

TESTING THE RELATIVE CONTRIBUTION OF POSITIVE AND NEGATIVE INTERACTIONS IN ROCKY INTERTIDAL COMMUNITIES

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Abstract. In contrast to many other biotic forces, such as competition and predation, the role played by habitat modification by plants and sessile animals in natural communities has not been given the experimental attention it deserves. To test the hypothesis that habitat modification by seaweed canopies can have direct positive effects on rocky intertidal communities, we quantified habitat amelioration by *Ascophyllum nodosum* canopies and its consequences on understory organisms in the Gulf of Maine, USA. At the upper and lower elevational borders of the algal canopy, we examined the recruitment, growth, and survivorship of common benthic organisms in canopy removal, canopy control, and shaded canopy removal plots intended to mimic canopy habitat modification.

The algal canopy greatly reduced potential physical stresses, particularly at high tidal heights. Maximum daily rock temperatures were 5°–10°C lower and evaporative water loss was an order of magnitude less under the canopy than in canopy removal plots. The response of understory organisms to canopy removal, however, was species specific and somewhat idiosyncratic. Nonetheless, in general, at the high intertidal border of the canopy the recruitment, growth, and survival of understory organisms were enhanced by the canopy, whereas at the low intertidal border canopy effects were negative or neutral. Nearly half of the interactions we studied were positive in the high zone. In contrast to positive canopy effects on understory organism recruitment and growth at high tidal heights, consumer pressure was severe under the canopy, particularly at low tidal heights. Green crab predation is likely responsible for limiting understory mussel densities, while grazing by the snail, *Littorina littorea*, keeps understory substrate clear of algal recruits.

The amelioration of harsh physical conditions by algal canopies can have strong direct positive effects in high rocky intertidal communities by enhancing organism recruitment, growth, and survival. These canopy effects, however, may often be offset by increased consumer pressure at low tidal heights. These types of habitat modification effects are likely to be pervasive in many other terrestrial and marine communities exposed to harsh physical conditions.

Key words: algal canopies; *Ascophyllum nodosum*; community ecology; Gulf of Maine; habitat amelioration; physical stress; rocky intertidal communities.

INTRODUCTION

The general role played by plants and sessile animals in structuring communities through habitat modification has not been emphasized by contemporary ecologists. While it is broadly perceived that common species (usually plants and occasionally sessile animals) alter the physical environment and thereby influence the abundance and distribution of associated species, these potentially important effects have not been rigorously documented in most systems. In marine systems, seaweed canopies (Dayton 1975, Menge 1978, Eckman et al. 1989), seagrass beds (Orth 1977, Peter-

son 1982, Irlandi and Peterson 1991), and mussel beds (Suchanek 1986, Witman 1987) have all been identified as playing important community structuring roles by modifying the physical and biological conditions in the habitats in which they dominate. The mechanisms whereby these habitat-modifying organisms influence marine communities, however, are diverse. Substrate stabilization (Orth 1977, Gambi et al. 1990), enhanced sedimentation, particulate food and larval deposition (Eckman et al. 1989), buffering residents from potential physical stress (Dayton 1975, Menge 1978), and providing refuge from predators (Peterson 1982, Witman 1987) are all common mechanisms by which larger sessile organisms can influence the success of smaller, associated organisms. In terrestrial habitats, vascular plants can play similar community structuring roles by protecting organisms from consumers (Atsatt and O'Dowd 1976) and physical stresses (Hunter and Aarsen 1988, Callaway 1995).

Recently, a number of authors have suggested that

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our lack of appreciation of the role played by biotic structure in influencing communities represents a major shortcoming in our understanding of natural communities (e.g., Bell et al. 1991). Wilson and Agnew (1992) compiled a long list of plants that are capable of shifting communities from one state to another through habitat modification and have termed these community shifts "positive switches." More recently, Jones et al. (1994) have suggested that organisms that have a large impact on the communities in which they live by modifying habitat quality or resource levels be termed "ecosystem engineers." More specifically, Jones and his colleagues (1994) define ecosystem engineers that affect communities through habitat modification that creates space for other organisms as "autogenic engineers." Forests, coral reefs, marsh plant communities, and kelp beds are all examples of ecosystems that are largely dependent on the success of dominant habitat modifiers or ecosystem engineers.

The community role played by direct positive interactions that result from habitat modification by dominant space holders has also not received the attention it deserves until quite recently. Earlier in this century direct positive interactions due to habitat amelioration were widely thought to be important community processes (Clements 1916, Allee et al. 1949). Over the past thirty years, perhaps in part as a backlash from the uncritical acceptance of the role of positive interactions by early ecologists (Odum 1969, Connell and Slatyer 1977), researchers have focused most of their attention on predation and competition. More recently, community ecologists have begun to recognize that direct positive interactions may be critical structuring forces in many physically stressful habitats. This may simply be a consequence of the ability of many dominant space holders to ameliorate the types of limiting stresses common in these habitats (Bertness and Callaway 1994).

For several reasons, rocky intertidal communities are a particularly attractive system to examine the role played by direct positive interactions and habitat modification in natural communities. First, we already know a great deal about these systems. For the past three decades rocky intertidal assemblages have been a model system for studying processes that generate pattern and structure in natural communities (e.g., Connell 1961, Paine 1966, Dayton 1971, Menge 1976). Second, one of the most valuable attributes of intertidal habitats is that they occur across very compact and severe gradients in physical stress. This makes it relatively easy to experimentally evaluate the impact of variation in physical stress on organism interactions. Finally, intertidal systems are ideal because the most conspicuous stresses in many rocky shore habitats (i.e., heat and desiccation) are often ameliorated by neighbors (Dayton 1975, Menge 1978, Bertness 1989, Bertness and Leonard 1997).

In this paper we examine habitat amelioration or eco-

system engineering by canopies of the intertidal seaweed *Ascophyllum nodosum* in wave-protected habitats in the Gulf of Maine. In subtidal kelp beds, the community structuring role of seaweeds is well known (Duggins et al. 1989, 1990, Eckman et al. 1989, Duggins and Eckman 1994). This previous work focused primarily on the effects of the canopy on water movement and its consequences on the recruitment and growth of organisms associated with the canopy. While these are important considerations in intertidal habitats as well, algal canopies likely play their most crucial role in the high intertidal zone by ameliorating thermal and desiccation stresses. It is these habitat-ameliorating effects on which we focused. In particular, we quantified habitat modification by *Ascophyllum* canopies and the effect of this habitat modification on the recruitment, survivorship, and growth of common understory organisms. These data were then used to examine the hypothesis that the effects of intertidal algal canopies shift from positive to neutral or negative from stressful high intertidal heights to more benign lower intertidal heights (see also Bertness and Leonard 1997). Thus we used these intertidal habitats to test the general hypothesis that positive species interactions due to habitat amelioration are a predictable feature of physically stressful, but not benign habitats (Bertness and Callaway 1994).

METHODS

Study sites

Our fieldwork was carried out on the shores of the Damariscotta River, an 18-km estuary in eastern Maine, USA. As is common of most rocky estuaries in the Gulf of Maine, its banks are characterized by a dense canopy of the large fucoid alga, *Ascophyllum nodosum* (see Plate 1). On wave-protected shores in the Gulf of Maine the *Ascophyllum* canopy typically covers the middle intertidal habitat as a dense relatively uniform canopy with usually discrete upper and lower borders. *Ascophyllum* plants can reach 2 m in length and achieve densities >50 individuals/m². Thus at high tide the intertidal habitat is a dense forest of *Ascophyllum*, while at low tide the beach is covered by a dense 20–30 cm thick layer of *Ascophyllum* stipes. The blue mussel *Mytilus edulis*, the acorn barnacle *Semibalanus balanoides*, the green crab *Carcinus maenas*, and the herbivorous snail *Littorina littorea* are the most conspicuous understory organisms in the estuary. As a result of heavy crab predation, the predatory gastropod *Nucella lapillus* was not present at our study site but was present at nearby high tidal flow habitats (Leonard et al. 1998). Our study site was located 7 km inland and occupied ~300 m of shoreline on both the eastern and western shores of the estuary. The site was exposed to moderate tidal currents. Flow within the estuary is mainly driven by tides, and flows were typically <10 cm/s (see Leon-

PLATE 1. Algal canopy of *Ascophyllum nodosum* exposed during a low tide on the Damariscotta River, Maine.



ard et al. 1998). As is typical of the Damariscotta River, there was little wave action and algal whiplashing.

