Oecologia (2000) 122:98–108

John F. Bruno · Coleman W. Kennedy

Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora*

Received: 2 November 1998 / Accepted: 15 July 1999

Abstract Most marine habitats are generated by the presence of habitat-modifying species. However, little is know about many aspects of this process, such as how individual- and population-level traits of habitat modifiers affect their ability to reduce environmental stress and thus facilitate other species. An important habitat modifier in New England is the intertidal grass *Spartina alterniflora* which facilitates the establishment and persistence of cobble beach plant communities by reducing wave-related disturbance. The objectives of this study were to (1) quantify the modification of cobble beach habitats by *S. alterniflora*, (2) determine how this process is related to *S. alterniflora* bed traits, and (3) determine why small patches of *S. alterniflora* generally remain unoccupied by cobble beach plants. Our results demonstrate that *S. alterniflora* substantially reduces flow-related physical disturbance on cobble beaches. Behind *S. alterniflora*, mean flow velocity was reduced by 40–60% and substrate stability was dramatically increased compared to portions of the shoreline not bordered by this species. These comparative results were supported by a *S. alterniflora* shoot removal experiment, which resulted in a 33% increase in average flow velocity and an 85% increase in substrate instability relative to control areas. There was a strong inverse logarithmic relationship between bed length and both average flow velocity and substrate instability behind *S. alterniflora*. Most *S. alterniflora* beds were small and bed length was significantly related to the presence of one or more cobble beach plant species. Only 13% of beds <25 m and 40% of beds 30–40 m in length were occupied, in contrast to an occupancy rate of 87% for beds >40 m long. Seeds of two annual cobble beach species (*Suaeda linearis* and *Salicornia europaea*) were added to plots behind large (>100 m in length) and small *S. alterniflora* (<25 m) beds with and without a substrate stabilization manipulation. Seedlings of both species only emerged and established behind small beds when the substrate was stabilized. These results indicate that smaller *S. alterniflora* patches are usually unoccupied because they do not stabilize the substrate to a degree that meets the establishment requirements of seedlings. Thus, both habitat modification and facilitation by *S. alterniflora* are patch-size dependent. The conditionality of this facilitation appears to generate a pattern of patchy yet predictable population and community distribution at a landscape spatial scale.

Key words Cobble beach · Facilitation · Flow velocity · Habitat modification · *Spartina alterniflora*

Introduction

Biological habitat generation is an important process within both aquatic and terrestrial landscapes (Ginsburg and Lowenstam 1958; Dayton 1972; Jones et al. 1994; Callaway 1995), but appears to be especially common in marine benthos (Bertness and Leonard 1997). Simply through their presence, species that create habitat modify numerous environmental parameters and reduce environmental stress and predation intensity to levels tolerable by other species (Hunter and Aarssen 1988; Bertness and Callaway 1994; Jones et al. 1994). Habitat modifiers can also facilitate (i.e., assist or benefit) dependent species by increasing propagule supply and retention and the availability of limiting resources (Eckman 1983, 1985; Jones et al. 1994). Because they facilitate the establishment and persistence of populations of many other species, these so-called foundation species (Dayton 1972) or keystone modifiers (Wilson and Agnew 1992; Bond 1993) can be responsible for the presence of an entire community. Marine examples include single species of large kelp in temperate kelp forests (Estes and Palmisano 1974; Jackson and Winant 1983; Eckman et al. 1989; Eckman and Duggins 1991) and bed-forming intertidal and subtidal mussels (Suchanek 1979, 1985; Witman 1985; Lohse 1993;

J.F. Bruno (✉) · C.W. Kennedy
Department of Ecology and Evolutionary Biology,
Brown University, Providence, RI 02912, USA
e-mail: john_bruno@brown.edu
Tel.: +1-401-8632619, Fax: +1-401-8632166

Seed 1996) that provide a refuge from predation for hundreds of infaunal species, thereby dramatically increasing local species diversity. In New England rocky intertidal habitats, fucoid algae often facilitate the recruitment and persistence of invertebrates and other algae by reducing thermal stress (Thompson et al. 1996; Leonard 1999; Bertness et al., in press). Sea grasses (Orth 1977; Fonseca et al. 1982; Peterson et al. 1984; Irlandi and Peterson 1991) and tropical reef-building corals (Goreau et al. 1979; Reaka-Kudla 1997) stabilize the substrate, increase habitat heterogeneity, and provide an important predation refuge for hundreds or even thousands of associated species. In fact it is difficult to think of a benthic marine habitat that is not defined by or dependent upon habitat creation by a single or a guild of species.

