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Shading impacts by coastal infrastructure on biological communities from subtropical rocky shores'

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1 **Shading impacts by coastal infrastructure on biological communities from**
2 **subtropical rocky shores**

3

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18

19 **Running title:** Effect of shading on biological communities

20

21

22 **Summary**

23 **1.** Artificial shading has been highlighted as an important human disturbance,
24 affecting both productivity and community organisation. However, studies of
25 shading have been poorly explored from an environmental impact perspective.

26 **2.** We compared community structure on subtropical rocky shores in areas
27 shaded by human constructions with those in unshaded areas. We then
28 implemented a manipulative field experiment to determine the effects of shading
29 on the macrobenthic community, biofilm biomass and larval recruitment.

30 **3.** Shading consistently affected the biological community of rocky shores. The
31 biomass and cover of macroalgae and the size of most sedentary grazers were
32 smaller in shaded habitat. In the infralittoral fringe, we recorded a shift in
33 dominance from macroalgae in unshaded habitats to invertebrate filter-feeders
34 in shaded ones. In a similar way, the community from the mesolittoral was also
35 affected by shading but not at all locations.

36 **4.** Experimental manipulation of shading led to a total loss of macroalgae from
37 the infralittoral fringe and no community replacement over a period of 220 days.
38 In the mesolittoral, oysters became more abundant in shaded conditions, while
39 barnacles decreased in abundance. Larval recruitment was also affected, with
40 oysters and barnacles recruiting more in shaded habitats.

41 **5. *Synthesis and applications.*** We demonstrate a clear impact of shading by
42 artificial man-made structures on patterns and processes regulating biodiversity
43 on rocky shores and thus consequences for coastal ecosystem functioning. We
44 argue that shading by artificial coastal structures, such as those proposed in the
45 port expansion in our study site in south-eastern Brazil, are potentially under-

46 estimated. Our work emphasises the importance of careful evaluations of
47 artificial structures in order to promote sustainable coastal development. As a
48 result, we do not recommend the proposed expansion by suspended structures
49 of the port of São Sebastião, as the consequent shading will negatively affect
50 the biodiversity and ecosystem functioning of the Araçá Bay and surrounding
51 areas.

52

53 **Key-words:** Araçá Bay, biofilm, filter-feeder invertebrates, grazers, human
54 disturbances, intertidal, larval recruitment, luminosity, macroalgae, port
55 expansion.

56

57 **Introduction**

58 Sunlight shading affects the structure and functioning of biological
59 communities in natural ecosystems, through a reduction in the incidence of
60 solar radiation, thus disturbing the growth and biomass production by
61 autotrophs in both terrestrial (Williams, Messier & Kneeshaw 1999; Pagès *et al.*
62 2003) and aquatic environments (Fitzprack & Kirkman 1995; Quinn *et al.* 1997;
63 Ruiz & Romero 2001). Sunlight limitation can influence animal communities by
64 affecting physical conditions (e.g., reducing heat stress) (Williams 1994; Kon,
65 Kurokura & Tongnunui 2010), decreasing energetic resources of herbivores
66 (Hill, Ryon & Schilling 1995; Harley 2002) and influencing larval recruitment of
67 marine organisms (Thorson 1964; Saunders & Connell 2001; Blockley &
68 Chapman 2006).

69 In both freshwater and marine environments, sunlight shading occurs
70 naturally due to riparian vegetation (Beschta 1997) or macroalgae coverage
71 (Clark, Edwards & Foster 2004). However, sunlight can also be blocked by
72 man-made structures, such as bridges, piers, wharfs, docks and ports. Although
73 the influence of the additional substrate provided by such structures on aquatic
74 biodiversity has been addressed (Bulleri & Chapman 2010), their role in artificial
75 shading has been overlooked. Results derived from salt marshes (Sanger,
76 Holland & Gainey 2004; Struck *et al.* 2004), seagrass beds (Burdick & Short
77 1999; Shafer 1999), estuaries (Able, Manderson & Studholme 1998) and hard
78 substrates (Glasby 1999; Blockley 2007) consistently show negative effects of
79 shading by artificial structures on autotrophs and alterations in the structure of
80 biological communities. Specifically on hard substrates, artificial shading has
81 been associated with shifts in the structure and the diversity of the community,
82 by reducing macroalgae cover (Glasby 1999; Blockley & Chapman 2006;
83 Blockley 2007; Miller & Etter 2008) and also by increasing the overall
84 abundances of some filter-feeding invertebrates and mobile consumers
85 (Williams 1994; Glasby 1999; Takada 1999; Blockley 2007; Miller & Etter 2008).

86 The accelerating urbanisation of coastal areas worldwide is well
87 recognised (Small & Nicholls 2003; NOAA 2004; EEA 2006). Intensification of
88 international commercial trade has increased the demand for construction or
89 expansion of ports and associated infrastructure (Van Gils & Klijn 2007; Hricko
90 2012). Such projects are usually of great magnitude and cause substantial
91 disturbance to the natural environment where they are installed and in nearby
92 locations. Loss of habitat and biodiversity, contamination by toxic substances,
93 introduction of exotic species and deterioration of air and water quality (Darbra

94 & Casal 2004; Gupta, Gupta & Patil 2005; Grech *et al.* 2013) are some
95 examples of potential impacts of ports. Quantifying the potential effects of such
96 urban structures on the organisation and functioning of biological communities
97 of natural ecosystems, has gained importance over the past decade, not only
98 from an academic viewpoint, but as tools for coastal management (Bulleri &
99 Airoidi 2005; Perkol-Finkel *et al.* 2012; Ferrario *et al.* 2016). However, in
100 considering the impacts of coastal development the effects of enhanced
101 shading, although recognised, are potentially under-estimated and have
102 received far less attention than other sources of disturbance.

