

Effects of physical ecosystem engineering and herbivory on intertidal community structure

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ABSTRACT: Physical ecosystem engineers play dominant roles in a wide variety of communities. While many of the direct, positive effects of ecosystem engineers are readily apparent, the roles of engineers are often mediated by indirect interactions stemming from the facilitation of one or a few key species. Although direct and indirect effects are both critical drivers of community dynamics, they are rarely considered together with regards to ecosystem engineering. In the present study barnacle and herbivorous gastropod densities are experimentally manipulated to investigate the direct positive effects of habitat provision by barnacles as well as indirect effects mediated by molluscan grazers. Molluscan grazers (*Littorina* spp.) and herbivorous arthropods were positively influenced by the presence of barnacles. Arthropod abundance and species richness were lower when *Littorina* spp. were present. This pattern was not influenced by barnacle cover, suggesting that competition among herbivore functional groups was strong but independent of biogenic habitat complexity. In addition, *Littorina* spp. had strong negative effects on the filamentous alga *Urospora penicilliformis*, but this effect was only seen in the absence of barnacles. Finally, *Littorina* spp. reduced the recruitment of the principal habitat-forming barnacle *Balanus glandula*, suggesting that *Littorina* spp. may mediate a negative feedback loop in *B. glandula* population dynamics. Given the ubiquity of ecosystem engineers, similar combinations of direct and indirect influences may have far-reaching consequences for community dynamics and species richness in a wide range of systems.

KEY WORDS: *Balanus glandula* · Biogenic habitat structure · *Chthamalus dalli* · Competition · Facilitation · Grazing · *Littorina plena* · Recruitment

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INTRODUCTION

Physical ecosystem engineers are prevalent in a diverse array of systems, and they are often the principal drivers of community structure, species diversity, and ecosystem function (Hacker & Gaines 1997, Reise 2002). Ecosystem engineers influence other species by altering environmental conditions and by providing habitat and other resources (Jones et al. 1994, 1997). Generally, the most apparent effects of ecosystem engineering are the direct positive effects that engineers have on other members of the community. Positive impacts of marine ecosystem engineers include increases in primary productivity (Bertness 1985), increases in the abundance of interacting species

(Wonham et al. 2005), and increases in overall species richness (Castilla et al. 2004). However, the importance of engineers may also manifest itself via indirect effects mediated by the species which they facilitate. For example, by providing a refuge for herbivores, habitat-forming corals can have indirect negative effects on algae and seagrasses both within and adjacent to the engineered habitat (Ogden et al. 1974, Stachowicz & Hay 1999). Furthermore, indirect effects can feed back into the population dynamics of the engineers themselves; coral-dwelling crabs help prevent their hosts from being overgrown and thus enhance coral growth and survivorship (Stachowicz & Hay 1999). Although the combination of direct and indirect effects will be crucial in determining the over-

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all importance of ecosystem engineers, simultaneous manipulations of ecosystem engineers and the species they facilitate are rare.

On rocky intertidal shores, many species rely on ecosystem engineers such as sessile invertebrates and seaweeds. Hydrodynamic forces at high tide, and thermal and desiccation stress at low tide can result in extensive mortality for many intertidal species (Dayton 1971, Paine & Levin 1981). Physical ecosystem engineers buffer these physical stresses by providing cool, moist, and hydrodynamically benign microhabitats. As a result, the abundance and diversity of many taxa and functional groups are much higher within biogenic habitats than in nearby areas lacking these habitat-forming organisms (Seed & Suchanek 1992, Bertness et al. 1999, Castilla et al. 2004).

One important group of intertidal ecosystem engineers are acorn barnacles. By providing protection from stressful environmental conditions, barnacle tests and crevices among barnacles serve as important refuges for a wide variety of taxa ranging from protozoans to invertebrates to fish (reviewed in Barnes 2000). On the Isle of Man (UK), the species richness and total abundance of macrobiota are approximately 3× and 40× greater, respectively, in barnacle matrix habitats than in adjacent areas of bare rock (Thompson et al. 1996). Barnacles also alter recruitment processes; *Fucus* spp. recruitment on the Isle of Man is enhanced by the presence of the barnacle *Semibalanus balanoides* (Hawkins 1981), and the settlement and early survival of *Balanus glandula* in the San Juan Islands (Washington) are higher inside of empty barnacle tests (Qian & Liu 1990, Schubart et al. 1995). Finally, barnacles alter the interactions among associated species. In the presence of barnacles, the top-down effect of littorine snails is strengthened, while that of limpets is weakened (Geller 1991, Kim 1997).

In this study, I examined the direct and indirect effects of the barnacles *Balanus glandula* and *Chthamalus dalli* on an assemblage which includes algae, herbivorous snails (*Littorina* spp.), and several species of small (<15 mm) arthropod herbivores (amphipods, isopods, and larval insects). I hypothesized that barnacles directly facilitate algae, littorine snails, and arthropod herbivores. However, I predicted that the positive effects of barnacles on many taxa would be offset by elevated abundances of littorine snails, which consume algae and compete with arthropod herbivores. Finally, I hypothesized

that the facilitation of *Littorina* spp. would create a positive feedback loop by limiting competitive interactions between barnacles and algae, and by increasing the amount of substrate available for barnacle recruitment. To test these hypotheses, I simultaneously manipulated barnacles and *Littorina* spp. to determine the direct effects of biogenic habitat structure and the indirect effects of altered littorine snail densities on the remainder of the community.

