

Intertidal macroalgae influence macroinvertebrate distribution across stress scenarios

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ABSTRACT: Intertidal macroalgae can create or modify habitats, potentially influencing ecosystem dynamics by altering the abundance and distribution of species within their community. However, the engineering ability of these organisms and the relative importance of their bioengineering potential may change rapidly in response to environmental stress. To better understand how bioengineering might influence macroinvertebrate community composition, several scenarios were assessed. First, we evaluated the effect of different macroalgal assemblages composed of single-species cultures at different densities on the attenuation of temperature, irradiance and water loss. Subsequently, we assessed the effect that these modifications had on the abundance and distribution of macroinvertebrates. Results showed that intertidal macroalgae differentially ameliorated physical factors depending on the composition of macroalgal aggregations and the level of environmental stress. Higher macroalgal densities attenuated physical factors the most during daytime low tides, modulated by macroalgal species composition. Moreover, macroalgal species composition was found to influence the community composition of macroinvertebrates under certain environmental baseline conditions. During the day, invertebrates were abundant underneath high-density canopies, regardless of the macroalgal species. At night, however, invertebrates showed specificity towards particular macroalgal species and densities. Bioengineers can influence the strength and nature of interspecific interactions in a variety of ways. Here, the differences in the abundance and distribution of macroinvertebrates associated with macroalgae show that the presence or absence of a bioengineer can result in completely different outcomes for associated organisms (feeding vs. shelter), which may, in turn, have feedback implications at many trophic and spatial scales in the intertidal ecosystem.

KEY WORDS: Amelioration · Bioengineering · Canopy · Macroalgal density · Rocky shore

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INTRODUCTION

An important challenge in marine ecology is to understand the structuring processes that determine species distributions and community composition. Recently, a number of authors have focused on understanding the mechanisms by which habitat-forming or habitat-modifying organisms (i.e. ecosystem engineers; Jones et al. 1994) influence marine communities. In marine coastal systems, macroalgal

canopies (Wright et al. 2014), mollusks such as mussels (Gutiérrez et al. 2003), and seagrasses (Holmquist 1998) are known to influence community structure by modifying biophysical conditions. In the intertidal, positive ecosystem engineer interactions are a major community structuring factor influencing the abundance and distribution of associated organisms such as macroinvertebrates, primarily because many ecosystem engineers are dominant space holders with the ability to ameliorate stressful

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forces acting within these habitats (Bertness & Callaway 1994).

Ecosystem engineers from the intertidal, such as small-size canopy-forming macroalgae, can ameliorate extreme physical conditions in their environment by modifying local hydrodynamic regimes, stabilizing sediments, and providing spaces free from competition and predation. For instance, *Ascophyllum* sp., a branched brown seaweed, significantly reduces physical pressure in the intertidal zone and positively affects the recruitment, survival, and growth of a range of macroinvertebrates (Bertness et al. 1999). And the red alga *Gracilaria vermiculophylla* provides milder biophysical conditions, increasing the survival of the amphipod *Gammarus mucronatus* (Wright et al. 2014).

Although the effects of ecosystem engineers on their environment are generally understood, the manner and magnitude by which they ameliorate physical conditions may differ based on the species of engineer, their density, and the baseline conditions of the environment. For example, in an experiment assessing the effect of different intertidal macroalgal species and densities on the settlement of microphytobenthic organisms below the canopy, the abundance of benthic diatoms were found to increase with the density and complexity of macroalgal cover because of a greater attenuation of particle transport (Umanzor et al. 2017). Similarly, different macroalgal morphologies can redirect particles differently, potentially affecting the abundance and distribution of suspension feeders in the subtidal (Morrow & Carpenter 2008). Also, blue mussel *Mytilus edulis* and Pacific oyster *Crassostrea gigas* beds can modify sediment characteristics in the intertidal; however, their ability to modify sediments differs as mussel beds can result in finer sediment grain-size when compared to oyster beds, which in turn affects the abundance and distribution of associated mobile organisms (Kochmann et al. 2008). Taken together, much of the information to date suggests that differences in ecosystem engineering could trigger differences in the abundance and distribution of associated organisms.

Intertidal zones are among the most popular sites to study ecosystem engineers. Several authors have examined ecosystem engineering processes, which structure local communities (e.g. Bertness et al. 1999, Borthagaray & Carranza 2007, Kochmann et al. 2008, Byers et al. 2010, Sueiro et al. 2011). Rocky intertidal zones are physically extreme marine environments (Tomanek & Helmuth 2002), in part because their vertical and horizontal stress gradients occur in a relatively small area (Crowe et al. 2000, Valdivia et al. 2011). As a result, intertidal invertebrates and macro-

algae must deal with strong selective pressures related to physical stress, in addition to competition and predation (Connell 1972, Denny 1985, Denny & Wetthey 2001). Because of the environmental heterogeneity in the intertidal zone and the multitude of biological interactions present, the rocky shore is an ideal study system to examine the effects that different ecosystem engineers at different densities could have on the abundance and distribution of intertidal organisms.