103 On the north coast of São Paulo State, Brazil, the expansion of the port
104 of São Sebastião has been discussed for many decades (see Appendix S1 in
105 supplementary information for details). The initial proposal was to increase port
106 facilities through infilling of an adjacent area, Araçá Bay (Fig. S1). However, this
107 small bay is a hot spot for benthic biodiversity in the Southwest Atlantic (Amaral
108 *et al.* 2010, 2015), and after some debate, it was proposed to avoid infilling of
109 the bay by construction of a structure suspended by pillars, covering 75% of
110 Araçá Bay. Among other disturbances, such plans would substantially restrict
111 sunlight to natural habitats. As a consequence we aimed to assess the effects
112 of shading on the rocky intertidal benthic community. Through a descriptive and
113 manipulative approach, we tested the hypotheses that shading (i) decreases
114 abundance or biomass of primary producers; (ii) reduces body size of sedentary
115 grazers, owing to bottom-up control from a reduced biofilm; and (iii) modifies the
116 organisation of sessile macrobenthic communities through effects on autotrophs
117 and on larval recruitment. We show consistent impacts, based on observational
118 surveys and experimental manipulation, of sunlight shading on patterns and

119 processes driving structure and functioning of biological communities of the
120 rocky intertidal, supporting the importance of the careful considerations of
121 shading disturbance in discussions regarding sustainable development and
122 policies for expansion of ports and man-made structures worldwide.

123

124 **Material and methods**

125 DESCRIPTIVE APPROACH

126 In September 2014, a survey was conducted in three subtropical
127 sheltered rocky shores in the Southwest Atlantic that are partially shaded by
128 man-made constructions, built at least five years before the study. Tidal range
129 for the sites is about 1.4 m (Fig. S1; Table S1). All shores are dominated by
130 filter-feeding invertebrates (e.g., barnacles, oysters and mussels) in the
131 mesolittoral, while macroalgae (e.g., corticoid and turf forming algae) dominate
132 the infralittoral fringe. Biological data were compared between two different
133 habitats within each of the three shores: (i) unshaded, naturally sunny areas;
134 and (ii) shaded, sunlight-restricted areas due to human-made structures. In the
135 shaded habitat, we sampled the area under the structure where no direct
136 sunlight reached the substrate. An area of approximately 50 m horizontal
137 distance was sampled in each habitat; these areas of shore were immediately
138 adjacent to each other (separated by 20 m) to avoid any differences in physical
139 environment such as degree of wave exposure. Response variables measured
140 included the biomass of primary producers, population structure of sedentary
141 grazers and sessile community organization.

142

143 **Primary producers.** Biofilm biomass was estimated by a field-based remote
144 sensing method using digital photographs (adapted from Murphy *et al.* 2005;
145 Murphy & Underwood 2006; Murphy, Underwood & Jackson 2009; see
146 Appendix S2 in supplementary materials for details). Ten images, each of 100
147 cm², were haphazardly taken in the upper mesolittoral of each location in
148 unshaded and shaded habitats. Macroalgal biomass was estimated by
149 destructive sampling. Five areas of 100 cm² in the infralittoral fringe in both
150 habitats on the three shores were scraped clear and the macroalgae collected
151 were dried at 60° C for 24h and weighed. The dry material was then burned at
152 500° C for 4h and we calculated the ash free dry weight.

153

154 **Sedentary grazers.** Population structure of three benthic grazers - the limpet
155 *Lottia subrugosa* (d'Orbigny 1846) in the lower mesolittoral and the littorinid
156 gastropods *Echinolittorina lineolata* (d'Orbigny 1840) and *Littoraria flava* (King
157 1832) in the upper mesolittoral was assessed through photography using
158 quadrats of 100 cm² (n = 20 per habitat) for *L. subrugosa* and 25 cm² (n = 10
159 per habitat) for littorinids. Due to the small body size, the littorinids were
160 collected and, photographed in the field on a white background to facilitate
161 counting and measurement. Size was defined as the longest length of the shell.
162 Comparisons of body size of consumers between unshaded and shaded areas
163 were performed only when we obtained at least 50 specimens in each habitat
164 on each shore.

165

166 **Community organization.** Sessile macrobenthic communities were compared
167 between unshaded and shaded habitats in three tidal zones: infralittoral fringe,

168 lower mesolittoral and upper mesolittoral, delimited according to Christofolletti *et*
169 *al.* (2011). Samples were taken haphazardly through photography (100 cm², n =
170 10 or 20 per habitat) and taxa abundance estimated as percentage cover using
171 100 regular intersection grids. Macroalgae were classified into functional
172 groups, according to Littler & Arnold (1982) and Littler, Litter & Taylor (1983).
173 Other taxa were identified to the lowest possible taxonomic group. We also
174 compared the abundance of the functional groups 'macroalgae' and 'filter-
175 feeding invertebrates' between different habitats to test the hypothesis of a
176 dominance shift in the infralittoral fringe due to shading.

177

178 MANIPULATIVE APPROACH

179 Experimental manipulations to test the effect of shading on biofilm
180 biomass and community organization were conducted on the shore of
181 Pernambuco island, within Araçá Bay (São Sebastião, São Paulo State, Brazil;
182 Fig. S1). The experiment lasted 221 days in two intertidal zones (infralittoral
183 fringe and upper mesolittoral) and was performed with three treatments: (i)
184 shaded, constructed with marine plywood sheets (40 x 40 cm) suspended 10
185 cm above the substrate by stainless steel bars in each corner; (ii) procedural
186 control, provided by transparent acrylic sheets, mimicking the physical structure
187 of the shaded treatment but allowing sunlight penetration to the substratum (\approx
188 90%); and (iii) control, unmanipulated areas. While all the 40 x 40 cm area is
189 under the influence of the treatment we only used the central 100 cm² for
190 analyses, to avoid artefacts caused by diffuse light at the perimeter. Although
191 partial shading (diffuse light) is a natural consequence of many artificial
192 structures our manipulative approach intended to simulate the effect of full

193 shade expected following potential port expansion We deployed 5 replicates of
194 each treatment in each intertidal zone. Replicates were separated by at least 2
195 m and the treatments were randomly allocated within each tidal zone. Acrylic
196 plates were regularly cleaned and damaged structures were replaced as soon
197 as possible. To test the efficacy of manipulations, luminosity and temperature
198 sensors were deployed on treatments at both tide heights. Both luminosity and
199 temperature were reduced by shading, but did not differ between control
200 treatments (more details in Appendix S3).

