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THE ROLE OF POSITIVE INTERACTIONS IN COMMUNITIES: LESSONS FROM INTERTIDAL HABITATS

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Abstract. Positive interactions that result from neighbors buffering one another from stressful conditions are predictably important community forces in physically stressful habitats. Here, we examine the generality of this hypothesis in marine intertidal communities. Intertidal communities have historically played a large role in the development of community ecology since they occur across pronounced physical gradients and are easily manipulated. Positive interactions, however, have not been emphasized in studies of intertidal communities.

We first review studies of intertidal marsh plant communities that suggest that positive interactions play a dominant role in the structure and dynamics of these common assemblages. We then present the results of an experimental manipulation on New England rocky shores that suggests that group benefits are as important in maintaining the upper intertidal limits of dominant spaceholders on rocky shores as the negative forces of competition and predation are in maintaining lower distributional limits.

We conclude by discussing the generality and implications of our results. We argue that biogeographic biases have limited appreciation of the role played by positive interactions in intertidal communities. Most of the work that has formed the foundation of marine intertidal ecology was done in cool temperate habitats, whereas positive interactions driven by the amelioration of thermal or desiccation stresses are likely more important in warmer climates. We further argue that many important positive feedbacks operate at large spatial scales, not conducive to experimental study, and thus have escaped critical attention and general acceptance. We suggest that recognizing the role of positive interactions in communities may be key to understanding population and community processes in physically stressful habitats, many large-scale landscape processes, and uncovering long-suspected linkages between biodiversity and community stability.

Key words: community ecology; distributional limits; group benefits; habitat amelioration; physical stress.

INTRODUCTION

Few contemporary ecologists would deny the role played by positive interactions in many natural communities, even though these interactions are not included in most current models of community dynamics (e.g., Tilman 1982, Menge and Sutherland 1987) and are not typically discussed as important community processes in contemporary textbooks (see Keddy 1990). Positive interactions can be simply defined as any direct or indirect interaction among two or more organisms that positively affects the growth or reproduction of one or more organisms without negatively affecting the other(s). Thus, positive interactions include facultative and obligatory mutualisms and facilitations, trophic and nontrophic interactions, and direct as well as indirect interactions.

The absence of positive interactions from most contemporary discussions of community dynamics is puzzling. Historically, positive interactions were considered crucial community processes by early ecologists (Clements et al. 1926, Allee et al. 1949). It was not until the last three decades when competitive and consumer processes at relatively small spatial scales were overwhelmingly emphasized that ecologists seemed to lose interest in the role of positive interaction in communities. Yet, evidence suggests that positive interactions play crucial roles in many communities. For example, most coral reef ecosystems would likely not exist without the mutualism between corals and their microscopic algal symbionts (Goreau and Goreau 1966), and positive feedbacks in communities involving nutrients are widespread (Carpenter et al 1985, Bianchi and Jones 1991, Stone and Weisburd 1992).

Recently, however, ecologists working in a range of natural systems have begun to develop a renewed appreciation for the role of positive interactions in communities. Positive feedbacks between organisms and their physical environment or supply of limiting re-

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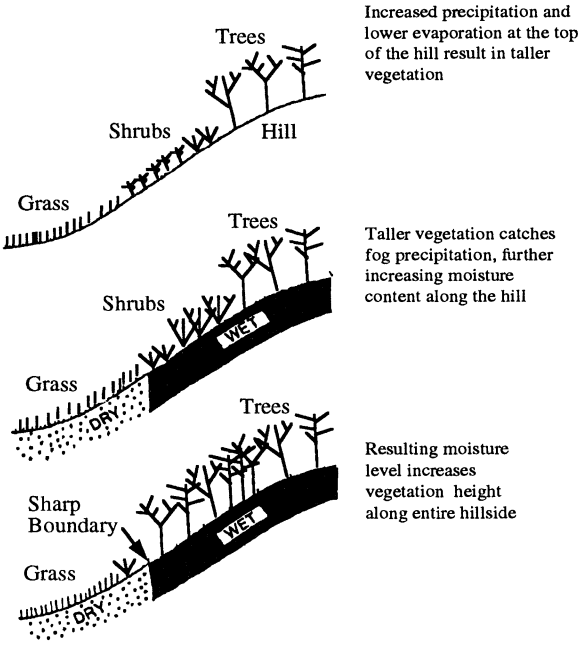

FIG. 1. Example of a positive switch (sensu Wilson and Agnew 1992) where plant cover, by ameliorating potentially limiting physical conditions, has positive feedbacks on plant community structure.

sources have been discussed conceptually (Odum 1969, Patten and Odum 1981, DeAngelis et al. 1986, Wilson and Agnew 1992) and empirical studies have begun to hint at their general importance (Levinton and Lopez 1977, Bertness 1984, 1985, Carpenter et al. 1985, Witman 1987, Bianchi and Jones 1991, Bertness and Hacker 1994). Indirect positive interactions that occur in food webs as a consequence of consumers sharing food resources and enemies have also been recently discussed theoretically (Levine 1976, Holt 1977, Vandermeer 1980, Abrams 1983) and shown to be widespread in complex natural communities (Dethier and Duggins 1984, Strauss 1991, Wootten 1993, Menge 1995).

Despite renewed interest in the community role of positive interactions, little has been done to incorporate them into the conceptual framework of ecology. Hunter and Aarssen (1988) and Callaway (1995) have reviewed the prevalence of positive interactions in plant communities. Wilson and Agnew (1992) have termed positive, nontrophic interactions among plants that are mediated by plant amelioration of physical stresses "positive switches." They suggest that positive switches are commonly important processes at large spatial scales (see Fig. 1 for an example) and have compiled a long list of probable examples. Jones et al. (1994, 1997) and Lawton (1994) have discussed the need to incorporate the often dramatic effects organisms have on their habitats into the conceptual framework of ecology. They suggest that organisms that affect habitats in ways that influence habitat use by other organisms be termed bioengineers and that many bioengineers have strong positive effects on other organisms.

Whereas many ecologists have recently recognized the potential importance of positive forces in the fabric of natural communities, work on the role of positive interactions in communities still largely lacks experimental analyses and a predictive understanding of the conditions under which positive interactions should and should not be expected to be important. Recent discussions of the community consequences of positive interactions have all emphasized the lack of critical experimental manipulations as a major stumbling block in accepting the role played by positive forces in communities (Strauss 1991, Jones et al. 1994, Lawton 1994). Many of the best correlative examples of potential positive interactions are convincing (see Wilson and Agnew 1992), but the speculative nature of their potential community consequences has limited appreciation of their importance.

Understanding under what conditions positive interactions are an important organizing force in communities is necessary if they are to be incorporated into the conceptual framework of community ecology. If the occurrence, strength, and consequences of positive interactions are not predictable, ecologists may be justified in ignoring them in general models and treating them as noise or natural history idiosyncrasies. Early in this century, ecologists emphasized the importance of facilitative interactions in succession (e.g., Clements et al. 1926), but later evidence suggested that facilitation only occurred during primary succession when early colonizers were necessary to ameliorate harsh physical conditions (Connell and Slayter 1977). Recent reviews have generally supported the hypothesis that group benefits of habitat amelioration are characteristic of physically harsh environments (Goldberg and Barton 1992, Huston 1994, Callaway 1995). Numerous authors have also suggested that palatable prey may typically be protected from consumers by living in association with less preferred prey (Atsatt and O'Dowd 1977, Hay 1986, Pfister and Hay 1988, Skilleter 1994, Littler et al. 1995). These associational defenses would be expected to occur most commonly under heavy consumer pressure where the benefits of association outweigh the potential costs of competition for resources. Based on correlations between group benefits and physically stressful habitats and associational defenses and high consumer pressure, Bertness and Callaway (1994) proposed a graphical model of the frequency and relative importance of positive interactions across physical stress gradients (Fig. 2). The model predicts that at low levels of physical stress where consumer pressure is typically high (Menge and Sutherland 1987), associational defenses will be important, whereas at high levels of physical stress where heavy consumer pressure is rare, positive interactions driven by habitat amelioration will be important. At intermediate levels of phys-