Experimental design

To experimentally examine the effects of the algal canopy on the dynamics of understory organisms, we established a set of canopy manipulation and control plots at the site in March 1995 (Fig. 1). We randomly positioned canopy removal, shaded canopy removal, and unmanipulated control plots at both the high and low intertidal border of the *Ascophyllum* canopy ($n = 16/\text{treatment}/\text{height}$ with $8/\text{treatment}/\text{height}$ on each side of the estuary). Plots were 1.5×1.5 m and separated by at least 3 m. High zone plots were placed 2.5

m above mean low water (MLW), while low zone plots were 0.5 m above MLW. Canopy removal treatments were cleared of all macroalgae by scraping and burning holdfasts until rock surfaces were completely cleared.

Shaded canopy removals were treated identically but included shades which mimicked the natural thermal buffering of the canopy. Shades consisted of an arched double layer roof of plastic mesh (0.5×0.5 cm Vexar, DuPont Chemical Corporation, Newark, Delaware) supported by plastic coated, metal wire mesh (5×5 cm Aquamesh, Riverdale Mills, Northbridge, Massachusetts). The open ends of these tunnel-shaped shades were also covered with a double layer of plastic mesh

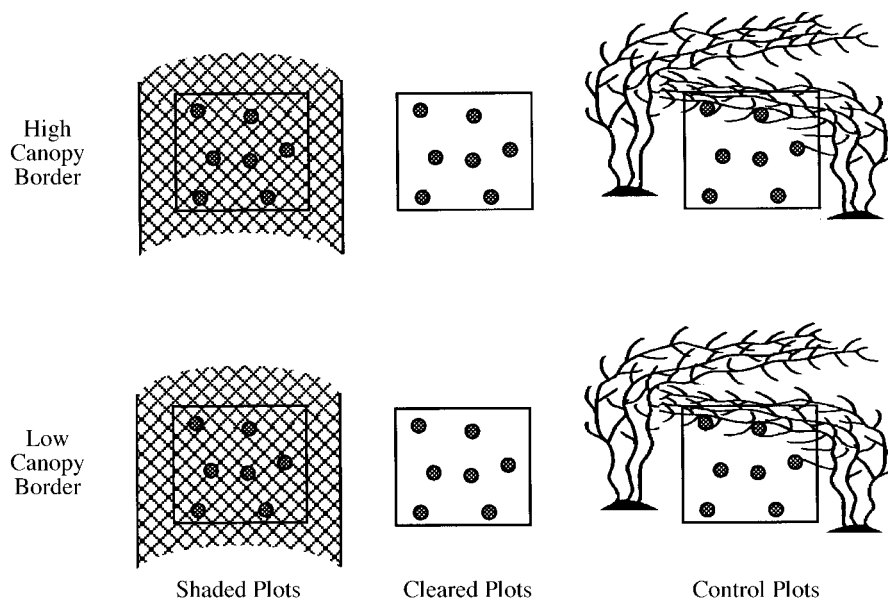


FIG. 1. Schematic of the experimental design. Cleared, control, and shaded plots were randomly located at the upper and lower border of the *Ascophyllum nodosum* canopy. Squares represent permanent quadrats in which recruitment, survival, and growth of organisms were evaluated with sampling devices and marked organisms (represented by circles).

and the shades arched ~20 cm above the rock surface. Physical characteristics (temperature, desiccation) that might be influenced by the presence of the shades were monitored during the experiment. Canopy control plots had a 100% cover of the undisturbed algal canopy at low tide. Within all plots, we monitored the recruitment, growth, and survival of dominant understory organisms for two field seasons (1995 and 1996). In addition, during the first year, we quantified crab predation on mussels and the effects of herbivory on algal recruitment in the treatments.

Habitat modification by Ascophyllum

Rock temperatures and desiccation were quantified to characterize abiotic conditions in the plots. Substrate temperatures were measured by attaching minimum/maximum thermometers to the rock in one-quarter of the tidal height \times canopy treatment replicates ($n = 4/\text{treatment/height}$). Maximum temperatures were recorded every 2 wk from June through September in 1995. Temperatures were sampled more frequently in 1996 in canopy and cleared treatments at both tidal heights with StowAway data loggers (Onset Corporation, Pocasset, Massachusetts; sample frequency = once per 15 min). Data loggers were deployed in late July 1996 for 2 wk. The influence of algal canopies on desiccation was evaluated by quantifying water loss from saturated sponges ($5 \times 5 \times 1$ cm, $n = 10/\text{treatment/height}$) on a cloudless day in July 1996. Water loss was calculated as the percentage difference in initial and final water masses of each sponge.

Recruitment of understory organisms

We quantified the effect of the *Ascophyllum* canopy on the recruitment of mussels (*Mytilus edulis*), grazers (*Littorina littorea*), and crabs (*Carcinus maenus*) using artificial settlement substrates (plastic kitchen scrub pads) bolted to the rock surface in all plots from May to September in both years. These substrates have a high surface area that has been shown to mimic natural settling substrates (Petraitis 1991). Recruits of each species were quantified under a $6\times$ dissecting microscope in the laboratory. Barnacle (*Semibalanus balanoides*) recruitment was assessed in permanent quadrats (25×25 cm) in each plot. Plots were scraped to bare rock each March and used to quantify *Semibalanus* recruitment annually. Quadrats were photographed immediately after each settlement season in late May. Photographs were projected to actual size and recruitment was quantified as the number of recruits in the central 125 cm^2 of the quadrat.

Survival and growth of understory organisms

The survival and growth of all common understory organisms were also examined as a function of plot treatment effects. For *Mytilus edulis*, juveniles (25–35 mm total length) collected from a site in the Damariscotta River (Upper Narrows High; see Leonard et al.

1998), were measured and individually marked with small numbered tags and outplanted to each plot in May 1995 in wire mesh cages ($20 \times 20 \times 5$ cm; mesh size = 0.5×0.5 cm) bolted to the substrate ($n = 8$ mussels/cage, 16 cages/treatment/height). Cages excluded all predators so that the direct influence of physical conditions on growth and survival could be assessed in the absence of predation. Mussels were monitored monthly (May–September) for survival and, in September, were measured for growth (change in overall length).

Growth of the herbivorous snail, *Littorina littorea*, was examined by caging marked snails in 50% of all tidal height \times canopy treatment replicates ($n = 8$ cages/treatment/height). Cages were identical to those described above. Four snails (15–20 mm total length), with the growing lip of the shell notched with a file for subsequent identification and growth measurements, were placed in these cages in June 1996 and collected 10 wk later. Growth was estimated by measuring the length of shell added beyond the notch.

Barnacle growth and survival were measured from photographs, taken each November, of the permanent quadrats. Survival was defined as the proportion of recruits that persisted until the fall sampling period. Growth was estimated from basal diameters of three randomly selected, solitary recruits in every plot each November. Growth was defined as body volume, assumed to be proportional to the cube of the radius.

Crab predation on understory organisms

To examine the hypothesis that consumer pressure varies as a function of tidal elevation and the presence of the algal canopy, predation on mussels by the green crab *Carcinus maenus* was quantified. *Carcinus maenus* was the only conspicuous large predator present at the study site (Leonard et al. 1998). Crab predation was estimated by tethering juvenile mussels (15–20 mm total length) to the rock substrate in July 1995. Individuals were marked with paint for subsequent identification and tethered to the rock with marine epoxy (Z-Spar Splash Zone Compound, Kopper's Company, Incorporated, Los Angeles, California) and 9.1 kg (20 pound) fishing line. Groups of ten mussels were located within five treatment \times height combinations and were deployed for a 12-h tidal cycle on two separate occasions. Direct observations of the tethered mussels during high tide revealed that green crabs were responsible for mussel losses. Green crabs typically left behind broken shell fragments still attached to the tether lines, making the detection of predation losses unambiguous.

