

## Effects of seaweed canopies and adult barnacles on barnacle recruitment: The interplay of positive and negative influences



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### ABSTRACT

Barnacles are dominant sessile invertebrates on many rocky shores worldwide. Hence, investigating the factors that affect their recruitment is important. Through field experiments done on the Atlantic coast of Canada, we investigated interspecific and intraspecific relationships affecting intertidal barnacle recruitment. Specifically, we evaluated the effects of seaweed canopies (*Ascophyllum nodosum*) and adult barnacles (*Semibalanus balanoides*) on the density of barnacle recruits at the end of the recruitment season. The effects of three canopy treatments on barnacle recruitment and understory environmental conditions allowed us to identify positive and negative effects of canopies. At mid-intertidal elevations subjected to a moderate wave action, we found that, during high tides, the flexible algal fronds damage wire sensors established on the substrate (whiplash effect) and limit barnacle recruitment. However, at low tide, algal canopies limit water loss and temperature extremes and enhance barnacle recruitment in understory habitats. The net effect of algal canopies on barnacle recruitment, however, was neutral, as the positive and negative influences balanced out. By manipulating the abundance of adult barnacles under the seaweed canopies, we found that adult barnacles enhance barnacle recruitment, likely due to the known attraction that adults exert on larvae seeking settlement and to the absence of post-settlement events that could otherwise have blurred such effects by the adults. The presence of adult barnacles, however, did not protect developing recruits from canopy whiplash effects. By understanding the contrasting influences that intertidal algal canopies have on understory abiotic conditions and barnacle recruitment, our ability to predict net canopy effects depending on the relative degree of physiological (e.g., high vs. low intertidal zone) and physical (e.g., sheltered vs. exposed shores) stresses should increase. This study also suggests that recruitment, considered as an important external factor in environmental models of community organization, can also be affected by components of the community itself, potentially triggering local feedbacks.

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### 1. Introduction

Barnacles are common organisms in rocky intertidal habitats worldwide. They are often the dominant sessile invertebrates because of their high resistance to emersion stress. As filter-feeders, barnacles convert pelagic biomass into benthic biomass, which eventually sustains upper trophic levels in benthic food webs. Hence, their ecological role is often important (Anderson, 1994; Foster, 1987). To understand how barnacle populations persist on the shore, several studies have investigated their recruitment. For intertidal sessile invertebrates with planktonic larvae, recruitment refers to the appearance of new individuals that have developed after larval settlement and have reached an arbitrary size that allows them to be counted (Cole et al., 2011). The transition from settler to recruit takes between a few days and weeks, depending on the species and abiotic conditions (Pineda et al., 2009). For such

species, recruitment is an important life-history step that affects population persistence (Bertness et al., 1992; Broitman et al., 2008; Menge, 2000).

Intertidal barnacle recruitment can be affected by non-trophic interspecific interactions. In particular, seaweeds that produce extensive canopies have a variety of positive and negative effects. Tides regularly expose intertidal habitats to aerial conditions, subjecting sessile organisms to abiotic stresses such as desiccation and temperature extremes (Eckersley and Scrosati, 2012; Raffaelli and Hawkins, 1999). Flexible macroalgal canopies lay mostly flat during low tides, limiting water loss and temperature variability in understory habitats. Thus, while seaweed canopies facilitate the performance of many understory species (Bertness et al., 1999; Watt and Scrosati, 2013), it has been suggested that canopies may also enhance barnacle recruitment by improving conditions for developing recruits during low tides (Dayton, 1971). During high tides, intertidal habitats are subjected to water movement caused by waves (Denny and Wethey, 2001). Thus, at high tide, flexible algal fronds hit and scour the substrate repeatedly (Dayton, 1975). Such a whiplash effect is considered to negatively affect barnacle

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recruitment, because developing recruits would be smashed or dislodged by algal fronds (Hancock and Petraitis, 2001; Hawkins, 1983; Jenkins et al., 1999; Leonard, 1999; Lewis, 1964; Menge, 1976).

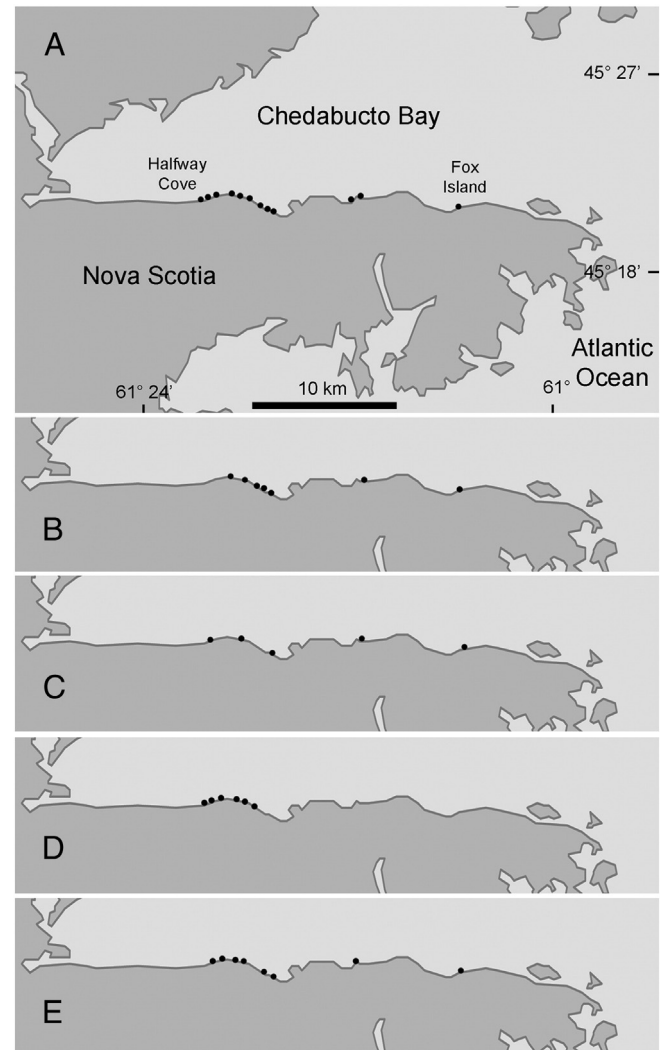
For those reasons, understanding canopy effects on barnacle recruitment requires an evaluation of the balance between the positive and negative influences. Through a factorial design, a field study applied clearing and caging treatments aiming to disentangle the positive and negative effects of algal canopies on barnacle recruitment, concluding that negative effects prevailed over facilitative effects in the studied system (Leonard, 1999). However, treatment effects on understory water retention, temperature extremes, and abrasion on the substrate were not evaluated. In fact, that has commonly been the case in studies of algal canopy effects on understory organisms (Cervin et al., 2004; Dayton, 1971, 1975; Hancock and Petraitis, 2001; Hawkins, 1983; Ingólfsson, 2008; Jenkins et al., 1999; Kiirikki, 1996; Lewis, 1964; Menge, 1976). Clearly, determining how canopy manipulations affect understory abiotic conditions in addition to barnacle recruitment would establish the environmental basis of canopy effects on recruitment more conclusively. Thus, our first objective was to investigate the positive and negative effects of algal canopies on barnacle recruitment by testing effects on recruitment as well as on understory abiotic conditions. Our hypotheses were that whiplash effects would be related to decreased recruitment and that limitation of water loss and temperature extremes would be related to increased recruitment.

