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

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2 **Southwestern Atlantic**

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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

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

65 encounter probability of prey by predators (Holling 1965), prey handling (Wieters and

66 Navarrete 1998), feeding rate (Moran 1985) and availability of refuges (Davenport et al. 1998).

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

80   feeding rates and hence the strength of top-down control. For example, variation in seawater

81   temperature can be responsible for variation in the strength of interactions due to effects on

82   predators' metabolism (Sanford 1999; O'Connor 2009; Kordas et al. 2011; Carr and Bruno

83   2013). Likewise, variation in nutritional quality of prey, which could be linked to large-scale

84   variability in phytoplankton availability, can affect consumers' feeding choices (Palmer 1984;

85   Simpson et al. 2010; Schmidt et al. 2012). Therefore, understanding variation in natural

86   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

110 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 $\log_{10}$ 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 cm^2)

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 cm^2 = 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 m^2 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

Experiment 2: Large-scale variation in predator-prey interactions and relationships to 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

173 treatment, we included one whelk per cage. The density of *T. stalactifera* was manipulated to

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 ± 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**

204   In both experiments, we calculated the mortality rate of the barnacle prey for each cage

205 *i* from the site *j* belonging to the treatments 'predator' *k* (k = 0: exclusion; k = 1: inclusion) and

206 'prey density' *l* (ambient, reduced: only for the Experiment 1) as the difference between the

207 number of live barnacles in the beginning (B_0) and at the end of the experiment (B_t) divided

208 by the time elapsed *t*:

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

210   (1)

211   Per capita consumption rate of barnacles by whelks ($CR_{ij(l)_{k=1}}$) was calculated by

212   subtracting the average mortality rate of prey in the absence of predators ($\overline{MR}_{j(l)_{k=0}}$) from the

213   mortality rate in the presence of the predator ($MR_{ij(l)_{k=1}}$) divided by the number of whelks *S.*

214   *brasiliensis* inside the cages ($S_{ij(l)_{k=1}}$). Since inclusion and exclusion plots were not paired,

215    $\overline{MR}_{j(l)_{k=0}}$ was obtained by averaging 1,000 averages calculated through bootstrapping. A few

216   negative values due to lack of predation and subtraction of background mortality were

217   replaced to zero since there cannot be a negative consumption rate.

$$CR_{ij(l)_{k=1}} = \left(\frac{MR_{ij(l)_{k=1}}}{S_{ij(l)_{k=1}}} \right) - \overline{MR}_{j(l)_{k=0}}$$

218

219   (2)

220   For calculating interaction strength, we assumed that the trajectory of the focal cohorts

221   of prey could be expressed as an exponential function (as in Navarrete and Menge 1996):

$$B_t = B_0 e^{(-(m-\alpha S)t)},$$

222

223   (3)

224   where B_t is the number of live barnacles at time *t*, B_0 is the initial number of live barnacles, *m*

225   is the mortality rate in the absence of predators, *S* is the abundance of the predatory whelk

226   and *α* is the per capita interaction strength (PCIS) of the whelk on the barnacle cohort.

227   Simplifying the formula by dividing both sides by B_0 and taking natural logarithms, we obtained

228   that:

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

229

230   (4)

231   The mortality rate in the absence of predators for each cage belonging to each site

232   and treatment (where pertinent) ($m_{ij(l)_{k=0}}$) was obtained using a similar formula to equation 4,

233   but without the term S. In both cases, B_t and B_0 were added to 1 to avoid natural logarithms

234   of zero. As before, the mortality rate in the absence of predators $\overline{\mathrm{m}}_{j(l)_{k=0}}$ was calculated by

235   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

253   pertinent relationships between variables (e.g., prey size and Chla, prey size and sea

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**

259   Mean ambient density of the barnacle prey *Tetraclita stalactifera* showed an increasing

260   trend with wave exposure (Fig. 1D), although the test was marginally non-significant (Linear

261   model on $\log_{10}$-transformed data: $F_{1,6} = 4.21$, $R^2 = 0.41$, P = *0.08*). At ambient densities,

262   barnacles varied on average from 45.0 to 99.3 individuals per 625 cm^2 in predator inclusion

263   plots and from 36.8 to 103.2 individuals in predator exclusion plots. Reduced prey density

264   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).

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

Relationships of prey size with ocean conditions and predation

311   The size of available prey in the plots for the whelks was not related to satellite Chla

312   (Table 3, Fig. 7A). The size of barnacles consumed by the whelks, on the other hand,

313   increased with the size of barnacles available in the plots and decreased with Chla (Fig. 7B).

314   Sea temperature did not relate to either the size of available or consumed prey. Moreover,

315   both size of the barnacles available and consumed did not affect PCIS, while consumption

316   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.

331   In our local experiment, wave exposure decreased the consumption rate of barnacles

332   by the predatory gastropod at reduced density but had no effect at ambient density, partially

333   confirming our expectations. We predicted consumption to decrease with increasing wave

334   exposure as a consequence of impairments on feeding activity of the predator (Menge and

335   Sutherland 1976, 1987; Lamb et al. 2020) and expected this reduction to occur to a greater

336   degree at reduced prey densities. The lack of effect of the wave exposure gradient on

337   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

357   exposure on whelk PCIS most likely as a consequence of decreased feeding activity. The

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

365 strength is also dependent on prey recruitment and growth (Laska and Wootton 1998; Berlow

366 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).

415   In considering patterns in PCIS it is worth considering the implications of conclusions

416   based on a relatively short-term experiment (e.g., Jenkins and Uyà 2016). The 'true' PCIS,

417   i.e., the per capita effect of the predator on the per capita population growth rate of the prey

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

We have shown that among-shore variation in the degree of exposure to wave action and prey density interact to determine a subtropical intertidal predator-prey interaction in the short term. These results reveal that disentangling the effects of covarying factors are required 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 nutritional quality relationships mediated by availability of food for the prey (Chla). Our work contributes to understand the interplay between ecological processes and environmental variability emerging at different spatial scales. To our knowledge, this is one of the few large-scale manipulative works along the southwestern Atlantic contributing to recent mensurative efforts in comprehending the structure and functioning of coastal ecosystems over a broad spatial range (e.g., Mazzuco et al. 2015; Kasten et al. 2019; Cruz-Motta et al. 2020; Pardal et al. 2021).

455

456   **Declarations**

457   **Ethics approval:** Ethics approval was not required for this study according to local legislation

458   (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-

465   interactions-rocky-shores-SE-Brazil/tree/main/codes

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469

470   **References**

471   Agrawal AA, Ackerly DD, Adler F, et al (2007) Filling key gaps in population and community

472   ecology. Front Ecol Environ 5:145–152. https://doi.org/10.1890/1540-

473   9295(2007)5[145:FKGIPA]2.0.CO;2

474   Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using

475   lme4. J Stat Softw 6:1–48

476   Berlow EL, Navarrete SA (1997) Spatial and temporal variation in rocky intertidal community

477   organization: Lessons from repeating field experiments. J Exp Mar Biol Ecol 214:195–229

478   Berlow EL, Navarrete SA, Briggs CJ, et al (1999) Quantifying variation in the strength of

479   species interactions. Ecology 80:2206–2224

480   Bertness MD, Gaines SD, Bermudez D, Sanford E (1991) Extreme spatial variation in the

481   growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. Mar Ecol

482   Prog Ser 75:91–100. https://doi.org/10.3354/meps075091

483   Bideault A, Loreau M, Gravel D (2019) Temperature modifies consumer-resource interaction

484   strength through its effects on biological rates and body mass. Front Ecol Evol 7:45.

485   https://doi.org/10.3389/fevo.2019.00045

486   Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory.

487   Trends Ecol Evol 18:119–125. https://doi.org/10.1016/S0169-5347(02)00045-9

488   Bueno M, Flores AAV (2010) Tidal-amplitude rhythms of larval release: Variable departure

489   from presumed optimal timing among populations of the mottled shore crab. J Mar Biol

490   Assoc U K 90:859–865. https://doi.org/10.1017/S0025315410000044

491   Burrows MT (2012) Influences of wave fetch, tidal flow and ocean colour on subtidal rocky

492   communities. Mar Ecol Prog Ser 445:193–207. https://doi.org/10.3354/meps09422

493   Burrows MT, Hughes RN (1991) Variation in Foraging Behaviour Among Individuals and

494   Populations of Dogwhelks, *Nucella lapillus*: Natural Constraints on Energy Intake. J Anim

495   Ecol 60:497–514

496   Burrows MT, Jenkins SR, Robb L, Harvey R (2010) Spatial variation in size and density of

497   adult and post-settlement *Semibalanus balanoides*: Effects of oceanographic and local

498   conditions. Mar Ecol Prog Ser 398:207–219. https://doi.org/10.3354/meps08340

499   Bustamante RH, Branch GM, Eekhout S, et al (1995) Gradients of intertidal primary
500   productivity around the coast of South Africa and their relationships with consumer
501   biomass. Oecologia 102:189–201. https://doi.org/10.1007/BF00333251

502   Carr LA, Bruno JF (2013) Warming increases the top-down effects and metabolism of a
503   subtidal herbivore. PeerJ 1:e109. https://doi.org/10.7717/peerj.109

504   Carr LA, Gittman RK, Bruno JF (2018) Temperature influences herbivory and algal biomass
505   in the Galápagos Islands. Front Mar Sci 5:1–10. https://doi.org/10.3389/fmars.2018.00279

506   Castro BM, Miranda LB (1998) Physical oceanography of the western Atlantic continental shelf
507   located between 4ºN and 34ºS. In: Robinson AR, Brink KH (eds) The sea. Wiley, New York,
508   pp 209–251

509   Christofoletti RA, Takahashi CK, Oliveira DN, Flores AAV (2011) Abundance of sedentary
510   consumers and sessile organisms along the wave exposure gradient of subtropical rocky
511   shores of the south-west Atlantic. J Mar Biol Assoc United Kingdom 91:961–967.
512   https://doi.org/10.1017/S0025315410001992

513   Connell JH (1961) Effects of Competition, Predation by *Thais lapillus*, and Other Factors on
514   Natural Populations of the Barnacle *Balanus balanoides*. Ecol Monogr 31:61–104

515   Contolini GM, Reid K, Palkovacs EP (2020) Climate shapes population variation in dogwhelk
516   predation on foundational mussels. Oecologia 192:553–564.
517   https://doi.org/10.1007/s00442-019-04591-x

518   Cruz-Motta JJ, Miloslavich P, Guerra-Castro E, et al (2020) Latitudinal patterns of species
519   diversity on South American rocky shores: Local processes lead to contrasting trends in
520   regional and local species diversity. J Biogeogr 47:1966–1979.
521   https://doi.org/10.1111/jbi.13869

522   Dahlhoff EP, Menge BA (1996) Influence of phytoplankton concentration and wave exposure
523   on the ecophysiology of *Mytilus californianus*. Mar Ecol Prog Ser 144:97–107.
524   https://doi.org/10.3354/meps144097

525 Davenport J, Moore PG, Magill SH, Fraser LA (1998) Enhanced condition in dogwhelks,

526   *Nucella lapillus* (L.) living under mussel hummocks. J Exp Mar Biol Ecol 230:225–234.