In this study, we investigated the ecosystem engineering potential of the canopies of the rocky intertidal macroalgae *Chondracanthus canaliculatus*, *Pyropia perforata*, and *Silvetia compressa*, during daytime and nighttime low tides, assessing how distinct species with distinct morphologies at different densities ameliorate extreme changes in temperature, irradiance, and water loss under the canopies. We also quantified the relative importance of their ecosystem engineering potential by examining the abundance and distribution of macroinvertebrates. The data collected was then used to test the hypothesis that, under harsh environmental conditions (i.e. daytime low tides), the provision of ameliorated conditions under the canopies would vary with the species composition and the density of the macroalgal assemblages. We predicted that macroinvertebrates would associate most with the macroalgal species and densities showing the most ameliorated environments. Furthermore, for relatively milder environmental conditions (i.e. nighttime low tides), macroalgal aggregations were not expected to provide any significant ecosystem engineering, and macroinvertebrates were expected to be similarly distributed among the macroalgal treatments.

Differences in the environmental baseline conditions of the rocky intertidal, in addition to differences in the physical attributes of macroalgae, could result in small-scale differences within the habitats provided below the canopies, reflected in the structure of the macroinvertebrate communities present. Therefore, understanding how differences related to form, species or density of macroalgae could affect the abundance and distribution of macroinvertebrates will provide a better understanding of the biodiversity and community stability controls present.

MATERIALS AND METHODS

Study site

Experiments were carried out on an exposed rocky shore in Ensenada, Baja California (31° 51' 41.6" N,

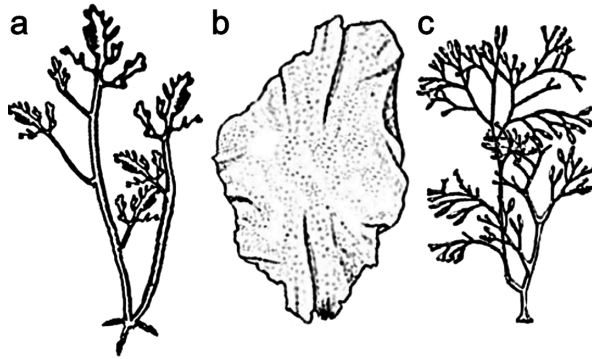


Fig. 1. General morphology of targeted macroalgae. (a) *Chondracanthus canaliculatus* (corticated form), (b) *Pyropia perforata* (foliose), and (c) *Silvetia compressa* (leathery)

116° 39' 58.1" W) for a 15 d period between May and June 2015. Targeted macroalgae were *Chondracanthus canaliculatus*, *Pyropia perforata* and *Silvetia compressa*, which are abundant in Ensenada during the spring/summer season. The study site was a rocky shore composed of extrusive basalt rock, along with boulders and coarse sand (Tellez-García 2003), with a semidiurnal mixed tidal cycle with 2 low tides and 2 high tides of different heights per day. Similar to other rocky shores, the heterogeneity present in this intertidal facilitates shelter, feeding, and settlement, while providing a nursery ground for gastropods, crustaceans, cnidarians, and macroalgae (Connell 1972). The sloped beach profile at this site (tidal range 0 to 1.5 m) creates habitats exposed to different desiccation, temperature, and irradiance regimes, making this site ideal for examining the effects of ecosystem engineering by macroalgae on the abundance and distribution of macroinvertebrates.

Experimental treatments

To examine how macroalgal canopies ameliorate extreme physical conditions and how these physical modifications affect the abundance and distribution of macroinvertebrates, we set up a series of canopy-manipulated quadrats. The quadrats consisted of single-species cultures of *C. canaliculatus*, *P. perforata*, and *S. compressa* (Fig. 1) at 3 densities (high, medium, and low) each. In addition, to avoid pseudo-replication of the controls (Hurlbert 1984), one control quadrat (zero density with no algae) was assigned to each species composition treatment (Fig. 2). Each experimental quadrat included 4 replicates, totaling 48 quadrats in the design and following an orthogonal approach (Underwood 1997). Therefore, the experimental design can be expressed as $3i \times 3\delta \times 4k + 12 \text{ ctrl}$, where i = species, δ = density, k = replicates, and ctrl = control. All quadrats were placed over bedrock in a section of the intertidal devoid of other macroalgae. This allowed us to quantify the relative importance of the targeted macroalgal canopies on the intertidal compared to areas with no macroalgal cover.