Intertidal barnacle recruitment may also be affected by intraspecific interactions. Cyprid larvae often settle near adult barnacles, which produce chemical cues that cyprids detect by contacting the adults when exploring a substrate for settlement (Gabbott and Larman, 1987; Hadfield and Paul, 2001; Raimondi, 1991). A waterborne cue released by the adults may initially orient cyprids towards the adults (Clare, 2011). Such an attraction is thought to have evolved to indicate to larvae that habitat conditions are suitable for development. Gregarious settlement is also considered to favor future reproductive success, because barnacle fertilization is internal and requires the proximity of mating individuals (Anderson, 1994; Foster, 1987). Whether the positive adult–settler relationship persists to the recruitment stage is unclear, but it is theoretically possible if post-settlement events do not modify the initial effects of the adult cues. Thus, our second objective was to investigate adult barnacle effects on barnacle recruitment, under the hypothesis that the presence of adults would locally enhance recruitment. In canopy-covered intertidal habitats, adult barnacles might further favor barnacle recruitment by protecting developing recruits from the whiplash effect of seaweed canopies, since adults are taller than recruits. Thus, our third objective was to test the hypothesis that the whiplash effect of canopies on barnacle recruitment would decrease when adult barnacles are present. We evaluated our hypotheses through field experiments done in rocky intertidal habitats on the NW Atlantic coast.

## 2. Materials and methods

### 2.1. Study system

We did the field work along a 27 km stretch of coastline in Chedabucto Bay, Nova Scotia, Canada, between Halfway Cove (45° 21' 0.5" N, 61° 21' 32.2" W) and Fox Island (45° 20' 43.8" N, 61° 5' 53.7" W; Fig. 1A). Rocky intertidal habitats with stable substrate (bedrock) are common on this coast. Maximum water velocity measured using dynamometers (see design in Bell and Denny, 1994) in the autumn of 2012 in intertidal habitats from this coast was  $5.3 \pm 0.3 \text{ m s}^{-1}$  (mean  $\pm$  SE,  $n = 15$ , range = 2.9–7.1  $\text{m s}^{-1}$ ). Thus, this coast is subjected to moderate levels of wave exposure, since maximum water velocity reaches  $12 \text{ m s}^{-1}$  on shores directly facing the open ocean in Nova Scotia (Hunt and Scheibling, 2001). The tidal amplitude (vertical extent between the highest and lowest tide marks) is approximately 1.8 m on this coast. Between 0 m (chart datum, or lowest normal tide



**Fig. 1.** Map of Chedabucto Bay (Nova Scotia, Canada) indicating the location of the experimental blocks used to evaluate (A) the effects of seaweed canopies and adult barnacles on barnacle recruitment, (B) canopy whiplash effects, (C) canopy effects on understory temperature, (D) canopy effects on substrate moisture, and (E) cage effects on water motion.

in Canada) and 1.2 m of elevation, rocky intertidal habitats are covered by dense canopies of the furoid seaweed *Ascophyllum nodosum* (Linnaeus) Le Jolis (hereafter *Ascophyllum*; Fig. 2). This is the norm for sheltered rocky intertidal habitats on the NW Atlantic coast (Adey and Hayek, 2005; Longtin et al., 2009). Fronds of this macroalga can locally reach 1.6 m in length and 10 years of age. Fronds stay upright at high tide owing to their gas bladders, but they lay on the substrate at low tide because of their high flexibility. On the studied coast, the barnacle *Semibalanus balanoides* (Linnaeus, 1767) is by far the most abundant sessile invertebrate and the only intertidal species of barnacle (Fig. 3). Barnacle recruitment occurs during the spring on this coast (Cole et al., 2011).