Despite the importance of foundation species, marine ecologists are just beginning to examine rigorously habitat modification and facilitation (Bertness and Leonard 1997; Bertness et al. 1999). Consequently, many reports of facilitation are largely anecdotal and the details of how this fundamental natural process operates are often quite vague (Bertness and Callaway 1994). In many cases, experimental data on the specific mechanism of facilitation from controlled manipulations are sparse or nonexistent (Callaway 1995). However, identifying the relevant factor that is ameliorated is rarely straightforward because several factors could restrict species distributions to the modified habitat and the importance of each could vary across life history stages as well as among species. Moreover, little is known about how basic individual and population-level traits of modifiers such as size, age, or density affect their ability to reduce environmental stress and thus to facilitate other species. We also have little data on how spatial and temporal variation in ambient stress or disturbance levels interact with modifier attributes to determine the differences between modified and unmodified habitat. Addressing such issues through a combination of comparative descriptive studies and field manipulations can help to advance the study of habitat modification and facilitation from a crude anecdotal narrative to a comprehensive and predictive science (Bertness et al. 1999, in press).

An important habitat modifier in southern New England is the grass *Spartina alterniflora* which facilitates the establishment and persistence of cobble beach plant communities. This intertidal assemblage of annual and perennial forbs is found on estuarine cobble beaches between 1.0–1.5 m above mean low water, behind the upper border of fringing *S. alterniflora* beds (Fig. 1A,B). *S. alterniflora* enables the seedlings of other plant species to emerge and survive in this physically stressful environment by stabilizing the substrate, thereby minimizing the burial of seeds and seedlings (Bruno, in press). As a result of this facilitation, plant population densities and species richness are dramatically increased relative to portions of the shoreline not bordered by *S. alterniflora* (Bruno, in press).

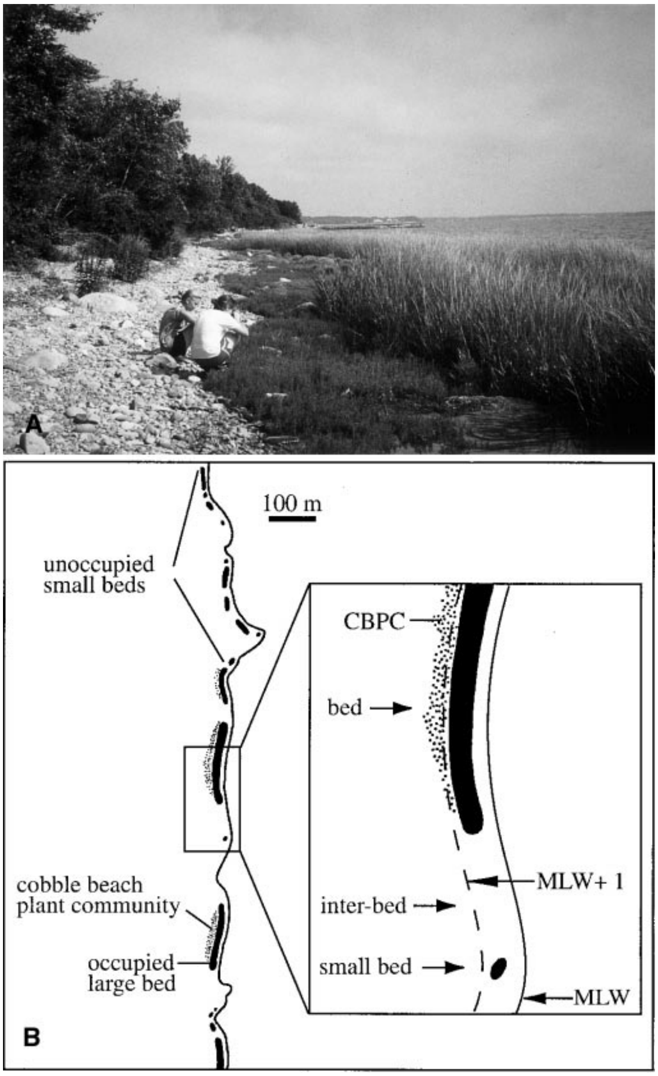

Fig. 1 **A** Photograph of a typical New England cobble beach plant community at the Brown University Haffenreffer Reserve. **B** Diagram of a cobble beach landscape illustrating the spatial arrangement of *Spartina alterniflora* beds, cobble beach plant communities (*CBPC*), and the experimental treatment locations (*MLW* mean low water mark, *MLW+1* 1.0 m above mean low water)

At a landscape scale, *S. alterniflora* beds can be viewed as biologically generated habitat patches that provide refuge from physical disturbance, whereas shoreline locations between patches represent an uninhabitable matrix environment. Interestingly, small patches of *S. alterniflora* (those <25 m in length) are usually unoccupied (i.e., no cobble beach plant species are present behind the bed), whereas larger patches are often occupied by dense populations of up to 11 species. Small beds may remain unoccupied for three reasons. (1) They may be less likely to be colonized due to their size (i.e., a target effect; MacArthur and Wilson 1967) or age as they may be younger than large beds (a temporal target effect). (2) They may be unable to reduce flow and stabilize the substrate sufficiently to facilitate seedling emergence and establishment. (3) Finally, they could be unsuitable habitat due to another attribute related to bed size (e.g., poor soil quality).