Each macroalgal species had a distinctive morphology (corticated, foliose, or leathery, sensu Steneck & Watling 1982) and was chosen based on its abundance in the intertidal and on cultivability. Prior to installing the quadrats in the intertidal, we used a random position allocator to assign the position of each quadrat within the preselected area. We then anchored each quadrat in the mid-intertidal using 2.5 kg diving weights. Quadrats consisted of 30 × 30 cm metal frames covered with a mesh net to which

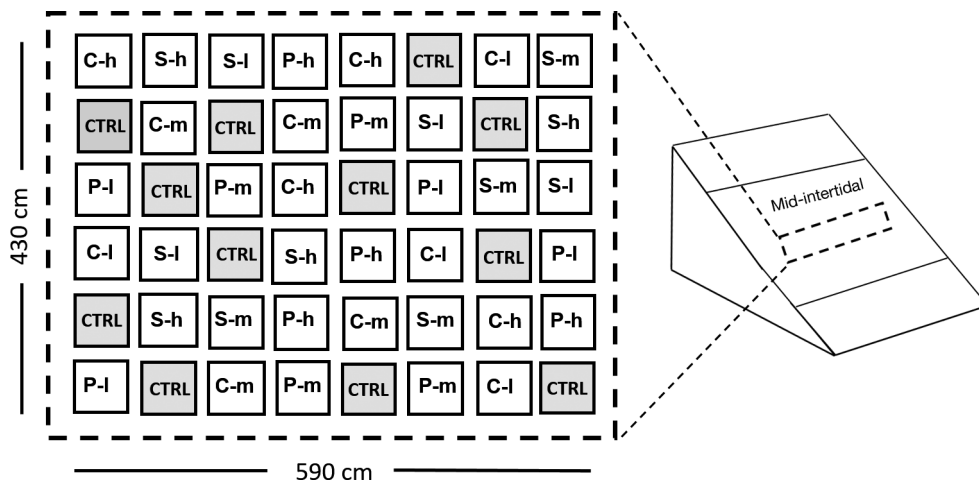


Fig. 2. Experimental system consisting of 48 randomly distributed quadrats containing either *Silvetia compressa* (S), *Chondracanthus canaliculatus* (C) or *Pyropia perforata* (P), at a given density: high (h), medium (m), low (l), or control (CTRL). Quadrats were assembled with ropes cultured with fragments of targeted macroalgae

ropes with macroalgae and data collection devices could be attached (Fig. 3). The distance between quadrats was at least 50 cm. The ecosystem engineering abilities of the macroalgae, as well as the effect that the canopies had on the abundance and distribution of associated macroinvertebrates during daytime and nighttime low tides as a function of macroalgal species composition and density, were compared.

Experimental quadrat setup

The 48 experimental quadrats were assembled prior to executing the experiment. To set up each quadrat, approximately 10 cm tall macroalgae fragments were collected from the intertidal, cleaned in freshwater, and immediately transferred to 1000 l seawater tanks and kept for 15 d under semi-controlled conditions. Daytime maximum net irradiance in the tanks was 699 W m^{-2} , resembling the irradiance levels in the intertidal. Water temperature in the tanks fluctuated between 16 and 26°C over a 24 h period. After the 15 d acclimation period, we outplanted the fragments by inserting them into pre-weighed polypropylene ropes (7 mm diameter) (Fig. 4). The densities utilized in the experiment were: high (1152 to 1246 ind. m^{-2}), medium (768 to 864 ind. m^{-2}), low (384 to 432 ind. m^{-2}), and control (zero density with no individuals). High-density treatments resembled the most abundant patches of thalli per square meter that naturally occurred at the site, while medium-density treatments approximated the mean density of the site and low-density treatments were calculated as approximately half of the typical mean density per square meter.

Cultured ropes were kept for at least 30 d under the same conditions until each fragment grew to at least 20 cm in length. Fragments larger than 20 cm

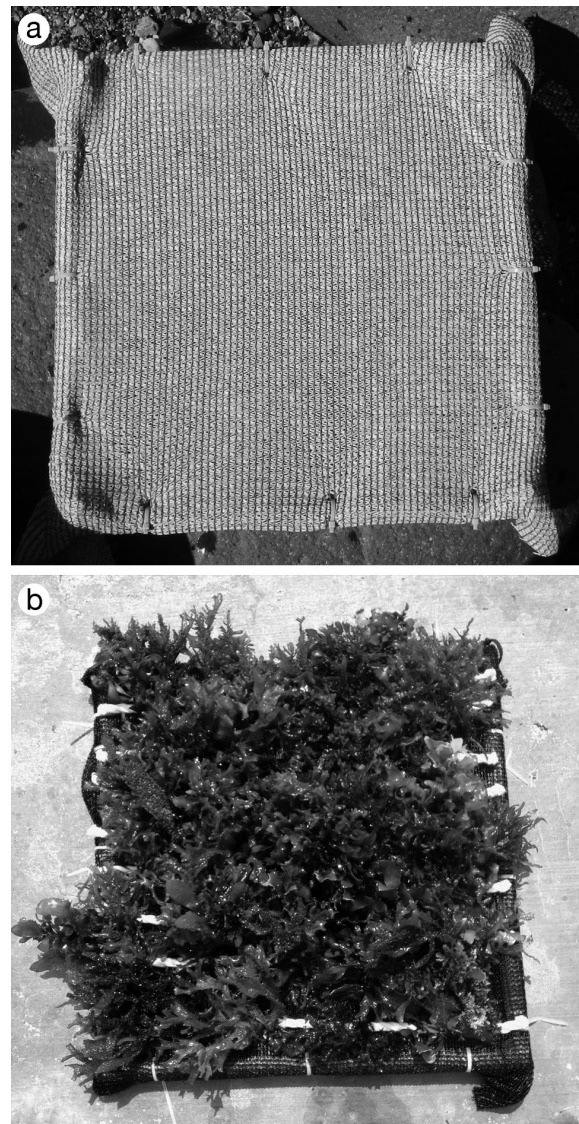


Fig. 3. (a) Experimental quadrats consisting of metal frames covered with mesh net to which (b) cultured ropes and data collection devices were attached