### 2.2. Effects of seaweed canopies and adult barnacles on barnacle recruitment

We did a field experiment based on a randomized complete block design with replicated treatments within blocks (Gotelli and Ellison, 2004). We created all treatments in the field between 3 and 16 April 2012, before barnacle larvae started to settle on the shore, as indicated by periodic observations with a magnifying glass. The experimental units where we measured recruitment (recruit density) were

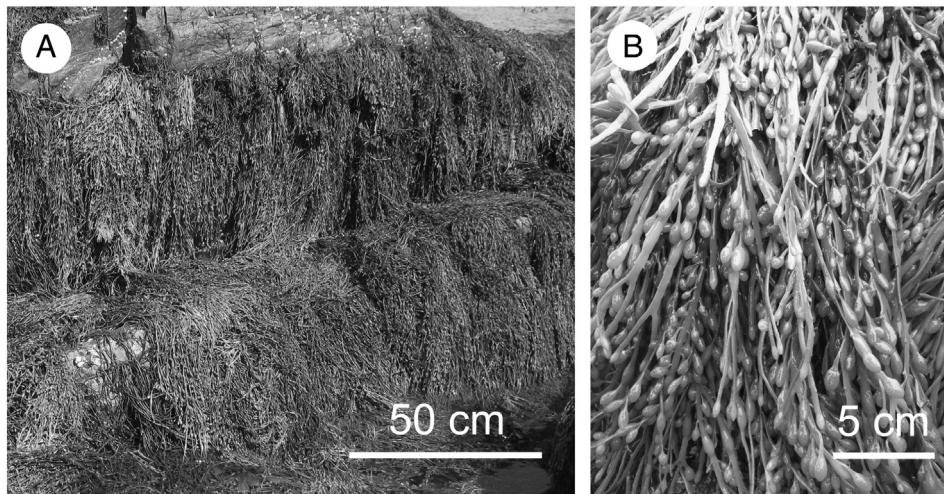


Fig. 2. A: Canopies of *Ascophyllum nodosum* covering most of the intertidal zone seen at low tide. B: Fronds of *A. nodosum* viewed at low tide.

10 cm × 10 cm quadrats delimited on the intertidal rocky substrate between 0.3 m and 0.9 m of elevation (relative to chart datum). The location of each quadrat was marked by establishing two screws on the substrate that indicated the position of two opposite vertices of the quadrat.

To investigate seaweed canopy effects on barnacle recruitment, we created three treatments. The first treatment (termed “canopy”) consisted of quadrats that were fully covered by a natural *Ascophyllum* canopy. The second treatment (termed “no canopy”) consisted of quadrats from which we removed the canopy that originally covered them, which exposed the quadrats to direct sunlight during low tides and prevented canopy whiplash effects. We also removed all neighboring *Ascophyllum* fronds that could otherwise have touched or shaded “no canopy” quadrats with successive tides. We evaluated the net effect of canopies on barnacle recruitment by comparing recruit density between the “canopy” and “no canopy” treatments. The third treatment (termed “cage”) consisted of quadrats that were each covered by a cage that was in turn fully covered by an *Ascophyllum* canopy (Fig. 4). The “cage” treatment was designed to evaluate the influence of canopies on barnacle recruitment with the exclusion of whiplash effects. Each cage was made of black plastic mesh (6 mm × 6 mm of window size) and consisted of a 13 cm × 13 cm roof that stayed 2.5 cm above the corresponding quadrat supported by mesh walls (Fig. 4). We secured each cage to the substrate using screws applied to 5-cm-wide strips of mesh that extended across the substrate from each cage wall (Fig. 4). We tested for negative canopy effects (whiplash) by comparing recruit

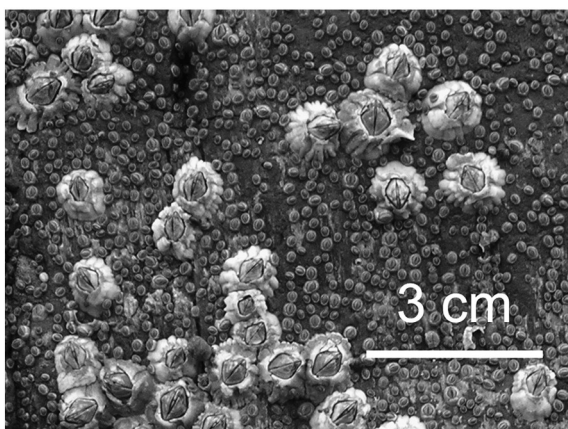


Fig. 3. Barnacle (*Semibalanus balanoides*) adults and recruits on an unmanipulated area of the substrate by the end of the recruitment season.

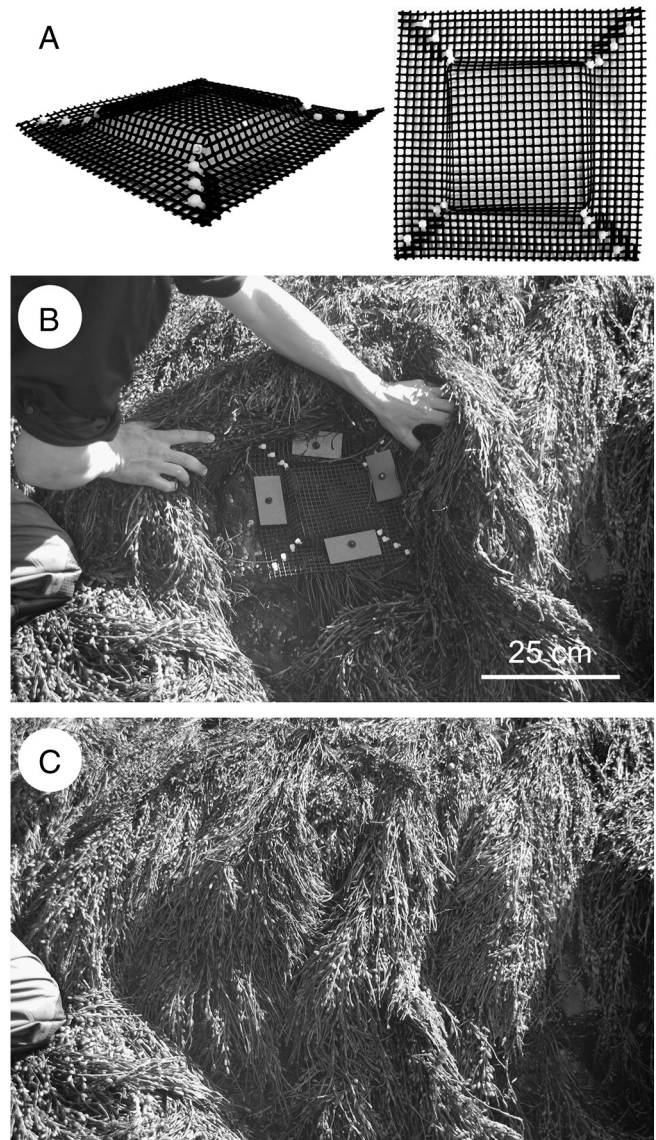


Fig. 4. A: Cage design used for the “cage” treatment (see Section 2.2 for cage dimensions). B: View of a cage installed on the substrate under a seaweed canopy. C: View of the same area once the canopy was left in its natural position at low tide, fully covering the cage.

density between the “canopy” and “cage” treatments, and positive canopy effects by comparing recruit density between the “no canopy” and “cage” treatments. We evaluated potential cage artifacts on water flow in the way described below.

