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

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Summary

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

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

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

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

5. *Synthesis and applications.* We demonstrate a clear impact of shading by artificial human-made structures on patterns and processes regulating biodiversity on rocky shores and thus consequences for coastal ecosystem functioning. We argue that shading by artificial coastal structures, such as those proposed in the port expansion in our study site in south-eastern Brazil, is potentially underestimated. Our work emphasizes the importance of careful evaluations of artificial structures in order to promote sustainable coastal development. As a result, we do not recommend the proposed expansion by suspended structures of the port of São Sebastião, as the consequent shading will negatively affect the biodiversity and ecosystem functioning of the Araçá Bay and surrounding areas.

Key-words: Araçá Bay, biofilm, filter-feeding invertebrates, grazers, human disturbances, intertidal, larval recruitment, luminosity, macroalgae, port expansion

Introduction

Sunlight shading affects the structure and functioning of biological communities in natural ecosystems, through a reduction in the incidence of solar radiation, thus disturbing the growth and biomass production by autotrophs in both terrestrial (Williams, Messier & Kneeshaw 1999; Pagès *et al.* 2003) and aquatic environments (Fitzpatrick & Kirkman 1995; Quinn *et al.* 1997; Ruiz & Romero 2001). Sunlight limitation can influence animal communities by affecting physical conditions (e.g. reducing heat stress) (Williams 1994; Kon, Kurokura & Tongnunui 2010),

decreasing energetic resources of herbivores (Hill, Ryon & Schilling 1995; Harley 2002) and influencing larval recruitment of marine organisms (Thorson 1964; Saunders & Connell 2001; Blockley & Chapman 2006).

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

The accelerating urbanization of coastal areas worldwide is well recognized (Small & Nicholls 2003; NOAA 2004; EEA 2006). Intensification of international commercial trade has increased the demand for construction or expansion of ports and associated infrastructure (Van Gils & Klijn 2007; Hricko 2012). Such projects are usually of great magnitude and cause substantial disturbance to the natural environment where they are installed and in nearby locations. Loss of habitat and biodiversity, contamination by toxic substances, introduction of exotic species and deterioration of air and water quality (Darbra & Casal 2004; Gupta, Gupta & Patil 2005; Grech *et al.* 2013) are some examples of potential impacts of ports. Quantifying the potential effects of such urban structures on the organization and functioning of biological communities of natural ecosystems has gained importance over the past decade, not only from an academic viewpoint, but as tools for coastal management (Bulleri & Airoldi 2005; Perkol-Finkel *et al.* 2012; Ferrario *et al.* 2016). However, considering the impacts of coastal development, the effects of enhanced shading, although recognized, are potentially underestimated and have received far less attention than other sources of disturbance.

On the north coast of São Paulo State, Brazil, the expansion of the port of São Sebastião has been discussed for many decades (see Appendix S1, Supporting Information). The initial proposal was to increase port facilities through infilling of an adjacent area, Araçá Bay (Fig. S1). However, this small bay is a hot spot for benthic biodiversity in the south-west Atlantic (Amaral *et al.* 2010, 2015), and after

some debate, it was proposed to avoid infilling of the bay by construction of a structure suspended by pillars, covering 75% of Araçá Bay. Among other disturbances, such plans would substantially restrict sunlight to natural habitats. As a consequence, we aimed to assess the effects of shading on the rocky intertidal benthic community. Through a descriptive and manipulative approach, we tested the hypotheses that shading (i) decreases abundance or biomass of primary producers; (ii) reduces body size of sedentary grazers, owing to bottom-up control from a reduced biofilm; and (iii) modifies the organization of sessile macrobenthic communities through effects on autotrophs and on larval recruitment. We show consistent impacts, based on observational surveys and experimental manipulation, of sunlight shading on patterns and processes driving structure and functioning of biological communities of the rocky intertidal, supporting the importance of the careful considerations of shading disturbance in discussions regarding sustainable development and policies for expansion of ports and human-made structures world-wide.