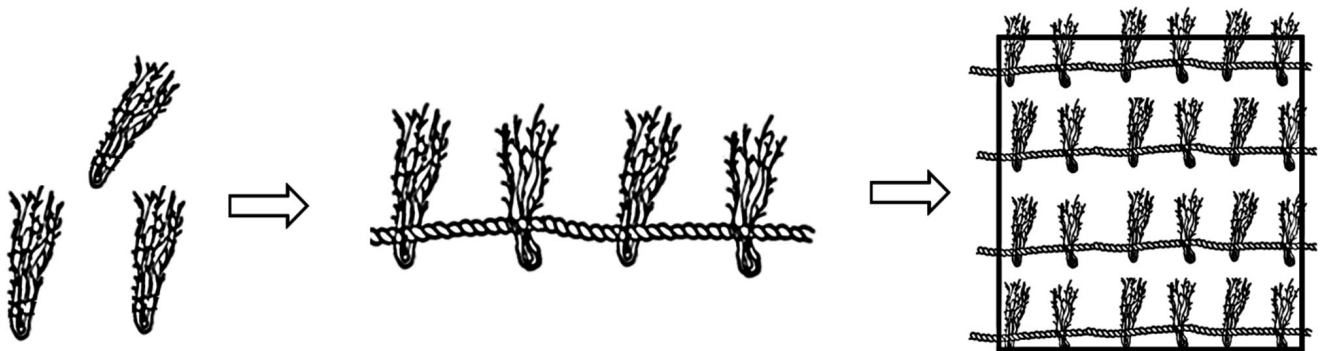


Fig. 4. Macroalgal fragments of *Silvetia compressa*, *Chondracanthus canaliculatus*, and *Pyropia perforate* were inserted into polypropylene ropes which were then attached to the $30 \times 30 \text{ cm}$ metal frames subsequently installed on the intertidal

were trimmed to normalize their length, while shorter fragments were replaced with 20 cm fragments. To ensure healthy macroalgal cultures, cultured ropes were fertilized twice a week ($0.3 \mu\text{M}$ NH_4NO_3 and $0.09 \mu\text{M}$ H_2PO_4), followed by a 100% water exchange 24 h later. After the cultivation period, cultured ropes with thalli growing on them were used to assemble the experimental quadrats (Fig. 4), which were subsequently deployed in the mid-intertidal to initiate the experimental period. Outplanted ropes showing any damage were replaced with fresh ones. Ropes with thalli that grew taller than 20 cm while in the intertidal were trimmed to maintain equal lengths; however, due to the brief period in the intertidal, trimming was rarely necessary.

Environmental modifications by macroalgae

Preliminary tests were performed prior to the experiment to determine if the allocation of the quadrats in the intertidal had an effect on low-tide temperature, irradiance, or water loss. Once we determined that there were no significant effects, quadrats were installed in the intertidal. Temperature, irradiance, and water loss were quantified under the canopies and in the control plots to characterize the abiotic conditions in each quadrat. Data collection devices were placed near the center of every quadrat. Light and temperature were measured using ONSET Hobo thermistors and irradiance meters ($\pm 0.53^\circ\text{C}$), programmed to record every 15 min, for a 5 d period. Water loss was assessed using an agarose bead assay (Brawley & Johnson 1993), where cylindrical beads ($0.7 \times 0.8 \text{ cm}$, $0.4 \pm 0.0035 \text{ g}$) were deployed on cloudless days and nights while all the quadrats were fully exposed to air. Six beads were concurrently deployed per quadrat, and pairs of beads from each quadrat were collected 45, 90, and 135 min after deployment. Water loss was determined by the weight difference caused by water evaporation over time. To compare average daytime and nighttime baseline conditions, physical parameters were evaluated using a weather station installed on-site.

Macroinvertebrate abundance in the quadrats

For a 15 d period, we quantified the effect of the canopies on small mobile macroinvertebrates by conducting daily visual surveys. These surveys

took place during daytime and nighttime low tides when all quadrats were fully exposed to air. We counted and identified *in situ* all macroinvertebrates associated with each one of the experimental quadrats. In addition, in order to help identify possible processes driving macroinvertebrate patterns in abundance and distribution, we logged information indicating whether macroinvertebrates were sheltering (e.g. mollusks with closed opercula) or feeding (e.g. actively scraping or grazing on macroalgal tissue).