527   https://doi.org/10.1016/S0022-0981(98)00082-3

528 Dayton PK (1971) Competition, Disturbance, and Community Organization: The Provision and

529   Subsequent Utilization of Space in a Rocky Intertidal Community. Ecol Monogr 41:351–

530   389

531 Dayton PK (1975) Experimental Evaluation of Ecological Dominance in a Rocky Intertidal Algal

532   Community. Ecol Monogr 45:137–159

533 Dunkin SB, Hughes RN (1984) Behavioural components of prey-selection by dogwhelks,

534   *Nucella lapillus* (L.), feeding on barnacles, *Semibalanus balanoides* (L.), in the laboratory.

535   J Exp Mar Biol Ecol 79:91–103. https://doi.org/10.1016/0022-0981(84)90032-7

536 Dunn RP, Hovel KA (2020) Predator type influences the frequency of functional responses to

537   prey in marine habitats. Biol Lett 16:20190758. https://doi.org/10.1098/rsbl.2019.0758

538 Elton CS (1927) Animal Ecology. Sidgwick & Jackson, Ltd, London

539 Emmerson MC, Raffaelli D (2004) Predator-prey body size, interaction strength and the

540   stability of a real food web. J Anim Ecol 73:399–409. https://doi.org/10.1111/j.0021-

541   8790.2004.00818.x

542 Giménez L, Torres G, Pettersen A, et al (2017) Scale-dependent natural variation in larval

543   nutritional reserves in a marine invertebrate: Implications for recruitment and cross-

544   ecosystem coupling. Mar Ecol Prog Ser 570:141–155. https://doi.org/10.3354/meps12081

545 Hacker SD, Menge BA, Nielsen KJ, et al (2019) Regional processes are stronger determinants

546   of rocky intertidal community dynamics than local biotic interactions. Ecology 100:e02763.

547   https://doi.org/10.1002/ecy.2763

548 Hairston NG, Smith FE, Slobodkin LB (1960) Community Structure, Population Control, and

549   Competition. Am Nat 94:421–425. https://doi.org/10.1086/282146

550 Holling CS (1965) The Functional Response of Predators to Prey Density and its Role in

551   Mimicry and Population Regulation. Mem Entomol Soc Canada 97:5–60.

552   https://doi.org/10.4039/entm9745fv

553 Hughes RN, Burrows MT (1991) Diet selection by dogwhelks in the field: an example of

554   constrained optimization. Anim Behav 42:47–55. https://doi.org/10.1016/S0003-

555   3472(05)80604-9

556 Hughes RN, Dunkin SB (1984) Effect of dietary history on selection of prey, and foraging

557   behaviour among patches of prey, by the dogwhelk, *Nucella lapillus* (L.). J Exp Mar Biol

558   Ecol 79:159–172. https://doi.org/10.1016/0022-0981(84)90217-X

559 Jenkins SR, Uyà M (2016) Temporal scale of field experiments in benthic ecology. Mar Ecol

560   Prog Ser 547:273–286. https://doi.org/10.3354/meps11659

561 Kasten P, Tremblay R, Flores AAV (2019) Mismatched seasonal patterns of larval production

562   and quality in subtropical barnacle populations along a coastal trophic gradient. Estuar

563   Coast Shelf Sci 224:43–50. https://doi.org/10.1016/j.ecss.2019.04.048

564 Kordas RL, Harley CDG, O'Connor MI (2011) Community ecology in a warming world: The

565   influence of temperature on interspecific interactions in marine systems. J Exp Mar Biol

566   Ecol 400:218–226. https://doi.org/10.1016/j.jembe.2011.02.029

567 Lamb RW, Smith F, Witman JD (2020) Consumer mobility predicts impacts of herbivory across

568   an environmental stress gradient. Ecology 101:e02910. https://doi.org/10.1002/ecy.2910

569 Laska MS, Wootton JT (1998) Theoretical concepts and empirical approaches to measuring

570   interaction strength. Ecology 79:461–476. https://doi.org/10.1890/0012-

571   9658(1998)079[0461:TCAEAT]2.0.CO;2

572 Leonard GH, Levine JM, Schmidt PR, Bertness MD (1998) Flow-Driven Variation in Intertidal

573   Community Structure in a Maine Estuary. Ecology 79:1395–1411

574 López MS, Coutinho R, Ferreira CEL, Rilov G (2010) Predator-prey interactions in a

575   bioinvasion scenario: Differential predation by native predators on two exotic rocky intertidal

576   bivalves. Mar Ecol Prog Ser 403:101–112. https://doi.org/10.3354/meps08409

577 Martinez AS, Mayer-Pinto M, Christofoletti RA (2019) Functional responses of filter feeders

578   increase with elevated metal contamination: Are these good or bad signs of environmental

579   health? Mar Pollut Bull 149:110571. https://doi.org/10.1016/j.marpolbul.2019.110571

Mazzuco ACA, Christofoletti RA, Coutinho R, Ciotti AM (2018) The influence of atmospheric cold fronts on larval supply and settlement of intertidal invertebrates: Case studies in the Cabo Frio coastal upwelling system (SE Brazil). J Sea Res 137:47–56. https://doi.org/10.1016/j.seares.2018.02.010

Mazzuco ACA, Christofoletti RA, Pineda J, et al (2015) Temporal variation in intertidal community recruitment and its relationships to physical forcings, chlorophyll-a concentration and sea surface temperature. Mar Biol 162:1705–1725. https://doi.org/10.1007/s00227-015-2689-6

McQuaid CD, Lindsay TL (2000) Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: Bottom-up regulation of intertidal populations. Mar Ecol Prog Ser 206:147–154. https://doi.org/10.3354/meps206147

Menge BA (1976) Organization of the New England Rocky Intertidal Community: Role of Predation, Competition, and Environmental Heterogeneity. Ecol Monogr 46:355–393

Menge BA (1978a) Predation intensity in a rocky intertidal community - Relation between predator foraging activity and environmental harshness. Oecologia 34:1–16. https://doi.org/10.1007/BF00346237

Menge BA (1978b) Predation intensity in a rocky intertidal community - Effect of an algal canopy, wave action and desiccation on predator feeding rates. Oecologia 34:17–35. https://doi.org/10.1007/BF00346238

Menge BA (1992) Community Regulation: Under What Conditions Are Bottom-Up Factors Important on Rocky Shores? Ecology 73:755–765

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250:257–289. https://doi.org/10.1016/S0022-0981(00)00200-8

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

Menge BA, Sutherland JP (1976) Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. Am Nat 110:351–369

608 Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition,

609   and predation in relation to environmental stress and recruitment. Am Nat 130:730–757.

610   https://doi.org/10.1086/284741

611 Menge BA, Daley BA, Wheeler PA, Strub PT (1997) Rocky intertidal oceanography: An

612   association between community structure and nearshore phytoplankton concentration.

613   Limnol Oceanogr 42:57–66. https://doi.org/10.4319/lo.1997.42.1.0057

614 Menge BA, Lubchenco J, Bracken MES, et al (2003) Coastal oceanography sets the pace of

615   rocky intertidal community dynamics. Proc Natl Acad Sci U S A 100:12229–12234.

616   https://doi.org/10.1073/pnas.1534875100

617 Moran MJ (1985) Effects of prey density, prey size and predator size on rates of feeding by

618   an intertidal predatory gastropod *Morula marginalba* Blainville (Muricidae), on several

619   species of prey. J Exp Mar Biol Ecol 90:97–105. https://doi.org/10.1016/0022-

620   0981(85)90112-1

621 Navarrete SA, Menge BA (1996) Keystone Predation and Interaction Strength: Interactive

622   Effects of Predators on Their Main Prey. Ecol Monogr 66:409–429

623 Navarrete SA, Wieters EA, Broitman BR, Castilla JC (2005) Scales of benthic-pelagic coupling

624   and the intensity of species interactions: From recruitment limitation to top-down control.