201 Biofilm biomass was evaluated in the upper mesolittoral using the same
202 remote sensing technique and protocols (Appendix S2). Samples were
203 undertaken 0, 15, 29, 44, 73, 149, 191 and 220 days after the start of the
204 experiment. Benthic community composition was sampled on the same dates in
205 the upper mesolittoral and, after 0, 15, 29, 75, 191 and 221 days in the
206 infralittoral fringe, as allowed by tidal conditions. Because communities were
207 dominated by a few species during the whole experiment, we tested how the
208 treatments affected the areas covered by macroalgae, oysters, the barnacle
209 *Chthamalus bisinuatus* (Pilsbry 1916) and open space.

210

211 **Larval recruitment.** To test whether alterations in adult populations were linked
212 to effects of shading on larval recruitment, we utilized acrylic plates (8 x 8 cm)
213 covered with gray slip-resistant tape (3M™ Safety-Walk, Minnesota, EUA).
214 Plates were screwed in the upper mesolittoral, under the procedural control and
215 shaded treatments, avoiding central sampling area, and close to replicates in
216 control. Plates were replaced approximately every 30 days. In the laboratory,
217 we identified and quantified recruits under a stereomicroscope. We tested the

218 effects of time and treatment on the recruitment rate (number of recruits per
219 days in the field) of barnacles and oysters, the two most abundant taxa in the
220 upper mesolittoral.

221

222 DATA ANALYSIS

223 In the descriptive approach, ecological parameters from primary
224 producers, sedentary grazers and univariate data from benthic community
225 (combined macroalgae and filter-feeding invertebrates) were analyzed using
226 factorial ANOVA, considering the factors 'habitat' (fixed, 2 levels: unshaded and
227 shaded) and 'location' (random, 3 levels). Specifically for the analysis of body
228 size of *Lottia subrugosa* and *Echinolittorina lineolata*, location had 2 levels as
229 we did not sample enough specimens at one of the shores. Variance
230 homogeneity was tested by Cochran's procedure and transformations were
231 applied when needed. Where heterogeneous variances persisted, the same
232 procedure was still performed using raw data, and attention is drawn to the
233 potential for increased probability of type I errors in these cases. Body size of
234 *Littoraria flava* was compared through a t-test after confirming homoscedasticity
235 (Levene's test), since we sampled this species in enough number only in one
236 shore.

237 Data from the sessile macrobenthic communities were converted to a
238 similarity matrix based on Bray-Curtis distance and compared between 'habitat'
239 (fixed, 2 levels: unshaded and shaded) and 'location' (random, 3 levels) using
240 PERMANOVA test (999 permutations) (Anderson 2001). Comparisons of
241 communities from different habitats within locations were performed by post-hoc
242 pair-wise tests. Non-metric multidimensional scaling (nMDS) was used for

243 visualization of data. SIMPER analysis was applied to identify the taxa which
244 contributed most to dissimilarity between habitats.

245 In the experimental approach, repeated measures ANOVA was used to
246 assess the differences between treatments through time on biofilm biomass,
247 area covered by macroalgae, oysters, barnacle *Chthamalus bisinuatus* and
248 open space. Mauchly's sphericity test was applied to verify time autocorrelation.
249 When this assumption was violated, we corrected statistical significances with
250 Greenhouse-Geisser adjustment. Post-hoc Student-Newman-Keuls (SNK) test
251 was used for multiple comparisons of means for both statistical techniques. The
252 effects of 'treatment' and 'time' (random factor) on recruitment rate during the
253 manipulative approach were evaluated using a factorial ANOVA.

254

255 **Results**

256 DESCRIPTIVE APPROACH

257 Primary producers

258 There was no influence of shading on biofilm biomass on shores under
259 the influence of man-made constructions (Table 1). On the other hand, shading
260 decreased the macroalgal biomass, which was about eight times lower in the
261 shaded (mean \pm SE: 1.01 ± 0.43 g) than in the unshaded habitat (8.33 ± 1.28 g)
262 (Table 1).

263

264 Sedentary grazers

265 Shading affected body size of the limpet *Lottia subrugosa* and the
266 littorinids *Echinolittorina lineolata* (Table 1) and *Littoraria flava* (t-test, $df = 121$, t
267 $= 5.36$, $P < 0.001$) (Fig. 1). Grazers from four of the five sampled populations
268 were smaller in the shaded habitat, although, *L. subrugosa* in one of the
269 localities was bigger in shaded habitat (SNK 'Habitat x Location' interaction:
270 Table 1).

271 There was a general trend across all three species at all shores for
272 greater abundance in unshaded areas (Fig 1). However only for *Echinolittorina*
273 *lineolata*, on one rocky shore, was this effect of shade significant (SNK 'Habitat
274 x Location' interaction: Table 1; Fig. 1).

275

276 Community organization

277 There was a significant, although spatially variable, effect of shading on
278 community organization. In the infralittoral fringe, there was a significant effect
279 of shading at all three shores, while the effect was significant on two shores in
280 the lower mesolittoral and one shore in the upper mesolittoral (Post-hoc pair-
281 wise test 'Habitat x Location' interaction: Table 2; Fig. 2).