Data analysis

Species composition (*C. canaliculatus*, *P. perforata*, and *S. compressa*) and density (high, medium, low, and control) were assigned as categorical and independent factors. Transformations (\ln and $\ln + 1$) were performed as required (Underwood 1997) to fulfill the assumptions of normality (Shapiro-Wilk test), independence of variables (Durbin-Watson test), and homogeneity of variances (Cochran's test) per factor and level.

Irradiance, temperature, water loss, and temporal patterns in the abundance of macroinvertebrates associated with the experimental quadrats were examined using a 2-way full factorial ANOVA. Because temperature and irradiance had multiple measurements over time, to summarize the overall effect of the canopy, measurements from a 2 h interval around the lowest tidal peaks across all days were averaged.

In order to determine if there was an effect of quadrat allocation in the intertidal that could affect the agarose bead assay, prior to the experiment we installed the 48 quadrat frames and mesh without macroalgae and ran the agarose bead assay. No significant differences were found. Then, to avoid any possible interaction of agarose beads with particles trapped by the targeted macroalgae, immediately after the algae were attached to the frames, the agarose bead desiccation assay was conducted before the plots came in contact with their first high tide and could have trapped particles. Because we still could not ensure complete non-independence between the experimental plots and exposure time for the agarose bead assay, we proceeded with separate analyses for each sampling exposure time (at 45, 90, and 135 min). The possible interactions between these 2 variables (time of exposure and allocation in the intertidal) did not appear to influence the general trend in water loss of the agarose beads.

For all data, where differences were found, post hoc (Tukey test) comparisons were conducted. Outputs from the preliminary experiments and raw data pertaining to the physical variables in this manuscript are available through the figshare repository (<http://dx.doi.org/10.6084/m9.figshare.5345221>).

RESULTS

Environmental modifications by macroalgae

During daytime low tides, average conditions were as follows: relative humidity 68%, air temperature 31°C, solar radiation 454 W m⁻², and wind velocity 2.5 m s⁻¹. Overall, during daytime low tides, control quadrats with no algae experienced higher temperatures, irradiance, and water loss than any other treatment (Table 1). The magnitude of these physical factors varied as a function of the interaction between species composition and density in the experimental quadrats ($p < 0.01$ for all; Table 2). Consistently, *Silvetia compressa* at higher densities attenuated below-canopy temperature the most (Table 1; Tukey $p < 0.001$). Temperature underneath *S. compressa* canopies at high and medium densities was at least 2°C cooler than for any other high-density treatment and approximately 7°C cooler than the control quadrats (Table 1). Moreover, *S. compressa* quadrats at high densities were most able to attenuate irradiance below the canopies, attenuating total irradiance by at least 60% compared to controls (Table 1; Tukey $p < 0.001$).

Similarly, water loss below the canopies resulted from the interaction between species composition and density ($p < 0.001$; Table 2). Results showed a trend of greater water loss from agarose beads after

Table 2. Statistical analyses on daytime low tide temperature, irradiance, and water loss (3 time periods: 45, 90 and 135 min, separate analysis for each time treatment) below the experimental canopies based on macroalgal species composition (*Chondracanthus canaliculatus*, *Pyropia perforata*, and *Silvetia compressa*), density (high, medium, low, and control), and their interaction using 2-way full factorial ANOVA

	df	MS	F	p
Temperature				
Species comp.	2	18.88	39.84	<0.001
Density	3	68.56	144.70	<0.001
Interaction	6	7.11	15.00	<0.001
Residual	36	0.47		
Irradiance				
Species comp.	2	1.23×10^7	7.18	0.002
Density	3	1.58×10^8	92.30	<0.001
Interaction	6	1.23×10^7	7.18	<0.001
Residual	36	1.71×10^6		
Water loss				
Minute 45				
Species comp.	2	0.00014	8.1	0.001
Density	3	0.00198	153.8	<0.001
Interaction	6	0.00002	2.3	0.060
Residual	36	0.00001		
Minute 90				
Species comp.	2	0.00025	11.2	<0.001
Density	3	0.02903	1283.9	<0.001
Interaction	6	0.00009	4.2	0.002
Residual	36	0.00002		
Minute 135				
Species comp.	2	0.00237	79.3	<0.001
Density	3	0.06725	2247.3	<0.001
Interaction	6	0.00079	26.5	<0.001
Residual	36	0.00003		

longer emersion times at lower macroalgal densities (Table 1). The post hoc test did not show any significant differences (Tukey $p > 0.05$) in water loss for

Table 1. Mean daytime low tide temperature, irradiance, and water loss underneath the canopies and control quadrats ($n = 4$ for each species and 12 controls). See Fig. 4 for full species names