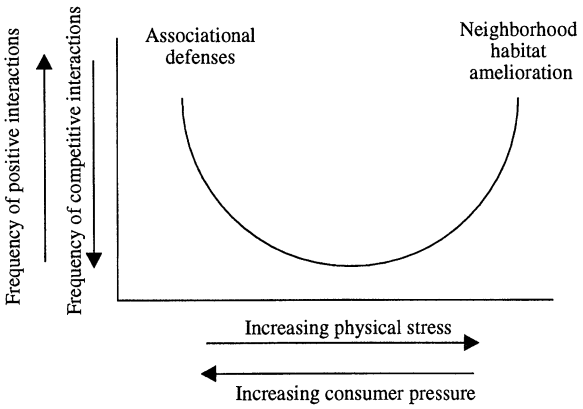

FIG. 2. Conceptual model of Bertness and Callaway (1994) predicting the conditions under which positive interactions are expected to be important forces in community structure. Positive interactions are predicted to be rare under mild physical conditions and low consumer pressure. Neighbor amelioration of physical stress and associational defenses are hypothesized to lead to positive interactions under harsh physical conditions and intense consumer pressure, respectively.

ical stress the model predicts that positive interactions are likely rare and of little consequence.

Intertidal communities are an attractive system to examine the association between physical stress and the importance of stress-ameliorating positive interactions. Historically, rocky intertidal communities have been valuable to explore mechanisms generating community structure because intertidal organisms are often easily manipulated. Intertidal systems occur across sharp environmental gradients. At high-tidal heights, organisms may be exposed to harsh terrestrial conditions of extreme temperatures and water loss, whereas only steps away organisms may never experience terrestrial conditions. Consequently, the role played by physical gradients in intertidal communities is much more easily described and examined than similar physical gradients in communities that occur across much larger spatial scales (e.g., latitude or altitude).

In this paper, we examine the predictability and pervasiveness of positive interactions driven by organism habitat amelioration in intertidal communities, and suggest that if positive interactions are characteristic of harsh environments, they should be generally important in intertidal environments. We begin by outlining recent evidence that positive interactions are predictable forces in marsh plant communities that fringe the shores of estuaries and other protected coastlines. Then, we present new evidence suggesting that positive interactions may play an equally powerful role in rocky intertidal communities. We close by discussing whether intertidal systems are representative of other natural communities in terms of the role played by positive interactions and the potential importance of biogeography and climate in mediating the relative importance of positive interactions in communities.

Positive Interactions in Salt Marsh Plant Communities

Salt marsh plant communities are characterized by striking vertical zonation that is particularly pronounced in regions with large tidal amplitude (Chapman 1974). The halophytic plants that dominate most marsh plant communities are clonal turfs that spread vegetatively to cover available surfaces, making many of these communities space limited. As is typical of intertidal space-limited systems (Jackson 1977, Paine 1984), competitive processes are conspicuously important in marshes. Research over the last decade in a variety of marsh plant systems has demonstrated the importance of interspecific competition in generating and maintaining marsh plant zonation (Silander and Antonivics 1982, Snow and Vince 1984, Bertness and Ellison 1987, Bertness 1991*a*, *b*, Pennings and Callaway 1991). The paradigm emerging from these studies is that marsh plant zonation is the product of competitively dominant plants monopolizing physically benign habitats and displacing competitively subordinate plants to physically harsh habitats where edaphic conditions preclude the persistence of the competitive dominants. Strong interspecific competitive dominance, a steep intertidal physical stress gradient, and an inverse relationship between competitive ability and physical stress tolerance combine to generate this striking zonation. In New England marshes, for example (see Fig. 3), the woody shrub *Iva frutescens* dominates the terrestrial borders of marshes, displacing the rush *Juncus gerardi* to lower elevations. *Juncus* in turn displaces salt hay, *Spartina patens,* from the terrestrial border of the high marsh, while *S. patens* likewise displaces the cordgrass *Spartina alterniflora* to the low marsh where tidal flooding occurs daily. In all cases, the role of interspecific competition in this strong zonation pattern is unambiguous and has been clearly demonstrated. Plants that dominate higher tidal heights die when moved to lower elevations with or without neighbors present. Conversely, plants found at lower elevations do well if moved to high elevations without neighbors, but are competitively displaced rapidly when neighbors are present (Bertness 1991*a*, *b*, Bertness 1992).

The strong role played by competitive processes in generating spatial patterns in marsh plant communities, however, masks the equally potent and predictable role played by habitat-ameliorating positive associations in marsh plant communities. Marsh habitats are physically stressful habitats for vascular plants, limiting their inhabitants only to those plants capable of tolerating extreme edaphic conditions. Two edaphic conditions in marsh habitats are particularly harsh: anoxic water-

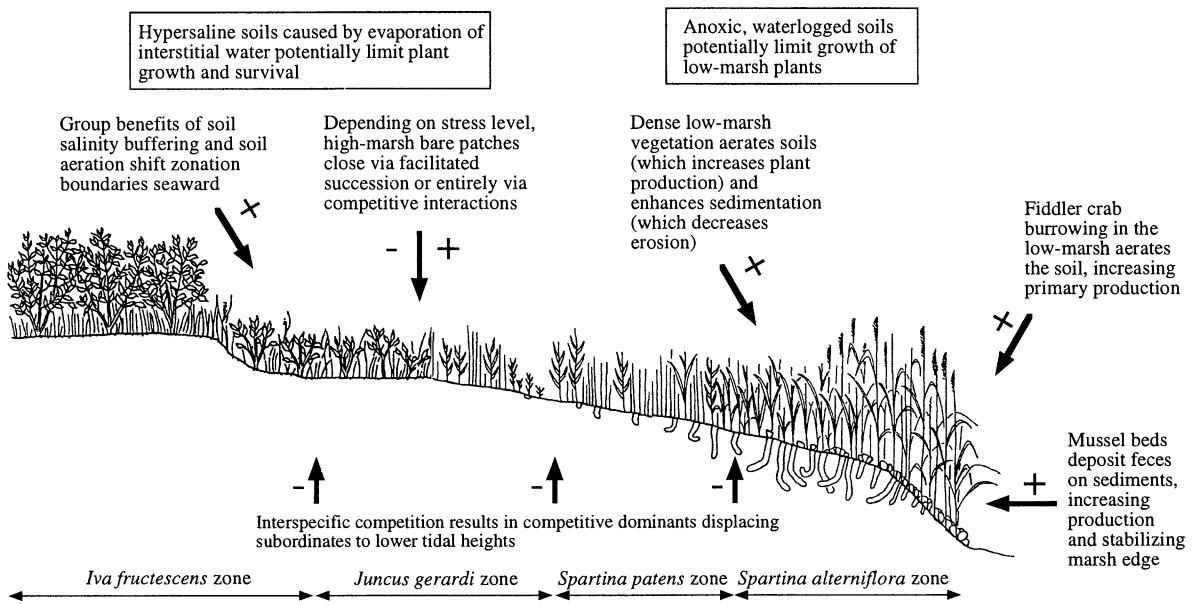

FIG. 3. Diagrammatic summary of the roles of positive and negative interactions on the structure of southern New England marsh plant communities, based on Howes et al. (1981, 1986), Bertness (1991*a*, *b*), Bertness and Shumway (1993), Bertness and Hacker (1994), and Bertness and Yeh (1994).

logged soils and high soil salinities. However, both of these are very strongly ameliorated by plant cover.