Materials and methods

DESCRIPTIVE APPROACH

In September 2014, a survey was conducted in three subtropical sheltered rocky shores in the south-west Atlantic that are partially shaded by human-made constructions (Fig. S1; Table S1), built at least 5 years before the study. Tidal range for the sites is about 1·4 m. All shores are dominated by filter-feeding invertebrates (e.g. barnacles, oysters and mussels) in the mesolittoral, while macroalgae (e.g. corticoid and turf-forming algae) dominate the infralittoral fringe. Biological data were compared between two different habitats within each of the three shores: (i) unshaded, naturally sunny areas; and (ii) shaded, sunlight-restricted areas due to human-made structures. In the shaded habitat, we sampled the area under the structure where no direct sunlight reached the substrate. An area of approximately 50 m horizontal distance was sampled in each habitat; these areas of shore were immediately adjacent to each other (separated by 20 m) to avoid any differences in physical environment such as degree of wave exposure. Response variables measured included the biomass of primary producers, population structure of sedentary grazers and sessile community organization.

Primary producers

Biofilm biomass was estimated by a field-based remote sensing method using digital photographs (adapted from Murphy *et al.* 2005; Murphy & Underwood 2006; Murphy, Underwood & Jackson 2009; see Appendix S2). Ten images, each of 100 cm^2, were haphazardly taken in the upper mesolittoral of each location in unshaded and shaded habitats. Macroalgal biomass was estimated by destructive sampling. Five areas of 100 cm^2 in the infralittoral fringe in both habitats on the three shores were scraped clear and the macroalgae collected were dried at 60 °C for 24 h and weighed. The dry material was then burned at 500 °C for 4 h, and we calculated the ash-free dry weight.

Sedentary grazers

Population structure of three benthic grazers – the limpet *Lottia subrugosa* (d'Orbigny 1846) in the lower mesolittoral and the littorinid gastropods *Echinolittorina lineolata* (d'Orbigny 1840) and *Littoraria flava* (King 1832) in the upper mesolittoral was assessed through photography using quadrats of 100 cm^2 ($n = 20$ per habitat) for *L. subrugosa* and 25 cm^2 ($n = 10$ per habitat) for littorinids. Due to the small body size, the littorinids were collected and photographed in the field on a white background to facilitate counting and measurement. Size was defined as the longest length of the shell. Comparisons of body size of consumers between unshaded and shaded areas were performed only when we obtained at least 50 specimens in each habitat on each shore.

Community organization

Sessile macrobenthic communities were compared between unshaded and shaded habitats in three tidal zones: infralittoral fringe, lower mesolittoral and upper mesolittoral, delimited according to Christofoletti *et al.* (2011). Samples were taken haphazardly through photography (100 cm^2, $n = 10$ or 20 per habitat) and taxa abundance estimated as percentage cover using 100 regular intersection grids. Macroalgae were classified into functional groups, according to Littler & Arnold (1982) and Littler, Littler & Taylor (1983). Other taxa were identified to the lowest possible taxonomic group. We also compared the abundance of the functional groups 'macroalgae' and 'filter-feeding invertebrates' between different habitats to test the hypothesis of a dominance shift in the infralittoral fringe due to shading.

MANIPULATIVE APPROACH

Experimental manipulations to test the effect of shading on biofilm biomass and community organization were conducted on the shore of Pernambuco island, within Araçá Bay (São Sebastião, São Paulo State, Brazil; Fig. S1). The experiment lasted 221 days in two intertidal zones (infralittoral fringe and upper mesolittoral) and was performed with three treatments: (i) shaded, constructed with marine plywood sheets (40 × 40 cm) suspended 10 cm above the substrate by stainless steel bars in each corner; (ii) procedural control, provided by transparent acrylic sheets, mimicking the physical structure of the shaded treatment but allowing sunlight penetration to the substratum (≈ 90%); and (iii) control, unmanipulated areas. While all the 40 × 40 cm area is under the influence of the treatment, we only used the central 100 cm^2 for analyses, to avoid artefacts caused by diffuse light at the perimeter. Although partial shading (diffuse light) is a natural consequence of many artificial structures, our manipulative approach intended to simulate the effect of full shade expected following potential port expansion. We deployed five replicates of each treatment in each intertidal zone. Replicates were separated by at least 2 m, and the treatments were randomly allocated within each tidal zone. Acrylic plates were regularly cleaned, and damaged structures were replaced as soon as possible. To test the efficacy of manipulations, luminosity and temperature sensors were deployed on treatments at both tide heights. Both luminosity and temperature were reduced by shading, but did not differ between control treatments (more details in Appendix S3).