Species	Interaction Density	Temperature (°C)		Irradiance (W m ⁻²)		Water loss, beads final weight (g)					
		Mean	±SE	Mean	±SE	45 min		90 min		135 min	
						Mean	±SE	Mean	±SE	Mean	±SE
<i>C. canaliculatus</i>	High	24.3	0.4	139.6	6.6	0.382	0.0029	0.376	0.0006	0.366	0.0016
<i>C. canaliculatus</i>	Medium	25.2	0.1	184.7	7.3	0.371	0.0026	0.360	0.0028	0.325	0.0042
<i>C. canaliculatus</i>	Low	26.4	0.2	218.0	6.0	0.371	0.0007	0.337	0.0021	0.299	0.0026
<i>P. perforata</i>	High	23.8	0.0	120.5	2.4	0.382	0.0025	0.380	0.0028	0.373	0.0008
<i>P. perforata</i>	Medium	26.4	0.4	153.4	7.8	0.380	0.0011	0.365	0.0027	0.359	0.0033
<i>P. perforata</i>	Low	26.9	0.7	180.1	25.5	0.373	0.0018	0.352	0.0007	0.339	0.0021
<i>S. compressa</i>	High	20.9	0.1	68.8	2.8	0.381	0.0015	0.378	0.0003	0.373	0.0016
<i>S. compressa</i>	Medium	21.5	0.5	128.7	10.4	0.382	0.0012	0.374	0.0014	0.374	0.0004
<i>S. compressa</i>	Low	26.2	0.4	239.0	13.5	0.378	0.0014	0.351	0.0035	0.339	0.0025
Control		28.5	0.2	236.8	5.7	0.353	0.0011	0.269	0.0026	0.205	0.0034

species composition treatments when present at high density. However, there was a trend of greater water loss under the *Chondracanthus canaliculatus* canopies at lower-density treatments, particularly after 90 min of exposure (Table 1; Tukey $p < 0.01$). Remarkably, after 135 min of emersion, even at low densities, macroalgae significantly ameliorated water loss compared to the control quadrats (Table 1; Tukey $p < 0.001$). Agarose beads in the control quadrats lost at least 20% more water than those under the *C. canaliculatus* canopies at low density, which was the macroalgal species least able to attenuate water loss (Table 1).

No significant differences ($p > 0.05$) were found in the physical parameters measured among the experimental quadrats during nighttime low tides. The absence of solar irradiance (0 W m^{-2}), reduced wind (0.6 m s^{-1}), and high relative humidity (89 to 94 %) contributed to stable, cool temperatures (20°C) that persisted underneath the canopies and in control quadrats. In addition, agarose beads showed no significant differences in water loss even after 135 min of emersion.

Macroinvertebrate abundance in the quadrats

The effect of macroalgal canopies on macroinvertebrate abundance varied with the baseline conditions of the environment. The 2-way full factorial ANOVA showed that during daytime low tides, only density treatments appeared to modulate the abundance of macroinvertebrates ($p < 0.001$; Table 3). *Chlorostoma* (formerly *Tegula*) *funnebralis* was the most abundant of these macroinvertebrates, and was often

Table 3. Statistical analyses on the abundance of macroinvertebrates at nighttime and daytime low tides based on macroalgal species composition (*Chondracanthus canaliculatus*, *Pyropia perforate*, and *Silvetia compressa*), density (high, medium, low, and control) and their interaction using a 2-way full factorial ANOVA

	df	MS	F	p
Nighttime low tides				
Species composition	2	19.08	13.37	0.000
Density	3	22.30	15.63	0.000
Interaction	6	4.28	2.99	0.017
Residual	36	1.42		
Daytime low tides				
Species composition	2	0.70	1.972	0.137
Density	3	6.20	17.36	0.000
Interaction	6	0.71	2.00	0.071
Residual	36	0.35		



Fig. 5. (a) Cluster of *Chlorostoma funnebralis* sheltering underneath high-density treatments of *Silvetia compressa* during daytime low tides, and (b) *Lottia* sp. feeding on *S. compressa* during nighttime low tides. Similar behavioral patterns were documented throughout the experimental periods

found motionless and grouped in compact aggregations below the canopies during the day (Fig. 5a).

On the other hand, during nighttime low tides, the abundance of macroinvertebrates was modulated by the interaction between species composition and density ($p < 0.05$; Table 3). *S. compressa* at high and medium densities showed the greatest abundance of associated macroinvertebrates (Fig. 6), mostly littorinids, and *C. funnebralis*. Nonetheless, *Pagurus samuelis*, *Lottia gigantea*, and *Pachygrapsus crasipes* were also distributed among the experimental quadrats. In contrast to daytime low tides, most macroinvertebrates were actively grazing or scraping on top of the canopies at night (Fig. 5b).