To investigate the effect of adult barnacles on barnacle recruitment, we created two treatments that were orthogonal to the three canopy treatments. The first adult-barnacle treatment (termed “adults present”) consisted of quadrats with 12 adult barnacles (5–10 mm in basal diameter) that had naturally grown on the substrate in previous years. We chose a density value of 12 adults  $\text{dm}^{-2}$  because preliminary measurements yielded that average for the studied elevation range on our shore. For some quadrats, we had to remove a few adults to create the desired density. The second treatment (termed “adults absent”) consisted of quadrats from which we removed all adult barnacles before the start of the experiment.

To prevent possible effects of snails on barnacle recruitment (bulldozing by grazing periwinkles or predation by dogwhelks), we surrounded each cage or non-caged quadrat with 5-cm-wide strips of artificial turf (RCR International, Quebec, Canada) bolted to the substrate (Fletcher and Underwood, 1987; Jernakoff, 1983; Kitting, 1980). Those barriers largely prevented snails from entering the quadrats. Through periodic checks every 3 days, we removed the few snails that had managed to cross. In any case, measurements taken among the experimental quadrats indicated that mean snail density was low at the studied elevations during our study: 0.24 individuals  $\text{dm}^{-2}$  ( $n = 192$  quadrats) for the common periwinkle (*Littorina littorea*) and 0.04 individuals  $\text{dm}^{-2}$  for dogwhelks (*Nucella lapillus*).

To create a randomized complete block design, we established 12 blocks at random along the studied coast (Fig. 1A). Each block consisted of two replicate quadrats of each treatment (three canopy treatments  $\times$  two adult-barnacle treatments = six treatments). In that way, each block had 12 quadrats and each treatment was replicated in 24 quadrats along the shore, yielding 144 quadrats in total. Within blocks, quadrats were separated from one another by nearly 1 m. The quadrats were located on steep substrate surfaces to ensure that seaweed canopies (whenever present) covered the quadrats during low tides (Fig. 4).

On 30–31 May 2012, we measured the number of barnacle recruits in all quadrats. Recruits were then 1–2 mm in basal diameter. Settling larvae were detected on the substrate as late as mid-May, while no new recruits appeared on the shore after the end of May. Thus, our counts were done at the end of the recruitment season. Under *Ascophyllum* canopies at the studied elevations, the substrate was largely bare rock, barnacles being the only conspicuous macroscopic organisms. Since adult barnacles reduced the substrate area available for settlement in “adults present” quadrats (compared with “adults absent” quadrats), we calculated recruit density for “adults present” quadrats in a way that density values were based on the available settlement area for both adult-barnacle treatments. Through the analysis of photographs using ImageJ software, for each “adults present” quadrat we first measured the substrate area that was not occupied by adult barnacles (available settlement area) and, then, we calculated recruit density by dividing the number of recruits counted in the quadrat by the value of available settlement area. For “adults absent” quadrats, recruit density was calculated simply by dividing the number of recruits by 1  $\text{dm}^2$  (quadrat area).

### 2.3. Canopy whiplash effects

We evaluated the physical effects of canopy whiplash using wire sensors glued to the rocky substrate. For this purpose, we used seven of the blocks established along the shore to investigate recruitment (Fig. 1B). In each of those seven blocks, we used one quadrat of each of the three canopy treatments (21 quadrats in total). On 7 June 2012, at the center of each of those quadrats, we established a 5-cm<sup>2</sup> round patch of epoxy glue (A-788 Splash Zone Compound, Z-Spar, Los

Angeles, California, USA), to which we attached six wire fragments (galvanized steel, 0.6 mm thick) that protruded 1 cm perpendicularly to the patch's surface. Because of the necessary installation of the wire sensors, the quadrats for this experiment were different from the quadrats used to measure recruitment. However, all of the quadrats for each canopy treatment were constructed in the same way. The quadrats for the different treatments were interspersed at the same elevation range in each block. On 14 June 2012, we measured the angle of departure of each wire sensor relative to their original position. For each quadrat, we calculated the mean deformation angle using the values for the six wire sensors. We used such quadrat means as replicates for data analysis.

### 2.4. Canopy effects on understory temperature

We evaluated canopy effects on understory temperature using submersible loggers (TidbiTs, Onset Computer, Bourne, Massachusetts, USA). For this purpose, we used five of the blocks established along the shore to investigate recruitment (Fig. 1C). In each of those five blocks, we used one quadrat of each of the three canopy treatments (15 quadrats in total). On 7 May 2012, in each quadrat (inside the cage, when present), we attached a temperature logger to the substrate using epoxy glue, an eye screw, and cable ties. The loggers were set to record temperature every 30 min. Because of the necessary installation of the loggers (which could have interfered with recruitment), the quadrats for this experiment were different from the quadrats used to measure recruitment. Nonetheless, the replicate quadrats for each canopy treatment were built in the same way. The quadrats for the different treatments were interspersed at the same elevation range in each block. We collected all loggers on 29 May 2012.