At low elevations in salt marshes that are routinely flooded by tides (low-marsh habitats), anoxic soil conditions can limit plant growth (Gleason 1980, Howes et al. 1981). Low-marsh plants like *Spartina alterniflora,* however, have aerenchyma tissue that supplies oxygen to belowground tissue, thus aerating anoxic soil. As a result, established plants can alleviate potentially limiting anoxic soil conditions, leading to a positive feedback between plant cover and growth both within and among plant species (Howes et al. 1981, 1986, Shat 1984, Bertness 1991*a*, Hacker and Bertness 1995).

At higher marsh elevations, high soil salinities can limit plant survival and growth. Soil salinity potential is highest at intermediate marsh elevations since tidal flushing at lower elevations and terrestrial influences (runoff) at higher elevations minimize salt accumulation. At intermediate elevations, however, by simply shading the soil and limiting evaporative water loss, plant cover can effectively limit salt accumulation.

As a direct consequence of the buffering of soil salinity by vegetation cover at higher marsh elevations, positive plant interactions driven by habitat amelioration are a predictable feature of physically stressful, but not physically benign, high-marsh habitats. This influences the predictability and importance of positive interactions in secondary succession, seedling establishment, and marsh plant zonation. Large bare patches in the high marsh close via facilitated succession, where initial colonizers reduce soil salinity, which leads to the invasion of less salt-tolerant competitive dominants (Bertness 1991*b*, Bertness and Shumway 1993). Since potential salt accumulation in bare patches is a function of patch size, tidal height, and rainfall, the relative importance of facilitation in patch closure is also a function of these variables. Similarly, seedling establishment in the high marsh can be dependent on the presence of seedling neighbors and/or adult nurse plants to ameliorate harsh soil conditions, but again only under conditions where salt accumulation is high. High seedling densities, for example, can be necessary for seedling establishment at intermediate elevations in New England marshes, but similar densities lead to intense seedling competition at higher, less stressful elevations (Bertness and Yeh 1994). Zonal boundaries in the high marsh are also sensitive to group benefits mediated by habitat amelioration (Bertness and Hacker 1994). In southern New England the seaward border of the distribution of marsh elders (*Iva*) is dependent on the presence of clonal turfs that ameliorate high soil salinities, but at the terrestrial border of the marsh elder zone, where high salinities do not occur either with or without plant cover, *Iva* competitively displaces its clonal turf neighbors (Bertness and Hacker 1994). These positive feedbacks between plants and local edaphic conditions can have a major impact on marsh food webs and plant species diversity. Clonal turf facilitation of marsh elders is necessary for the local persistence of marsh elder herbivores and their predators (Hacker and Bertness 1996), and clonal turfs are also responsible for maintaining the high diversity of

fugitive plants in high-marsh habitats (Hacker and Gaines 1997).

Patterns in marsh plant communities clearly represent a delicate balance between competitive and facilitative interactions (see Callaway and Walker 1997 in this Special Feature for further discussion). Under benign physical conditions, both intra- and interspecific plant competition, is the driving force in secondary succession, seedling establishment, and zonation. Equally important in understanding marsh plant community structure, however, is that under harsh physical conditions intra- and interspecific positive interactions driven by habitat amelioration are as predictable a driving force in secondary succession, seedling establishment, and zonation patterns as are competitive forces under physically benign conditions. How common these sorts of positive feedbacks are in the underlying fabric and dynamics of other marine and terrestrial communities is unknown and largely untested.

Are Positive Interactions Important Forces on Rocky Shores?

If positive interactions caused by stress amelioration by neighbors are predictably important processes in harsh physical environments, they should be common in other intertidal environments where inhabitants are exposed to harsh physical conditions. In particular, rocky intertidal habitats where sessile organisms attached to rock surfaces cannot burrow into sediments to escape low-tide exposure to heat and desiccation should be ideal habitats to test this general hypothesis.

For the last three decades, rocky intertidal assemblages have been an important model system for elucidating processes that generate community pattern and structure (Connell 1961, 1970, Paine 1966, 1974, Dayton 1971, Menge 1976, 1995, Lubchenco 1978). Although experimental intertidal ecologists have taken advantage of gradients in intertidal habitats to quantify how environmental stress affects competitive and consumer processes, most of the focus on these shoreline assemblages has not been explicitly on the role of physical stresses in directly affecting these communities. It could be argued, in fact, that modern experimental marine community ecology developed as a reaction to the emphasis of earlier ecologists on physical stress-based explanations of intertidal community patterns (e.g., Stephenson and Stephenson 1954, Lewis 1960, Newell 1976). Experimental marine ecologists over the last few decades have tended to downplay the role of physical stresses other than disturbance on intertidal communities in favor of focusing on biotic interactions.

One of the most robust paradigms that has emerged from work in rocky intertidal communities is that the upper distribution limits of intertidal invertebrates and seaweeds are typically set by physical processes (e.g., heat, desiccation), whereas lower distributional limits are typically set by biotic processes, (e.g., competition for space and consumer pressure; Connell 1972, Carefoot 1977, Menge and Sutherland 1987). This oversimplified dichotomy has had the unfortunate effect of setting physical stresses and biotic interactions as opposing rather than interacting forces. In addition, a general preoccupation with competitive and consumer processes over the last two decades has also focused the attention of rocky intertidal ecologists on lower intertidal habitats rather than high-intertidal habitats. As pointed out by Wethey (1984), it is not uncommon for intertidal ecologists to dismiss high-intertidal limits as "likely due to physical stresses" while devoting most of their attention and much more rigor to carefully dissecting the processes that generate low-intertidal zone patterns. It is also common to consider competitive and consumer interactions as density-dependent processes, while dismissing responses to physical stresses and disturbance as density independent (Connell 1972). Thus, a cursory look at the rocky intertidal community literature would suggest that positive interactions are not particularly common and that work in this habitat is not consistent with the prediction that positive interactions due to habitat amelioration should be common in stressful, high-intertidal rocky habitats.

More careful examination of interactions of organisms on high-intertidal hard substrates, however, suggests that something may be missing from our understanding of these habitats. On tropical shores, high algal densities buffer individuals from desiccation at high tidal heights (Hay 1981) and snails often live in dense groups, which serve to minimize individual water loss (Garrity 1984). Similarly, on temperate rocky shores high densities of barnacles, mussels, and seaweeds have been shown to buffer neighbors from physical stress at high-tidal heights, but lead to competition among neighbors at low-tidal heights (Bertness and Grosholz 1985, Lively and Raimondi 1987, Bertness 1989, Stephens and Bertness 1991). Are these aberrant results or do they suggest that positive density-dependent interactions are characteristic of high-intertidal rocky beach communities?

Testing the Role of Positive Interactions on Rocky Shores

We recently tested the general hypothesis that group benefits are as common an organizing force in high rocky intertidal assemblages as competitive effects are in lower intertidal assemblages on southern New England shores. As study organisms, we used four of the most common sessile space holders at middle-to-high tidal heights in this region. The study organisms were the mussels *Mytilus edulis* and *Geukensia demissa,* which typically occur in dense intertidal beds in southern New England on rocky shores and salt marshes, respectively (see Menge 1976, Bertness and Grosholz 1985 for details) and the brown seaweeds, *Ascophyllum nodosum* and *Fucus distichus,* which occur in dense