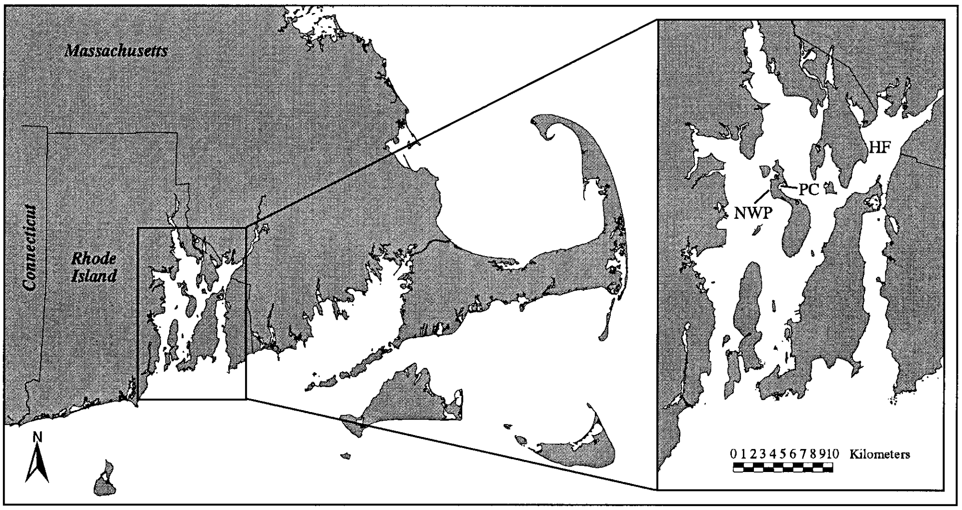

Fig. 2 Map of study sites in Narragansett Bay, R.I. (*HF* Haffenreffer, *NWP* northwest Prudence Island, *PC* Potter Cove)

The purpose of this study was to quantify the modification of cobble beach habitats by *S. alterniflora* and to determine how attributes of *S. alterniflora* patches are related to this process and why small patches generally remain unoccupied. Specifically, we quantified the effects of *S. alterniflora* on flow velocity and substrate stability and examined the effect of patch size on the ability of *S. alterniflora* beds to reduce these measures of wave-related disturbance. We also documented the restriction of cobble beach plant communities to large *S. alterniflora* patches in Narragansett Bay, R.I. Finally, we performed a manipulative seed addition experiment to test three hypotheses that explain why cobble beach plants are not found behind small beds:

Ha1: limited seed supply excludes plants from small beds.
Ha2: substrate instability excludes plants from small beds.
Ha3: other environmental factors exclude plants from small beds.

Materials and methods

Study system

Some representative cobble beach forbs are the annuals *Suaeda linearis* (sea-blite, Chenopodiaceae), *Salicornia europaea* (common glasswort, Chenopodiaceae), and *Spergularia marina* (sand spurrey, Caryophyllaceae), and the perennials *Limonium nashii* (sea-lavender, Plumbaginaceae) and *Salicornia virginica* (woody glasswort, Chenopodiaceae). Some of these species are also abundant in salt marsh habitats in southern New England (e.g., *S. europaea* and *L. nashii*), while others are generally, though not totally, restricted to cobble beaches (e.g., *S. linearis* and *S. marina*) which appears to be their primary habitat. Cobble beach plant species have small seeds (1–3 mm in diameter across the maximum axis) that are usually water dispersed during the fall and winter and can remain buoyant for weeks or even months (Ungar 1987). Although most seeds are released from the parent plant before dispersal, many are also dispersed while still attached to the inflorescence when adult plants are removed from the substrate by wave action.

S. alterniflora is generally considered to be a salt marsh species; however, in portions of southern New England such as Narragansett Bay, R.I., it is equally abundant on cobble beaches where it forms long fringing beds and is usually the only grass species present. Hence, on cobble beaches, halophytic forbs dominate the zone above and behind *S. alterniflora* that is occupied in New England salt marsh and fringing salt marsh habitats by grasses and rushes such as *Spartina patens* and *Juncus gerardi*. Although there is some overlap in species composition between cobble beaches and marshes, these habitats differ in a number of important aspects including the density of forb populations and the environmental factors that affect them. For example, in marshes, the grasses that dominate the substrate generally outcompete forbs for light and nutrients, thus severely limiting the abundance and restricting the distribution of the forbs (Bertness et al. 1992; Chmura et al. 1997). Additionally, salt and fringing marshes are characterized by a stable peat substrate in contrast to the highly unstable gravel and cobble substrate of cobble beaches. Furthermore, the frequency and intensity of wave-related physical disturbance is many times greater on relatively exposed cobble beaches than in salt marshes, which are usually found within protected bays and other low-energy, depositional environments (Adam 1990). Important physical stress factors in marshes including soil waterlogging and salt accumulation on the soil surface (Adam 1990; Bertness 1992) are not likely to be important in cobble beach plant communities because the coarse substrate is well-drained.