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

Larval recruitment

To test whether alterations in adult populations were linked to the effects of shading on larval recruitment, we utilized acrylic plates (8 × 8 cm) covered with grey slip-resistant tape (3M™ Safety-Walk, Saint Paul, MN, USA). Plates were screwed in the upper mesolittoral, under the procedural control and shaded treatments, avoiding central sampling area, and close to replicates in control. Plates were replaced approximately every 30 days. In the laboratory, we identified and quantified recruits under a stereomicroscope. We tested the effects of time and treatment on the recruitment rate (number of recruits per days in the field) of barnacles and oysters, the two most abundant taxa in the upper mesolittoral.

DATA ANALYSIS

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

Data from the sessile macrobenthic communities were converted to a similarity matrix based on Bray–Curtis distance and compared between 'habitat' (fixed, two levels: unshaded and shaded) and 'location' (random, three levels) using PERMANOVA test (999 permutations) (Anderson 2001). Comparisons of communities from different habitats within locations were performed by post hoc pairwise tests. Non-metric multidimensional scaling (nMDS) was used for visualization of data. SIMPER analysis was applied to identity the taxa which contributed most to dissimilarity between habitats.

In the experimental approach, repeated-measures ANOVA was used to assess the differences between treatments through time on biofilm biomass, area covered by macroalgae, oysters, barnacle *Chthamalus bisinuatus* and open space. Mauchly's sphericity test was applied to verify time autocorrelation. When this assumption was violated, we corrected statistical significances with

Greenhouse–Geisser adjustment. Post hoc Student–Newman–Keuls (SNK) test was used for multiple comparisons of means for both statistical techniques. The effects of 'treatment' and 'time' (random factor) on recruitment rate during the manipulative approach were evaluated using a factorial ANOVA.

Results

DESCRIPTIVE APPROACH

Primary producers

There was no influence of shading on biofilm biomass on shores under the influence of human-made constructions (Table 1). On the other hand, shading decreased the macroalgal biomass, which was about eight times lower in the shaded habitat (mean ± SE: 1·01 ± 0·43 g) than in the unshaded habitat (8·33 ± 1·28 g) (Table 1).

Sedentary grazers

Shading affected body size of the limpet *Lottia subrugosa* and the littorinids *Echinolittorina lineolata* (Table 1) and *Littoraria flava* (*t*-test, d.f. = 121, t = 5·36, P < 0·001)

(Fig. 1). Grazers from four of the five sampled populations were smaller in the shaded habitat, although *L. subrugosa* in one of the localities was bigger in shaded habitat (SNK 'Habitat × Location' interaction: Table 1).

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

Community organization

There was a significant, although spatially variable, effect of shading on community organization. In the infralittoral fringe, there was a significant effect of shading at all three shores, while the effect was significant on two shores in the lower mesolittoral and one shore in the upper mesolittoral (*Post hoc* pairwise test 'Habitat × Location' interaction: Table 2; Fig. 2).

In the infralittoral fringe, cover of combined macroalgae decreased from about 70% in unshaded habitat to 17% in shaded habitat. On the other hand, combined invertebrate filter feeders increased from 5% in unshaded

Table 1. Effect of habitats (unshaded and shaded) (two-way ANOVA) on primary producers and sedentary grazers on subtropical rocky shores

Effect	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
	Primary producers							
	Biofilm biomass				Macroalgae biomass			
Habitat = H	1	0·004	0·16	0·72	1	4·02	137·25	**
Location = L	2	0·094	3·84	0·20	2	0·49	16·92	0·05
H × L	2	0·024	2·92	0·06	2	0·03	0·25	0·78
Error	54	0·008			24	0·11		
Cochran's test	C = 0·47 (***)				C = 0·45 (ns)			
	Grazers' body size							
	L. subrugosa				*E. lineolata*			
Habitat = H	1	0·52	0·001	0·97	1	34·66	3·28	0·32
Location = L	1	11·52	0·027	0·89	1	38·18	3·61	0·30
H × L	1	416·12	42·56	***	1	10·55	11·95	***
Error	1066	9·77			606	0·88		
Cochran's test	C = 0·51 (***)				C = 0·39 (***)			
	Grazers' abundance							
	L. subrugosa				*E. lineolata*[†]			
Habitat = H	1	2226·05	5·26	0·26	1	1·97	2·17	0·28
Location = L	1	61·25	0·14	0·76	2	2·99	3·30	0·23
H × L	1	423·20	3·37	0·07	2	0·90	9·79	***
Error	76	125·46			54	0·09		
Cochran's test	C = 0·47 (***)				C = 0·28 (ns)			