Herbivory and algal recruitment

To examine the hypothesis that the algal canopy influences herbivory and algal recruitment, we manipulated the density of herbivorous snails in all treatment by tidal height combinations. Although *Littorina obusata* was present, *Littorina littorea* was by far the

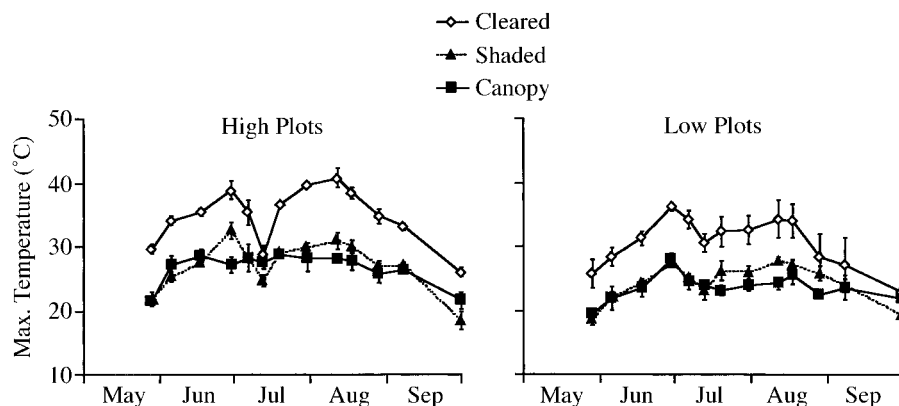


FIG. 2. Maximum rock temperatures quantified approximately every 2 wk during summer 1995 using minimum/maximum thermometers. Values are means \pm 1 SE.

most common herbivore. Exclusion cages, cage controls, and unmanipulated controls were randomly located within all canopy treatment plots ($n = 16/\text{treatment/height}$). The herbivore exclusion cages were identical to the mussel cages described above, but cage controls had only two sides to allow access to mobile organisms.

Recruitment of *Ascophyllum nodosum* and *Fucus* spp. into the plots was quantified after 1 yr (in May 1996). The two fucoid species which recruited (*Fucus spiralis* and *Fucus vesiculosus*) could not be distinguished due to their small size so their numbers were pooled. Recruits typically measured 3–5 mm and were counted visually in the field. Percent cover of algal recruits in each quadrat was determined using a 100-point random dot grid (10 \times 10 cm).

Data analysis

Most data were analyzed with two-factor analysis of variance with canopy treatment and tidal height as fixed factors. Since initial analysis found that side of the river did not significantly affect any of the physical or biological variables we measured, data from plots on both sides of the river were pooled for final analysis. A significant canopy treatment \times tidal height interaction was taken as evidence of canopy-mediated variation in species interactions across tidal heights. A priori, planned comparisons were used to test the direction of the change in species interactions with tidal height. To summarize the overall effect of the canopy on species interactions, we summed the number of positive, negative, and statistically neutral interactions at each tidal height. To ensure homogeneity of variances and normality, proportion data were arcsine square-root transformed and other data were transformed as necessary (Zar 1984). Independence of error terms was evaluated by visually examining plots of the residuals of each analysis. Untransformed means (\pm 1 SE) are presented graphically. Temporal patterns in mussel survival and long-term rock temperatures were evaluated using repeated-measures analysis of variance.

RESULTS

Abiotic conditions

Cleared plots at the high intertidal border of the algal canopy experienced higher temperatures and water loss over periods of longer duration than in other plots. The magnitudes of these factors were lower and less variable in shaded and canopy plots, especially in the low zone. Biweekly maximum rock temperatures revealed that the canopy's capacity to buffer thermal stress varied with tidal height and over time (Fig. 2, Table 1). Average maximum temperatures generally increased from May through July, peaked in August, and returned to initial values by October. Temperature differences among canopy treatments between tidal heights varied over time (Table 1), but in all time periods, cleared plots were generally 8°–10°C higher than both the shaded and canopy plots. Shaded and canopy plots remained at similar temperatures throughout the experiment (typically $<5^{\circ}\text{C}$ difference at any given time), and maximum temperatures were generally 4°–5°C higher in high tidal height plots than in low height plots (Fig. 2 and Table 1). The highest temperature recorded ($\sim 41^{\circ}\text{C}$) was in the high cleared plots in mid-August. This was also the period of greatest temperature difference between high cleared and high shade and canopy plots (see Fig. 2). Low zone temperatures mirrored trends in the high zone. Maximum temperatures in the low zone cleared plots were highly variable in July and August (note wide error bars in low plots), but were still 5°–8°C higher than both the low zone shaded and control plots.

Higher frequency temperature records from data loggers corroborated these biweekly maximum temperatures (Fig. 3). The highest daily temperature readings ($\sim 35^{\circ}\text{C}$) with the longest duration (up to 6 h) were found in the high cleared plots. Canopy plots at both heights experienced much lower temperatures (average temperatures $\sim 22^{\circ}\text{C}$). During midday low tides, temperatures increased from morning readings near 15°C (water temperature) to maximum readings slightly after

TABLE 1. Results of three-factor, repeated-measures analysis of variance on maximum substrate temperatures during the summer of 1995.

Source of variation	df	MS	F	MS†	P
Height	1	879.92	15.05	a	0.001
Treatment	2	1843.59	31.52	a	<0.001
Height × Treatment	2	11.96	0.21	a	0.817
Subject (group) error	18	58.48			
Time	12	219.38	55.13	b	<0.001
Time × Height	12	11.28	2.83	b	0.003
Time × Treatment	24	14.42	3.62	b	<0.001
Time × Height × Treatment	24	6.48	1.63	b	0.050
Time × Subject (group) error	216	3.98			

† Denominator MS for the *F* ratios: a = Subject (group) error, b = Time × Subject (group) error.

midday, and fell again by evening. High cleared and canopy plots initially heated at similar rates, but canopy plots reached an asymptote in the low 20°C range, while cleared plots continued to heat, eventually reaching the mid-30's by the afternoon. Rock temperatures in the low plots rose at a rate comparable to those in the high zone, but due to longer immersion times began later and leveled off at a lower temperature than high plots. This effect was not related to time of exposure but may have been due to the thermal buffering of the seawater in close proximity to the plots in the low zone.

The algal canopy also drastically reduced understory rate of water loss, especially in the high zone (Fig. 4). Water loss was three to five times higher in high zone than in low zone plots but the relative effects of the algal canopy on water loss varied with tidal height ($F_{2,55} = 167.56$, $P < 0.001$). In the high zone, differences between the water loss buffering ability of the canopy were more dramatic than in the low zone plots, most likely because of the differences in time of exposure at the two heights. Water loss in high zone cleared plots was more than 10 times the water loss in canopy plots,

while differences between low zone cleared and canopy plots were more subtle. In both the low and high zone, water loss under the canopy was negligible (Fig. 4). Our artificial shades only partially mimicked canopy effects on water loss (Fig. 4). At both high and low tidal heights, the shades reduced water loss to only about half that of the canopy.