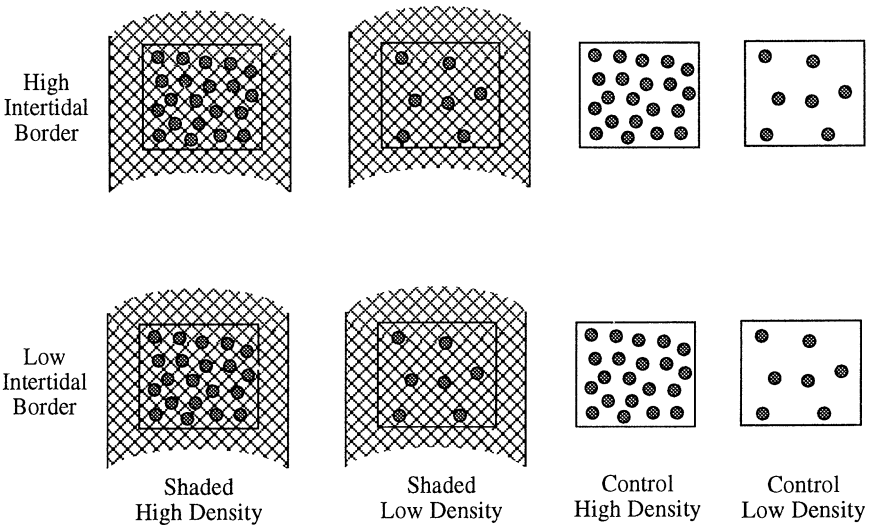

FIG. 4. Design of the density manipulations of southern New England high intertidal zone sessile spaceholders to test the relative importance of positive and negative density effects on individual survivorship and growth. This experiment was performed on the mussels *Mytilus edulis* and *Geukensia demissa* and the seaweeds *Ascophyllum nodosum* and *Fucus distichus*, the most prominent primary spaceholders on southern New England shorelines.

stands at middle-to-high tidal heights on rocky beaches throughout New England (see Menge 1976, and Lubchenco 1983 for details). Together, these species and the northern acorn barnacle, *Semibalanus balanoides*, are the most dominant rocky intertidal spaceholders at middle-to-high tidal heights throughout the Gulf of Maine. *Semibalanus* was not included in our experiments since it has already been shown to benefit at high-tidal heights from high densities due to thermal buffering, but that high densities decreased individual survivorship at low-tidal heights due to competition for space (Bertness 1989). Thus, our experiment was designed as a community-wide test of the role of positive interactions in dictating the high-intertidal limits of sessile spaceholders on southern New England shorelines. As study sites, we used Rhode Island shoreline habitats that are described in detail elsewhere. *Mytilus* and *Geukensia* experiments were performed at Portsmouth Narrows (Sanford et al. 1994) and Rumstick Cove (Bertness 1992), respectively. Seaweed experiments were all performed at Sakonnet Point (Bertness et al. 1991).

To test the hypothesis that the high-intertidal borders of sessile high-intertidal species are set by positive interactions, but that their lower borders are influenced more by negative, competitive interactions, we performed the same basic experiment on all four species (Fig. 4). At both the high- and low-intertidal limits of each species' distribution we marked and monitored the survivorship and growth of individuals in replicated control treatments (where individuals were left at natural high densities) and thinned treatments (where individuals were thinned to low densities). At both high- and low-tidal heights we also followed shaded control and thinned replicates to experimentally reduce potential thermal and desiccation stress and to mimic the habitat-ameliorating influence of aggregated organisms. For shades, we used a double layer of 5-mm plastic mesh (Vexar) suspended 20 cm over shaded replicates (see Bertness and Gaines 1993 for methods).

For both mussel species we used plastic flower pots (15 cm diameter) filled with ambient substrate and imbedded flush into the surrounding substrate as replicate units (16 density × shade × tidal height replicates). At each tidal height and for each mussel species, shaded replicates were placed under two 2 × 2.5 m shades (8 high-density and 8 low-density replicates). Unshaded replicates were similarly grouped in unshaded areas adjacent (2 m) to each shade. Four mussels were marked and placed in each pot. To minimize the influence of mussel size variation on the results, a single size class of individuals was used for each mussel species. For *Mytilus*, 30–40 mm individuals were used and for *Geukensia*, 60–70 mm individuals were used. Marked individuals were measured (length) with calipers, individually labeled with 2 mm diameter plastic tags, and then lip marked with acrylic paint to quantify shell growth (see Bertness and Grosholz 1985 for methods). For high-density replicates, randomly selected high-density mussel clumps from the study site were placed in the pots and marked mussels were added in natural positions. For low-density replicates, only the four marked mussels were placed in the pots and allowed to attach. A 4 × 4 cm wire mesh cover was cable tied to the top of each replicate pot to limit the access of bird and crab predators to the marked individuals. The smaller mussels used in these experiments are known to be vulnerable to large mobile predators when

not protected by neighbors in dense mussel beds (Bertness and Grosholz 1985, Okamura 1986, Stiven and Gardner 1992). Identical *Mytilus* and *Geukensia* experiments were set up in mid-May 1993, and monitored for dead mussels weekly for 13 wk. At the end of August, remaining mussels were scored as live or dead and remeasured to quantify growth.

In analogous seaweed experiments, we manipulated naturally occurring dense stands of *Ascophyllum* and *Fucus*. For each species, at the upper and lower tidal limits of their distributions, we randomly assigned five density × shade replicates. In low-density replicates, seaweeds were thinned by removing individuals at the holdfast to densities of 20–25 marked individuals/m^2. In high-density replicates, 20–25 random individuals in a 1 m^2 area were marked. Each shaded seaweed plot was individually shaded. For *Fucus,* we numbered the base of small, 4–8 cm high sporlings (juveniles) with 4-mm cloth markers (Brady wire markers) covered with superglue. Marked *Fucus* were initially measured in May 1993 and censused and remeasured every other week until September 1993. *Ascophyllum* replicates were set up identically, but instead of monitoring sporlings (which were not available) we monitored growing tips on marked plants (Northeast Utilities Services Company 1994). Five growing tips were marked with 2 mm diameter cable ties on each marked *Ascophyllum* plant in each replicate (20–25 individuals/replicate). Marked *Ascophyllum* in all replicates were monitored for growth and survival every other week from May to August 1993.

Growth and survival data from the four experiments were analyzed with a three-factor, nested analysis of variance. The data were transformed as necessary to meet assumptions of normality and homogeneity of variance. Treatments consisted of tidal height, density, and shading and were all considered fixed factors. Individual pots (*Mytilus* and *Geukensia* experiments) or individual plants (*Ascophyllum* and *Fucus* experiments) were nested within each tidal height × density × shade replicate. Survival was calculated as the percentage alive (*Mytilus* and *Geukensia* experiments) or percentage still present (*Ascophyllum* and *Fucus* experiments) at the end of the summer. Growth of the two mussel species was calculated as the absolute length of new shell added at the growing margin. Growth of *Ascophyllum* was calculated as the length of the growing tip at the end of the summer, while for *Fucus* it was calculated as percentage change in the length of the sporlings.

The results strongly suggest that group benefits are important determinants of the upper intertidal distribution of sessile rocky shoreline organisms in southern New England. Both mussel species showed a significant density × shading × tidal height interaction on survivorship, revealing that mussel density influenced survivorship differently across tidal heights and with shading (Fig. 5, Table 1). At high-tidal heights, mussel survivorship for both species decreased dramatically when neighbors were removed, but this group benefit was not seen under shades or at lower tidal heights where physical stresses were reduced (Fig. 5).

Similar but less clear patterns were seen with seaweed survivorship (Fig. 5, Table 1). *Ascophyllum* density influenced individual survivorship differently at high- and low-tidal heights (tidal height × density interaction), but this interaction was not affected by shading. At high-tidal heights without shading, survivorship of solitary individuals was half that of individuals in groups, whereas solitary and crowded individuals had similar survivorship at low-tidal heights (Fig. 5). For *Fucus,* the results were less striking, possibly reflecting the fact that small *Fucus* sporlings are vulnerable to herbivory (Lubchenco 1978). Thinning *Fucus* strongly reduced individual survival in unshaded plots at both low- and high-tidal heights, but shading eliminated the survivorship advantages of dense stands (Fig. 5, Table 1). Shading the *Fucus* plots at low-tidal heights was particularly detrimental to marked sporlings either because of reduced light, increased herbivore pressure, or both. Thus, in terms of survivorship, positive group interactions play a prominent role in the persistence at high-tidal heights of at least three of the four species tested.