**P < 0·01; ***P < 0·001; ns = not significant.
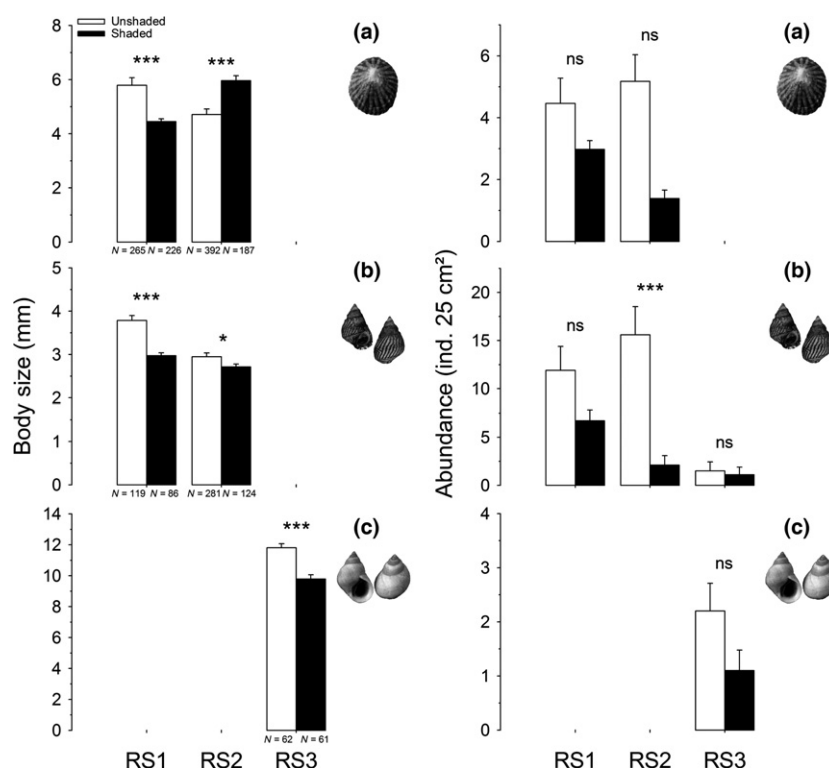[†]Data transformed to ln (x + 1).

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).

Table 2. Effects of habitats (unshaded and shaded) (PERMANOVA) on sessile macrobenthic communities on different zonation ranges in subtropical rocky shores

Effect	d.f.	MS	Pseudo-F	P	d.f.	MS	Pseudo-F	P	d.f.	MS	Pseudo-F	P
	(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	1521·10	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	1102·40			54	17·91		

Pairwise tests 'unshaded' vs. 'shaded' inside location

	(a) Infralittoral fringe		(b) Lower mesolittoral		(c) Upper mesolittoral	
	t	P	*t*	P	*t*	P
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

All data were transformed to arcsine ($\sqrt{x}$) + 1. ***$P < 0.001$.

to 65% in shaded habitats (ANOVA, effect of 'Habitat', macroalgae: $F_{1,54} = 23\,470.89$; filter-feeding invertebrates: $F_{1,54} = 491.84$; $P < 0.01$). Macroalgae morphofunctional groups combined were responsible for more than 45% of dissimilarity between habitats (SIMPER: Table S2). For both other zones, while the same species occurred in shaded and unshaded habitats, the relative abundance of organisms was affected by shading (SIMPER: Table S2). In the lower mesolittoral, oysters were more abundant in shaded than in unshaded areas, while *Brachidontes* sp.