MATERIALS AND METHODS

This research was conducted on Tatoosh Island (48° 23.5' N, 124° 44.2' W), located 0.6 km off the tip of the Olympic Peninsula in Washington State, USA (Fig. 1). Experimental manipulations were performed on a south-facing wall at the head of a moderately exposed inlet (Fig. 1). The high intertidal zone at this site featured a broad vertical band of the barnacles *Balanus glandula* and *Chthamalus dalli* that extended from roughly 1.7 to 2.7 m above mean lower low water (MLLW). Summertime mean higher high water (MHHW) is 2.2 m above MLLW on Tatoosh Island, although wave run-up consistently delivers water to higher shore levels (Harley & Helmuth 2003). Larger physical ecosystem engineers (e.g. *Semibalanus cariosus*, *Pollicipes polymerus*, and *Mytilus* spp.) were not present in this zone. Living amongst the *Balanus glandula* and *Chthamalus dalli* were 4 species of littorine snails: *Littorina plena*, *L. subrotundata*, *L. sitkana*, and

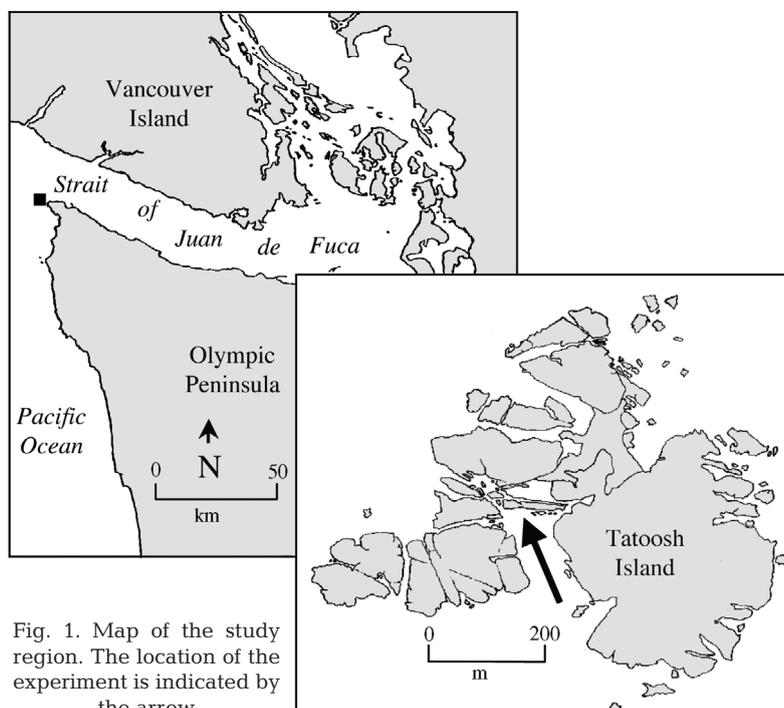


Fig. 1. Map of the study region. The location of the experiment is indicated by the arrow

L. scutulata. Of the adults (snails ≥ 2 mm, 77% of the total population), 77% were *L. plena*, 10% were *L. subrotundata*, 9% were *L. sitkana*, and 4% were *L. scutulata*. Juvenile (< 2 mm) snails (23% of the total population) could not be distinguished to species. Presumably, however, the majority of these juvenile snails were *L. plena*. All *Littorina* spp. at the study site were < 8 mm long. Other molluscan herbivores (e.g. limpets) were rare. Conspicuous predators (e.g. crabs, whelks, and sea stars) were absent.

To test for barnacle effects mediated by littorine snails, I manipulated barnacle cover and littorine abundance in a 2×3 factorial design (barnacles present or removed, and *Littorina* spp. fenced out, fenced in, or not manipulated; see Fig. 4). Each treatment combination was replicated 6 times, for a total of 36 experimental plots. Barnacles, predominantly *Balanus glandula*, were removed from half of the plots with a hammer and chisel, and left at their natural density (approximately 60% cover) in the control plots. Although potential sources of barnacle-related settlement cues (e.g. basal plates) remained in the barnacle removal plots, the near-sterilization of plots that would have been required to eliminate any barnacle cue was judged to be a severe experimental artifact and was therefore not attempted. *Littorina* spp. were excluded with metallic copper fences (17 cm in diameter and 2.5 cm tall) attached to the substrate with Sea Goin' Poxy Putty (Permalite Plastics). Differences between these exclusions and unmanipulated control plots could either be due to differences in littorine snail abundance or to unintended experimental artifacts (e.g. the hydrodynamic influence of the fence or the potential chemical effects of the copper). To control for these artifacts, I included a procedural control treatment in which snail densities were maintained at ambient densities inside of a full copper fence. Note that ambient snail densities differed between plots with and without barnacles; *Littorina* spp. densities in plus-barnacle and minus-barnacle snail inclusion plots were intended to reproduce natural snail densities in plus-barnacle and minus-barnacle control plots, respectively. By allowing snail densities to differ between these 2 inclusion treatments, the manipulation avoids biologically implausible and experimentally unsustainable densities in those snail inclusion plots which lacked barnacles. From a statistical standpoint, this experimental design is equivalent to conducting a factorial, cage-controlled experiment in which a species is removed in 2 contexts (e.g. locations, years) in which the abundance of that species differed. The detection of a significant interaction term could indicate that the effects of a species depended on its abundance, and that its abundance depended on the context. Thus, in the case of the experiment reported here,

a significant barnacle \times snail interaction could emerge if snails were more abundant in plots with barnacles than plots lacking barnacles and snail effects were density dependent (see 'Discussion' for further consideration).