In terms of growth, both mussel species and *Ascophyllum* showed strong density × shade × tidal height interactions (Fig. 6, Table 2). For each of these species, at the high end of their distributions, individuals grew more with neighbors than when neighbors were removed, but the positive effect of neighbors was eliminated when physical stress was reduced either by shading or at low-tidal heights. Neighbors significantly depressed individual growth in both mussel species at low-tidal heights. This was the only strong competitive effect seen in our density manipulations (Fig. 6).

Of the four species examined, *Fucus* was the only one that did not show strong positive density-dependent growth at high-tidal heights (Fig. 6). With the exception of shading, which strongly reduced its growth, *Fucus* growth was not affected by any of the experimental treatments, suggesting that its growth may be influenced by other variables. *Fucus* appeared to be the only species tested that was influenced by consumers. No evidence of predation was observed on the mussels, which were protected from large predators, and large *Ascophyllum* individuals are thought to be too large to be eaten by most intertidal herbivores (Steneck and Watling 1982). *Fucus* sporlings are known to be vulnerable to grazing snails (Lubchenco 1978, 1980, 1983), and increased periwinkle (*Littorina littorea*) densities under the shades and in dense *Fucus* stands may have acted to eliminate any potential group benefits in these experiments.

Together, our results suggest that the upper intertidal

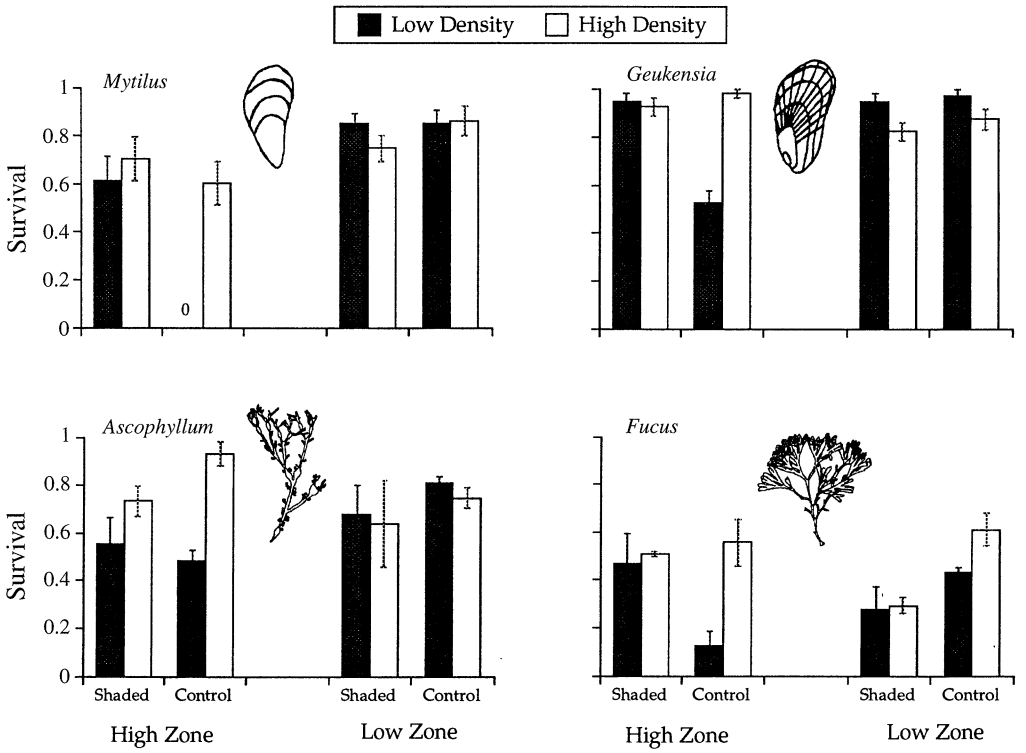

FIG. 5. Results of the density manipulation experiments on the survivorship of: (A) *Mytilus edulis* (n = 10 density × shade treatments), (B) *Geukensia demissa* (n = 10 density × shade treatments), (C) *Ascophyllum nodosum* (n = 3 density × shade treatments), and (D) *Fucus distichus* (n = 3 density × shade treatments). Each bar represents mean values ±1 SE. See Table 1 for statistics summary.

limits of the dominant sessile spaceholders on southern New England rocky shores are strongly influenced by positive interactions or group benefits and that without habitat-ameliorating feedbacks the dominant high-intertidal sessile organisms in these habitats could not survive at the high elevations that they are typically found. Moreover, while our experiments were designed to detect both competitive and positive interactions, group benefits were a more common consequence of crowding at high-tidal heights than negative competitive effects were at lower tidal heights (Figs. 5 and 6). Finally, while all of these examples of group benefits at high-tidal heights are intraspecific examples, since the interactions all appear to be mediated by simple shading and buffering from heat and desiccation stress, there is no reason to suspect that interspecific positive group benefits among high intertidal species are not just as common.

TABLE 1. Summary of ANOVA results on the survivorship of individuals (per replicate, see Fig. 3) in the density manipulations by species. Table entries are P values. All treatment and interaction df = 1.

Treatment	*Mytilus*	*Geukensia*	*Ascophyllum*	*Fucus*
Tidal height (HT)	0.0001	0.018	0.481	0.906
Density (D)	0.003	0.044	0.048	0.007
Shade treatment (S)	0.002	0.004	0.150	0.720
HT × D	0.0002	0.0001	0.008	0.177
HT × S	0.0001	0.0001	0.655	0.003
D × S	0.002	0.0001	0.328	0.024
HT × D × S	0.044	0.0001	0.237	0.192
Error df	71	72	16	16

ARE POSITIVE INTERACTIONS MORE COMMONLY IMPORTANT IN INTERTIDAL SYSTEMS THAN IN OTHER SYSTEMS?

Positive interactions driven by the amelioration of potentially limiting harsh physical conditions appear to be common in intertidal assemblages. This is likely because intertidal habitats are physically rigorous habitats and the major spaceholding organisms in many intertidal habitats are capable of ameliorating potentially limiting stresses. A nonexhaustive list of habitat-ameliorating positive associations in intertidal systems (Table 3) suggests that these sorts of interactions are a pervasive force in intertidal communities.

Are intertidal systems unusual in the role played by positive forces? Probably not. Positive neighbor interactions among vascular plants have long been known to be characteristic of physically harsh environments such as deserts. Recent reviews by Callaway (1995) and Goldberg and Barton (1992) have pointed to a