showed an opposite pattern. These two species contributed 55% of the dissimilarity between the sessile communities from shaded and unshaded habitats at this shore height. In the upper mesolittoral, the barnacle *Microeuraphia rizophorae* (De Oliveira 1940) was more abundant in shaded than in unshaded habitats, while *Chthamalus bisinuatus* showed an opposite pattern. These two species contributed 91% of the dissimilarity between the sessile communities from shaded and unshaded habitats in the upper mesolittoral.
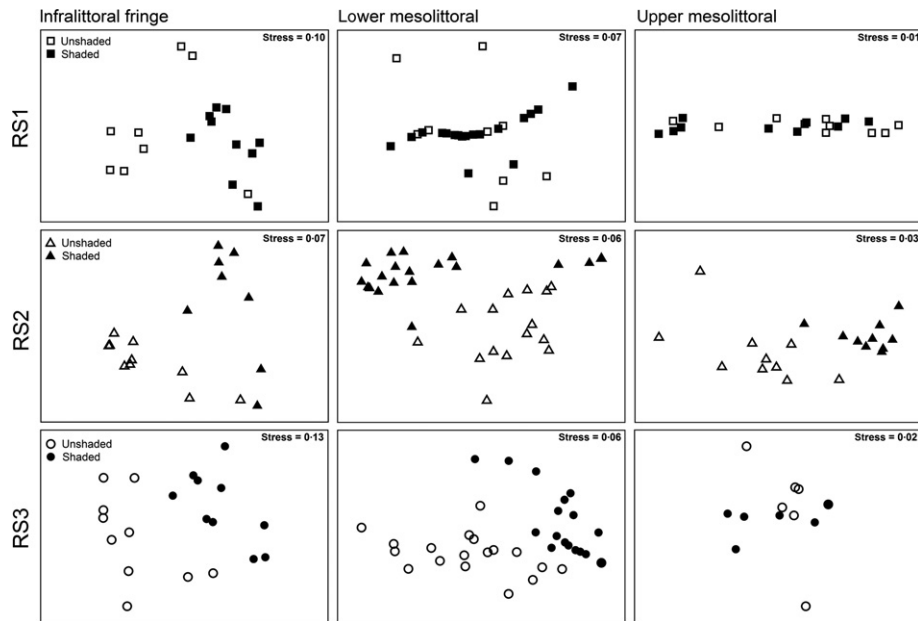
Fig. 2. nMDS diagrams of macrobenthic communities of different zonation ranges in unshaded and shaded habitats in subtropical rocky shores (RS).
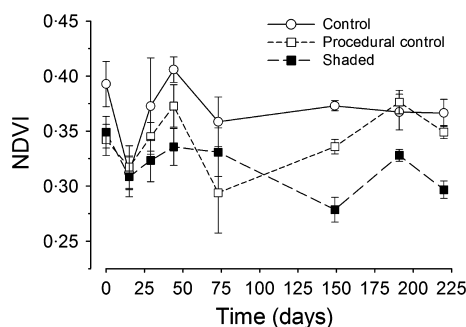

Fig. 3. Biofilm biomass (NDVI) (mean ± standard error) in treatments of shading manipulation in the upper mesolittoral.

MANIPULATIVE APPROACH

Biofilm biomass

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

Community organization

In the infralittoral fringe, macroalgae covered almost 100% at the beginning of the experiment and quickly decreased in the shading treatment during the first 2 months, completely disappearing at day 221 (SNK

'Treatment × Time' interaction: Table 3, Fig. 4). Shading also affected the structure of the macrobenthic community in the upper mesolittoral. In the shaded treatment, oysters increased in abundance from 1·2% at the beginning of the experiment to 37·8% after 220 days, while there was no change in other treatments. Conversely, the barnacle *Chthamalus bisinuatus* decreased in abundance due to shading, reaching a cover of about 10% by the end of the experiment (SNK 'Treatment × Time' interaction: Table 3; Fig. 4).

Larval recruitment

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

Discussion

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

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

	d.f.	MS	F	P	MS	F	P	MS	F	P
		Upper mesolittoral								
Effect		Biofilm			Oysters†			*C. bisinuatus*†		
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			Open space					
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					

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
†P-values corrected by Greenhouse–Geisser adjustment. All response variables except biofilm were transformed to arcsine ($\sqrt{x}$).