Preliminary trials indicated that copper-based paint and copper fences were ineffective barriers to littorine snail movement on horizontal or gently sloping surfaces because snails could crawl or wash into exclusion areas. Therefore, the experiment was conducted on a near-vertical ($80 \pm 5^\circ$ slope) surface. The abundance of barnacles, littorine snails, and other species on this wall was similar to nearby horizontal and gently sloping barnacle beds (pers. obs.). Treatment plots were established at a constant intertidal height (MLLW + 2.2 m, which is coincidentally equal to MHHW) on 31 March 1998. Snails were removed from *Littorina* spp. exclusion plots every 2 wk (with the exception of early April and late September, when the site was not visited), and snails were added to snail inclusions when necessary to maintain levels similar to unmanipulated controls. Large swells damaged several of the exclusion fences between experimental initiation and the first sampling date; these fences were repaired in late April.

The experiment was monitored until 6 October 1998. Snails were counted prior to resetting their densities. To assess the effects of *Littorina* spp. grazing and barnacle cover on macroalgae, macroalgal percent cover was estimated visually with the aid of a small quadrat. This technique works well for large, discrete entities such as patches of prostrate algae (Dethier et al. 1993). The impact of *Littorina* spp. grazing on barnacle recruitment was assessed in the barnacle removal treatments (from which recruits were removed to prevent barnacle reestablishment). Barnacle recruits were counted and carefully removed with forceps on 12 July, and counted again on 6 October 1998. Recruitment was not measured in plots with adult barnacles. The relationship between *Littorina* spp. and adult barnacle mortality was investigated in barnacle inclusion plots at the end of the experiment by recording the proportion of all tests with intact lateral plates that did not contain a live barnacle. Adult barnacles were defined as *Balanus glandula* > 5 mm basal diameter and *Chthamalus dalli* > 3 mm basal diameter. Mobile, non-molluscan invertebrates were rare or absent in the study plots for the first 3 mo of the experiment (pers. obs.), and were not quantified during this period. However, the abundance of dipteran larvae, isopods *Ligia pallasii*, and gammarid amphipods increased in mid-summer. To assess the combined and potentially interactive effects of facilitation by barnacles and competition with littorine snails, the abundance and species richness of these herbivorous arthropods were

visually quantified at low tide once per month from July through October. This method was sufficient to produce reliable counts of the relatively sedentary insect larvae, which did not immigrate or emigrate rapidly in response to diel or tidal cycles. However, my low-tide counts of highly mobile amphipods may be underestimates of their abundance at high tide.

Statistics were performed in JMP 5.1 (SAS Institute). To meet the assumption of normality, *Urospora penicilliformis* percent cover was arcsine square root transformed, and herbivore abundance and herbivore species richness were both $\log(x+1)$ transformed. The mean, and therefore the variance, for algal cover, herbivorous arthropod abundance, and herbivorous arthropod species richness was zero in certain treatments. This led to heterogeneity of variances for several individual sampling dates, which violated the assumptions of both the parametric 2-factor ANOVA and the nonparametric Friedman test (Day & Quinn 1989). Because there were no striking temporal trends in herbivore abundance from July through October, herbivore abundance and species richness within each of the 36 individual plots were averaged over the 4 sampling dates. The resulting 36 means were $\log(x+1)$ transformed to meet the assumptions of normality and homogeneity of variances. Temporal trends in *Urospora penicilliformis* cover were marked, thus precluding this approach. To explore the consequences of heterogeneity of variances, I compared 2-factor ANOVA results based on the original data to results obtained from a modified dataset in which variance across treatments was homogenized by the addition of 5% cover to 1 plot from every treatment combination in which *U. penicilliformis* was absent. Because there were no qualitative differences between the 2 sets of tests (when significant differences existed, both approaches yielded highly significant results in all cases), I assume that the *U. penicilliformis* results are robust to heterogeneity of variances. Therefore, I present the results of tests performed on the original data.

RESULTS

Littorina abundance

In plots where snails were not manipulated, *Littorina* spp. were approximately 8 (range: 5.0 to 16.6) times more abundant in plots with barnacles than in plots from which barnacles were removed (Fig. 2). Abundances similar to unfenced controls were maintained in littorine inclusion plots. Although there were slightly fewer snails (relative to controls) in snail inclusions with barnacles, the differences in littorine

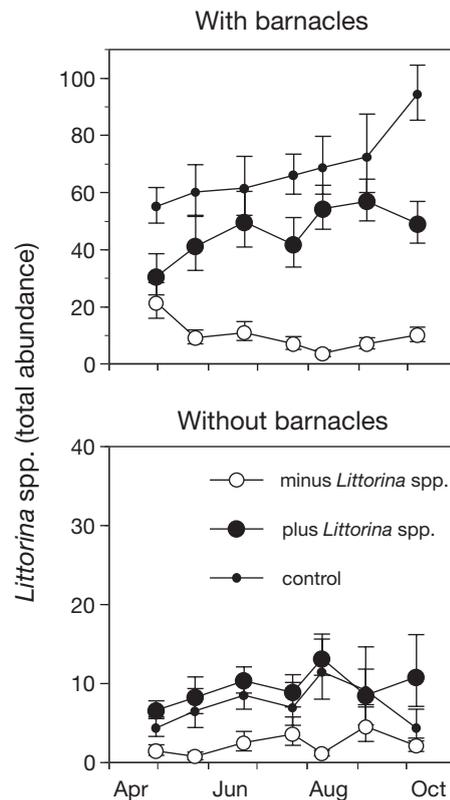


Fig. 2. *Littorina* spp. abundance. Data are back-transformed means \pm 1SE (note different y-axis scales). At each sampling date, abundance data were recorded prior to resetting densities to zero in exclusion plots, and before adding snails (if necessary) to inclusion plots. Several snail exclusion fences were damaged prior to the first sampling point, resulting in relatively high snail abundances in the *Littorina* spp. removal plots in April