282 In the infralittoral fringe, cover of combined macroalgae decreased from
283 about 70% in unshaded habitat to 17% in shaded habitat. On the other hand,
284 combined invertebrate filter-feeders increased from 5% in unshaded to 65% in
285 shaded habitats (ANOVA, effect of 'Habitat', macroalgae: $F_{1,54} = 23,470.89$;
286 filter-feeding invertebrates: $F_{1,54} = 491.84$; $P < 0.01$). Macroalgae
287 morphofunctional groups combined were responsible for more than 45% of
288 dissimilarity between habitats (SIMPER: Table S2). For both other zones, while

289 the same species occurred in shaded and unshaded habitats, the relative
290 abundance of organisms was affected by shading (SIMPER: Table S2). In the
291 lower mesolittoral, oysters were more abundant in shaded than in unshaded
292 areas, while *Brachidontes* sp. showed an opposite pattern. These two species
293 contributed 55% of the dissimilarity between the sessile communities from
294 shaded and unshaded habitats at this shore height. In the upper mesolittoral,
295 the barnacle *Microeuraphia rizophorae* (De Oliveira 1940) was more abundant
296 in shaded than in unshaded habitats, while *Chthamalus bisinuatus* showed an
297 opposite pattern. These two species contributed 91% of the dissimilarity
298 between the sessile communities from shaded and unshaded habitats in the
299 upper mesolittoral.

300

301 MANIPULATIVE APPROACH

302 Biofilm biomass

303 Biofilm biomass showed a high degree of variation among replicates and
304 over time (Fig. 3). Although there was a significant effect of treatment (Table 3),
305 this was a consequence of the control being placed in plots of higher NDVI at
306 the start of the experiment (Fig. 3). There was no significant interaction between
307 treatment and time which might indicate divergence of the treatments over time
308 (Table 3).

309

310 Community organization

311 In the infralittoral fringe, macroalgae covered almost 100% at the
312 beginning of the experiment and quickly decreased in the shading treatment

313 during the first 2 months, completely disappearing at day 221 (SNK 'Treatment
314 x Time' interaction: Table 3, Fig. 4). Shading also affected the structure of the
315 macrobenthic community in the upper mesolittoral. In the shaded treatment,
316 oysters increased in abundance from 1.2% at the beginning of the experiment
317 to 37.8% after 220 days, while there was no change in other treatments.
318 Conversely, the barnacle *Chthamalus bisinuatus* decreased in abundance due
319 to shading, reaching a cover of about 10% by the end of the experiment (SNK
320 'Treatment x Time' interaction: Table 3; Fig. 4).

321

322 Larval recruitment

323 Larval recruitment rate was affected by shade. Oyster larvae recruited
324 more in the shaded treatment than in the control treatments (SNK 'Treatment':
325 Table 4; Fig. 5). For the barnacle *Chthamalus bisinuatus*, larval recruitment was
326 smaller in the control than in shaded and procedural control (SNK 'Treatment':
327 Table 4; Fig. 5). Also, there was variation among sampling dates, with larger
328 numbers of *C. bisinuatus* larvae recruiting in April/2015 than in all 5 months
329 before, which did not differ from one another (SNK 'Time': Table 4).

330

331 **Discussion**

332 Many studies have shown how artificial structures can influence local
333 ecosystems by the addition of substrate (see Bulleri & Chapman 2010 for
334 review). We showed important ecological changes on natural rocky substrates
335 associated with such structures and demonstrated through experiments that the
336 changes were a consequence of shading. Under shading disturbance, biomass

337 of primary producers, body size of primary consumers, community structure and
338 larval recruitment changed, and the results were consistent for both descriptive
339 and manipulative approaches. The changes in communities are likely explained
340 by physical factors and biological processes such as competition, recruitment
341 rates and physiological status of the organisms, as discussed below. Our
342 observational and experimental results contribute quantitatively to the extensive
343 debate on coastal management under pressure from urbanization (Bulleri &
344 Chapman 2010; Dugan *et al.* 2011).

345 The results highlighted more pronounced changes in the intertidal
346 communities found at the lower levels in the shore, suggesting that this zone is
347 more vulnerable to shading. There was a strong negative influence of shading
348 on macroalgae, expected since light restriction limits photosynthesis and
349 prevents autotrophs survival, as observed for other ecosystems (e.g., Glasby
350 1999; Shafer 1999; Struck *et al.* 2004; Blockley 2007; Miller & Etter 2008).
351 Surveys showed that in areas shaded by human-made structures, macroalgae
352 coverage and biomass were low, while experimental manipulation of shade
353 caused progressive loss of existing macroalgae, with total loss in about 6
354 months. Differences in abundance of macroalgae between unshaded and
355 shaded habitats can also be linked to recruitment, as macroalgae tend to recruit
356 less in light-limited areas (Clark, Edwards & Foster 2004; Blockley & Chapman
357 2006) due to high post-settlement mortality of spores and low growth (Goldberg
358 & Foster 2002).

359 With the reduction in macroalgae in the infralittoral zone affected by man-
360 made structures, dominance shifted toward filter-feeding invertebrates. This
361 shift to invertebrates was not observed following shade manipulation, possibly

362 as a consequence of limited recruitment over the 220 day experimental period,
363 but also potentially owing to high mortality of early settlers caused by
364 sedimentation observed in experimental plots (Airoldi 2003). It was not clear the
365 extent to which such sedimentation was an artefact of the shade structures,
366 since sedimentation on rock throughout Araçá Bay is common depending on
367 prevailing weather and sea conditions. Whether shading leads to dominance by
368 filter feeding invertebrates, or to open bare space, there was a clear reduction in
369 local biodiversity, considering the loss of macroalgae species and their
370 associated fauna (Christie, Norderhaug & Fredriksen 2009). An additional
371 consequence of loss of turf macroalgae cover is the opening up of bare space
372 and an enhanced probability of invasive species establishment (Arenas *et al.*
373 2006). This shading may be an additional mechanism by which urban
374 infrastructure in port facilities can facilitate the introduction and spread of exotic
375 species (Bulleri & Airoldi 2005; Vaselli, Bulleri & Benedetti-Cecchi 2008;
376 Dafforn, Johnston & Glasby 2009).