625   Proc Natl Acad Sci U S A 102:18046–18051. https://doi.org/10.1073/pnas.0509119102

626 Novak M, Wootton JT (2010) Using experimental indices to quantify the strength of species

627   interactions. Oikos 119:1057–1063. https://doi.org/10.1111/j.1600-0706.2009.18147.x

628 O'Connor MI (2009) Warming strengthens an herbivore-plant interaction. Ecology 90:388–

629   398. https://doi.org/10.1890/08-0034.1

630 Paine RT (1966) Food Web Complexity and Species Diversity. Am Nat 100:65–75

631 Paine RT (1980) Food Webs: Linkage, Interaction Strength and Community Infrastructure. J

632   Anim Ecol 49:666–685

633 Palmer AR (1984) Prey selection by thaidid gastropods: some observational and experimental

634   field tests of foraging models. Oecologia 62:162–172. https://doi.org/10.1007/BF00379009

635 Pardal A, Cordeiro CAMM, Ciotti AM, et al (2021) Influence of environmental variables over

636   multiple spatial scales on the population structure of a key marine invertebrate. Mar Environ

637   Res 170:105410. https://doi.org/10.1016/j.marenvres.2021.105410

638 Pardal-Souza AL (2021) Estrutura de populações e comunidades de costões rochosos: o

639   papel de fatores naturais e antrópicos em diferentes escalas espaciais. PhD dissertation,

640   Centre for Natural and Human Sciences, Federal University of ABC, Santo André, São

641   Paulo, Brazil

642 Poore AGB, Graba-Landry A, Favret M, et al (2013) Direct and indirect effects of ocean

643   acidification and warming on a marine plant-herbivore interaction. Oecologia 173:1113–

644   1124. https://doi.org/10.1007/s00442-013-2683-y

645 Power ME (1992) Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy.

646   Ecology 73:733–746

647 R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation

648   for Statistical Computing, Vienna, Austria. URL. https://www.R-project. org/

649 Richardson TD, Brown KM (1990) Wave exposure and prey size selection in an intertidal

650   predator. J Exp Mar Biol Ecol 142:105–120. https://doi.org/10.1016/0022-0981(90)90140-

651   8

652 Rovero F, Hughes RN, Chelazzi G (1999) Effect of experience on predatory behaviour of

653   dogwhelks. Anim Behav 57:1241–1249. https://doi.org/10.1006/anbe.1999.1102

654 Rovero F, Hughes RN, Chelazzi G (2000) When time is of the essence: Choosing a currency

655   for prey-handling costs. J Anim Ecol 69:683–689. https://doi.org/10.1046/j.1365-

656   2656.2000.00426.x

657 Ruesink JL (1998) Variation in per capita interaction strength: Thresholds due to nonlinear

658   dynamics and nonequilibrium conditions. Proc Natl Acad Sci U S A 95:6843–6847.

659   https://doi.org/10.1073/pnas.95.12.6843

660 Sanford E (1999) Regulation of keystone predation by small changes in ocean temperature.

661   Science 283:2095–2097. https://doi.org/10.1126/science.283.5410.2095

662   Sanford E, Swezey DS (2008) Response of predatory snails to a novel prey following the

663   geographic range expansion of an intertidal barnacle. J Exp Mar Biol Ecol 354:220–230.

664   https://doi.org/10.1016/j.jembe.2007.11.007

665   Schmidt JM, Sebastian P, Wilder SM, Rypstra AL (2012) The Nutritional Content of Prey

666   Affects the Foraging of a Generalist Arthropod Predator. PLoS One 7:e49223.

667   https://doi.org/10.1371/journal.pone.0049223

668   Sellers AJ, Leung B, Altieri AH, et al (2021) Seasonal upwelling reduces herbivore control of

669   tropical rocky intertidal algal communities. Ecology e03335.

670   https://doi.org/10.1002/ecy.3335

671   Silliman BR, He Q (2018) Physical Stress, Consumer Control, and New Theory in Ecology.

672   Trends Ecol Evol 33:492–503. https://doi.org/10.1016/j.tree.2018.04.015

673   Simpson SJ, Raubenheimer D, Charleston MA, Clissold FJ (2010) Modelling nutritional

674   interactions: from individuals to communities. Trends Ecol Evol 25:53–60.

675   https://doi.org/10.1016/j.tree.2009.06.012

676   Underwood AJ, Denley EJ (1984) Paradigms, explanations and generalizations in models for

677   the structure of intertidal communities on rocky shores. In: Strong Jr DR, Simberloff D,

678   Abele LG, Thistle AB (eds) Ecological Communities: Conceptual Issues and the Evidence.

679   Blackwell Scientific, United States, pp 151–180

680   Valentin JL (2001) The Cabo Frio Upwelling System, Brazil. In: Seeliger U, Kjerfve B (eds)

681   Coastal Marine Ecosystems of Latin America. Springer Berlin Heidelberg, Berlin,

682   Heidelberg, pp 97–105

683   Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York

684   (ISBN 978-3-319-24277-4). https://ggplot2.tidyverse.org.

685   Wieters EA, Navarrete SA (1998) Spatial variability in prey preferences of the intertidal whelks

686   *Nucella canaliculata* and *Nucella emarginata*. J Exp Mar Biol Ecol 222:133–148.

687   https://doi.org/10.1016/S0022-0981(97)00142-1

688   Wood SA, Lilley SA, Schiel DR, Shurin JB (2010) Organismal traits are more important than

689   environment for species interactions in the intertidal zone. Ecol Lett 13:1160–1171.

690   https://doi.org/10.1111/j.1461-0248.2010.01508.x

691   Wootton JT, Emmerson M (2005) Measurement of interaction strength in nature. Annu Rev

692   Ecol Evol Syst 36:419–444. https://doi.org/10.1146/annurev.ecolsys.36.091704.175535

693   Zuur AF, Ieno EN, Walker NJ, Savelier AA, Smith GM (2009) Mixed Effects Models and

694   Extensions in Ecology with R. Springer, New York, USA

695 **Tables**

696

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	SE	t-value	P	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 = wf	-0.044	0.052	-0.854	0.425			
tr:wf	-0.121	0.049	-2.465	**0.016***			

effect of wave fetch by prey density 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 'site'		
parameters	estimate	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 = wf	0.005	0.002	2.645	0.038			
tr:wf	0.015	0.005	3.038	**0.003****			

effect of wave fetch by prey density treatment[1]:

ambient	intercept	slope	R^2	*reduced*	intercept	slope	R^2
	-0.022***	0.005*	0.15		-0.077***	0.020***	0.34

701 *Notes*: Both linear mixed models were fitted with different variance structure by prey density

702 treatment to meet homoscedasticity assumption. [1]Significance of slopes of regressions were

703 tested by fitting ordinary linear models for wave fetch and responses (consumption rate and

704 PCIS) separately per prey density treatment (N = 41). Reported P-values for slopes of such

705 models were adjusted using Bonferroni correction.

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

consumption rate fixed effects parameters	estimate	SE	t-value	P	random effects of 'site' 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 parameters	estimate	SE	t-value	P	random effects of 'site' 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			

710

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

713   **Table 3.** Linear models testing the effect of large-scale conditions (Chla, chlorophyll-a

714   concentration; and sea temperature) on the size of available and consumed barnacles and

715   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	N	intercept	slope	R^2
~ Chla	46	6.80***	-0.15ns	0.02
~ sea temperature	46	12.23ns	-0.26ns	0.00

| size of barnacles consumed | | | | |
predictor	N	intercept	slope	R^2
~ size of available barnacles	37	0.46ns	**1.00***	0.49
~ Chla	37	8.49***	**-0.68**	0.23
~ sea temperature	37	26.57ns	-0.88ns	0.02

| consumption rate | | | | |
predictor	N	intercept	slope	R^2
~ size of available barnacles	46	0.27**	**-0.026***	0.09
~ size of barnacles consumed	37	0.18**	-0.008ns	0.02

| PCIS | | | | |
predictor	N	intercept	slope	R^2
~ size of available barnacles	46	-8.55e-03*	9.22e-04ns	0.05
~ size of barnacles consumed	37	-7.42e-03*	5.96e-04ns	0.04

717   *Notes:* A replicate for size of available and consumed barnacles was the average opercular

718   length per plot. The plots that remained in the field for about 30 days were not included in this

719   analysis (4 out of 51) neither the plots with less than 2 barnacles consumed. The size of

720   'consumed barnacles' was the size of dead barnacles (i.e., empty shells or missing individuals)

721   since background mortality was low and it was not possible to separate it from mortality caused

722   by predation itself.

724

725   **Fig. 1.** (**A**) Map of the Southeast coast of Brazil showing domain of wave fetch model (proxy

726   to wave exposure). (**B**) Details of the region of Ubatuba in the north coast of São Paulo State

727   where experiments were carried out in 2018 (*Experiment 1*). Size of black circles represents

728   mean wave fetch. (**C**) Wave fetch (mean ± SE) of sites. (**D**) Ambient density of the barnacle

729   *Tetraclita stalactifera* along the gradient of wave fetch. Black circles are mean values per site

730   (N = 8), line and shaded area are linear prediction ± 95% confidence interval

731

732   **Fig. 2.** Initial density of the barnacle *Tetraclita stalactifera* (mean ± SE) in the treatments of

733   exclusion or inclusion of the predatory whelk *Stramonita brasiliensis* (–P, +P) and prey density

734   (ambient, reduced) in eight sites in Ubatuba (São Paulo state, SE Brazil) (*Experiment 1*). Grey

735   dashed lines represent the global mean of barnacle density for each prey density treatment

736

737   **Fig. 3.** Initial density of the barnacle *Tetraclita stalactifera* (mean ± SE) in the treatments of

738   exclusion or inclusion of the predatory whelk *Stramonita brasiliensis* (–P, +P) in ten sites along

739   the Southeast coast of Brazil (*Experiment 2*)

740

741   **Fig. 4.** (**A**) Consumption rate and (**B**) per capita interaction strength (PCIS) of the whelk

742   *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera* along a gradient of wave fetch

743   (proxy to wave exposure) and between prey density treatments (ambient, reduced). Small

744   symbols are raw data (N = 82), lines and shaded areas are model predictions ± 95%

745   confidence interval

746

747   **Fig. 5.** Satellite chlorophyll-a concentration (Chla) and sea temperature (mean ± SE) in the

748   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 in

750 situ data from loggers

751

752 **Fig. 6.** Relationships among consumption rate and per capita interaction strength (PCIS) of

753 the whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera* and chlorophyll-a

754 concentration (Chla) and sea temperature in the Southeast coast of Brazil. Small symbols are

755 raw data (N = 51), lines and shaded areas are model predictions ± 95% confidence interval

756

757 **Fig. 7.** Relationships between (**A**) size of barnacles *Tetraclita stalactifera* available to the

758 predatory whelk *Stramonita brasiliensis* and mean satellite chlorophyll-a concentration (Chla)

759 (N = 46) and (**B**) size of barnacles consumed by the predatory whelks and Chla (N = 37).