Fig. 4. Cover percentage (mean ± 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 ≠ shaded.
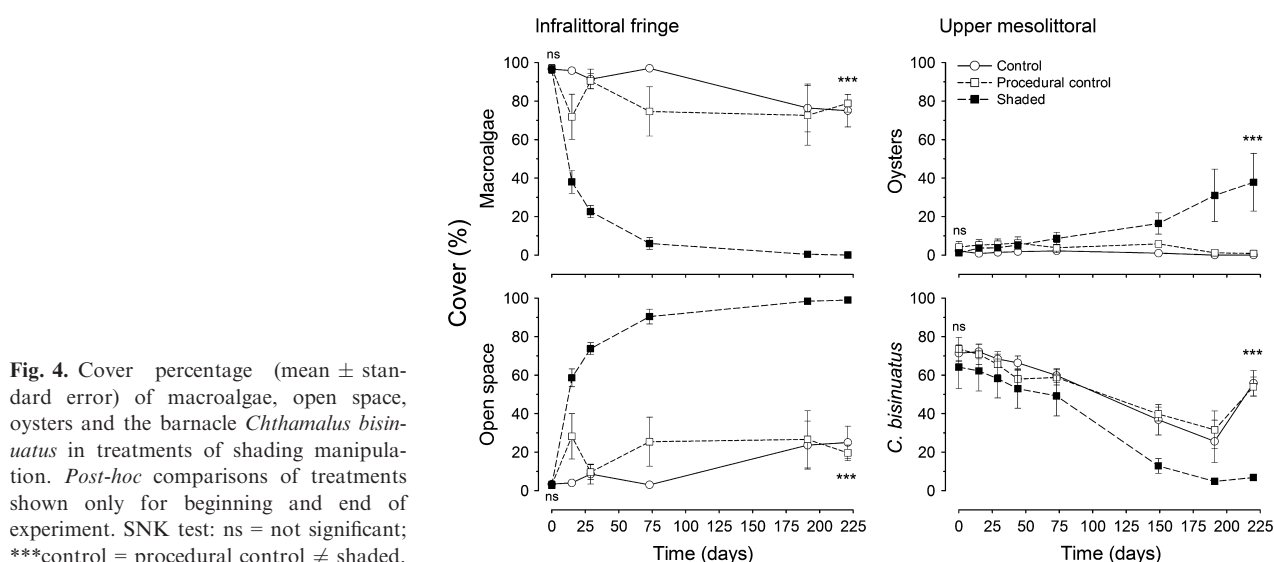
larval recruitment changed, and the results were consistent for both descriptive and manipulative approaches. The changes in communities are likely explained by physical factors and biological processes such as competition, recruitment rates and physiological status of the organisms, as discussed below. Our observational and experimental results contribute quantitatively to the extensive debate on coastal management under pressure from urbanization (Bulleri & Chapman 2010; Dugan *et al.* 2011).

The results highlighted more pronounced changes in the intertidal communities found at the lower levels in the shore, suggesting that this zone is more vulnerable to shading. There was a strong negative influence of shading on macroalgae, expected since light restriction limits

photosynthesis and may prevent autotrophs survival (e.g., Glasby 1999; Shafer 1999; Blockley 2007; Miller & Etter 2008). Surveys showed that in areas shaded by human-made structures, macroalgae coverage and biomass were low, while experimental manipulation of shade caused progressive loss of existing macroalgae, with total loss in about 6 months. Differences in abundance of macroalgae between unshaded and shaded habitats can also be linked to recruitment, as macroalgae tend to recruit less in light-limited areas (Clark, Edwards & Foster 2004; Blockley & Chapman 2006) due to high post-settlement mortality of spores and low growth (Goldberg & Foster 2002).

With the reduction in macroalgae in the infralittoral zone affected by human-made structures, dominance

Table 4. Effects of treatments (two-way ANOVA) on recruitment rate of oysters and the barnacle *Chthamalus bisinuatus* on shading manipulation in the upper mesolittoral

Effect	d.f.	MS	F	P	MS	F	P
		Chthamalus bisinuatus			Oysters		
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 (***)		

*P < 0·05; **P < 0·01; ***P < 0·001.
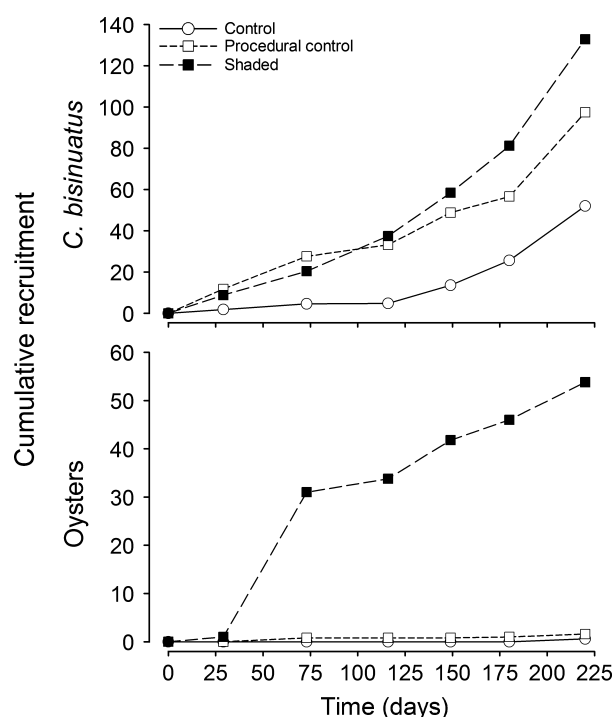
Fig. 5. Cumulative recruitment (mean number of accumulated recruits in each time) of oysters and the barnacle *Chthamalus bisinuatus* in treatments of shading manipulation.