### 2.5. Canopy effects on substrate moisture

To evaluate canopy effects on substrate moisture (a proxy for desiccation stress for developing recruits), we measured the amount of water on the substrate near the end of a typical daytime low tide for the three canopy treatments. For this purpose, we used six of the blocks used to measure recruitment (Fig. 1D), using for this experiment the 12 original quadrats from each block (72 quadrats in total). On 8 June 2012, we measured the amount of water on the substrate of each quadrat at low tide 1–2 h before the incoming tide washed the substrate again. We quantified water content using make-up pads of 6.5 cm in diameter. We pressed the pads to the substrate with a uniform pressure for 1 min, which was enough to collect all visible water. The moist pads were immediately stored in tightly closed plastic bags inside a cooler and transported to the laboratory for weighing within 3–4 h. The water content of each pad was determined with a balance (to the nearest 0.1 mg) by subtracting the dry mass value for each pad (measured before field work) from the pad's value of moist mass (measured after field work). To assess the possible effect of our transportation method on the values of pad water content, we did a preliminary study. In the laboratory, using the procedure described above, we used 16 dry pads to collect the water from Petri dishes that had been wetted to simulate a moist intertidal substrate. We then determined those pads' water content as described above, stored them in plastic bags inside the cooler, transported them in a vehicle away from the laboratory for 6 h and, finally, determined their water content in the laboratory again. On average, those pads only lost 1% (SE = 0.01%) of their water content after the 6 h. Thus, we increased the values of water content obtained for the pads used for field work by 1%.

### 2.6. Water motion in cages

To ensure that the cages did not reduce water motion near the substrate (which could have affected larval supply or food supply for recruits), we estimated water motion for the canopy treatments

by measuring the mass loss of gypsum pieces during high tides (Jonsson et al., 2006). For this purpose, we used eight of the blocks established along the shore to investigate recruitment (Fig. 1E). Each of those eight blocks consisted of two quadrats of each of the three canopy treatments (48 quadrats in total). We prepared 48 gypsum pieces by mixing plaster of Paris and seawater in a mass ratio of 1.2:1 and, then, by filling with that mixture the compartments of a muffin baking pan that we stored at 60 °C for 24 h for drying (Howerton and Boyd, 1992). We determined the dry mass of each gypsum piece to the nearest 0.1 mg, which yielded an average of 14.77 g (SE = 0.04 g). Then, using Z-Spar, we glued each gypsum piece to a PVC plate (9 cm × 4.5 cm) that had a previously drilled hole for field deployment. Once the glue dried, we weighed each resulting unit (PVC plate with a gypsum piece) to the nearest 0.1 mg. On 5 May 2012, we bolted each of the 64 PVC/gypsum units to the substrate of a different quadrat. The gypsum pieces did not touch the cages. Because of the necessary installation of the PVC/gypsum units, the quadrats for this experiment were different from the quadrats used to measure recruitment. However, the replicate quadrats for each canopy treatment were built in the same way. The quadrats for the different treatments were interspersed at the same elevation range in each block. We collected all PVC/gypsum units on 7 May 2012, dried them at 60 °C for 24 h, and weighed them. The difference in dry mass of each PVC/gypsum unit between the end and start of this experiment represented the mass loss due to gypsum erosion. Through a preliminary study, we ensured that the mass loss in the gypsum pieces resulted from water motion and not from passive dissolution. For that aim, we built six PVC plates that had each a glued gypsum piece and placed them in still seawater in the fridge (4 °C) for 2 days. The dry mass of the gypsum pieces did not change between the start and end of this preliminary study (paired *t*-test,  $t_5 = 2.32$ ,  $P = 0.68$ ), indicating that our field values of gypsum mass loss resulted from water motion.

### 2.7. Data analyses

To evaluate the effects of seaweed canopies and adult barnacles on barnacle recruit density, we did an analysis of variance (ANOVA) for a randomized complete block design with replicated treatments within blocks (Quinn and Keough, 2002). Seaweed canopy (with three levels: “canopy”, “no canopy”, and “cage”) and adult barnacle presence (with two levels: “adults present” and “adults absent”) were considered as fixed factors, while “block” (with twelve levels) was a random factor. We used square-root-transformed data to meet the normality assumption (verified with the Shapiro–Wilk test) and the homoscedasticity assumption (verified with Cochran’s *C* test). After the ANOVA, we did pairwise comparisons between treatments using Tukey HSD (honestly significant difference) tests.

To evaluate whether canopy whiplash effects on barnacle recruitment decreased when adult barnacles were present, we compared the effect size between the “canopy” and “cage” treatments containing adult barnacles (“adults present” treatment) with the effect size between the “canopy” and “cage” treatments lacking adult barnacles (“adults absent” treatment). We measured effect size as the squared point-biserial correlation coefficient (Howell, 2002). Expressed as a percentage, this coefficient measured the percentage of the observed variability in recruit density that was attributable to canopy whiplash effects in the presence and absence of adult barnacles, respectively.

The deformation angle data from the wire sensors (to measure the physical effect of canopy whiplash) were not normally distributed even after several data transformations were applied. Thus, we evaluated the effects of the three canopy treatments through a non-parametric Kruskal–Wallis test (Quinn and Keough, 2002). Blocks cannot be included in such a test. However, this method was appropriate for our objective, because including blocks in an ANOVA aims to increase precision when testing for factor effects (Quinn and Keough, 2002) and significant factor effects were identified anyway by the Kruskal–Wallis test

(see Results). We compared treatment means with Mann–Whitney *U* tests (Dytham, 2010).

Two temperature loggers failed during the experiment, each one in a different block. Thus, to maintain a balanced design when evaluating the effects of the three canopy treatments on understory temperature, we used three blocks. We used maximum daily temperature as the dependent variable, because this measure is directly related to the thermal stress that understory organisms experience at low tide (Bertness et al., 1999). The data failed to meet the normality assumption even after applying several transformations, so we evaluated treatment effects through a Kruskal–Wallis test followed by Mann–Whitney *U* tests to compare treatment means.

To evaluate the effects of the canopy treatments on substrate moisture at low tide, we carried out a Kruskal–Wallis test because the data were not normally distributed even after applying several transformations. We compared treatment means with Mann–Whitney *U* tests.