760 Small circles are averaged opercular length per plot, lines and shaded areas are model
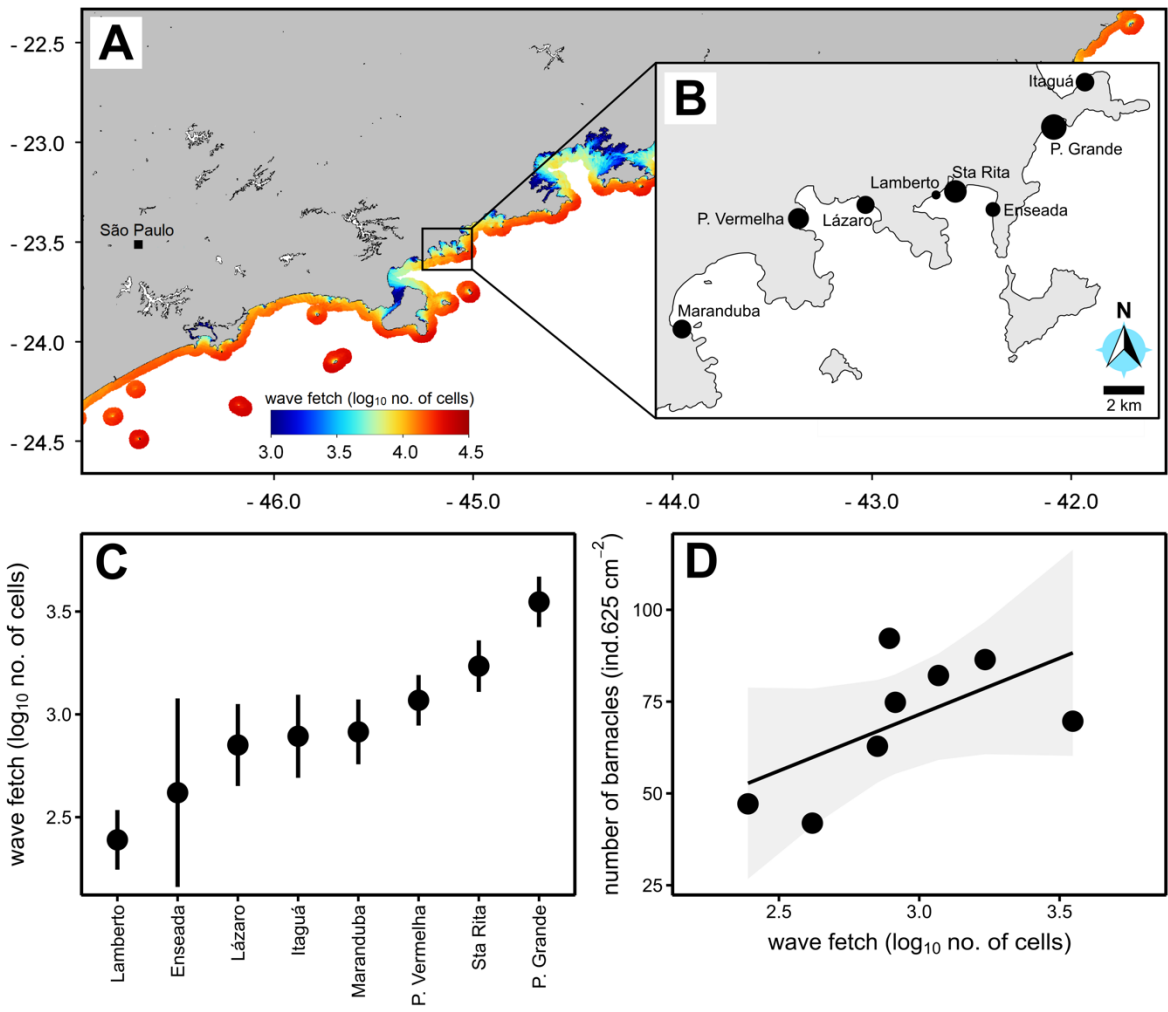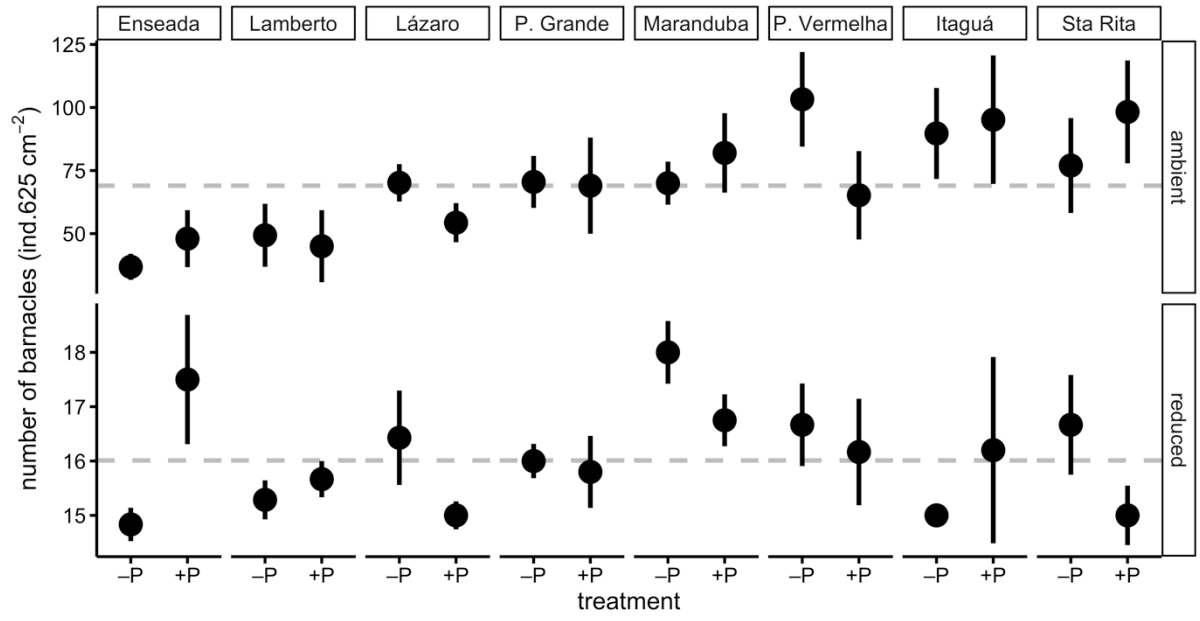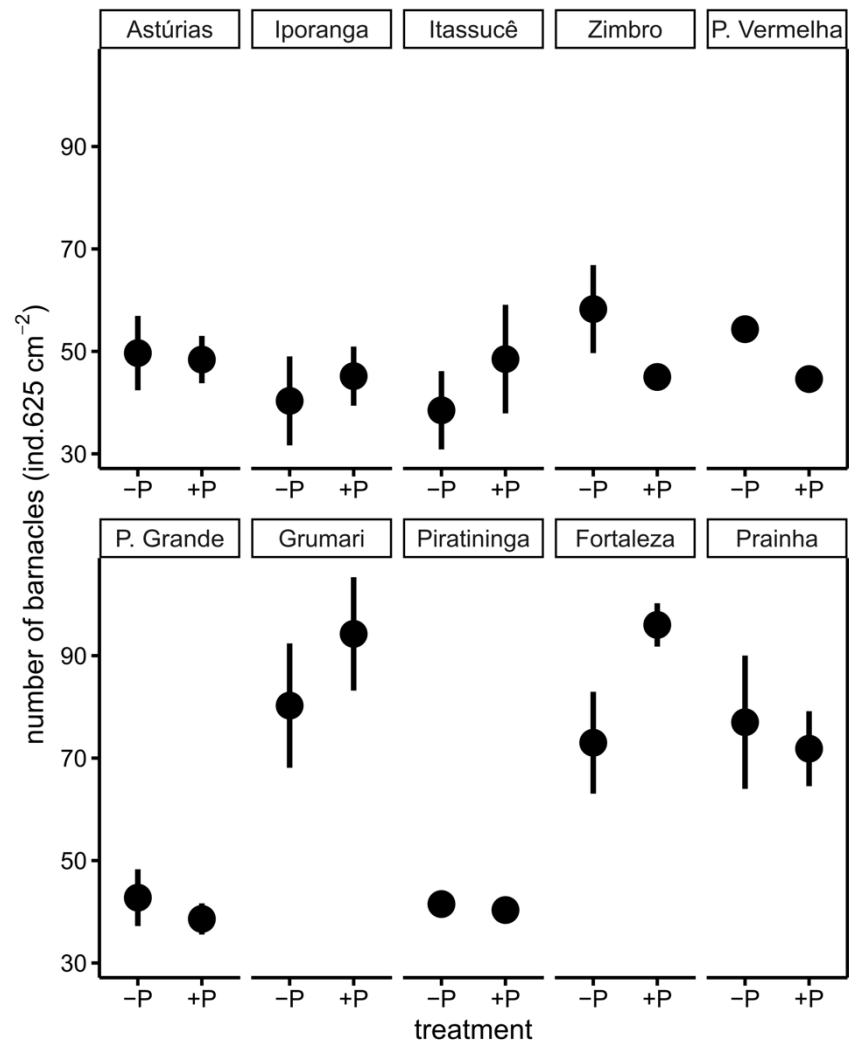
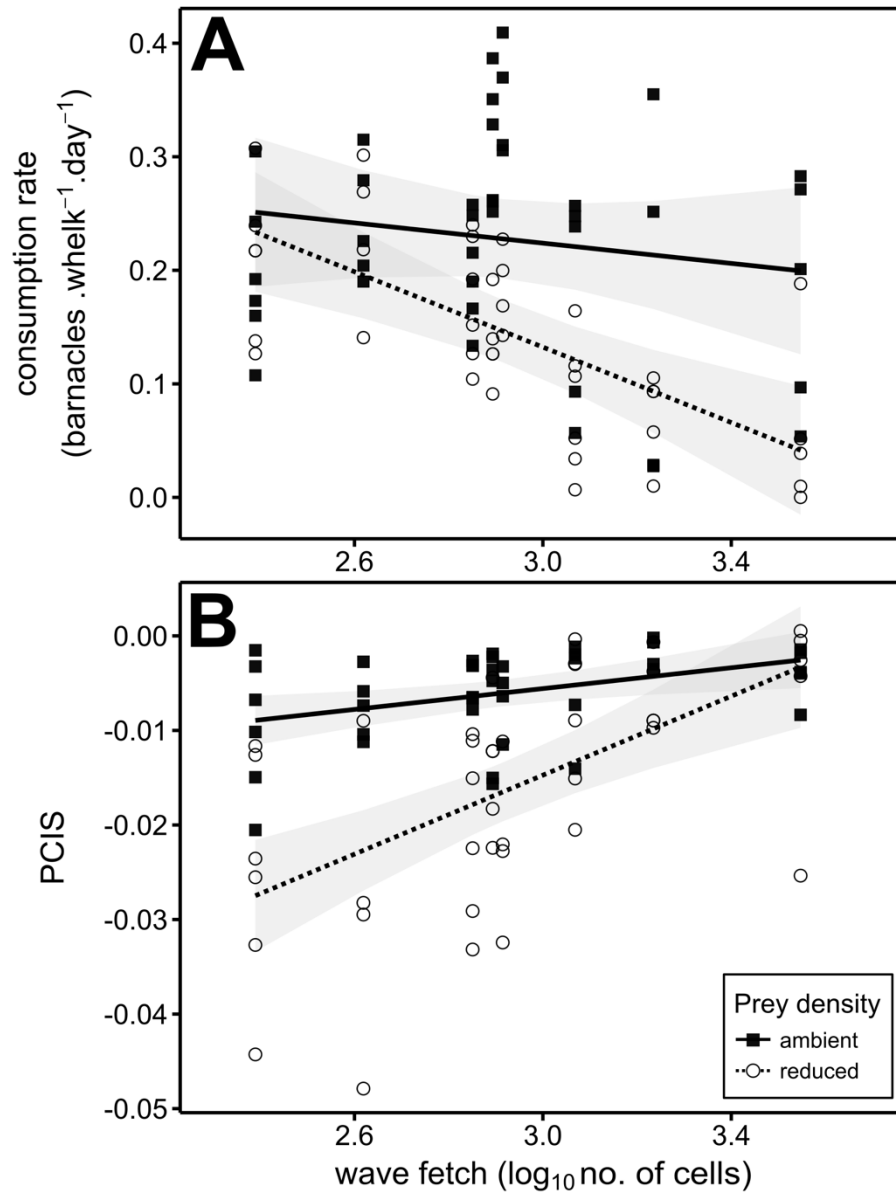761 predictions ± 95% confidence interval