377 We predicted, based on previous observations (Hill, Ryon & Schilling
378 1995; Harley 2002), that shading would have a negative effect on the intertidal
379 epilithic biofilm, but we found no support for this hypothesis. The intertidal
380 biofilm is a complex system and the influence of light on its dynamics is still
381 controversial. Biofilm biomass can increase due to shading or reduced sunlight
382 regimes (Jenkins *et al.* 2001; Thompson, Norton & Hawkins 2004) or show
383 restricted growth when exposed to excess sunlight, due to photoinhibition or
384 thermal stress (Serôdio, Vieira & Cruz 2008; Coelho, Vieira & Serôdio 2009).
385 Also, it is important to note that our manipulation did not exclude biofilm
386 grazers. Previous work in the study region has shown that fast-moving grazers

387 mask the effect of sedentary grazers on biofilm, while grazing pressures of both
388 together mask environmental influences (Christofoletti, Almeida & Ciotti 2011).
389 Although the influence of shading on biofilm was not seen, our prediction of
390 negative shade effects on grazers was confirmed at most locations. Another,
391 non-exclusive hypothesis to explain bigger animals in sunny habitats is that
392 grazer size is related to increased heat stress in sunny habitats, which would
393 select specimens with larger shells due to optimized water storage (Vermeij
394 1973; Tanaka, Duque-Estrada & Magalhães 2002) and also increasing growth
395 rate due a higher metabolism (Chelazzi, Williams & Gray 1999).

396 Shading can also promote differences between communities by changing
397 the recruitment regime (Chapman & Blockley 2006). Many late-stage larvae
398 show active choice at settlement (Keough & Downes 1982); available light is an
399 important cue with many larvae of marine organisms exhibiting negative
400 phototactic behaviour, thus settling in light-limited habitats (Thorson 1964;
401 Young & Chia 1984; Saunders & Connell 2001). Blockley & Chapman (2006)
402 showed that shading increased recruitment of some filter-feeding invertebrates
403 but reduced macroalgae recruitment on seawalls. Such results are consistent
404 with the abundance of these taxa in established shaded communities in the
405 present study, supporting the conclusion that changes in community
406 organisation in the infralittoral fringe and mesolittoral following shading may be
407 linked to larval recruitment. Oysters became more abundant in the upper
408 mesolittoral in the shaded treatment and barnacle recruitment increased in
409 shaded habitats. However, interestingly, the abundance of adult barnacles
410 reduced under shading. Such patterns, both in the natural environment and
411 experiments indicate the need to differentiate between effects of shade on

412 settlement/ early post settlement mortality and the development of adult
413 populations.

414 Our study shows the consequences of shading from artificial structures
415 on the biota of intertidal rocky shores. Coastlines worldwide are being
416 increasingly modified through constructions ranging from artificial sea defences
417 to port facilities (Bulleri & Chapman 2010; Dugan *et al.* 2011). Such urban
418 infrastructures alter landscape via loss, addition or fragmentation of habitat
419 (Chapman 2006; Goodsell, Chapman & Underwood 2007), and modify
420 biodiversity, since artificial and natural habitats do not support the same
421 communities (Bulleri & Chapman 2004). Our study was prompted by the
422 proposal for expansion of the port of São Sebastião which would result in a
423 shaded area of approximately 1 km² of the Araçá Bay, impacting rocky shores,
424 soft sediment habitats and mangroves. Results indicate such a development
425 would cause substantial decreases in macroalgae cover on hard substrate
426 leading to a reduction in primary production, carbon exchange and habitat for
427 associated fauna. Shading is also predicted to increase filter-feeding
428 invertebrate cover strongly influencing the dynamics of the pelagic environment.
429 The Araçá Bay, like many other coastal sites threatened by development is a
430 hot spot in marine biodiversity (Amaral *et al.* 2010, 2015) supporting a wide
431 range of ecosystem services. Understanding the impact of shading contributes
432 to a wider view of the consequences of such development and hence informs
433 discussions regarding sustainable development, in this and other regions
434 around the world. Specifically regarding the expansion plans of the port of São
435 Sebastião, our results suggest that covering the bay with a suspended structure
436 will have major negative effects on biodiversity and ecosystem functioning. As a

437 result, we recommend that stakeholders carefully evaluate the expansion plan,
438 and, based on the likely shade effects (as well as many other potential impacts)
439 across much of the bay, we do not recommend it.

440

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450

451 **Data accessibility**

- 452 - Study sites locations: uploaded as online supporting information (Table S1).
- 453 - Data archived in Figshare <https://dx.doi.org/10.6084/m9.figshare.3205285.v1>
454 (Pardal-Souza *et al.* 2016).

455

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644 Supporting Information

645 TABLES

646

647

648 **Table 1.** Effect of habitats (unshaded and shaded) (2-way ANOVA) on primary
 649 producers and sedentary grazers on subtropical rocky shores. ** $P < 0.01$; *** P
 650 < 0.001 ; ns = not significant. §Data transformed to $\ln(x + 1)$

651

652	Effect	df	MS	F	P	df	MS	F	P	
653	Primary producers									
654	Biofilm biomass					Macroalgae biomass				
655	Habitat = H	1	0.004	0.16	0.72	1	4.02	137.25	**	
656	Location = L	2	0.094	3.84	0.20	2	0.49	16.92	0.05	
657	H*L	2	0.024	2.92	0.06	2	0.03	0.25	0.78	
658	Error	54	0.008			24	0.11			
659	Cochran's test		C = 0.47 (***)				C = 0.45 (ns)			
660	Grazers body size									
661	<i>L. subrugosa</i>					<i>E. lineolata</i>				
662	Habitat = H	1	0.52	0.001	0.97	1	34.66	3.28	0.32	
663	Location = L	1	11.52	0.027	0.89	1	38.18	3.61	0.30	
664	H*L	1	416.12	42.56	***	1	10.55	11.95	***	
665	Error	1066	9.77			606	0.88			
666	Cochran's test		C = 0.51 (***)				C = 0.39 (***)			
667	Grazers abundance									
668	<i>L. subrugosa</i>					<i>E. lineolata</i> §				
669	Habitat = H	1	2,226.05	5.26	0.26	1	1.97	2.17	0.28	
670	Location = L	1	61.25	0.14	0.76	2	2.99	3.30	0.23	
671	H*L	1	423.20	3.37	0.07	2	0.90	9.79	***	
672	Error	76	125.46			54	0.09			
673	Cochran's test		C = 0.47 (***)				C = 0.28 (ns)			