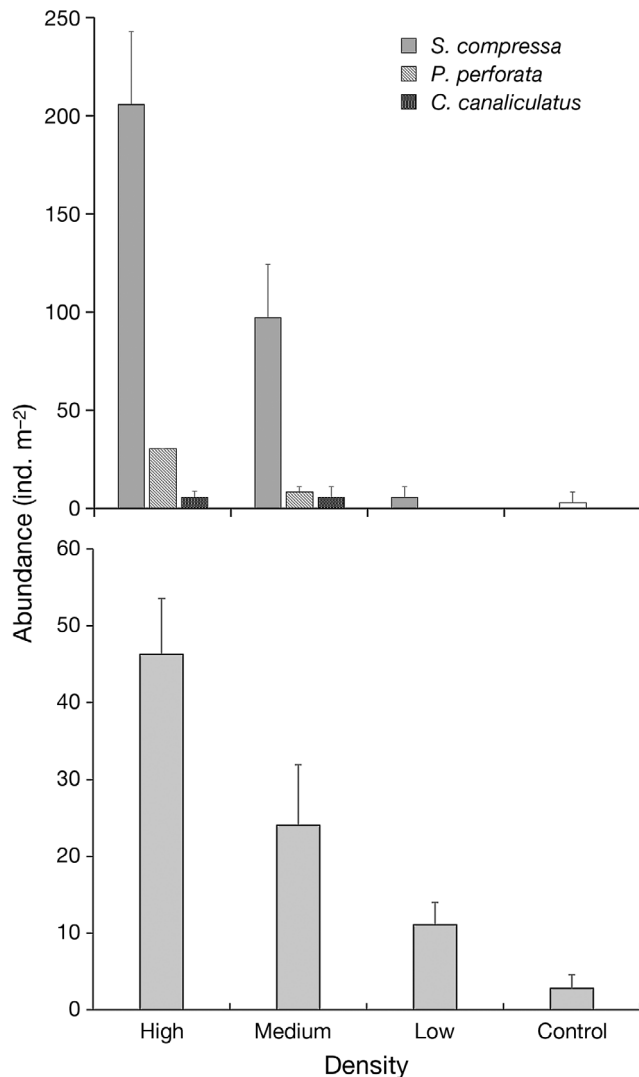


Fig. 6. Average abundance of macroinvertebrates associated with the experimental quadrats consisting of *Silvetia compressa*, *Chondracanthus canaliculatus*, and *Pyropia perforata* during (a) nighttime and (b) daytime low tides. Note y-scale differences. During daytime there were no statistical differences in the invertebrate density among species treatments. Quadrats were installed at the same tidal level in the mid-intertidal. Data are mean \pm SE

DISCUSSION

As expected, our results showed that on an exposed rocky intertidal shore, the ability of macroalgae to ameliorate conditions below the canopies varied with the baseline conditions of the environment, as well as with the species composition and density of macroalgal aggregations. Results showed that macroalgal canopies can have a major influence on the abundance and distribution of intertidal

macroinvertebrates. The reasons for this relationship appear to differ between harsh daytime low tides and milder environments, such as nighttime low tides. By reducing heat, irradiance, and water loss, high-density canopies positively affected the abundance and distribution of macroinvertebrates during daytime low tides. Yet at the low tides at night, despite the fact that no significant differences in the measured physical parameters were found between experimental quadrats, macroinvertebrates still showed greater abundances associated with the higher densities of *Silvetia compressa*.

Environmental modifications by macroalgae

Habitat-forming macroalgae play a key role in rocky intertidal systems because they provide shelter to other organisms and support secondary production. Macroalgae, as well as invertebrates, experience physical stress due to the constant variation of physical parameters such as salinity, nutrient availability, hydrodynamic regimes, heat, irradiance, and water loss (Mueller et al. 2015). However, high temperatures, irradiance variability, and water loss are the main daytime physical stressors in intertidal habitats affecting the development and survival of both macroinvertebrates and macroalgae (Bertness et al. 1999). It appears that differences in the morphological traits of the seaweeds tested herein, along with their density, significantly contributed to their ability to attenuate extreme physical conditions, as in other studies. For example, after assessing the ability of different *Caulerpa* species to retain particles, Hendriks et al. (2010) found that even though all canopies enhanced particle retention rates compared to bare sediment, retention per surface area varied as a function of morphology.

In this study, we found that the effect of the canopies on the attenuation of physical stressors was only significant during daytime low tides. Higher densities of *S. compressa* and *Pyropia perforata* were most able to attenuate light below the canopies. Moreover, higher densities of *S. compressa* also showed slightly cooler temperatures below the canopies when compared to *P. perforata* and *Chondracanthus canaliculatus* at the same densities. The canopies, particularly when present at high densities and for shorter emersion periods, also significantly reduced water loss compared to the control quadrats. These results suggest that even at low densities, macroalgae can protect a range of macroinvertebrates from desiccation. It is well documented that the potential for water

loss, exposure to high temperatures, and irradiance can all influence macroinvertebrate survival rates and behavior (Foster 1969, 1971, Doering & Phillips 1983, Gleason & Burton 2013).

Macroinvertebrate abundance below the canopies

Many authors have studied the macroinvertebrate communities of the rocky intertidal (Cardoso et al. 2004, Pereira et al. 2006, Sueiro et al. 2011, Londoño-Cruz et al. 2014). Similar to what has been reported, we also found a relationship between intertidal macroinvertebrates and macroalgal aggregations. However, the abundance and distribution of macroinvertebrates as a function of macroalgal canopies was not always as expected. During daytime low tides, high temperature, irradiance, and desiccation can limit the mobility of macroinvertebrates, similarly to what was previously described by Connell (1961), comparing the distribution of *Chthamalus stellatus* and *Balanus balanoides* in the intertidal. Under these harsh scenarios, macroinvertebrates showed greater abundance underneath high-density canopies, regardless of species composition. These results suggest that under extreme environmental conditions, density might be the main factor driving the abundance and distribution of small and mobile macroinvertebrates.