Recruitment of understory organisms

The effect of the algal canopy on the recruitment of understory organisms varied among the species and zones we examined (Fig. 5). In the high zone, mussel and crab recruitment were positively influenced by the presence of the canopy while recruitment of herbivorous snails was inhibited by the canopy. The algal canopy had no influence on barnacle recruitment in the high zone. Recruitment into the low zone was generally greater than the high zone for all species examined, presumably reflecting the greater submergence time of low zone plots. Nonetheless, canopy effects on recruitment in the low intertidal zone were similar to the

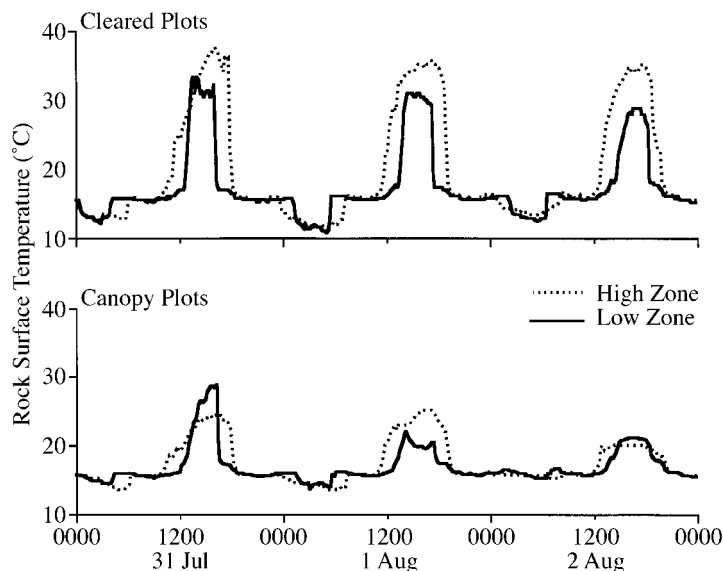


FIG. 3. Short-term rock temperatures quantified over a 2-wk period in mid-June 1996 using StowAway thermistors. The figure shows a representative 3-d period during which there were midday low tides. Data plotted are instantaneous temperatures (°C) sampled every 15 min. Values on the x-axis are time (0000 = midnight, 1200 = noon).

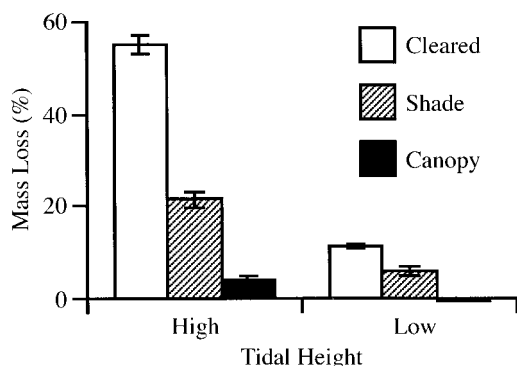


FIG. 4. Water loss rates sampled on a clear, windless day in July 1996 during which there was a midday low tide. Data are the percentages of water lost from saturated sponges placed in the treatments immediately after the tide recessed and recovered immediately before they were covered by the incoming tide. Values are means \pm 1 SE.

high zone except for strong canopy inhibition of barnacle recruitment in the low zone.

Mussel recruitment was much higher in 1996 than in 1995. When recruitment was higher (1996), the effect of the canopy on mussel recruitment varied with tidal height but not when it was lower (1995) (Fig. 5, Table 2). The magnitude of the canopy effect on mussel recruitment in 1996 was strong in high plots, with most recruitment occurring under the canopy and little occurring in cleared plots. This canopy effect, however, was not observed in the low zone where there was no difference in mussel recruitment between canopy treatments. In 1995, when recruitment was lower, it varied with tidal height and canopy treatment, with higher recruitment in the low zone and under the algal canopy.

As with mussels, the algal canopy facilitated crab recruitment (Fig. 5, Table 2), but only during 1995. Recruitment of crabs under the canopy was generally three times greater than into the cleared plots, while recruitment was intermediate in shaded treatments. Like mussels, crab recruitment in both years was greater in the low zone than in the high zone (Table 2).

In both years, barnacle recruitment was negatively influenced by the algal canopy in the low zone, but was not influenced by the canopy in the high zone (Fig. 5, Table 2). Barnacle recruitment into the low zone was more than double that in the high intertidal. In low plots, the canopy plots had ~35% lower recruitment than cleared plots. In both years and at both tidal heights, snail recruitment was also negatively influenced by the presence of the algal canopy (Fig. 5, Table 2) but the effect did not vary with tidal height. Snail recruitment was highest in cleared plots but lowest in the canopy plots.

Survival of understory organisms

Survival of the two benthic filter feeders examined was positively affected by the presence of the canopy at high tidal heights while survival of the snail was not

influenced by the canopy. The effects of the canopy on mussel survival varied with canopy treatment, tidal height, and time (Fig. 6, Table 3). In June (before summer temperatures had increased substantially), there was no difference in survival among any canopy or tidal height treatments. Mussel survival declined, however, in cleared plots in the high zone over the course of the summer. By July, 25% of the mussels in high cleared plots had died and by August nearly 35% had died. Survivorship of mussels in all other treatments was >95%.

Barnacle survival was enhanced by the algal canopy in both years, especially at high tidal heights (Fig. 6, Table 3). In the high zone, the effect of the canopy was much stronger than in the low zone. In 1995, the low zone algal canopies did not influence barnacle survival but in 1996 the algal canopy enhanced survival. In both

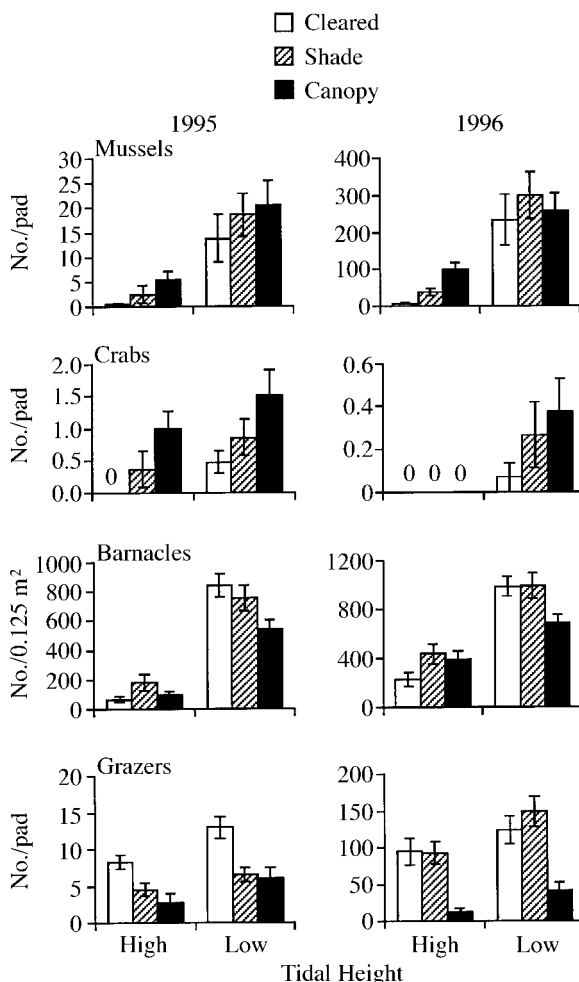


FIG. 5. Recruitment of mussels, crabs, barnacles, and grazers during 1995 and 1996. Barnacles were sampled in permanent quadrats on the rock substrate, while the other three species were sampled from settlement substrates. Values are means \pm 1 SE. Note that recruitment for mussels and grazers was an order of magnitude higher in 1996 than in 1995.

TABLE 2. Results of two-factor analyses of variance on recruitment of mussels, crabs, barnacles, and grazers during 1995 and 1996.