674

675

Table 2. Effects of habitats (unshaded and shaded) (PERMANOVA) on sessile macrobenthic communities on different zonation ranges in subtropical rocky shores. All data was transformed to arcsine $(\sqrt{x}) + 1$. *** $P < 0.001$

Effect	df	MS	Pseudo-F	<i>P</i>	df	MS	Pseudo-F	<i>P</i>	df	MS	Pseudo-F	<i>P</i>
		(a) Infralittoral fringe				(b) Lower mesolittoral				(c) Upper mesolittoral		
Habitat = H	1	315.96	1.77	0.24	1	138.69	0.55	0.60	1	150.98	0.63	0.57
Location = L	2	156.02	7.36	***	2	1,521.10	147.30	***	2	376.64	21.03	***
H*L	2	177.87	8.40	***	2	252.02	26.06	***	2	240.12	13.41	***
Error	54	21.17			114	1,102.40			54	17.91		
Pair-wise tests 'unshaded' vs. 'shaded' inside Location												
		(a) Infralittoral fringe				(b) Lower mesolittoral				(c) Upper mesolittoral		
		<i>t</i>	<i>P</i>			<i>t</i>	<i>P</i>			<i>t</i>	<i>P</i>	
	RS1	3.06	***			1.02	0.36			1.44	0.16	
	RS2	3.43	***			4.84	***			5.31	***	
	RS3	3.30	***			4.69	***			0.40	0.80	

Table 3. Effects of treatments (repeated measures ANOVA) on abundance of primary producers, sessile invertebrates and open space on shading manipulation in the upper mesolittoral and infralittoral fringe. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; § P -values corrected by Greenhouse-Geisser adjustment. All response variables except biofilm were transformed to arcsine (\sqrt{x})

Effect	df	MS	F	P	MS	F	P	MS	F	P
Upper mesolittoral										
Biofilm										
Treatment = Tr	2	0.0240	8.87	**	0.60	12.31	***	0.62	4.13	*
Error	12	0.0028			0.05			0.15		
Time = Ti	7	0.0058	3.79	**	0.02	1.48	0.25	0.70	50.40	***
Tr*Ti	14	0.0021	1.36	0.19	0.10	6.45	**	0.05	4.10	**
Error	84	0.0015			0.01			0.01		
Infralittoral fringe										
Macroalgae										
Treatment = Tr	2	5.75	64.22	***	5.16	61.05	***			
Error	12	0.09			0.08					
Time = Ti	5	0.98	30.87	***	0.94	29.09	***			
Tr*Ti	10	0.34	10.64	***	0.32	10.03	***			
Error	60	0.03			0.03					
Open space										
<i>C. bisinuatus</i> §										

Table 4. Effects of treatments (2-way ANOVA) on recruitment rate of oysters and the barnacle *Chthamalus bisinuatus* on shading manipulation in the upper mesolittoral. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Effect	df	<i>Chthamalus bisinuatus</i>			Oysters		
		MS	F	<i>P</i>	MS	F	<i>P</i>
Treatment = Tr	2	0.98	10.97	**	0.48	5.32	*
Time = Ti	5	1.34	15.01	***	0.10	1.07	0.42
Tr*Ti	10	0.09	0.84	0.58	0.09	1.79	0.07
Error	72	0.10			0.05		
Cochran's test		C = 0.25 (***)			C = 0.83 (***)		

FIGURE CAPTIONS

Fig. 1. Body size and abundance (mean + standard error) of sedentary grazers (a) *Lottia subrugosa*, (b) *Echinolittorina lineolata* and (c) *Littoraria flava* in unshaded and shaded habitats in subtropical rocky shores (RS). * $P < 0.01$; *** $P < 0.001$; ns = not significant; according to SNK test (items a and b) or t-test (c).

Fig. 2. nMDS diagrams of macrobenthic communities of different zonation ranges in unshaded and shaded habitats in subtropical rocky shores (RS).

Fig. 3. Biofilm biomass (NDVI) (mean \pm standard error) in treatments of shading manipulation in the upper mesolittoral.

Fig. 4. Cover percentage (mean \pm standard error) of macroalgae, open space, oysters and the barnacle *Chthamalus bisinuatus* in treatments of shading manipulation. Post-hoc comparisons of treatments shown only for beginning and end of experiment. SNK test: ns = not significant; ***control = procedural control \neq shaded.

Fig. 5. Cumulative recruitment (mean number of accumulated recruits in each time) of oysters and the barnacle *Chthamalus bisinuatus* in treatments of shading manipulation.