Figure 1

Figure 2

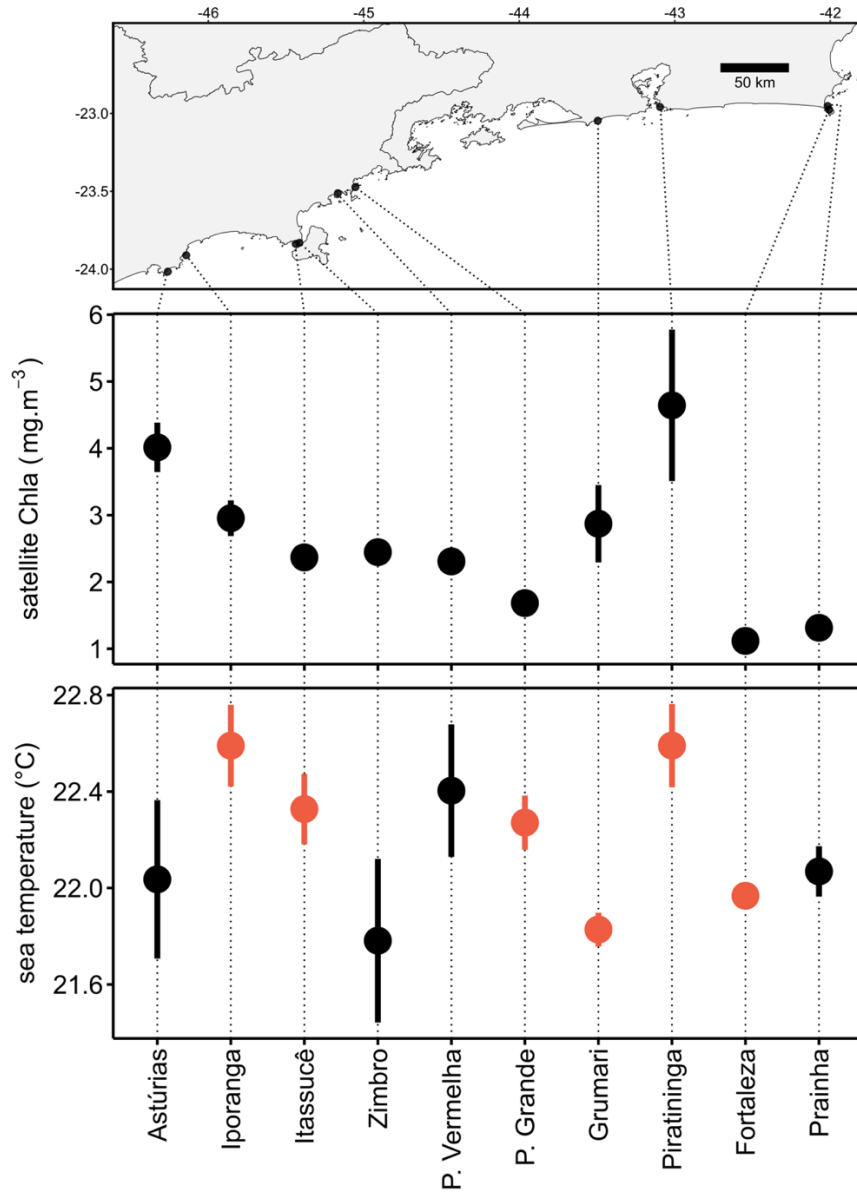Figure 3

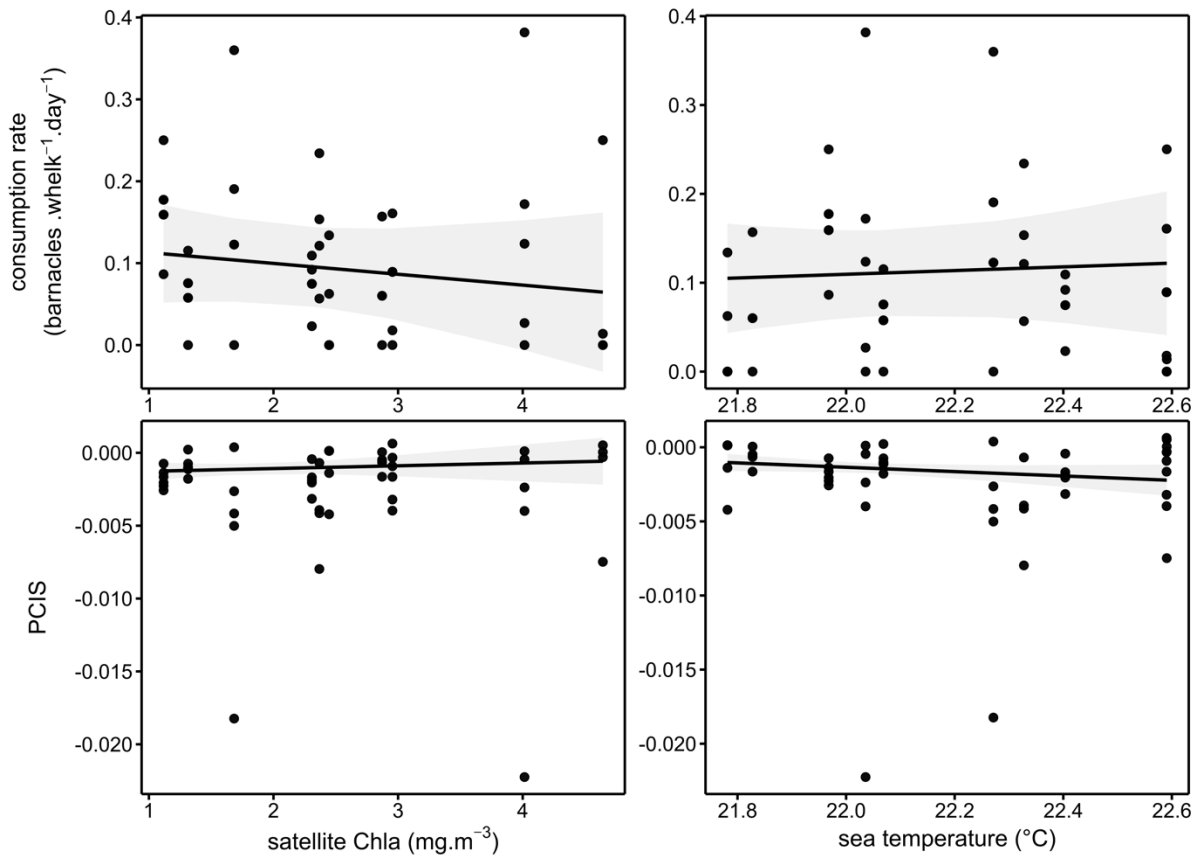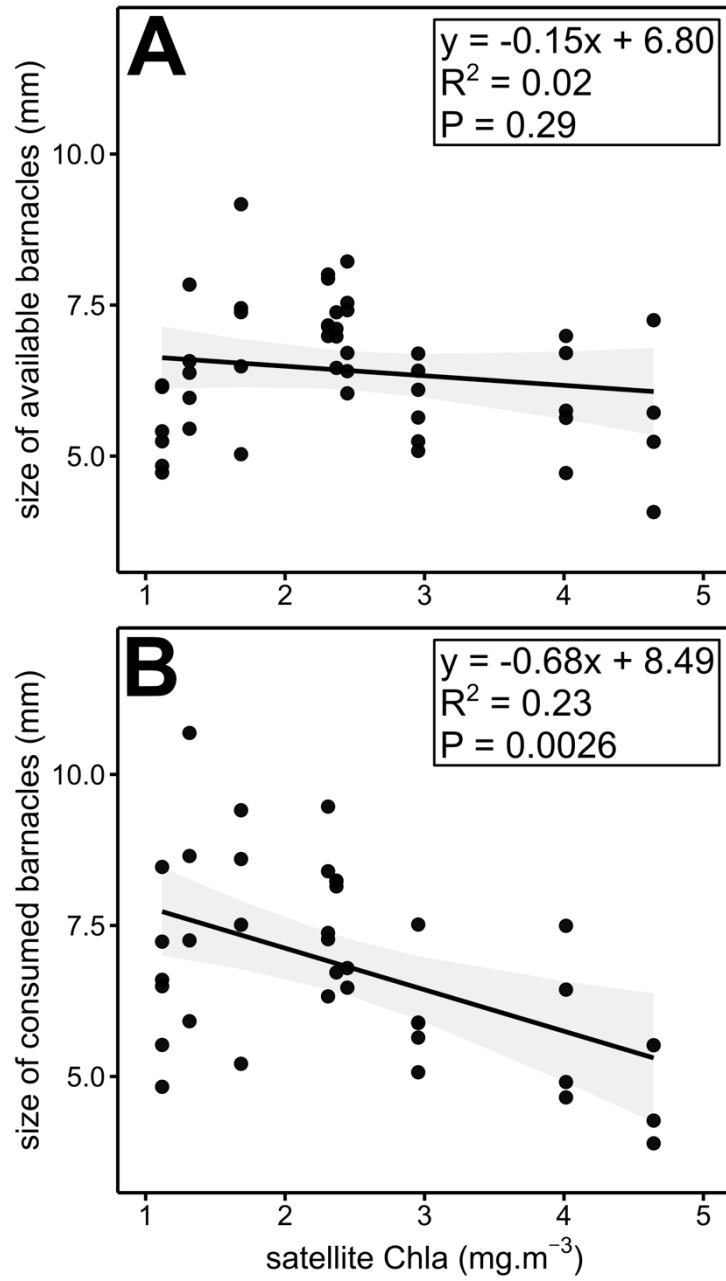Figure 4