Source of variation	1995				1996			
	df	MS	F	P	df	MS	F	P
<i>Mytilus edulis</i>								
Height	1	44.57	38.82	<0.001	1	117.46	109.31	<0.001
Treatment	2	6.23	5.42	0.006	2	18.92	17.61	<0.001
Height \times Treatment	2	1.11	0.96	0.386	2	9.54	8.87	<0.001
Residual	75	1.15			87	1.08		
<i>Carcinus maenus</i>								
Height	1	4.68	4.47	0.038	1	1.31	9.92	0.002
Treatment	2	7.13	6.81	0.002	2	0.19	1.45	0.239
Height \times Treatment	2	<0.01	0.00	0.999	2	0.19	1.45	0.239
Residual	75	1.05			88	0.13		
<i>Semibalanus balanoides</i>								
Height	1	79.90	142.41	<0.001	1	71.80	70.11	<0.001
Treatment	2	2.04	3.63	0.031	2	2.58	2.52	0.086
Height \times Treatment	2	2.17	3.87	0.025	2	4.55	4.44	0.014
Residual	85	0.56			95	1.02		
<i>Littorina littorea</i>								
Height	1	226.21	10.36	0.002	1	7.57	5.93	0.017
Treatment	2	292.49	13.40	<0.001	2	44.48	34.82	<0.001
Height \times Treatment	2	11.20	0.51	0.601	2	3.02	2.37	0.100
Residual	75	21.83			87	1.28		

years, high zone survival was markedly greater in canopy plots than cleared plots. For example, survival in high canopy plots was >60% while in high cleared plots survival was ~20%. Barnacles in shaded plots had intermediate survival, with values closer to those of cleared plots. Snail survival was not affected by the algal canopy and was uniformly high (nearly 100%) in all canopy treatments and at both tidal heights (Fig. 6, Table 3).

Growth of understory organisms

In the high intertidal, mussel growth was positively affected by the presence of the canopy while barnacle growth was unaffected (Fig. 7). Gastropod growth was negatively influenced by the algal canopy. The effect of the canopy on mussel growth varied with tidal height, with no difference evident in low zone treatments but a strong positive effect of the canopy in the high zone (Fig. 7, Table 4). Growth in high canopy plots was over three times greater than that in high cleared plots, while shaded plots exhibited intermediate growth. Barnacle growth was not influenced by the algal canopy and the effect of the canopy on barnacle growth did not vary with tidal height (Fig. 7, Table 4). Barnacle growth, however, was strongly affected by tidal height and was two times greater in low zone plots than high zone plots in both 1995 and 1996 (Fig. 7).

The algal canopy had a strong negative effect on the growth of *Littorina littorea* (Fig. 7, Table 4) and the negative effect of the canopy on snail growth was more evident in high plots than in low zone plots. Snails in the low zone grew an average of three times more than

those in high zone. Maximum shell addition averaged 3.7 mm in the low cleared plots, while snails in high canopy plots experienced the least growth with an average of 0.13 mm of new shell added.

Predation on understory organisms

Survival of mussels in our predation assays varied with tidal height and canopy treatment with no height \times canopy treatment interaction (Fig. 8; Tidal height, $F_{1,22} = 14.28$, $P < 0.001$; Treatment, $F_{2,22} = 12.63$, $P < 0.001$; Height \times Treatment, $F_{2,22} = 1.85$, $P = 0.181$). Planned comparisons revealed that at both tidal heights, predation in cleared and canopy plots was similar but predation was markedly more intense under these conditions in the low zone than in the high zone. Less than 20% of the mussels survived the 12-h experiment in the low zone, while >60% of the mussels survived in the high zone. Survival was highest in the shaded treatments. Direct observations at high tide revealed that shades excluded large crabs and resulted in 90–100% survival under shades at both tidal heights.

Herbivory and algal recruitment

Herbivory by *Littorina littorea* significantly inhibited the recruitment of fucoid seaweeds in all treatment types (Fig. 9, Table 5). Grazing effects, however, varied with height, canopy treatment, and cage treatment for densities and percent cover of both algal species. In the cage treatments, where grazing was precluded, algal recruits reached maximum densities of >3 recruits/cm² (*Ascomyllum*) and 2 recruits/cm² (*Fucus*). Virtually no algal recruitment was found in control or cage-control

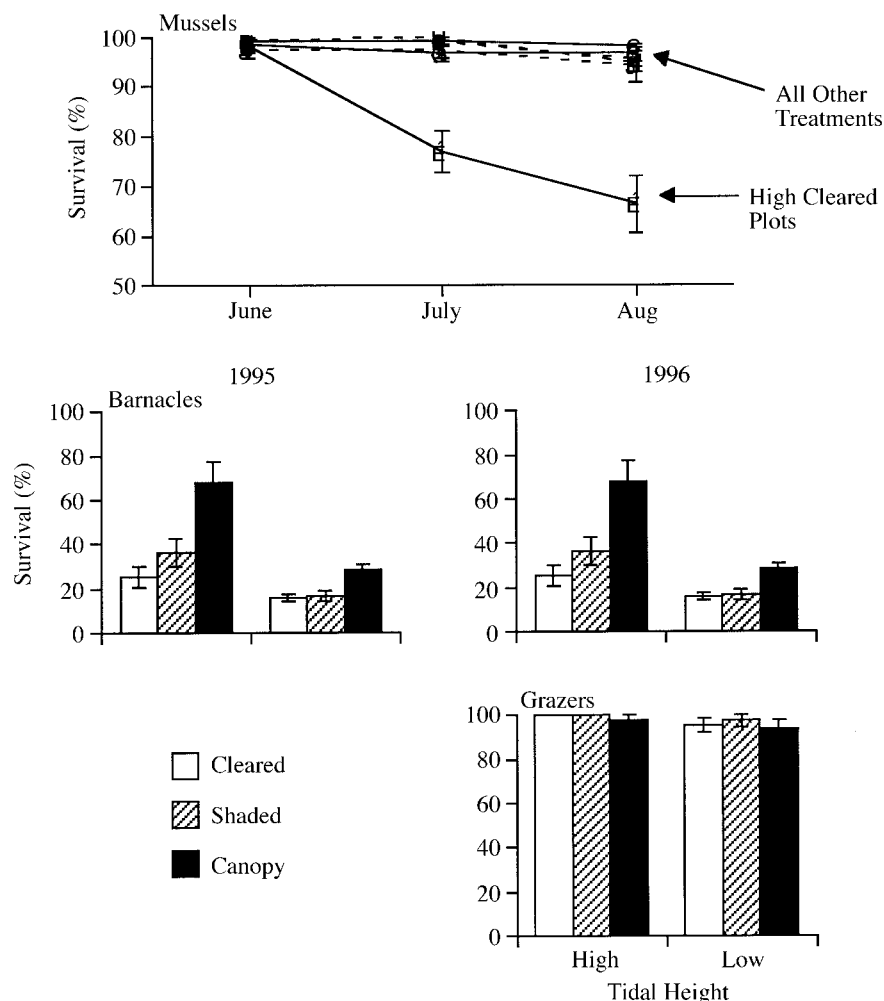


FIG. 6. Survival of mussels, barnacles, and grazers in 1995 and 1996. Barnacles were sampled in both years, but mussels were evaluated only during 1995. Grazers were evaluated only during 1996. Mussels were sampled monthly after deployment in May. Barnacle and grazer survival was evaluated once at the end of the summer (September). Values are means \pm 1 SE.

quadrats in any of the canopy treatments at either tidal height (Fig. 9). When recruitment did occur in the presence of grazers, it was extremely patchy. For example, the range of densities for algal recruits in the open or cage-control plots was 0–0.3 recruits/cm² for both *Fucus* and *Ascophyllum*.

The presence of the algal canopy and the artificial shades had a strikingly different effect on the recruitment of the two algal species (Fig. 9, Table 5). When grazers were removed, *Ascophyllum* recruits were over two orders of magnitude more abundant under the algal canopy than in canopy removal plots. *Ascophyllum* recruitment was also much more dense under shades than in canopy removal plots. *Fucus* recruits showed the opposite pattern. In the absence of grazers, *Fucus* recruitment was much more common in cleared plots than in shaded or canopy plots (Fig. 9). *Fucus* and *Ascophyllum* recruitment were generally more abundant in high intertidal plots than in low intertidal plots.