FIGURES

Figure 1

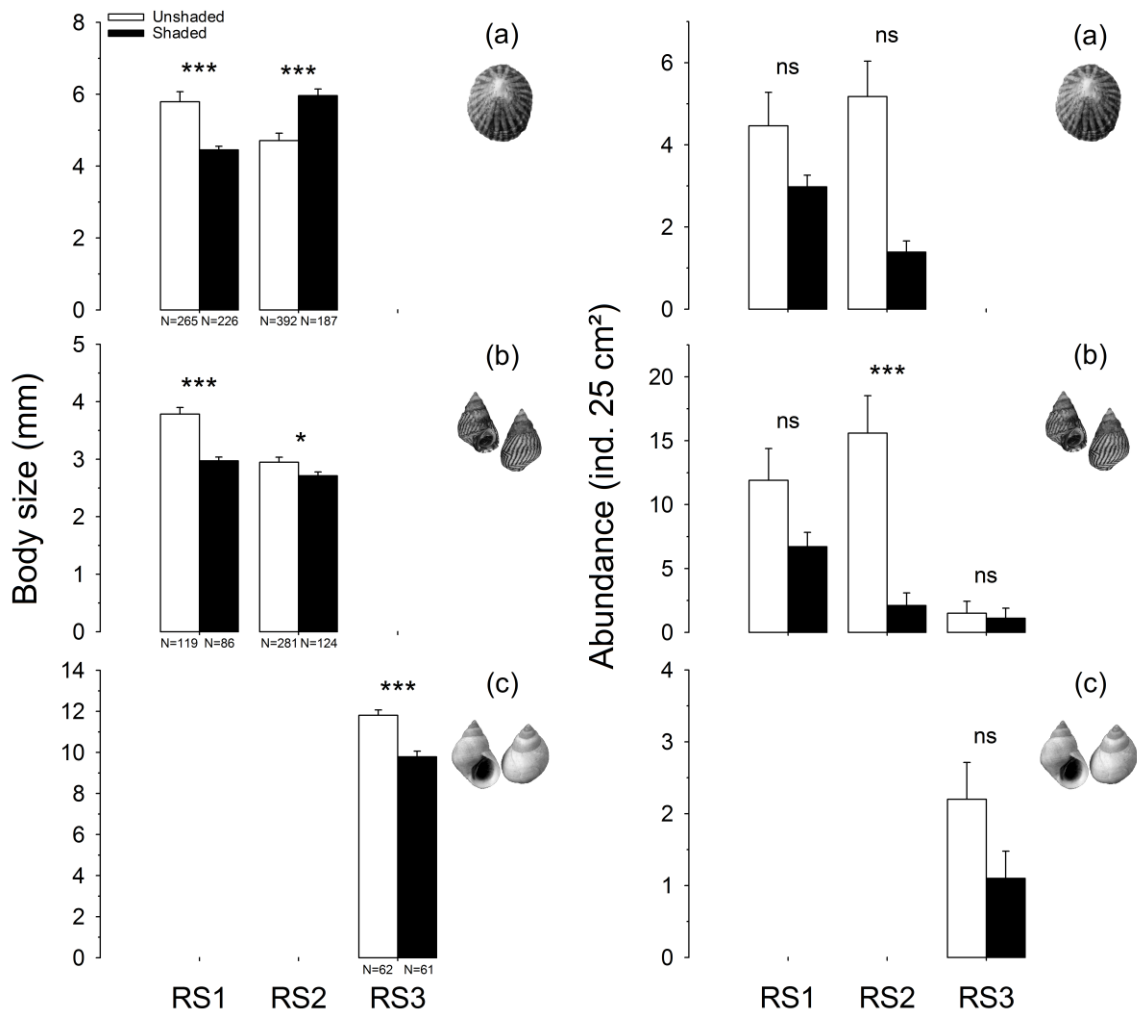


Figure 2

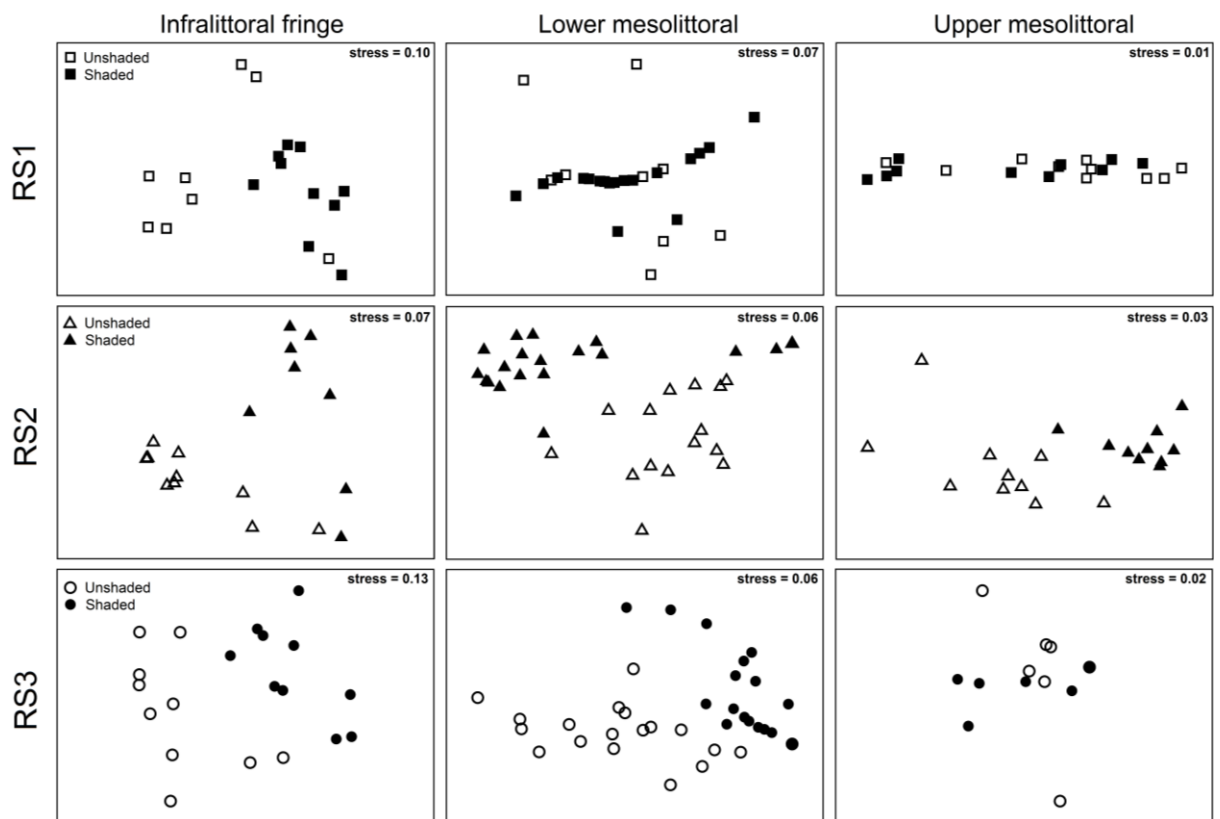