abundance between snail inclusions and controls was never significant (Tukey HSD, $p > 0.05$ for all sampling dates). At every sampling date over the course of the experiment, adult *Littorina* spp. abundance responded significantly to the main effects of barnacle and littorine manipulation, but not to their interaction (Table 1). Identical patterns were observed when *Littorina plena* was analyzed alone (data not shown). In summary, barnacles facilitated *Littorina* spp., littorine snail manipulations were successful, and the magnitude of the snail treatment effect was consistent between barnacle treatments.

Algal cover

The filamentous green alga *Urospora penicilliformis* was the only macroalga to recruit into the study plots. It never occurred in plots with littorine snails present, and was rare in plots with barnacles. However, there

Table 1. Statistical analyses of the effects of barnacle and littorine manipulation on *Littorina* spp. abundance (see Fig. 2). $L \times b$: *Littorina* \times barnacles. Data were $\log(x+1)$ transformed and analyzed with 2-factor ANOVAs. Effects that are significant following Bonferroni correction of α to 0.007 are indicated in bold

Date (1998)	Source	df	MS	F	p
30 April	<i>Littorina</i>	2	0.47	8.97	<0.001
	Barnacles	1	6.69	127.4	<0.001
	$L \times b$	2	0.14	2.58	0.092
	Error	30	0.05		
24 May	<i>Littorina</i>	2	1.84	78.9	<0.001
	Barnacles	1	5.39	27.0	<0.001
	$L \times b$	2	0.05	0.71	0.499
	Error	30	0.07		
23 June	<i>Littorina</i>	2	1.30	67.4	<0.001
	Barnacles	1	4.00	21.9	<0.001
	$L \times b$	2	0.06	1.01	0.378
	Error	30	0.06		
23 July	<i>Littorina</i>	2	1.22	40.4	<0.001
	Barnacles	1	3.24	15.3	<0.001
	$L \times b$	2	0.35	4.40	0.021
	Error	30	0.08		
10 August	<i>Littorina</i>	2	3.64	57.6	<0.001
	Barnacles	1	2.80	74.8	<0.001
	$L \times b$	2	0.13	2.70	0.083
	Error	30	0.05		
6 September	<i>Littorina</i>	2	1.34	30.3	<0.001
	Barnacles	1	3.26	12.5	<0.001
	$L \times b$	2	0.44	4.08	0.027
	Error	30	0.11		
6 October	<i>Littorina</i>	2	1.43	72.9	<0.001
	Barnacles	1	5.86	17.8	<0.001
	$L \times b$	2	0.44	5.46	0.010
	Error	30	0.08		

was a conspicuous spring bloom of *U. penicilliformis* in treatments that lacked both barnacles and snails (Figs. 3 & 4). This bloom peaked at almost 90% cover in June, and had disappeared by August. Both main effects of littorines and barnacles were significant during the bloom (late May to early July), and these main effects were always accompanied by a significant interaction term (Table 2). The barnacle \times littorine interaction reflects the fact that *U. penicilliformis* only became abundant in plots lacking both barnacles and snails.

Arthropod herbivore abundance and diversity

Arthropod herbivores were rare and not quantified during the first half of the experiment, but the abundance and species richness of arthropods were quantified monthly from July through October. There were consistently more herbivorous arthropods (amphipods, isopods, and larval insects) in plots without *Littorina*

spp., and in plots with barnacles (Fig. 5A). Similarly, the species richness of arthropod herbivores was consistently higher in plots without snails and in plots with barnacles (Fig. 5B). The main effects of barnacles and littorine treatments were highly significant and roughly equivalent for both arthropod abundance and species richness (Table 3). The interaction terms were not significant.

Because arthropod abundance was highest in treatments with barnacles and/or without *Littorina* spp., the elevated richness in these plots could be attributable to larger samples of individuals (Sanders 1968). Unfortunately, the rarity of herbivorous arthropods in the treatments accessible to snails but lacking barnacles precludes a formal analysis of this rarefaction effect (Heck et al. 1975). However, it is worth noting that species richness, summed across replicates and sampling dates, was lower in the barnacle removal/littorine exclusion treatment (49 individuals representing 3 species) than in any of the treatments with barnacles present (28, 166, and 31 individuals representing 4, 5, and 5 species in the littorine inclusion, exclusion, and control plots, respectively). Although further research is needed to verify this pattern, these results suggest that barnacles may enhance herbivorous arthropod diversity independent of their effects on arthropod abundance.