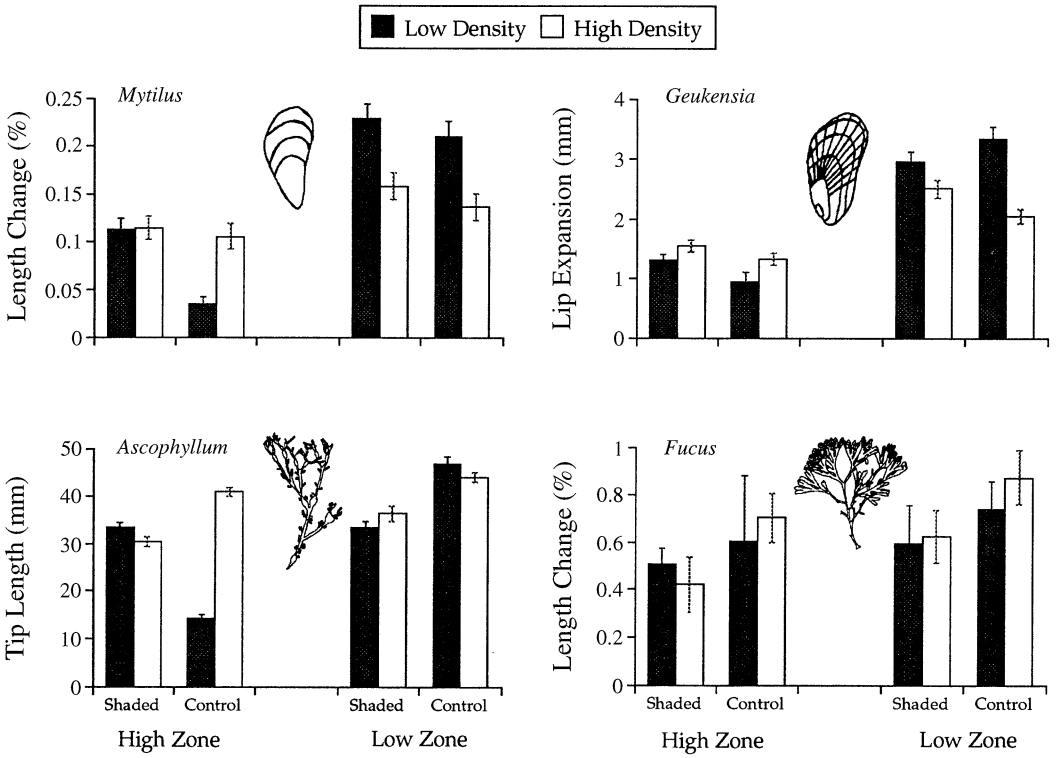

FIG. 6. Results of the density manipulation experiments on the growth of: (A) *Mytilus edulis* (n = 287 individuals), (B) *Geukensia demissa* (n = 260 individuals), (C) *Ascophyllum nodosum* (n = 321 individuals), and (D) *Fucus distichus* (n = 287 individuals). Treatment effects were tested by using the error mean square from the individuals nested within each replicate. If the nested term was nonsignificant, it was dropped from the analysis and all individuals were considered the replicate. Each bar represents mean values ± 1 SE. See Table 2 for statistics summary.

strong relationship between physically stressful environments and the importance of positive plant associations as community-level processes.

Compact physical gradients and the small spatial scale at which shoreline organisms strongly modify their environment simply appear to make intertidal systems particularly amenable to elucidating the role of positive interactions in communities. Gradients in physical factors that affect terrestrial plant communities most conspicuously operate at latitudinal and altitudinal spatial scales so that changes in physical conditions that can influence species interactions probably are best measured in kilometers to hundreds of kilometers rather than meters or less in intertidal habitats. Because of this large difference in scale, effects of changing physical conditions and particularly the causal relationship between physical stress and group benefits is likely more clear in intertidal habitats. Moreover, the spatial scale at which organisms ameliorate harsh physical conditions in intertidal habitats appears to be small in comparison to similar effects in terrestrial habitats. In rocky beach and salt marsh habitats, for example, dominant spaceholders buffer potentially limiting physical factors at spatial scales often less than a meter (Bertness 1989, Bertness et al. 1991, Bertness and Hacker 1994). In contrast, in most terrestrial vascular plant and freshwater communities, habitat-ameliorating positive feedbacks typically appear to occur on much larger spatial scales that are difficult to work with and experimentally manipulate (Wood and Del Moral 1987, Wilson and Agnew 1992, Jones et al. 1994). Forest canopies, for example, clearly play a large role in affecting understory microhabitats, but experimentally examining these effects is typically not practical. There is no reason to believe, however, that positive feedbacks from forest canopies are not as pow-

TABLE 2. Summary of ANOVA results on the growth of individuals (see Fig. 4) in the density manipulation by species. Table entries are P values. All treatment and interaction df = 1.

Treatment	*Mytilus*	*Geukensia*	*Ascophyllum*	*Fucus*
Tidal height (HT)	0.0001	0.0001	0.0001	0.125
Density	0.142	0.002	0.002	0.645
Shade treatment (S)	0.0002	0.327	0.407	0.050
HT × D	0.0001	0.0001	0.003	0.680
HT × S	0.153	0.243	0.0007	0.946
D × S	0.020	0.225	0.0012	0.447
HT × D × S	0.017	0.089	0.0001	0.819
Error df	279	66	18	15

TABLE 3. Stress alleviation by neighbors in shallow-water shoreline habitats.

Habitat	Stress	Mechanism	Reference
Salt marshes	low soil oxygen potentially limits plant growth	dense stands of plants oxygenate soil	Howes et al. 1981, Shat 1984, Hacker and Bertness 1995
		fiddler crabs oxygenate soil	
	high soil salinity potentially limits plant growth	plant cover shades soil, preventing soil salt accumulations	Bertness et al. 1992, Bertness and Shumway 1993
	low soil nutrients limit plant growth	mussel filter feeding and feces deposition increase soil nutrients	Bertness 1984
Mangroves	low soil oxygen potentially limits plant growth	mangroves oxygenate soil	McKee et al. 1988
		fiddler crabs oxygenate mangrove soil	Smith et al. 1991
	low nutrient levels limit plant growth	epiphytic sponges provide nitrogen to plants	Ellison et al. 1996
Soft bottoms	substrate instability limits infaunal populations	seagrasses bind substrate, limiting disturbance	Orth 1977
	low nutrient levels limit seagrass colonization	initial seagrass colonizers add organic material to substrate	Williams 1980
		mussels attached to seagrass enhance production	Valentine and Heck 1993
	low nutrient levels limit deposit feeder growth	deposit feeding enhances food supply	Levinton and Lopez 1977
Rocky shores	heat and desiccation potentially limit sessile invertebrates and/or seaweed growth	dense assemblages buffer group members from stress	Hay 1981, Lively and Raimondi 1987, Bertness 1989, Stephens and Bertness 1991
	wave stress potentially dislodges sessile invertebrates	dense groups buffer members from wave stress	Holbrook et al. 1991, Denny et al. 1985

erful a force at large spatial scales in forests as they appear to be at smaller spatial scales in intertidal communities.

The Biogeography of Positive Interactions in Shoreline Communities

A largely unappreciated aspect of the role played by positive interactions in shoreline communities is the potential importance of biogeography. Just as we have argued that positive forces due to habitat amelioration are important in many physically stressful areas of intertidal habitats, the relative importance of positive forces in intertidal communities may also be spatially predictable at larger, biogeographic spatial scales. In particular, for intertidal communities where neighborhood buffering from heat and desiccation stresses commonly lead to positive associations among sessile organisms, the importance of these types of positive associations may increase with decreasing latitude and increasing solar radiation.

Biogeographic biases, in fact, may have played a role in preventing marine ecologists from appreciating the role of habitat amelioration in structuring high-intertidal communities. Most early experimental work in rocky intertidal communities was done in temperate zone habitats with cool summers, e.g., the north Pacific coast of North America (Paine 1966, 1974, Connell 1970, Dayton 1971) Northern New England (e.g., Menge 1976, Lubchenco 1978), and Northern Europe (e.g., Connell 1961, Kitching and Ebling 1961). All these studies were done at latitudes with mild climates and minimal high-temperature stresses. In contrast, studies from southern New England have found thermal stress to be of increased importance to intertidal organisms (Wethey 1984, Etter 1988) and positive interactions driven by thermal buffering by neighbors to be common (Bertness 1989, Stephens and Bertness 1991). Similarly, on the Pacific coast of North America, group benefits have not been emphasized by studies on the Oregon and Washington coasts (Dayton 1971, Paine 1974, Menge et al. 1994) but at lower latitudes in the Gulf of California, positive interactions due to thermal buffering appear to be common (Lively and Raimondi 1987). We suggest that a biogeographic bias has led to a paradigm of the forces generating pattern in rocky shore communities that has underestimated the importance of positive interactions in these communities.