DISCUSSION

Our results show that in wave-protected rocky intertidal habitats in New England, algal canopies can have a large effect on the settlement, growth, and survival of common understory species. By reducing heat and desiccation stresses, particularly at high tidal heights, the canopy positively influenced the distribution and abundance of benthic organisms. The nature of this relationship between the canopy and understory organisms, however, often shifts with tidal height for many of these species. At stressful high tidal heights, canopy effects on understory organisms were largely positive, whereas at lower, more benign, tidal heights, canopy effects were entirely negative or statistically neutral. These results highlight the prominent role that habitat-modifying organisms can have in communities and support the hypothesis that the nature and strength of interspecific species interactions are highly dependent on the physical environment in which they occur.

TABLE 3. Results of statistical analyses on survival of mussels, barnacles, and grazers during 1995 and 1996.

Source of variation	1995					1996			
	df	MS	F	MS†	P	df	MS	F	P
<i>Mytilus edulis</i>									
Height	1	0.180	12.82	a	0.001				
Treatment	2	0.261	18.55	a	<0.001				
Height × Treatment	2	0.181	12.88	a	<0.001				
Subject (group) error	80	0.014							
Time	2	0.123	39.87	b	<0.001				
Time × Height	2	0.044	14.19	b	<0.001				
Time × Treatment	4	0.056	18.07	b	<0.001				
Time × Height × Treatment	4	0.058	18.88	b	<0.001				
Time × Subject (group) error	160	0.003							
<i>Semibalanus balanoides</i>									
Height	1	1.12	31.21		<0.001	1	0.005	0.22	0.642
Treatment	2	0.56	15.54		<0.001	2	0.684	30.79	<0.001
Height × Treatment	2	0.16	4.36		0.016	2	0.069	3.11	0.050
Residual	81	0.04				86	0.022		
<i>Littorina littorea</i>									
Height						1	0.018	3.25	0.077
Treatment						2	0.004	0.77	0.470
Height × Treatment						2	0.001	0.10	0.906
Residual						52	0.005		

Notes: Mussel data were not collected in 1996. Grazer data were not collected in 1995. Mussel data were analyzed with repeated-measures ANOVA.

† Denominator MS for the *F* ratios: a = Subject (group) error, b = Time × Subject (group) error.

Habitat modification by seaweed canopies

In northern New England estuaries, algal canopies can sharply modify physical conditions. Both high temperatures and water loss, two of the most important stresses in intertidal habitats for invertebrates and algae, were strongly buffered by the canopy. Maximum substrate temperatures under the canopy were typically 8°–10°C cooler than when the canopy was removed. This canopy effect was documented at high and low tidal heights, but was more pronounced at higher tidal heights. In addition, the time exposed to these temperatures was often 3 h less in the low zone than in the high zone (Fig. 3) and this likely contributed to the differences in organism mortality among heights. It is well known that the absolute temperature as well as the length of exposure can influence invertebrate survival rates (Evans 1958, Foster 1969, 1971). Water loss was also reduced by the canopy, particularly at high tidal heights (Fig. 4). While water loss during a single daytime exposure to low tide was <5% under the canopy at high tidal heights, it was >50% in cleared plots. At low tidal heights water loss in the presence and absence of the canopy was five times less than at high tidal heights.

The experimental shades closely mimicked the habitat-modifying effects of the algal canopy in terms of reducing thermal stress, but poorly mimicked canopy effects on desiccation. Temperatures under the canopy and in shades were usually very similar (Fig. 2). The structures, however, did not adequately mimic the effect of being covered by a dense, waterlogged, 10–25 cm thick layer of algal fronds. Accordingly, desiccation

under the shades was over twice that under the canopy (Fig. 4).

While we did not quantify the effect of the canopy on physical conditions during the winter, it is likely just as substantial as during the summer. During especially severe winter low tides, temperatures under the canopy are markedly warmer than in cleared areas (G. Leonard, *unpublished data*). Moreover, mortality from ice scour is likely to be limited by the canopy's tendency to shield the substrate from direct ice abrasion (Mathieson et al. 1982).

Although sedimentation rates could have been modified by the presence of the canopy, we did not explicitly address this issue in our study. We intentionally worked at sites with enough water movement so that sedimentation under the canopy was minimal. In the subtidal zone, these habitat-modifying effects of algal canopies are well studied. By slowing flows, canopies can increase the resuspension and deposition of sediment, enhance larval settlement and increase food supply to filter feeders (Duggins et al. 1989, 1990, Eckman et al. 1989, Duggins and Eckman 1994). While all these effects are likely to be important in many intertidal habitats as well, at our sites where surface sediment was not common, heat and desiccation buffering were probably more important. In many wave-protected habitats in the Gulf of Maine, the *Ascophyllum* canopy is often denser than at our study sites, and the substrate is often covered with a layer of sediment that appears to limit the distribution of barnacles, encrusting algae, and other substrate-dependent organisms (M. Bertness, *personal observation*).

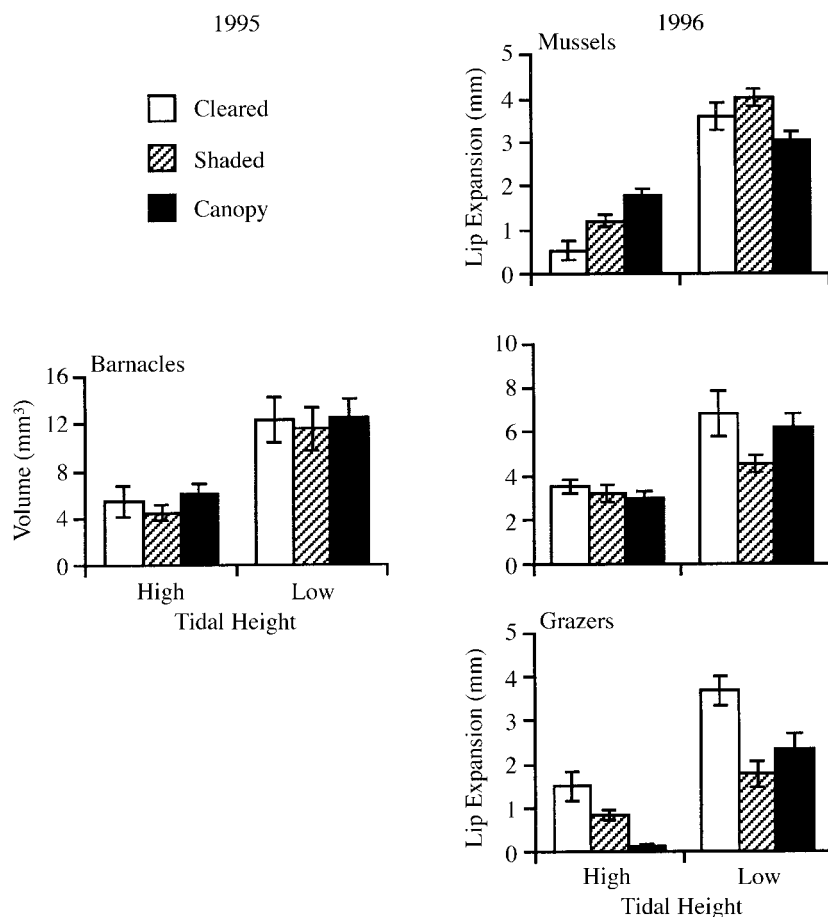


FIG. 7. Growth of mussels, barnacles, and grazers during 1995 and 1996. Barnacles were sampled in both years, but mussels were evaluated only during 1995. Grazers were evaluated only during 1996. Growth of mussels and grazers was estimated from new shell material added to marked individuals. Barnacle growth was defined as body volume, assumed to be proportional to the cube of the radius of solitary individuals. Values are means \pm 1 SE.

TABLE 4. Results of statistical analyses on growth of mussels, barnacles, and grazers during 1995 and 1996.