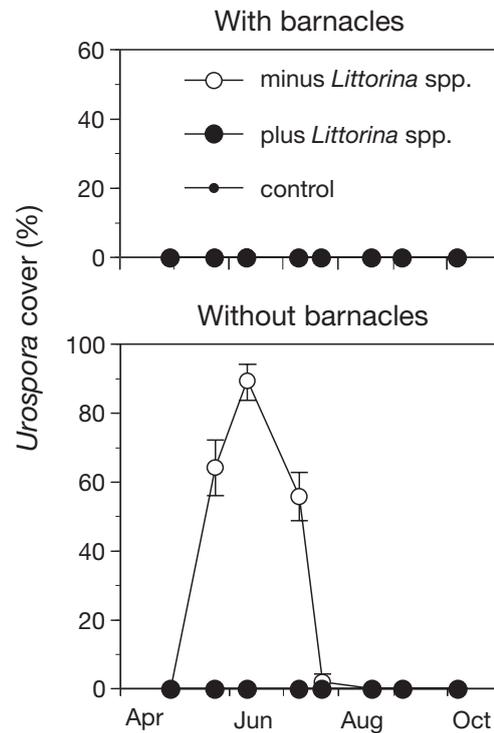


Fig. 3. Percent cover of *Urospora penicilliformis*. Control data and treatments with *Littorina* spp. overlap at or near zero. Data are back-transformed means \pm 1 SE

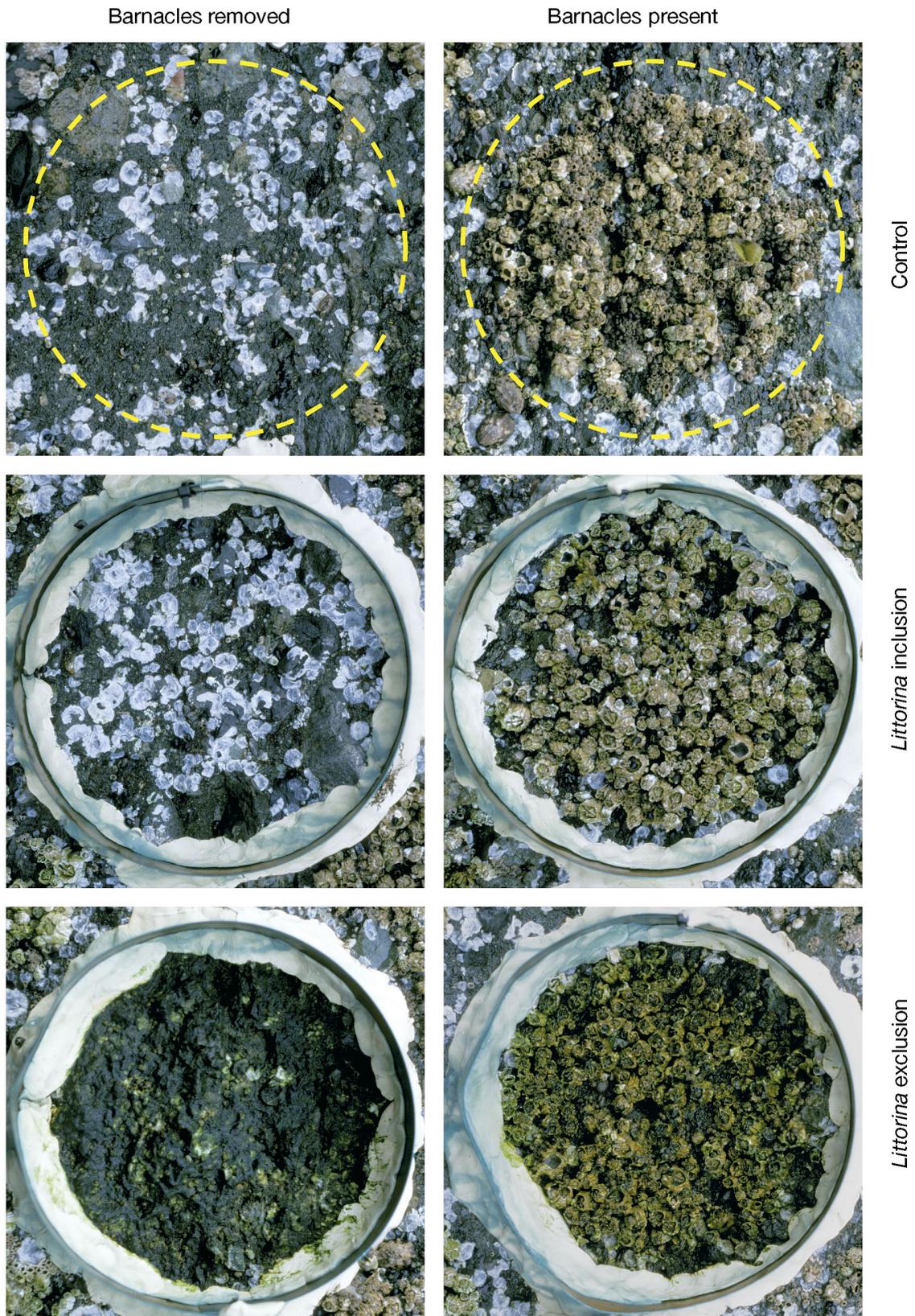


Fig. 4. Photographs of representative treatment plots, taken on 23 June 1998. Note the visual similarities between snail inclusion plots and the corresponding unmanipulated controls. Snail removal resulted in a darkening of barnacle tests (compare middle right and lower right panels) due to the growth of a microbial biofilm. The filamentous green alga in the barnacle and snail removal plot (lower left) is *Urospora penicilliformis*

Table 2. Statistical analyses of the effects of *Littorina* spp. and barnacle manipulations on the percent cover of *Urospora penicilliformis* (see Fig. 3). *L* × *b*: *Littorina* × barnacles. Data were arcsine square root transformed and analyzed using 2-factor ANOVAs. Significant effects ($\alpha = 0.0125$ to correct for multiple tests) are highlighted in bold