The data on percent loss of gypsum dry mass (to evaluate cage effects on water motion) met the normality and homoscedasticity assumptions after logarithmic transformation ( $\log_{10} X$ ). Thus, we evaluated the effects of the three canopy treatments through an ANOVA for a randomized complete block design with replicated treatments within blocks. We compared treatment means using Tukey HSD tests. We did all of the data analyses with STATISTICA 10 (StatSoft, Tulsa, Oklahoma, USA).

## 3. Results

### 3.1. Effects of seaweed canopies and adult barnacles on barnacle recruit density

Seaweed canopy treatments and adult barnacles significantly affected recruit density at the end of the recruitment season (Table 1). The interaction between the two main factors was not significant (Table 1), indicating that the effects of each factor on recruit density were similar at each level of the other factor. There were significant differences in recruit density among the blocks (Table 1). However, none of the interactions between the blocks and the other factors (and their interaction) were significant (Table 1), indicating that the effects of the canopy treatments and adult barnacles on recruit density were consistent along the shore.

Seaweed canopies had no overall effect on recruit density, as the statistical similarity between the “canopy” and “no canopy” treatments indicated (Fig. 5). The lack of a net effect, however, resulted from a balance between positive and negative influences. Negative canopy influences were revealed by the fact that excluding whiplash effects through the use of cages significantly increased recruit density under canopies (“canopy” vs. “cage” comparison; Fig. 5). Positive canopy influences were revealed by the fact that recruit density was significantly higher under canopies with whiplash effects excluded than on the substrate without any canopy cover (“cage” vs. “no canopy” comparison; Fig. 5).

**Table 1**

Results of the analysis of variance that evaluated the effects of seaweed canopy treatments (referred to as “Canopy” below) and presence of adult barnacles (referred to as “Adults” below) on barnacle recruitment using a randomized complete block design with replicated treatments within blocks.

Source of variation	df	SS	MS	F	P
Canopy	2	3591.88	1795.94	49.88	<0.001
Adults	1	715.58	715.58	19.88	<0.001
Canopy × Adults	3	82.88	41.44	1.15	0.322
Blocks	11	2289.87	208.17	5.78	<0.001
Blocks × Canopy	22	395.04	17.96	0.50	0.965
Blocks × Adults	11	323.24	29.39	0.82	0.624
Blocks × Canopy × Adults	22	525.67	23.89	0.66	0.859
Error	72	2592.18	36.00		
Total	144	10516.33			

The presence of adult barnacles caused a 51% increase in the density of barnacle recruits, considering all canopy treatments together (Fig. 5, Table 1). However, adult barnacles did not protect recruits from the whiplash effect of canopies, as the effect size between the “canopy” and “cage” treatments was 41% in the presence of adult barnacles and 39% in their absence (Fig. 5).

### 3.2. Canopy whiplash effects

The deformation angle of the wire sensors on the substrate was significantly affected by the canopy treatments ( $H_2 = 13.61$ ,  $P = 0.001$ ). Deformation angle was significantly higher for the “canopy” treatment than for the other two treatments (530% higher, on average; Fig. 6A). The lack of significant differences between the “no canopy” and “cage” treatments (Fig. 6A) indicates that the cages eliminated canopy whiplash effects effectively.

### 3.3. Canopy effects on understory temperature

Daily maximum temperature near the substrate was significantly affected by the canopy treatments ( $H_2 = 25.92$ ,  $P < 0.001$ ). The absence of a seaweed canopy (“no canopy” treatment) caused daily maximum temperature to be significantly higher than in the two treatments with understory environments (59% higher, on average; Fig. 6B). The highest recorded value of temperature was 35 °C for the “no canopy” treatment but only 19 °C for the two understory treatments. Moreover, temperature in the “no canopy” treatment reached values higher than 30 °C in 30% of the surveyed days and higher than 20 °C in 70% of the surveyed days. The lack of significant differences between the “canopy” and “cage” treatments (Fig. 6B) indicates that the cages were successful in retaining the canopies' ability to moderate temperature during low tides.

### 3.4. Canopy effects on substrate moisture

Substrate moisture at low tide shortly before re-submersion was significantly affected by the canopy treatments ( $H_2 = 45.31$ ,  $P < 0.001$ ). The “canopy” and “cage” treatments promoted a significantly higher water retention on the substrate (nearly 3000% higher, on average) than the “no canopy” treatment (Fig. 6C). The lack of significant differences between the “canopy” and “cage” treatments (Fig. 6C) indicates that the cages were successful in retaining the canopies' ability to limit understory water loss at low tide.

### 3.5. Water motion in cages

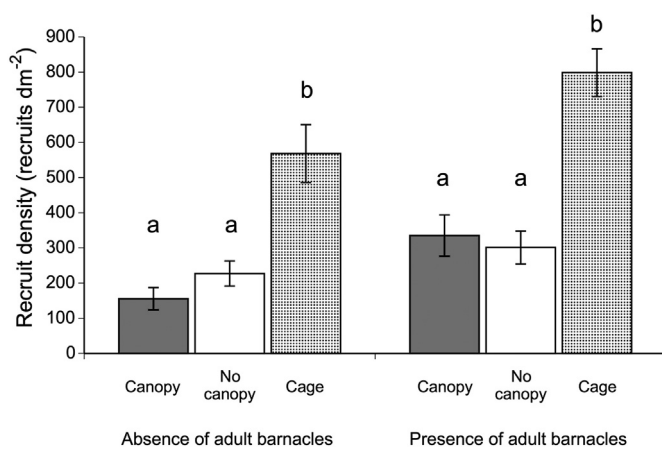
The percent loss of mass in gypsum pieces (measured to evaluate water motion) was significantly affected by the canopy treatments ( $F_{2, 14} = 5.19$ ,  $P = 0.021$ ). However, there were no significant differences between the “canopy” and “cage” treatments (Fig. 6D), indicating that the cages did not artificially reduce water motion near the substrate under seaweed canopies.