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

André Pardal[1,2,*], Stuart R. Jenkins[3] and Ronaldo A. Christofoletti[2]

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[2]Institute of Marine Science, Federal University of São Paulo (IMar/UNIFESP), Rua Dr Carvalho de Mendonça 144, Santos, SP, 11070-100, Brazil

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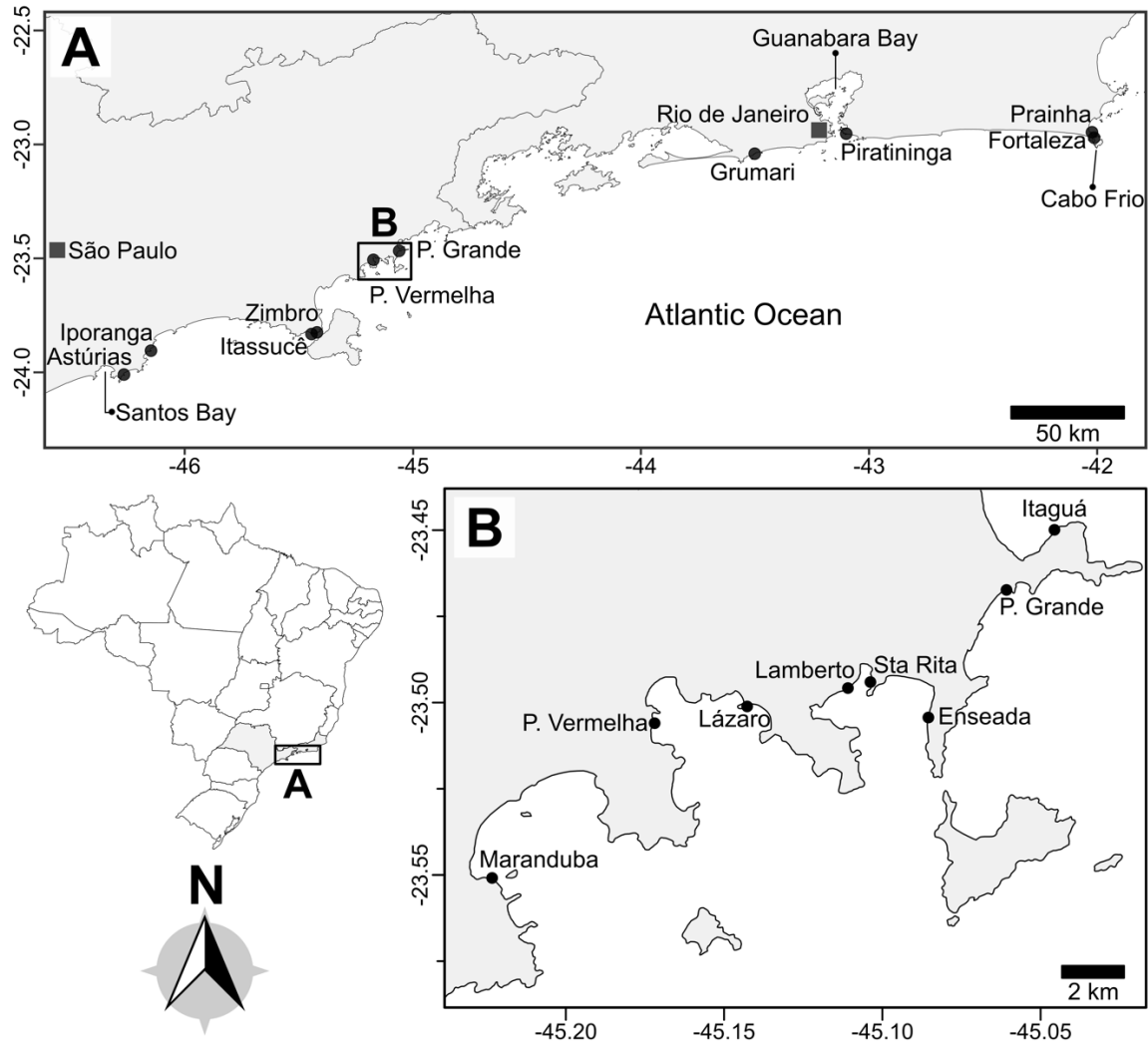**Fig. A1.** Map of the study areas. (**A**) Location of the ten sites along Southeast coast of Brazil where the large-scale experiment was carried out in 2019. (**B**) Detail of the north coast of São Paulo State (Ubatuba municipality) showing the eight sites where experiments were carried out in 2018. 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

Table A1. Continuation.

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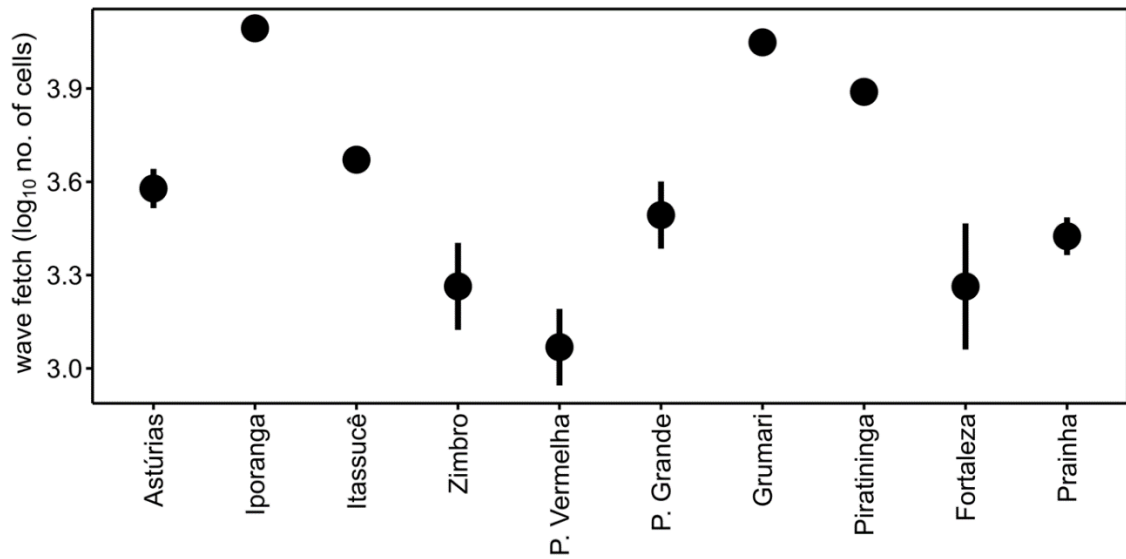
Fig. A2. Wave fetch (mean ± SE) of the ten sites along the Southeast coast of Brazil where the large-scale experiment was done in 2019 (*Experiment 2*). Sites are shown from south to north (see Fig. A1 above).
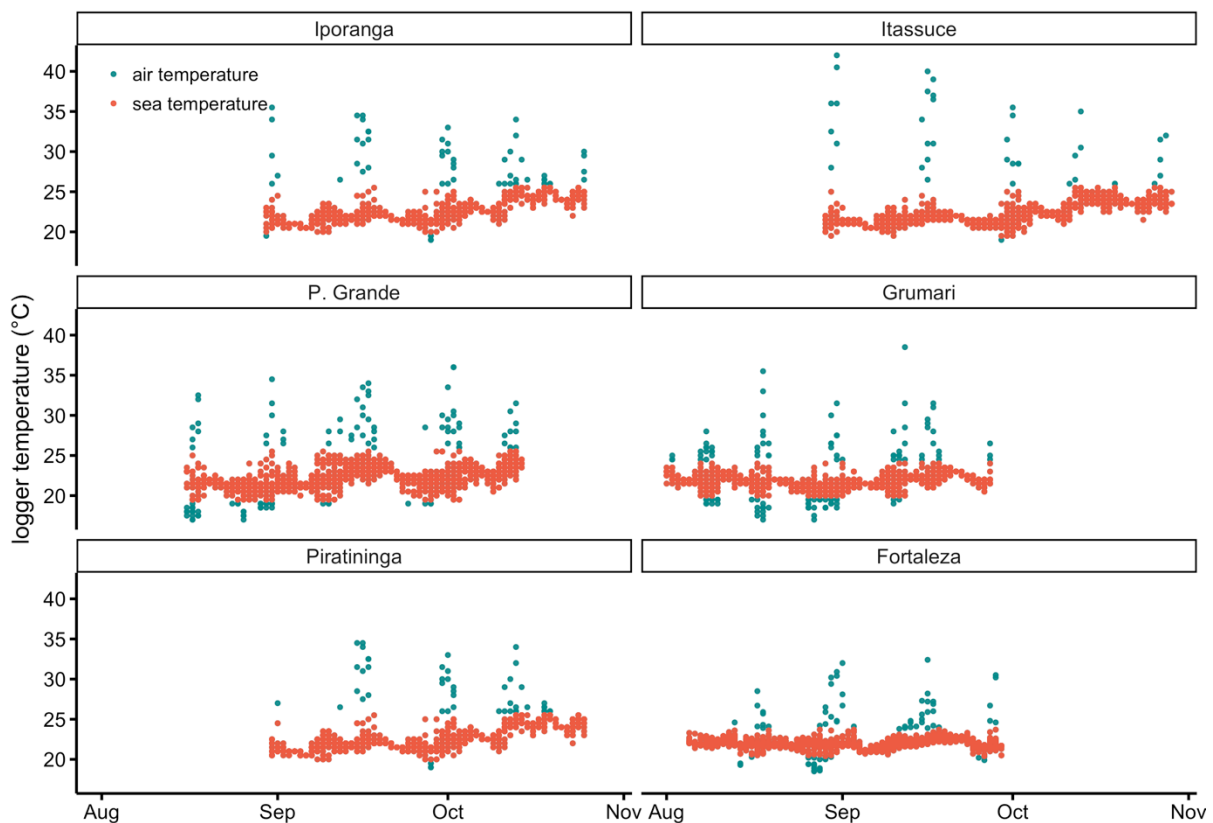