Date (1998)	Source	<i>F</i>	<i>p</i>
24 May	<i>Littorina</i>	119	<0.001
	Barnacles	111	<0.001
	<i>L</i> × <i>b</i>	111	<0.001
11 June	<i>Littorina</i>	192	<0.001
	Barnacles	161	<0.001
	<i>L</i> × <i>b</i>	161	<0.001
10 July	<i>Littorina</i>	144	<0.001
	Barnacles	144	<0.001
	<i>L</i> × <i>b</i>	144	<0.001
23 July	<i>Littorina</i>	4.77	0.037
	Barnacles	4.77	0.016
	<i>L</i> × <i>b</i>	4.77	0.016

Barnacle recruitment and mortality

Barnacles recruited into all plots over the course of the study, but recruits were only censused in the barnacle removal plots (from which they were being removed). At the first recruitment sampling date (12 July 1998, Fig. 6A), *Balanus glandula* recruitment was similar between treatments ($F_{2,15} = 1.21, p = 0.33$). *Chthamalus dalli* recruitment was somewhat lower in the *Littorina* spp. removal plots, but this difference was only marginally statistically significant ($F_{2,15} = 4.74, p = 0.025$). On the second sampling date (6 October 1998), strong treatment effects were evident for both species (Fig. 6B). *B. glandula* recruitment was much higher ($F_{2,15} = 9.74, p = 0.002$), and *C. dalli* recruitment much lower ($F_{2,15} = 15.5, p < 0.001$), in the *Littorina* spp. removal plots than in the *Littorina* spp. inclusion plots or controls.

By the end of the experiment, adult barnacle mortality did not differ between *Littorina* spp. treatments for either species of barnacle ($F_{2,15} < 1.2, p > 0.3$ in both cases). The proportion of all intact tests that did not contain a live barnacle (mean ± 1SE of raw data) for

Table 3. Statistical analyses (2-factor ANOVAs) of the effects of *Littorina* spp. and barnacle manipulations on the abundance and species richness of non-molluscan herbivores (see Fig. 5). *L* × *b*: *Littorina* × barnacles. Abundance and richness data were log(x+1) transformed prior to analysis. Significant effects ($\alpha = 0.05$) are highlighted in bold

Source	df	— Total abundance —			— Species richness —		
		MS	<i>F</i>	<i>p</i>	MS	<i>F</i>	<i>p</i>
<i>Littorina</i>	2	0.911	59.3	<0.001	0.214	40.6	<0.001
Barnacles	1	0.891	57.9	<0.001	0.260	49.3	<0.001
<i>L</i> × <i>b</i>	2	0.037	2.38	0.110	0.001	0.22	0.806
Error	30	0.015			0.005		

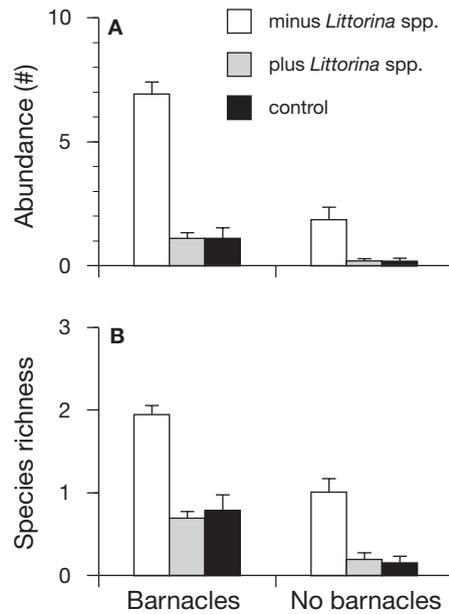


Fig. 5. Arthropod herbivores (gammarid amphipods, the isopod *Ligia pallisi*, and larval insects): (A) total abundance, averaged across sampling dates, (B) species richness, averaged across sampling dates. Data are back-transformed means ± 1SE

Balanus glandula was $0.250 \pm 0.055, 0.194 \pm 0.088,$ and 0.216 ± 0.068 for *Littorina* spp. inclusions, exclusions, and controls, respectively ($n = 6$ in all cases). For *Chthamalus dalli*, mortality was $0.107 \pm 0.027, 0.087 \pm 0.027,$ and 0.147 ± 0.035 for *Littorina* spp. inclusions, exclusions, and controls, respectively ($n = 6$ in all cases).

DISCUSSION

Barnacles, algae, and herbivores form a distinct assemblage on rocky shores throughout the world (Knox 2001). Barnacles play an important role as physical ecosystem engineers (e.g. Thompson et al. 1996); barnacles alter patterns of algal establishment (Hawkins 1981) and provide cool, moist refugia for invertebrates (Barnes 2000). These taxa, in turn, interact via trophic and competitive interactions, which can propagate back to influence the population dynamics of the barnacles (Bertness et al. 1983, Dungan 1986).