In this study, *Chlorostoma funebris* was the most abundant organism, possibly because this invertebrate is highly tolerant to heat stress (Gleason & Burton 2013). However, because high levels of irradiance can greatly restrict the mobility of *C. funebris* (Doering & Phillips 1983), they were found sheltering underneath our high-density treatments. Other facilitation outcomes are also strongly density-dependent, regardless of the species involved. For instance, high densities of macroalgae and oysters positively affect epifaunal richness and abundance by providing greater surface area for colonization (Bishop et al. 2012). Additionally, when abundant, suspension feeders appear to facilitate growth and recruitment of seagrasses by clearing the water column and allowing for increased light penetration (Wall et al. 2008).

Conversely, for nighttime low tides, our data showed no significant differences between the control and experimental quadrats. This result might indicate that when environmental conditions and their associated physical stressors are milder, the effect that macroalgae could have as ecosystem engineers is of limited relative importance. Remarkably, although we expected no pattern in the abundance

and distribution of macroinvertebrate as a function of our macroalgal treatments at night, a significantly higher abundance of macroinvertebrates did associate with the higher densities of *S. compressa*.

Theoretical models summarize that, under relatively milder environmental conditions, competition and predation become the most relevant community structuring processes and organisms tend to associate with ecosystem engineers providing competition and/or predation-free spaces (Menge & Sutherland 1987, Crain & Bertness 2006). As an example, in a relatively low-stress seagrass meadow with mild physical stressors, blades provide clinging surfaces for shrimp where they can attach and find protection from predators (Main 1987). Because nighttime low tides showed relatively milder environmental conditions than daytime low tides in our study, we expected a similar protective interaction between macroinvertebrates and macroalgae in which invertebrates would use algal cover as protection from potential predators.

However, we did not find any indication of this interaction that could explain the abundance and distribution patterns found at night. It is possible that the relatively short canopy of the macroalgae assessed did not provide macroinvertebrates with effective shelter or that local predators did not represent an immediate threat during low tides. Although we did not assess any processes that occurred at high tides, it is also probable that predation and competition would have been greater when predators such as octopi and fish had had access to the mid-intertidal. Under this scenario, it is likely that macroalgae would have provided some shelter, which merits further testing.

Our observations indicate that during nighttime low tides, the relationship between macroalgae and macroinvertebrates is trophically driven, rather than macroinvertebrates actively searching for shelter. In fact, the most abundant macroinvertebrate (*C. funebris*) as well as littorinids have shown a preference for feeding on brown seaweeds such as *S. compressa*, compared to red macroalgae such as *P. perforata* and *C. canaliculatus* (Steinberg 1985, Granado & Caballero 1991, Kubanek et al. 2004). In addition, some authors have found that branched-articulated macroalgae such as *S. compressa* support high densities of epiphytic diatoms (Al-Handal & Wulff 2008, Totti et al. 2009) and understory biofilms (Umanzor et al. 2017). Because several of the macroinvertebrates found (for instance, *C. funebris*, littorinids, and *Lottia gigantea*) are grazers (Mak & Williams 1999, Shanks 2002), it is plausible that the greater abundance of diatoms and other epiphytes associated with

experimental macroalgae canopies could have had an effect on the abundance and distribution of macroinvertebrates at nighttime low tides.

Although the former hypothesis needs further testing, it suggests that the presence of a particular macroalgal species can strengthen trophic connections between a variety of primary producers and macroinvertebrates (Bulleri et al. 2013). Direct, but also indirect, positive effects via facilitation and/or trophic cascades (Borer et al. 2005, Thomsen et al. 2010) can also affect species abundances and distributions. For instance, the intertidal macroalgae *Homosira banksii* is the host for its obligate epiphyte, *Notheia anomala*. Although invertebrates directly associate with *H. banksii* alone, this epiphyte seems to diminish desiccation stress, which in turn increases the abundance and richness of associated invertebrates (Thomsen et al. 2015). Likewise, in this study limpets and snails found within the quadrats could have attracted the predatory crab *Pachygrapsus crasipes* (Barry & Ehret 1993).

Our results highlight the key role played by relatively small-sized ecosystem engineers inhabiting variable environments. The differences found in the abundance and distribution of macroinvertebrates associated with our experimental macroalgae show the varying outcomes that can be driven by the presence of ecosystem engineers. Still, further experimental fieldwork is required to fully comprehend different feedback mechanisms occurring across the intertidal system. Nevertheless, we show that environmental conditions and the physical attributes of bioengineers contribute to modulating ecosystem engineering and the strength and nature of interspecific interactions (Wootton & Emmerson 2005, Boström-Einarsson et al. 2014). In addition, we suggest that it is essential to evaluate the scale at which these interactions occur to properly determine the relative effectiveness and importance of organisms as ecosystem engineers.

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