Fig. A3. Data logger temperature in 6 sites along the Southeast coast of Brazil (*Experiment 2*). Values outside of the range of site average ± 1.5 SD were excluded to separate seawater from air temperature. Red and blue dots correspond to sea and air temperatures, respectively.
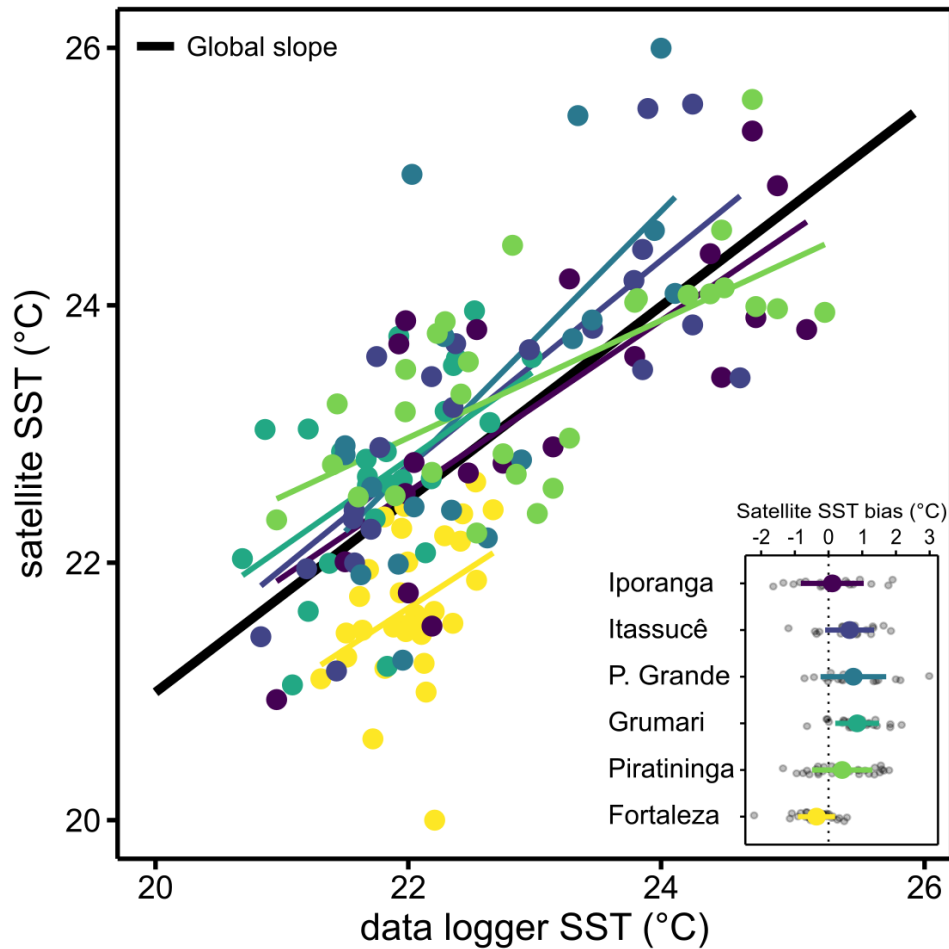
Fig. A4. Match-up between *in situ* and satellite-borne sea surface temperature (SST) measurements from the sites along SE Brazil. For data logger SST, each circle represents daily averages while for satellite SST, each circle is the average of all pixels from an image (4-km resolution, spatial buffer of 3 x 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 ± SE. Colours represent the same sites in both graphs.

Table A2. Linear models of the match-up between satellite and *in situ* sea surface temperature (SST). Ordinary linear models were fitted for the global data and for each site where we obtained both data. $*P < 0.05$; $**P < 0.01$, $***P < 0.001$; ns = not significant.

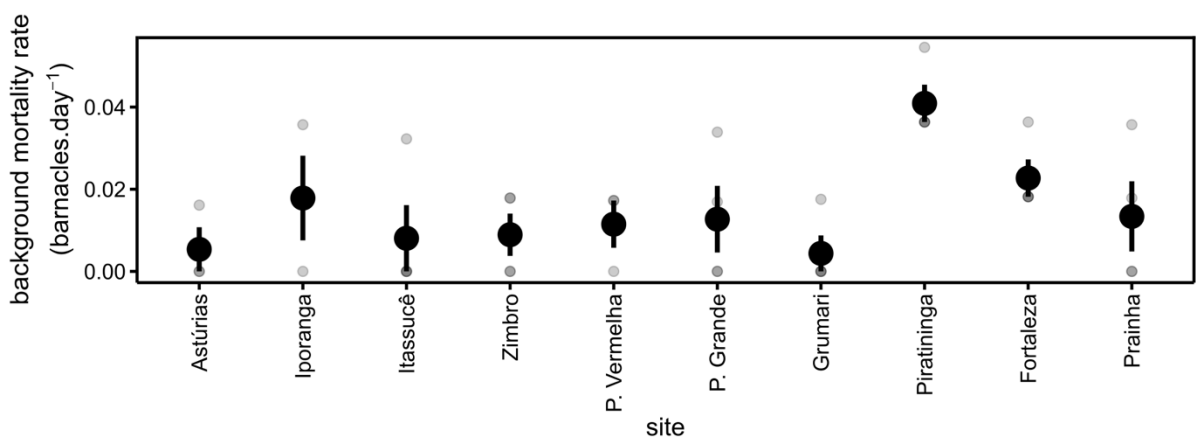| Match-up satellite SST *vs.* data logger SST | | | | | | |
model	intercept	slope	R^2	N	average bias	site corrected
Global	**5.70*****	**0.76*****	**0.47**	**144**	**+0.35**	**-**
Iporanga	5.66ns	0.76***	0.56	21	+0.11	Astúrias
Itassucê	5.18ns	0.80***	0.66	21	+0.62	Zimbro
P. Grande	0.86ns	0.99**	0.46	18	+0.74	P. Vermelha
Grumari	7.68ns	0.69**	0.30	25	+0.85	-
Piratininga	12.94***	0.45***	0.46	29	+0.40	-
Fortaleza	7.60ns	0.64*	0.14	30	–0.35	Prainha
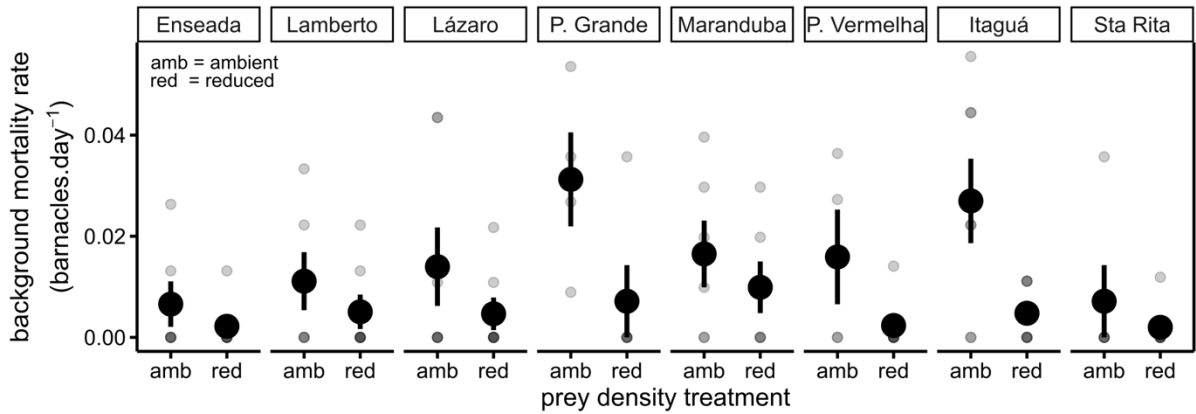
Fig. A5. Mortality of the barnacle prey *Tetraclita stalactifera* in the absence of predators (background mortality) in the experiment done in (**A**) Ubatuba (São Paulo state) in 2018 (*Experiment 1*) and (**B**) along the SE coast of Brazil in 2019 (*Experiment 2*). Small circles are raw data, big circles with error bars are mean ± 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 effects of 'site'		
parameters	estimate	SE	t-value	P	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 effects of 'site'		
parameters	estimate	SE	t-value	P	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).
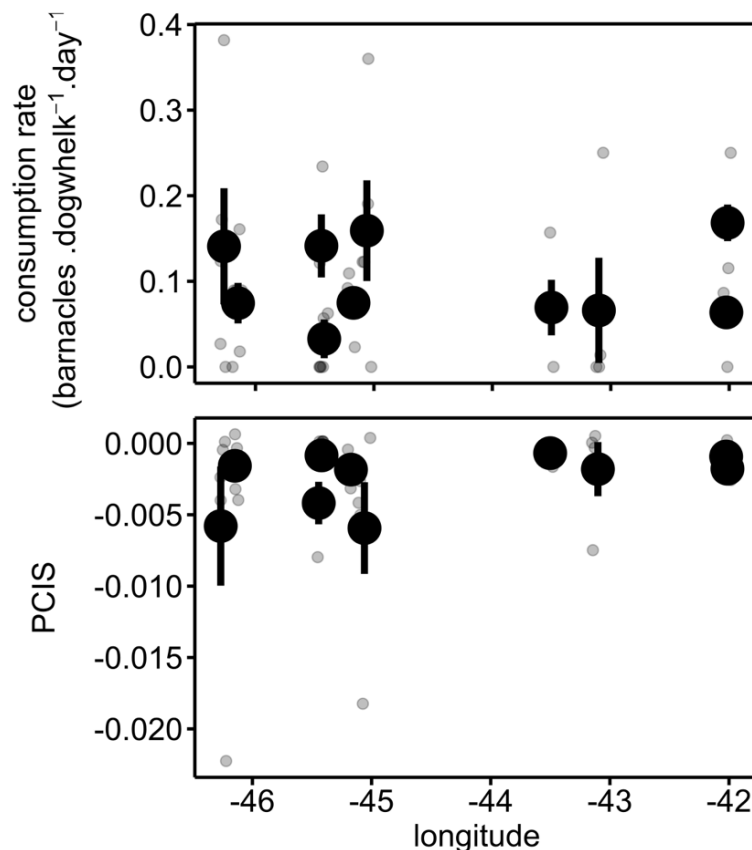