## 4. Discussion

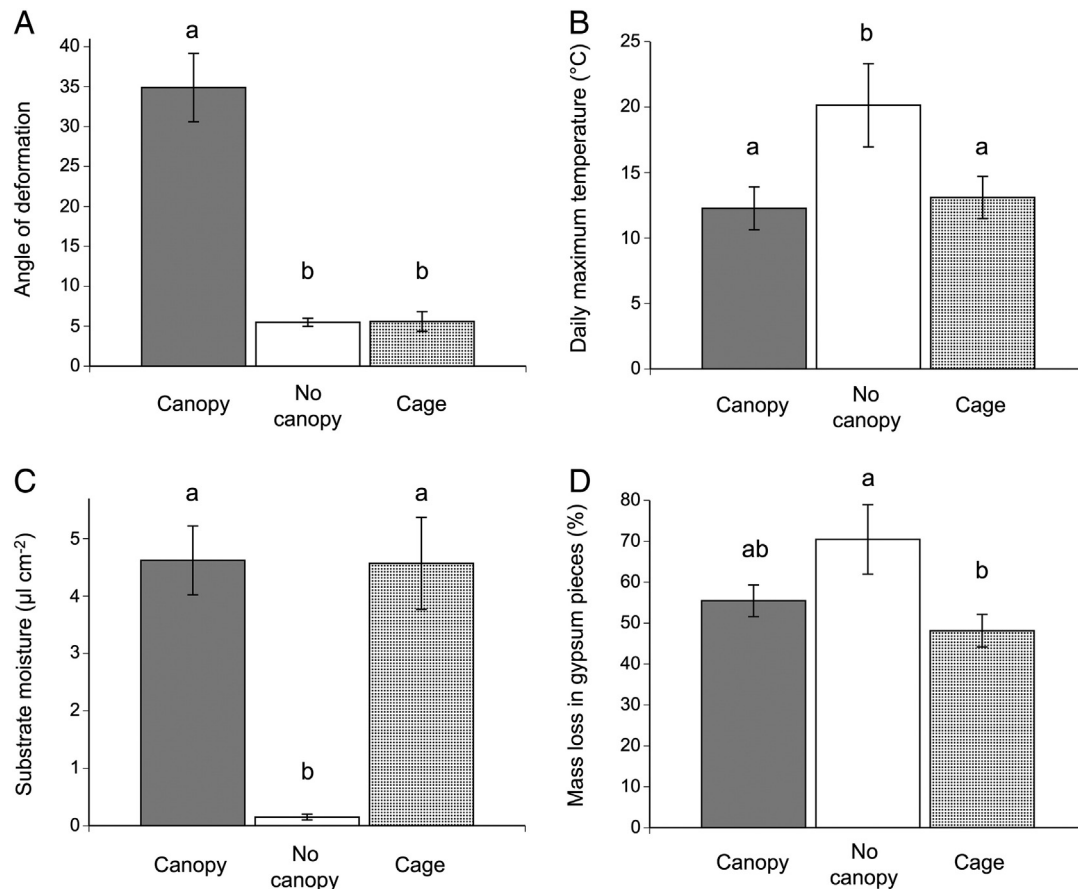
This study has found that seaweed canopies had no net effect on barnacle recruitment in the studied system. The lack of an overall effect, however, resulted from the combined action of positive and negative influences in a way that neither prevailed. Canopies negatively influenced barnacle recruitment by whipping the substrate during high tides, which was revealed by the observations that cages located under canopies protected wire sensors and increased barnacle recruitment compared with unmanipulated canopies. The physical effect of canopy whiplash was measured two weeks after measuring barnacle recruitment, but we consider whiplash data to be representative because wave action is a normal phenomenon on the studied shore. In fact, a repetition of measurements done in November 2012 for a different project also revealed a strong whiplash effect ( $F = 23.68$ ,  $P < 0.001$ ; J. Ellrich, unpublished data). The positive influence of canopies was revealed by the finding that barnacle recruitment was lower without canopy cover than in cages located under canopies, which maintained benign understory conditions at low tide while excluding whiplash effects at high tide. We could not measure desiccation and temperature in the bodies of recruits, but our data for surrogate variables yielded a clear picture. Barnacle recruits are very sensitive to water loss during low tides (Connell, 1961; Foster, 1971) and we found that canopies greatly promote water retention on the substrate's surface at low tide, which likely benefited recruits because of their small size. We measured substrate moisture just one week after quantifying recruitment, which suggests that such data were representative of conditions during recruitment. Strong canopy effects on substrate moisture are in fact likely the norm, as measurements taken in November 2012 for a different project revealed a similar pattern ( $F = 36.12$ ,  $P < 0.001$ ; J. Ellrich, unpublished data). Regarding temperature, although values recorded by loggers may not match invertebrate body temperature exactly (Helmuth, 2002), canopies were nonetheless found to prevent high temperatures from occurring near the substrate during low tides.

Overall, the combined results on recruit density and abiotic variables support our hypotheses that seaweed canopies influence barnacle recruitment positively by limiting understory water loss and thermal extremes during low tides and negatively through whiplash effects during high tides. Research about canopy effects on understory organisms has a rich history in marine ecology (Cervin et al., 2004; Dayton, 1975; Hancock and Petraitis, 2001; Hawkins, 1983; Ingólfsson, 2008; Jenkins et al., 1999; Kiirikki, 1996; Lewis, 1964; Menge, 1976). However, the environmental effects were often assumed. By collecting abiotic data in addition to biological data, our study establishes the environmental basis of canopy influences on barnacle recruitment more conclusively.