Source of variation	1995					1996				
	df	MS	F	MS†	P	df	MS	F	MS†	P
<i>Mytilus edulis</i>										
Height	1	868.20	175.56	a	<0.001					
Treatment	2	14.28	2.89	a	0.056					
Height \times Treatment	2	54.60	11.04	a	<0.001					
Cage (Height, Treatment)	7	9.07	1.83	b	0.078					
Residual	651	4.95								
<i>Semibalanus balanoides</i>										
Height	1	1086.96	32.92		<0.001	1	160.28	28.09		<0.001
Treatment	2	12.86	0.39		0.679	2	12.58	2.20		0.117
Height \times Treatment	2	1.08	0.03		0.968	2	9.43	1.65		0.198
Residual	90	33.02				87	5.71			
<i>Littorina littorea</i>										
Height						1	118.14	58.98	a	<0.001
Treatment						2	36.37	18.16	a	<0.001
Height \times Treatment						2	6.28	3.14	a	0.046
Cage (Height, Treatment)						10	3.19	1.59	b	0.114
Residual						160	2.00			

Notes: Mussel data were not collected in 1996. Grazer data were not collected in 1995. Mussel and grazer data were analyzed with a nested ANOVA.

† Denominator MS for the F ratios: a = Cage (Height, Treatment), b = Residual.

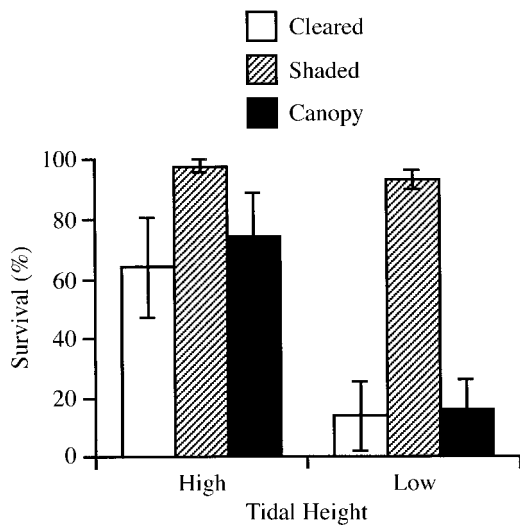


FIG. 8. Survival of mussels exposed to crab predators for a single high tide. Mussels were deployed in groups of 10, and assays were run on two consecutive days. Data were pooled. Values are means \pm 1 SE.

Positive and negative effects of the canopy on understory organisms

Our results support the hypothesis that the relationship between the canopy and its associated organisms

shifts with tidal height and the potential of exposure to extreme physical stress. Recruitment (Fig. 5), survival (Fig. 6), and growth (Fig. 7) of understory organisms were often, but not exclusively, positively affected by the canopy at high tidal heights, and negatively affected at low tidal heights. We can summarize this shifting effect of the canopy on understory organisms with tidal height by calculating the frequency of statistically significant interactions across tidal height as a function of (1) demographic process (recruitment, growth, and survival), (2) organism functional group (filter feeders and grazers) and (3) the community (all direct interactions combined). Calculations were made by pooling information across each of these three levels. For each level, the percentage of statistically positive, negative, or neutral (i.e., $P > 0.05$) interactions was tallied as a function of tidal height.

This approach revealed that the positive effects of the canopy operated only at high tidal heights and in a process-specific manner (Table 6). At the process level at high tidal heights, there was a 50/50 mix of positive and negative effects of the canopy on recruitment and growth and canopy effects on survivorship were 66% positive (Table 6). In contrast, at lower tidal heights no positive canopy effects on recruitment or growth were documented and all canopy effects on survival were statistically neutral. Pooling the same data

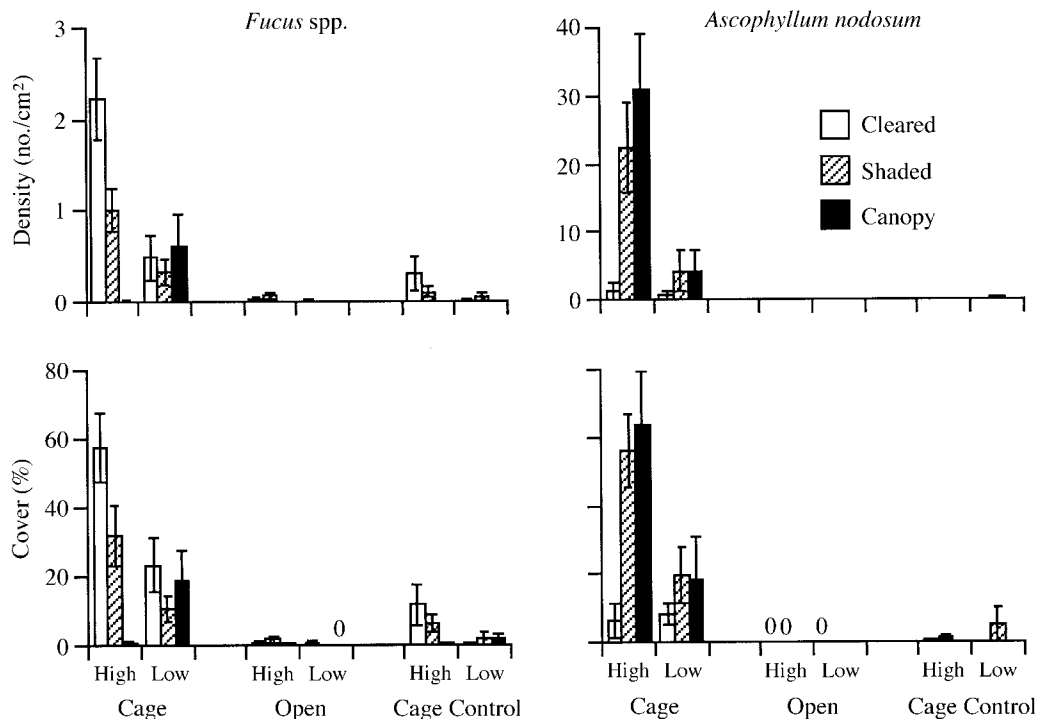


FIG. 9. Recruitment of *Fucus* spp. (*F. spiralis* and *F. vesiculosus*) and *Ascophyllum nodosum* after 1 yr in quadrats that had been initially cleared to bare rock. Cage, cage control, and open (control) quadrats were set out at high and low tidal heights in the three canopy treatments. Density and percent cover were sampled in the field. Zeros indicate no (nil) recruitment. Areas of the figure with no bar visible but without zeros are indicative of non-zero but very low recruitment. Note that patterns of recruitment for the two species as a function of the canopy treatments are mirror images of each other.

TABLE 5. Results of three-factor analyses of variance on the density and percent cover of *Ascophyllum nodosum* and *Fucus* spp. recruits as a function of tidal height, canopy treatment, and grazer treatment.

Source of variation	Density				Percent cover			
	df	MS	F	P	df	MS	F	P
<i>Ascophyllum nodosum</i>								
Height	1	1.45	31.51	<0.001	1	4135.19	20.12	<0.001
Treatment	2	0.66	14.20	<0.001	2	3432.84	16.70	<0.001
Grazers	2	2.38	51.57	<0.001	2	16 640.39	80.95	<0.001
Height \times Treatment	2	0.38	8.22	<0.001	2	1293.02	6.29	0.002
Height \times Grazers	2	1.20	25.94	<0.001	2	3800.35	18.49	<0.001
Algal \times Grazers	4	0.54	11.72	<0.001	4	2569.58	12.50	<0.001
Height \times Treatment \times Grazers	4	0.32	6.87	<0.001	4	1249.86	6.08	<0.001
Residual	242	0.05			242	205.57		
<i>Fucus</i> spp.								
Height	1	4.68	10.32	0.002	1	2.67	7.63	0.006
Treatment	2	4.22	9.33	<0.001	2	3.78	10.79	<0.001
Grazers	2	18.15	40.04	<0.001	2	15.85	45.30	<0.001
Height \times Treatment	2	5.08	11.21	<0.001	2	3.18	9.09	<0.001
Height \times Grazers	2	2.42	5.35	0.005	2	0.92	2.63	0.074
Algal \times Grazers	4	2.76	6.08	<0.001	4	2.33	6.65	<0.001
Height \times Treatment \times Grazers	4	3.50	7.72	<0.001	4	1.77	5.06	0.001
Residual	284				284	0.35		

Notes: Data were collected in March 1996, one year after the treatments were installed. The grazer treatment had three levels: an exclusion cage, a cage control, and a true control (uncaged) quadrat.

across functional types revealed that the positive effects of the canopy were not only restricted to high tidal heights, but were also restricted to the sessile filter feeders (i.e., barnacles and mussels; Table 6). This result must be viewed with caution, however, since only one grazer (i.e. *Littorina littorea*) was examined. Pooling across demographic process and functional type showed that the overall effect of the canopy was mostly positive or neutral at high tidal heights, but shifted to neutral or negative at low tidal heights.