Climate-driven physical forces may also lead to strong latitudinal gradients in the importance of positive forces in marsh plant communities. As already discussed, positive feedback between plants and soil salinity leads to strong positive associations among plant neighbors in southern New England marshes (Fig. 3), which in turn affects mechanisms of secondary succession, seedling establishment, and the distributions of adult plants. Because these positive associations are

directly dependent on solar radiation, their importance in marsh communities is likely a function of climate and latitude. In northern New England, for example, where soils are not exposed to extended periods of high heat and solar radiation, positive associations from soil shading would not be expected to occur. Conversely, in the southern marshes of the Carolinas and Georgia intense nearly year-round heat and solar radiation typically lead to persistent salt pans in the high intertidal. In these marshes, positive feedbacks between plants and soil salinity may be essential for plant persistence. Latitudinal gradients in feedbacks between physical stresses and sessile organisms may be common in many other systems.

Do Ecologists Need to Understand the Role of Positive Associations in Communities?

We have argued that positive interactions play a major, but largely unappreciated role in shoreline communities and that they are predictable under physically stressful conditions across spatial scales ranging from tidal to latitudinal gradients. We have also suggested that positive forces are probably just as important in terrestrial communities as recently suggested by Wilson and Agnew (1992), Jones et al. (1994, 1997) and Callaway and Walker (1997), but that they typically occur at large spatial scales that are difficult to work with and are therefore easily ignored. How important is it for ecologists to come to terms with the role played by positive interactions in communities? We suggest that understanding the role of positive forces in communities may be critical to resolving a number of pervasive problems in ecology.

Understanding the role of positive feedbacks in natural communities could elucidate linkages between ecosystem and community-level processes. Traditionally, ecosystem ecologists have been concerned with larger scale processes of energy and nutrient flow through ecosystems and have always considered feedbacks to be important for ecosystem function and stability (e.g., Patten and Odum 1981). Community ecologists, in contrast, have traditionally been concerned with pattern generation and species interactions in natural assemblages. These different, but equally valuable perspectives have led to vastly different approaches to ecological questions and virtually different fields of study. Recognizing the interplay between species interactions in communities and large-scale positive feedbacks in energy, nutrients, and/or potentially limiting physical conditions could help unify ecosystem- and community-level approaches to natural systems (see Jones et al. 1994, 1997 and Lawton 1995 for further discussion of this argument).

Understanding the role of positive feedbacks in communities may also be necessary for ecologists to successfully deal with landscape ecology issues. As numerous authors have pointed out (e.g., Wilson and Agnew 1992, Jones et al. 1994) positive feedbacks that operate by habitat amelioration of physical stresses or nutrient regeneration typically occur at larger spatial scales than usually addressed by community ecologists. Since landscape ecology typically tackles large-scale community problems, ecologists may need to incorporate positive feedbacks into their thinking before landscape ecology issues can be solved.

An understanding of the role of positive interactions in communities may also be necessary to predict community responses to global climate change. As already discussed, climate variation may often lead to latitudinal variation in the intensity and relative importance of positive feedbacks in communities. Consequently, predicting climate change effects simply based on current community process and pattern may fail to consider potentially dramatic shifts in the importance of positive feedbacks in systems with changing climate. For example, global warming and increased solar radiation levels could lead to positive feedbacks playing a more important role in intertidal communities than is now the case.

Finally, consideration of the role played by positive interactions in communities could contribute to understanding biodiversity and community stability issues. While ecologists have long been suspicious of connections among positive interactions, species diversity, and system stability (May 1973), recent field and microcosm experiments (Frank and McNaughton 1991, Lawton 1994, Tilman and Downing 1994, Hacker and Bertness 1996) and modeling efforts (DeAngelis et al. 1986, Dobbs 1988, Wilson and Nisbet 1997) have renewed interest in the potential role played by positive interactions in maintaining community diversity and stability. In particular, positive feedbacks among primary spaceholders that provide habitats for other organisms through bioengineering and/or enhancing primary productivity, may, in general, be a potent, but largely underappreciated force in generating and maintaining local species diversity (see Lawton 1994, Hacker and Bertness 1996, and Hacker and Gaines 1997 for further discussion).

We suggest that it is time for ecologists to re-evaluate the general role of positive interactions in natural communities. It is only by understanding their cause and effects that we can hope to better understand how natural systems are structured.

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Literature Cited

Abrams, P. A. 1983. Arguments in favor of higher order interactions. American Naturalist **121**:887–891.

Allee, W. C., A. E. Emerson, O. Park, and K. P. Schmidt.

1949. Principles of animal ecology. W. B. Saunders, New York, New York, USA.

Atsatt, P. R., and D. J. O'Dowd. 1976. Plant defense guilds. Science **193**:24–29.

Bertness, M. D. 1984. Ribbed mussels and the productivity of *Spartina alterniflora* in a New England salt marsh. Ecology **65**:1794–1807.

———. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. Ecology **66**: 1042–1055.

———. 1989. Intraspecific competition and facilitation in a northern acorn barnacle population. Ecology **70**:257–268.

———. 1991*a*. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology **72**:138–148.

———. 1991*b*. Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology **72**:125–137.

———. 1992. The ecology of a New England salt marsh. American Scientist **80**:260–268.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities: a post cold war perspective. Trends in Ecology and Evolution **9**:191–193.

Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England marsh plant community. Ecological Monographs **57**:129–147.

Bertness, M. D., and S. D. Gaines. 1993. Larval dispersal and local adaptation in acorn barnacles. Evolution **47**:316–320.

Bertness, M. D., S. D. Gaines, D. Bermudez, and E. Sanford. 1991. Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series **75**:91–100.

Bertness, M. D., and T. Grosholz. 1985. Population dynamics of the ribbed mussel *Geukensia demissa*: the costs and benefits of a clumped distribution. Oecologia **67**:192–204.

Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. American Naturalist **144**:363–372.

Bertness, M. D., and S. W. Shumway. 1993. Competition and facilitation in marsh plants. American Naturalist **142**: 718–724.

Bertness, M. D., and S. M. Yeh. 1994. Cooperative and competitive interactions in the recruitment of marsh elders. Ecology **75**:2416–2429.

Bianchi, T., and C. G. Jones. 1991. Density-dependent positive feedback between consumers and their resources. Pages 331–339 *in* J. Cole, G. Lovett, and S. Findley, editors. Comparative analysis of ecosystems. Springer-Verlag, New York, New York, USA.

Callaway, R. 1995. Positive interactions among plants. Botanical Review **61**:306–349.

Callaway, R., and L. W. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology **78**:1958–1965.

Carefoot, T. 1977. Pacific seashores. University of Washington Press, Seattle, Washington, USA.

Carpenter, S. F., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634–639.

Chapman, V. J. 1974. Salt marshes and salt deserts of the world. J. Cramer, Lehre, Germany.

Clements, F. E., J. Weaver, and H. Hanson. 1926. Plant competition: an analysis of the development of vegetation. Carnegie Institute, Washington, D.C., USA.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710–723.

———. 1972. The ecology of rocky shores. Annual Review of Ecology and Systematics **3**:169–192.

Connell, J. H. 1970. A predator-prey system in the marine intertidal. Ecological Monographs **40**:49–78.

Connell, J. H., and R. O. Slatyer 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **111**:1119–1144.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs **41**:351–389.

DeAngelis, D. L., V. M. Post, and C. C. Travis. 1986. Positive feedback in natural systems. Springer-Verlag, Berlin, Germany.

Denny M., T. Daniel, and M. A. R. Koehl. 1985. Mechanical limits to size in wave swept organisms. Ecological Monographs **55**:69–102.

Dethier, M. N., and D. O. Duggins. 1984. An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. American Naturalist **124**:205–219.

Dobbs, W. K. 1988. Community structure and selection for positive and negative species interactions. Oikos **53**:387–390.

Ellison, A. M., E. J. Farnsworth, and R. R. Twilly. 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangel. Ecology **77**:2431–2444.

Etter, R. J. 1988. Physiological stress and color polymorphism in the intertidal snail *Nucella lapillus*. Evolution **42**: 660–680.

Frank, D. A., and S. J. McNaughton. 1991. Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. Oikos **62**:360–362.