Net canopy effects on barnacle recruitment are not always neutral. Other studies using furoid algae (*Ascophyllum* and *Fucus* spp.) have found positive as well as negative overall effects (Cervin et al., 2004; Hancock and Petraitis, 2001; Hawkins, 1983; Jenkins et al., 1999; Leonard, 1999; Menge, 1976). The results of those studies suggest that, for the same combination of seaweed and barnacle species, positive canopy effects would prevail in habitats under high physiological stress and low physical stress (such as high-intertidal habitats on wave-sheltered shores), while negative effects would prevail under low physiological stress and high physical stress (such as in low-intertidal habitats on wave-exposed shores). Since our study was



**Fig. 5.** Density of barnacle recruits (mean  $\pm$  SE) for the six treatments that resulted from combining three canopy treatments (“canopy”, “no canopy”, and “cage”) and two adult-barnacle treatments (presence and absence of adult barnacles). For each adult-barnacle treatment, significant differences between any two canopy treatments are indicated by the occurrence of different letters above the corresponding bars.



**Fig. 6.** Effects of three canopy treatments on (A) angle of deformation of wire sensors on the substrate, (B) daily maximum temperature near the substrate, (C) substrate moisture at the end of a typical low tide, and (D) percent loss of mass in gypsum pieces used to measure water motion near the substrate (mean  $\pm$  SE). For each variable, significant differences between any two canopy treatments are indicated by the occurrence of different letters above the corresponding bars.

done at the middle of the elevation range where *Ascophyllum* and barnacles occur, the above expectations could be assessed by repeating our experiments at higher and lower elevations. Assuming a similar degree of wave action across elevations, the net effect of canopies on barnacle recruitment could thus be positive at high elevations and negative at low elevations on our studied shore.

It has been suggested that furoid algal canopies may also negatively affect barnacle recruitment by reducing understory water flow, which would reduce the arrival of larvae to the substrate. This seems to be the case for bushy species such as *Fucus serratus*. However, our studied species, *Ascophyllum*, has relatively long and slender stipes. Accordingly, this species has been found not to inhibit the arrival of cyprid larvae that are seeking substrate for settlement (Jenkins and Hawkins, 2003; Jenkins et al., 1999). The similar degree of water motion found between our “canopy” and “no canopy” treatments supports this notion.

Our experimental design excluded gastropods from all quadrats to evaluate the effects of algal canopies on barnacle recruitment more clearly. Nonetheless, periwinkles normally have small or no effects on barnacle recruitment under furoid canopies (Hancock and Petraitis, 2001; Menge, 1976); grazing periwinkles negatively affect barnacle recruits through bulldozing only at high periwinkle densities (Buschbaum, 2000), which our sites did not experience (see Materials and methods). The density of dogwhelks on our shore was even lower than for periwinkles during our study (it often increases towards the autumn). In addition, dogwhelks largely prefer preying on adults over recruits (Dunkin and Hughes, 1984). Limpets are rare on our shore. Thus, our results on barnacle recruitment would likely have remained similar had gastropods been allowed to move freely on the experimental quadrats.

Our results on canopy effects secondarily bear importance for the understanding of the role of ecosystem engineers. Canopy-forming

seaweeds fit the definition of allogenic bioengineers, which are species that modify the abiotic conditions of habitats (Jones et al., 1994). Such bioengineers are often considered to enhance environmental conditions for understory species, contributing to increases in local biodiversity (Koivisto and Westerbom, 2010; Pillay et al., 2011; Suiro et al., 2011). However, even though our study evaluated canopy effects on only one species, it nonetheless indicates that a bioengineer may actually have neutral effects on understory species, as negative influences may neutralize the positive influences commonly ascribed to such bioengineers.

Our study has also found that the presence of adult barnacles enhances the recruitment of conspecifics. It has long been known (Knight-Jones, 1953) that cyprid larvae often settle near barnacle adults. Such an attraction is mediated by a cuticular protein present in the adults (which cyprids can detect through physical contact when seeking substrate for settlement; Gabbott and Larman, 1987; Hadfield and Paul, 2001) and probably also by waterborne cues released by adults (which initially attract larvae towards the adults; Clare, 2011). As cyprids explore more frequently the substrate on those areas, the chemical footprints resulting from their temporary adhesion to the substrate accumulate. Such footprints also attract new cyprids, which stimulates further settlement (Clare et al., 1994; Yule and Walker, 1985). Adult barnacles also increase benthic rugosity, which may also favor larval settlement because cyprids have a preference for rough surfaces (Crisp, 1961; Wethey, 1986). Although factors such as hydrodynamic, thermal, and nutritional stresses can cause the mortality of barnacle settlers during their transition to recruits (Jarret, 2003; Larsson and Jonsson, 2006; Lathlean et al., 2013), the positive effects of the adult signals on settlement may persist to the recruitment stage when post-settlement events do not blur such effects (Jenkins et al., 2000). This

appears to have been the case in our study system. Adult barnacles, however, did not reduce the negative effects of canopy whiplash on barnacle recruitment. Either adult barnacles were not tall enough to protect the developing recruits or higher adult densities would have been required to reduce whiplash effects (Jenkins et al., 1999). Regardless of the mechanism, it is clear that the average density of adult barnacles on our shore cannot mitigate the negative influence that canopies have on barnacle recruitment.

Recruitment is an essential step in the life history of sessile invertebrates, especially in intertidal habitats where extreme environmental events may decimate populations unexpectedly (Denny et al., 2009). At regional scales, factors such as coastal oceanography and planktonic food supply often determine barnacle recruitment rates (Cole et al., 2011; Connolly et al., 2001). At local scales, species interactions may be more important (Menge and Branch, 2001). Our study clarifies the environmental basis of the positive and negative influences that algal canopies have on barnacle recruitment, and suggests approaches to test the relative contribution of such influences depending on the environmental context. We also demonstrate that adult barnacles have a positive influence on barnacle recruitment, building on previous studies that had shown positive effects of adults on larval settlement. Recruitment is an important variable that modulates the predictions of environmental stress models of community structure and biodiversity (Bruno et al., 2003; Menge and Sutherland, 1987; Scrosati et al., 2011). The present study offers evidence that interspecific and intraspecific influences in local communities may affect recruitment, in addition to external factors such as coastal oceanography and planktonic food supply. Such influences could thus trigger internal feedbacks ultimately affecting community organization.

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