Fig. A6. Consumption rate and per capita interaction strength (PCIS) of the whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera* along longitude coordinates of sites from SE Brazil. Longitude coordinates represent better the spatial gradient since this coastline runs mostly from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

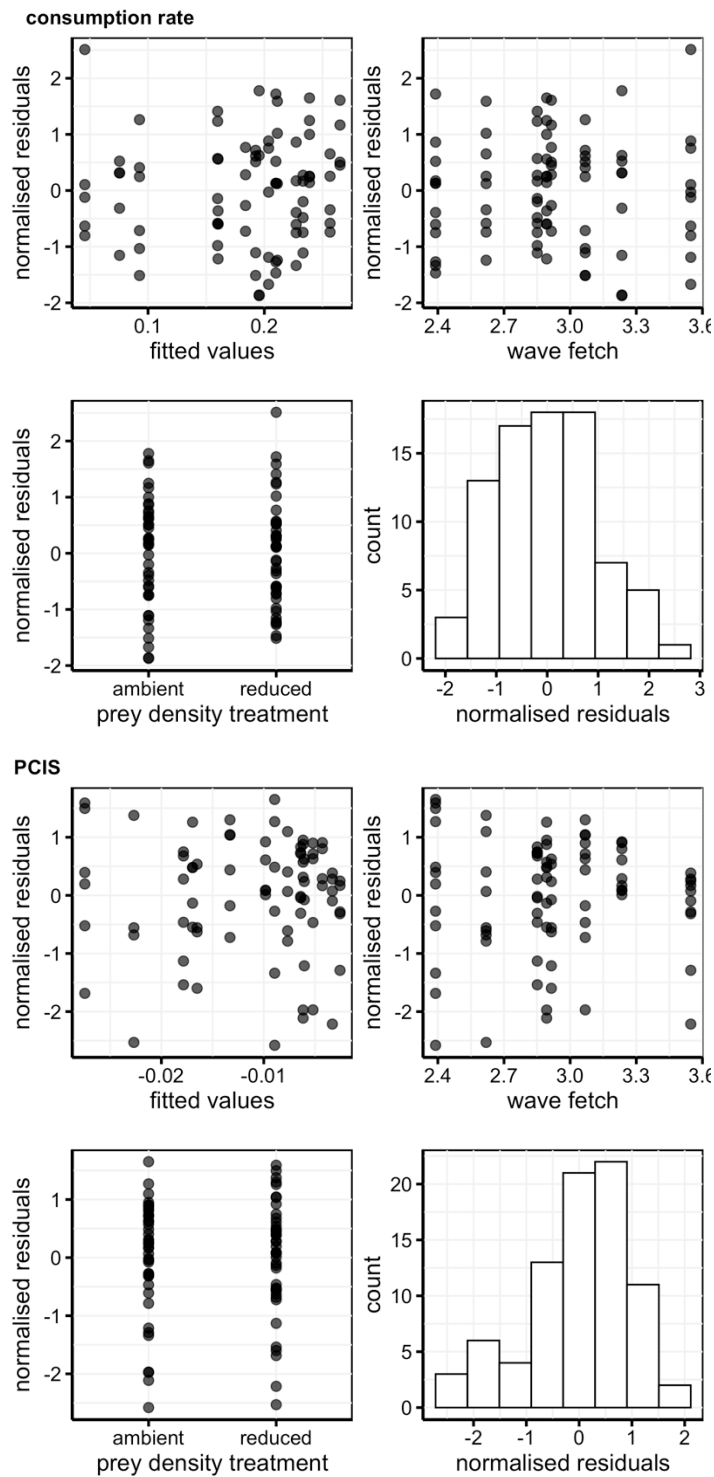**Appendix B:** Validation of the linear mixed models

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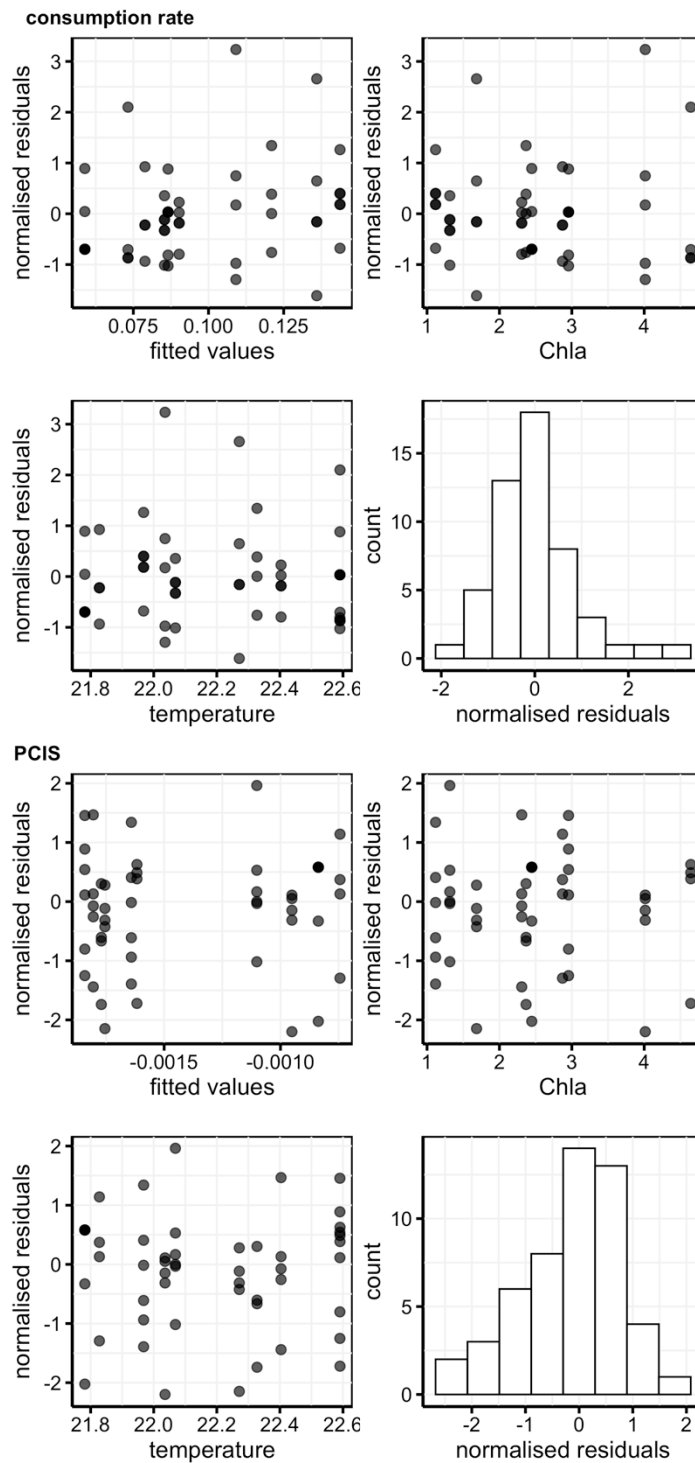
Fig. B2. Residuals of the linear mixed models (Gaussian distribution, identity link) testing the effect of chlorophyll-a concentration (Chla) and sea temperature on the consumption rate and per capita interaction strength (PCIS) of the whelk *Stramonita brasiliensis* on the barnacle *Tetraclita stalactifera*.