Garrity, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology **65**:559–574.

Gleason, M. L. 1980. Influence of tidal inundation on internal oxygen supply of *Spartina alterniflora* and *Spartina patens*. Dissertation. University of Virginia, Charlottesville, Virginia, USA.

Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. American Naturalist **139**:771–801.

Goreau, T. F., and N. I. Goreau. 1966. Corals and coral reefs. Scientific American **241**:124–136.

Hacker, S. D., and M. D. Bertness. 1995. Morphological and physiological consequences of a positive plant interaction. Ecology **76**:2165–2175.

Hacker, S. D., and M. D. Bertness. 1996. Trophic consequences of a positive plant interaction. American Naturalist **148**:559–575.

Hacker, S. D., and S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. Ecology **78**:1990–2003.

Hay, M. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology **62**:739–750.

———. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. American Naturalist **128**:617–641.

Holbrook, N., M. Denny, and M. Koehl. 1991. Intertidal trees: consequences of aggregation on properties of sea palms. Journal of Experimental Marine Biology and Ecology **146**:39–67.

Holt, R. 1977. Predation, apparent competition and the structure of prey communities. Theoretical Population Biology **12**:197–229.

Howes, B. L., J. W. Dacey, and D. D. Goehringer. 1986 Factors controlling the growth of *Spartina alterniflora*: feedbacks between aboveground production, sediment ox-

idation, nitrogen and salinity. Journal of Ecology **74**:881–898.

Howes, B. L., R. W. Howarth, J. M. Teal, and I. Valiela. 1981. Oxidation-reduction potentials in salt marshes: spatial patterns and interactions with primary production. Limnology and Oceanography **26**:350–360.

Hunter, A. F., and L. W. Aarssen. 1988. Plants helping plants. BioScience **38**:34–40.

Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, England.

Jackson, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. American Naturalist **111**:743–767.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373–386.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946–1957.

Keddy, P. A. 1990. Why don't ecologists study positive interactions? Bulletin of the Ecological Society of America **71**:101–102.

Kitching, J. A., and F. J. Ebling 1961. The ecology of Lough Ine. XI. The control of algae by *Paracentrotus lividus*. Journal of Animal Ecology **30**:373–383.

Lawton, J. H. 1994. What do species do in ecosystems? Oikos **71**:367–374.

Levine, S. H. 1976. Competitive interactions in ecosystems. American Naturalist **110**:903–910.

Levinton, J. S., and G. R. Lopez. 1977. A model of renewable resources and limitation of deposit-feeding benthic populations. Oecologia **31**:177–190.

Lewis, J. R. 1960. The ecology of rocky shores. English University Press, London, England.

Littler, M. M. D. Littler, and P. R. Taylor. 1995. Selective herbivore increases biomass of its prey: a chiton–coralline reef building association. Ecology **76**:1666–1681.

Lively, C. M., and P. T. Raimondi. 1987. Desiccation, predation, and mussel barnacle interactions in the northern Gulf of California. Oecologia **74**:304–309.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community importance of herbivore food preference and algal competitive abilities. American Naturalist **112**:23–39.

———. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology **61**:333–344.

———. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity and plant escapes during succession. Ecology **64**:1116–1123.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

McKee, K. L., I. Mendelssohn, and M. Hester. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. American Journal of Botany **75**: 1352–1359.

Menge, B. A. 1976. Organization of the New England Rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs **46**: 355–393.

———. 1995. Indirect effects on marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs **65**:21–74.

Menge, B. A., E. Berlow, A. Blanchette, S. Navarrete, and S. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs **64**:249–286.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress. American Naturalist **130**:730–757.

Newell, R. C. 1976. The biology of intertidal organisms. Elsevier, New York, New York, USA.

Northeast Utilities Services Company. 1994. Monitoring the marine environment of Long Island Sound at Millstone Nuclear Power Station. 1993 Annual Report. Waterford, Connecticut, USA.

Odum, E. P. 1969. The strategy of ecosystem development. Science **164**:262–270.

Okamura, B. 1986. Group living and the effects of spatial position in aggregates of *Mytilus edulis*. Oecologia **69**:341–347.

Orth, R. J. 1977. The importance of sediment stability in seagrass communities. Pages 281–300 *in* B. C. Coul, editor. Ecology of marine benthos. University of South Carolina Press, Columbia, South Carolina, USA.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:67–75.

———. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia **15**:93–120.

Paine, R. T. 1984. Ecological determinism in the competition for space. Ecology **65**:1339–1348.

Patten, B. C., and E. P. Odum. 1981. The cybernetic nature of ecosystems. American Naturalist **118**:886–895.

Pennings, S., and R. Callaway. 1991. Salt marsh zonation: the relative importance of competition and physical factors. Ecology **73**:681–690.

Pfister, C. A., and M. Hay. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from different mechanisms. Oecologia **77**:118–129.

Sanford, E., D. Bermudez, M. D. Bertness, and S. D. Gaines. 1994. Flow, food supply and acorn barnacle population dynamics. Marine Ecology Progress Series **104**:49–62.

Shat, H. 1984. A comparative ecophysiological study of the effects of waterlogging and submergence on dune slack plants: growth, survival and mineral nutrition in sand culture experiments. Oecologia **62**:279–286.

Silander, J., and J. Antonivics. 1982. Analysis of interspecific interactions in a coastal plant community—a perturbation approach. Nature **289**:557–560.

Skilleter, G. A. 1994. Refuges from predation and the persistence of estuarine clam populations. Marine Ecology Progress Series **109**:29–42.

Smith, T. J., K. G. Boto, S. D. Frusher, and R. L. Giddins. 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. Estuarine, Coastal and Shelf Science **33**:419–432.

Snow, A., and S. Vince. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. Journal of Ecology **72**:669–684.

Steneck, R. S., and L. Watling 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Marine Biology **68**:299–319.

Stephenson, T. A., and A. Stephenson. 1954. The universal features of zonation between tide-marks on rocky coasts. Journal of Ecology **37**:289–305.

Stephens, E. G., and M. D. Bertness 1991. Mussel facilitation of barnacle survival in a sheltered bay habitat. Journal of Experimental Marine Biology and Ecology **145**:33–48.

Stiven, A. E., and S. A. Gardner. 1992. Population processes in the ribbed mussel *Geukensia demissa* in a North Carolina salt marsh tidal gradient. Journal of Experimental Marine Biology and Ecology **160**:81–102.

Stone, L., and R. S. Weisburd. 1992. Positive feedback in aquatic ecosystems. Trends in Ecology and Evolution **7**: 263–267.

Strauss, S. Y. 1991. Indirect effects in communities: their definition, study and importance. Trends in Ecology and Evolution **6**:206–210.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. Nature **367**:363–365.

Valentine, J. F., and K. L. Heck 1993. Mussels in seagrass meadows: their influence on macroinvertebrate abundance and secondary production in the Gulf of Mexico. Marine Ecology Progress Series **96**:63–74.

Vandermeer, J. 1980. Indirect mutualism: variations on a theme by Stephen Levine. American Naturalist **116**:441–448.

Wethey, D. S. 1984. Geographical limits and local zonation: the barnacles *Semibalanus* and *Chthamalus* in New England. Biological Bulletin **165**:330–341.

Williams, S. L. 1980. Experimental studies of Caribbean seagrass bed development. Ecological Monographs **60**: 449–469.

Wilson, J. B., and A. D. Agnew. 1992. Positive feedback switches in plant communities. Advances in Ecological Research **23**:263–336.

Wilson, W. G., and R. M. Nisbet. 1997. Cooperation and competition along smooth environmental gradients. Ecology **78**:2004–2017.

Witman, J. D. 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. Ecological Monographs **57**:167–187.

Wood, D., and R. Del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mt. Saint Helens. Ecology **68**:780–790.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community—interaction chains and interaction modifications. American Naturalist **141**:71–89.