Facilitative effects of barnacles

The physical structure of intertidal barnacles provides important refuges for many invertebrate species (Barnes

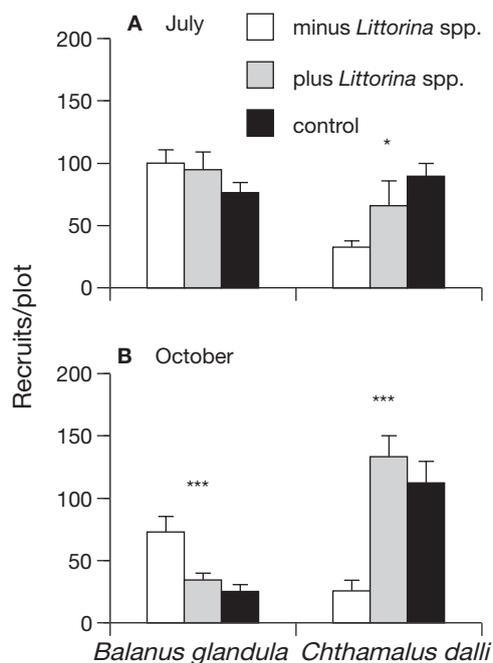


Fig. 6. *Balanus glandula* and *Chthamalus dalli*. Recruitment in barnacle removal plots. Data are means \pm 1SE. Because all recruits were removed following the June sampling, the October samples do not include any individuals from the June samples. Statistically significant differences are indicated by asterisks (* p < 0.05, *** p < 0.001)

2000). In the experiment reported here, this facilitation was observed for both littorine snails and arthropod herbivores. In plots where barnacles had been manipulated but grazers had not, littorine snails were roughly 8 times more abundant in plots with barnacles than in plots from which barnacles had been removed. Across all treatments and dates, herbivorous arthropods were approximately 5 times more abundant in plots with barnacles relative to plots without barnacles. Barnacles have also been shown to facilitate algal establishment (Hawkins 1981). However, algae did not appear to be facilitated by the presence of barnacles in the present study (see 'Interactive effects of engineers and herbivores').

Effects of *Littorina* spp. grazing

Like barnacles, littorine snails are ubiquitous members of intertidal communities world-wide (Reid 1996). Littorine grazing reduces micro- and macroalgal biomass (Castenholz 1961, Bertness et al. 1983, Lubchenco 1983, Cervin et al. 2004). In the present study, *Littorina plena* prevented the establishment of the filamentous macroalga *Urospora penicilliformis*, presumably through herbivory. *U. penicilliformis* is rare on

Tatoosh Island, and typically only appears in areas where grazers are absent (e.g. recent, large disturbance patches). The littorine snails also appeared to influence the abundance of microalgae. Although I did not directly quantify microalgal abundance, a conspicuous biofilm developed in littorine exclusion treatments, and the color of barnacles in snail exclusion treatments was distinctly darker than the color of barnacles in littorine inclusions and controls (Fig. 4).

Herbivorous intertidal snails are known to alter the abundance and diversity of other invertebrate taxa (Anderson & Underwood 1997). In the present study, *Littorina* spp. reduced the species richness and total abundance of herbivorous arthropods. Littorine suppression of both macro- and microalgae may have been responsible for the differences in non-molluscan herbivore abundance and diversity among treatments, with the appearance of highly mobile amphipods and isopods and moderately mobile insect larvae in snail exclusion treatments reflecting an increase in food availability.

Littorine manipulations also affected patterns of barnacle recruitment, and these effects varied between barnacle species. As expected, the presence of snails increased the recruitment of *Chthamalus dalli*; a similar positive association between herbivores and *Chthamalus* spp. has been documented in southern California (Van Tamelen 1987). This association may be driven by grazer removal of algae which otherwise would have preemptively dominated the space available for settling barnacle cyprids. Alternatively, *C. dalli* recruitment could be enhanced by the presence of *Littorina* spp. mucus. For example, the recruitment of *Semibalanus balanoides* is higher in the presence of *Littorina littorea* mucus in the laboratory, although this effect was not found in the field (Holmes 2002). In contrast to the results for *C. dalli*, *Littorina* spp. significantly decreased the recruitment of *Balanus glandula*. The mechanisms underlying this unexpected result remain unclear. The presence of *L. littorea* can reduce barnacle recruitment (Buschbaum 2000, Holmes et al. 2005), and it is possible that release from littorine disturbance may explain the increase in *B. glandula* recruitment in snail exclusion treatments. However, the small size of the snails in this experiment (<6 mm) relative to *L. littorea* (11 to 53 mm; Reid 1996) makes it seem less likely that *L. plena* were bulldozing settled cyprids or recently metamorphosed *Balanus* recruits. Alternatively, herbivory could indirectly reduce barnacle recruitment by removing macroalgal biomass that would otherwise facilitate cyprids and recently metamorphosed adults. This pathway has been demonstrated for *Balanus* spp. in Australia (Anderson 1999), where the removal of algal biomass by grazers or herbicide resulted in reduced barnacle

recruitment. However, macroalgae were absent during the latter half of the experiment reported here (when recruitment differences among treatments were strongest), suggesting that stress reduction by algal cover was unlikely. It is also possible that cues provided by the microscopic biofilm or by snail mucus resulted in enhanced *B. glandula* recruitment in snail removal plots. Although Holmes et al. (2005) did not find support for a microalgal pathway when examining the relationship between the presence of *L. littorea* and settlement of *S. balanoides*, Johnson and Strathmann (1989) did find that limpet mucus reduced the recruitment of *B. glandula*. Intraspecific competition between barnacle species could also create the observed pattern of *B. glandula* recruitment. However, the low density of barnacle recruits ($<1 \text{ cm}^{-2}$) suggests that competition for space was unlikely. Further elucidation of the true nature of the relationship between *L. plena* and barnacle recruitment will await further experimentation.