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

We predicted, based on previous observations (Hill, Ryon & Schilling 1995; Harley 2002), that shading would have a negative effect on the intertidal epilithic biofilm, but we found no support for this hypothesis. The intertidal biofilm is a complex system and the influence of light on its dynamics is still controversial. Biofilm biomass can increase due to shading or reduced sunlight regimes (Jenkins *et al.* 2001; Thompson, Norton & Hawkins 2004) or show restricted growth when exposed to excess sunlight, due to photoinhibition or thermal stress (Serôdio, Vieira & Cruz 2008; Coelho, Vieira & Serôdio 2009). Also, it is important to note that our manipulation did not exclude biofilm grazers. Previous work in the study region has shown that fast-moving grazers mask the effect of sedentary grazers on biofilm, while grazing pressures of both together mask environmental influences (Christofoletti, Almeida & Ciotti 2011). Although the influence of shading on biofilm was not seen, our prediction of negative shade effects on grazers was confirmed at most locations. Another, non-exclusive hypothesis to explain bigger animals in sunny habitats is that grazer size is related to increased heat stress in sunny habitats, which would select specimens with larger shells due to optimized water storage (Vermeij 1973; Tanaka, Duque-Estrada & Magalhães 2002) and also increasing growth rate due a higher metabolism (Chelazzi, Williams & Gray 1999).

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

Our study shows the consequences of shading from artificial structures on the biota of intertidal rocky shores.

Coastlines world-wide are being increasingly modified through constructions ranging from artificial sea defences to port facilities (Bulleri & Chapman 2010; Dugan *et al.* 2011). Such urban infrastructures alter landscape via loss, addition or fragmentation of habitat (Chapman 2006; Goodsell, Chapman & Underwood 2007) and modify biodiversity, as artificial and natural habitats do not support the same communities (Bulleri & Chapman 2004). Our study was prompted by the proposal for expansion of the port of São Sebastião which would result in a shaded area of approximately 1 km² of the Araçá Bay, impacting rocky shores, soft sediment habitats and mangroves. Results indicate such a development would cause substantial decreases in macroalgae cover on hard substrate leading to a reduction in primary production, carbon exchange and habitat for associated fauna. Shading is also predicted to increase filter-feeding invertebrate cover strongly influencing the dynamics of the pelagic environment. The Araçá Bay, like many other coastal sites threatened by development, is a hot spot in marine biodiversity (Amaral *et al.* 2010, 2015) supporting a wide range of ecosystem services. Understanding the impact of shading contributes to a wider view of the consequences of such development and hence informs discussions regarding sustainable development, in this and other regions around the world. Specifically regarding the expansion plans of the port of São Sebastião, our results suggest that covering the bay with a suspended structure will have major negative effects on biodiversity and ecosystem functioning. As a result, we recommend that stakeholders carefully evaluate the expansion plan, and based on the likely shade effects (as well as many other potential impacts) across much of the bay, we do not recommend it.

Acknowledgements

Data accessibility

Study sites locations: uploaded as online supporting information (Table S1). Data archived in Figshare https://dx.doi.org/10.6084/m9.figshare.3205285.v2 (Pardal-Souza 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Map of study sites and representation of port of São Sebastião expansion.

Table S1. Details of study sites.

Table S2. SIMPER analysis of biological communities in shaded and unshaded habitats.

Appendix S1. History of alterations in the Araçá Bay and judiciary status of the expansion of port of São Sebastião.

Appendix S2. Methodological details for estimating biofilm biomass.

Appendix S3. Details on measuring physical data.