In short, these results support the predictions of Bertness and Callaway (1994) that the frequency of habitat-ameliorating positive interactions should increase with increasing physical stress. Nearly half of the interactions in the high zone were positive while none were positive in the low zone. In contrast to Bertness and Callaway (1994), however, we found that most of the interactions in the low stress habitat (i.e., the low intertidal) were statistically neutral rather than negative. One explanation is that thermal and desiccation stresses were lower but still appreciable, in the low zone. A second explanation is that we had little statistical power to detect negative interactions there. Our ability to detect variable species interactions in the high zone, however, makes this latter explanation unlikely. We suspect that the lower intertidal border of the canopy is still a relatively stressful environment during low tide exposures for many of these rocky shore organisms.

Positive feedbacks, consumers, and the dominance of Ascophyllum canopies in wave-protected habitats

Dense canopies of *Ascophyllum* are characteristic of wave-sheltered rocky shores throughout the Gulf of Maine (A. R. O. Chapman 1974, Vadas et al. 1990). They are one of the most conspicuous features of these

rocky shores, and yet have been relatively understudied. While our work has not specifically examined why these canopies are so dominant in these habitats or why they occur as such discrete stands with sharp borders, it does contribute to understanding these issues.

We found no evidence that the canopy influenced grazing intensity in this system. Both under the canopy and in cleared areas, the herbivorous snail, *Littorina littorea*, virtually eliminated algal recruitment (Fig. 9). The presence or absence of the *Ascophyllum* canopy, however, dictated which species of algae recruited in the absence of grazing. In cleared areas, the rockweed *Fucus* spp. recruited in high densities (i.e., 2 recruits/cm²) when grazers were experimentally removed. *Fucus* did recruit in the presence of natural *Littorina* densities, but at very low densities. In marked contrast to the pattern seen with *Fucus*, *Ascophyllum* recruitment (in the absence of grazers) was largely restricted to shaded and canopy treatments (Fig. 9). These findings suggest that *Fucus* is intolerant of low light levels but relatively immune to thermal and desiccation stress while *Ascophyllum* tolerates low light but is sensitive to physical stress. They also suggest that once established, *Ascophyllum* canopies can persist by facilitating their own recruitment. Average longevity for individual *Ascophyllum* thalli in the Gulf of Maine is 5–8 yr, with some individuals living >25 yr (R. Steneck, *personal communication*). The longevity of this alga, combined with these intra-generational positive interactions, may contribute to its dominance in protected estuaries.

Our finding of high *Ascophyllum* recruitment in sheltered habitats is also interesting because it is at odds with previous work done in more wave-exposed habitats. Vadas et al. (1990) studied *Ascophyllum* recruitment at nearby open coast sites in Maine and found

TABLE 6. Percentage of positive, negative, and statistically neutral interactions ($n = 9$ interactions) among invertebrates and the *Ascophyllum* canopy as a function of tidal height and (1) demographic process (top), (2) species functional group (middle) and (3) community (all direct interactions; bottom).

Interaction category	Tidal height					
	High zone			Low zone		
	Positive (%)	Neutral (%)	Negative (%)	Positive (%)	Neutral (%)	Negative (%)
Demographic process						
Recruitment	33	33	33	0	33	66
Survival	66	33	0	0	100	0
Growth	33	33	33	0	33	66
Functional type						
Filter Feeder	66	33	0	0	66	33
Grazer	0	33	66	0	33	66
Community level						
All Direct Interactions	44	33	22	0	56	44

Note: Interaction types and statistical significance were taken from Tables 2–4 and Figs. 5–7.

that recruitment was rare. Recruitment appeared to be severely limited by wave stress and the weak attachment strength of recently settled *Ascophyllum* zygotes. Without grazers in shaded habitats, we found extremely heavy *Ascophyllum* recruitment (i.e., 20–30 recruits/cm²). Thus, in more wave-protected habitats in the Gulf of Maine, recruitment may not be a severe bottleneck as previously assumed.

Our quantification of predation pressure by crabs suggests that predation, like grazing, may limit the abundance of prey under the canopy. In a previous paper (Leonard et al. 1998) we showed that in these habitats, mussel beds dominate high flow sites but that *Ascophyllum* dominates nearby low flow sites. Mussels are numerous at high flow habitats because of higher recruitment and because their major predator, the green crab *Carcinus maenas*, is an ineffective forager in high flows (Leonard et al. 1998). At low flow sites, crab predation limits mussels to crevices and other refugia (Leonard et al. 1998). Results from our crab predation assays (Fig. 8) show that predation on mussels is intense under the canopy and was not reduced in cleared areas. Since our clearings were relatively small in comparison to the mobility of this predator, however, we suspect predation would have been lower if much larger clearings (P. Petraitis, *unpublished data*) had been used. It is also worth noting that mussels recruited to many of our grazer exclusion cages under the *Ascophyllum* canopy (G. Leonard, *personal observation*). While we could not maintain these cages long enough to quantify this observation (the cages were lost over the winter), the absence of mussel recruits under the canopy except in predator exclusion cages suggests that crab predation may exclude mussels from living under the canopy.

Habitat modification, direct positive interactions, and shoreline ecology

Our results contribute to growing evidence that habitat modification and direct positive interactions play

too important a role in natural communities to be ignored in general models of community organization (Wilson and Agnew 1992, Bertness and Callaway 1994, Jones et al. 1994). Intertidal communities, in particular, appear to be strongly organized by habitat-modifying organisms because they occur in physically rigorous environments where the major stresses can be ameliorated by the presence of organisms.

A short list of organisms that could be argued to play crucial structuring roles in intertidal habitats include marsh grasses (Redfield 1965, 1972, V. J. Chapman 1974; J. Bruno, *unpublished manuscript*), seagrasses (Orth 1977, Peterson 1982), seaweed canopies (Eckman et al. 1989, Duggins and Eckman 1994), mussel beds (Suchanek 1986, Witman 1987, Dame 1996), and oyster reefs (Dame 1976). Each of these species plays a critical role in the habitats they dominate by ameliorating potentially limiting stresses. The stresses that are alleviated, however, are different in each habitat. Heat and desiccation (Hay 1981, Suchanek 1986), high water currents and disturbance (Orth 1977, Bertness 1984, Eckman et al. 1989, Holbrook et al. 1991) and consumer pressure (Bertness and Grosholz 1985, Hay 1986, Witman 1987) are some of the most prominent abiotic and biotic stresses alleviated by dominant shoreline organisms.

An appreciation of the role of habitat-modifying organisms and direct positive interactions in the structure and organization of natural communities is important if we are ever to develop accurate models of how natural assemblages work (Wilson and Agnew 1992, Bertness and Callaway 1994, Jones et al. 1994, Bertness and Leonard 1997, Hacker and Gaines 1997). While considerable recent attention has been given to exploring the importance of indirect interactions in natural communities (Wootton 1992, 1993, Menge 1995), less attention has been given to the community role or significance of direct positive interactions in natural

communities. Further insight into the dependencies of natural communities in stressful habitats on the presence of dominant habitat modifiers can only come from studies that quantify the role of such organisms. By identifying and quantifying the role played by dominant habitat modifiers, such as *Ascophyllum* canopies, we may learn just how dependent some natural communities in stressful habitats are on the presence of habitat modifiers.

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