By altering patterns of recruitment, littorine grazing may influence barnacle population dynamics. Specifically, the facilitation of *Littorina* spp. by *Balanus glandula* may introduce a negative feedback loop in *B. glandula* population dynamics by indirectly reducing *B. glandula* recruitment. Although this mechanism is plausible, further work on the influence of *Littorina* spp. impacts on barnacle recruitment in the presence of adult barnacles will be necessary to establish its generality. I had also hypothesized that *Littorina* spp. would influence barnacle population dynamics by preventing algae from smothering barnacles. Although some studies have found that herbivory indirectly reduces barnacle mortality by preventing overgrowth by algae (Dungan 1986), other studies have not (Jernakoff 1985), and I did not observe such an interaction here. Algal cover remained low in all plots containing barnacles, and adult barnacle mortality was unrelated to the presence of *Littorina* spp. for both *B. glandula* and *Chthamalus dalli*.

Interactive effects of engineers and herbivores

Barnacles are known to modify the interactions between herbivores and their algal resources. For example, Geller (1991) determined that *Littorina plena* is capable of suppressing macroalgal recruitment and growth, but only in areas where barnacles were abundant. Conversely, the presence of barnacles weakens the top-down effects of limpets on macroalgae (Farrell 1991, Geller 1991, Kim 1997). I did not observe either pattern on Tatoosh Island. Although there was a statistically significant interaction between barnacle and littorine effects on the cover of *Urospora penicilliformis*,

this cannot be unambiguously attributed to a shift in littorine grazing pressure. It is possible that a threshold abundance of 5 to 10 *Littorina* spp. per plot was sufficient to prevent the establishment of *U. penicilliformis*; the plots lacking both barnacles and littorines were the only plots below this threshold and the only ones with significant *U. penicilliformis* cover. Threshold effects have been demonstrated in other algal-herbivore interactions (Ruesink 1998). However, because the surface area available for grazing in the barnacle removal plots is considerably lower than in plots with barnacles, the evidence for such a density threshold (relative to the area of grazable surface) in the present experiment is difficult to interpret. It is also possible that barnacles remained clear of filamentous algae by some mechanism other than herbivory. Similar negative associations between green algal taxa and barnacles have been observed elsewhere (Hawkins 1981). Filter-feeding barnacles may have intercepted incoming algal spores, or interfered with recently recruited sporelings. Barnacle feeding can prevent the recruitment of other species from the plankton (Berlow & Navarrete 1997). It is also possible that, by facilitating arthropod herbivores, barnacles had an indirect negative effect on *U. penicilliformis* (see below). Finally, although ecosystem engineers have been shown to alter interspecific interactions in other systems (Palmer 2003), the presence of barnacles had no bearing on the competitive relationships between molluscan and arthropod herbivores in the high intertidal community studied here. Apparently, both herbivore guilds were favored approximately equally by the biogenic habitat structure provided by barnacles, and the presence of barnacles did not change the nature of inter-guild competitive interactions.

Temporal trends

Several seasonal patterns were evident over the course of this 7 mo experiment. The most obvious of these was the spring bloom and subsequent disappearance of *Urospora penicilliformis*. The rarity of this species on Tatoosh Island makes it difficult to know whether the initiation of the bloom reflects seasonality in the abiotic environment or a time lag between the initial removal of grazers in late March and the recruitment of *U. penicilliformis* in late May. Similarly, the disappearance of *U. penicilliformis* could be a response to either increased physiological stress or to the higher abundance of arthropod grazers beginning in July. The appearance of arthropods in July may reflect seasonal abundance patterns that are well documented for marine insect larvae and amphipods (Hashimoto 1976, Johnson 1976).

Barnacle recruitment in Washington is strongly seasonal (Connell 1970). *Balanus glandula* typically recruits in the late spring/early summer, and *Chthamalus dalli* typically recruits in a more protracted pulse throughout the summer months (C. D. G. Harley unpubl. data). These general trends, while not strong, were observed in this study as well. More intriguing were the strong *Littorina*-related recruitment differences in October that were weak or absent in July, particularly for *B. glandula*. It is possible that the abundance of *Urospora penicilliformis* throughout the spring inhibited *B. glandula* recruitment in the snail removal treatments, obscuring a trend that would only become evident in the October samples.

CONCLUSIONS

Physical ecosystem engineers play dominant roles in their communities by modifying environmental conditions and providing habitat and other resources. By so doing, they alter the strengths of interactions among other components of the community, which subsequently modify the direct effects of habitat provision and may feed back into the population dynamics of the habitat-forming species themselves. In the rocky intertidal community explored here, the habitat structure provided by barnacles was expected to enhance *Littorina* spp. abundance, which was predicted to indirectly favor barnacles by reducing pre-emptive and interference competition with algae. Although barnacles did facilitate littorine snails as expected, algae did not appear in barnacle plots even when snail densities were dramatically reduced, and the expected indirect mutualism between barnacles and snails never developed. Rather, littorines had unexpected negative impacts on *Balanus glandula* recruitment that may generate a negative feedback loop in the population dynamics of this competitively dominant barnacle. Finally, although ecosystem engineers may alter interspecific interactions in other systems, there was no evidence to suggest that the presence of barnacles influenced the competitive relationships between molluscan and arthropod herbivores in the high intertidal community studied here. In sum, the effects of ecosystem engineers and herbivores, and to a lesser extent interactions among these effects, had far reaching consequences for the abundance and composition of the high intertidal community.

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