Figure 3

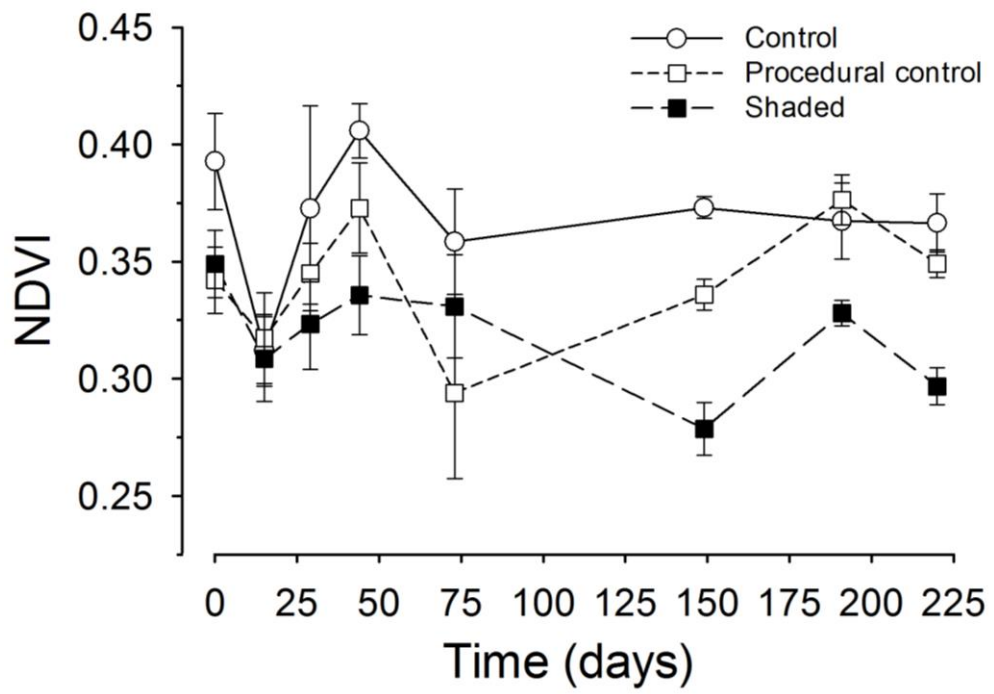


Figure 4

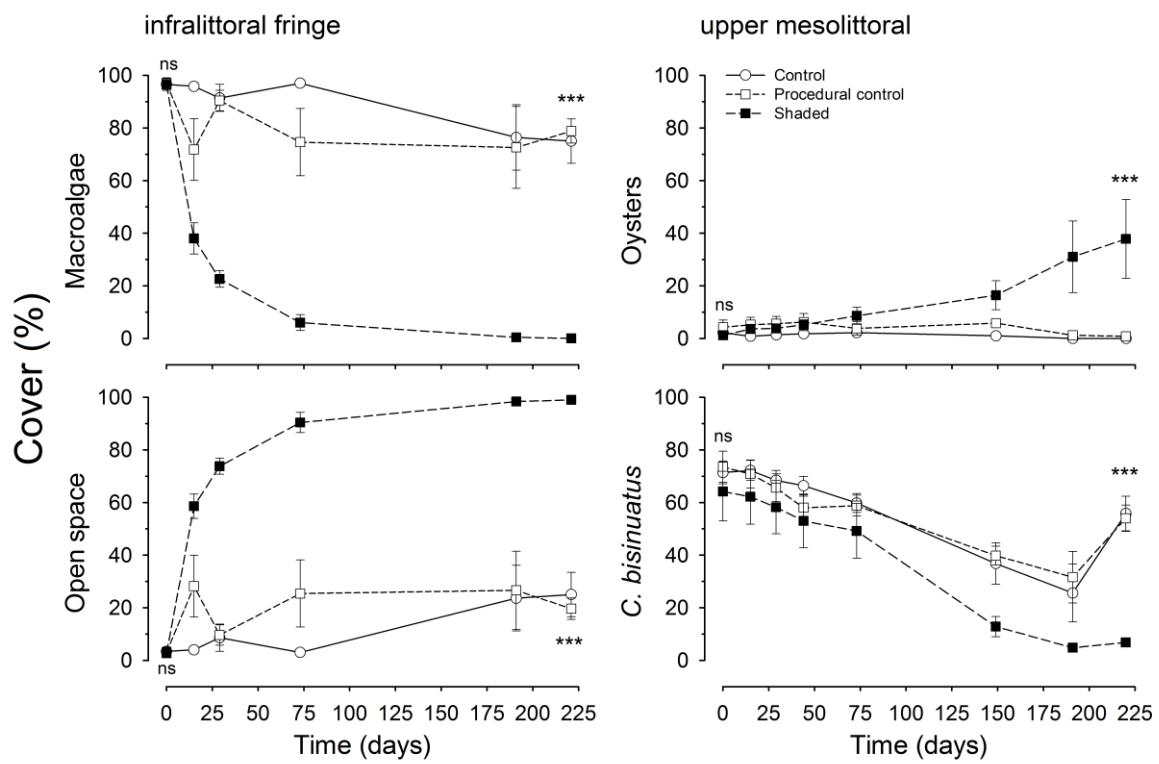


Figure 5