Study location

Research was performed in Narragansett Bay, Rhode Island, USA (Fig. 2), a well-mixed estuary with semi-diurnal tides (range 0.8–2.0 m). The shoreline of Narragansett Bay is dominated by beaches made up of unconsolidated, glacially deposited boulders, cobbles, gravel, and sediment. Waves in the middle and upper bay are generated by local winds and boat traffic and rarely exceed 1 m in height. Most measurements and manipulations were performed at the Brown University Haffenreffer Reserve and on Prudence Island in the Narragansett Bay National Estuarine Research Reserve. The exception was the bed trait measurements that were made on *S. alterniflora* beds distributed throughout Narragansett Bay. Each “site” consisted of a 1–3 km linear section of shoreline that contained 3–25 *S. alterniflora* beds. The shoreline at Haffenreffer is 3 km long and was considered to be a single “site,” while the perimeter of Prudence Island is 36 km and thus contains several distinct “sites” (Fig. 2).

Habitat modification

The effect of large (>100 m in length) *S. alterniflora* beds on substrate stability and short- (5 min.) and long-term (10 days) water velocity was initially quantified in a comparative manner by measuring each parameter at two locations: (1) behind *S. alterniflora* beds (bed locations), and (2) on portions of the shore not bordered by a bed (inter-bed locations), but that were at the same tidal height as the corresponding bed locations (Fig. 1B). The bed treatments were located >20 m from one of the two lateral edges of a given *S. alterniflora* patch. This distance was chosen to avoid any "edge effects" (i.e., waves wrapping around the ends of beds) and was based on lateral flow velocity profiles behind patches (J. Bruno, unpublished data). No other factors (e.g., beach slope, cobble size, direction or distance of fetch, water depth) varied between the bed and inter-bed treatment locations.

Long-term flow was measured using plaster cylinders which dissolve at a rate proportional to bulk fluid flux and thus represent an integrated measure of flow velocity at each location (dissolution block technique; Thompson and Glenn 1994). Our dental plaster (calcium sulfate) cylinders were 4 cm in height and 7.5 cm in diameter. Each cylinder was attached to a small piece of galvanized steel mesh (10×10 cm, 0.5 inch mesh size) which was fastened to the substrate with 20-cm nails. The bottom surface and sides were coated with clear polyurethane so that only the top surface could erode. Each cylinder was weighed before and after deployment so that total mass loss could be calculated. Cylinders were deployed for 10 days to bed and inter-bed treatment locations at two tidal elevations: (1) mean low water (MLW), an elevation below *S. alterniflora* beds, at two sites (Haffenreffer and NW Prudence; *n*=15 cylinders/treatment location per site, May 1999), and (2) above beds, at 1.0 m above MLW at each of three sites (Haffenreffer, NW Prudence, and Potter Cove; *n*=12 cylinders/treatment location per site, July 1997). The deployment below beds was to test the hypothesis that ambient flow does not vary between locations on the shoreline with and without *S. alterniflora*. We compared log-transformed total mass loss between bed and inter-bed locations and among sites with a separate two-factor ANOVA for each tidal elevation (fixed factor=location, random factor=site). This and all other analyses were performed with JMP statistical software (SAS Institute, Cary, NC).

A portable acoustic current meter (ADV; Sontek, model ADV-1) was used to measure instantaneous, short-term, three-dimensional flow. Measurements were made 5 cm above the substrate during high tide, at a tidal elevation of 1.0 m above MLW (water depth ≈20 cm, sample duration 5 min, sample frequency 10 Hz). Short-term flow was measured at eight bed and inter-bed locations in a paired sampling design at Haffenreffer, over the course of several days in July 1997. Each bed measurement was made behind a different *S. alterniflora* patch, and each inter-bed measurement was made 10 m from the edge of the corresponding patch; thus for each pair, the measurements were separated by ≈30 m. Only a single probe was available and the two measurements for each pair could not be made simultaneously. However, they were made within 10 min of each other and a hand-held anemometer was used to ensure that ambient wind speed did not vary by more than 10% between each measurement for a given pair. The ADV measures three components of flow: the vector perpendicular to the shore (onshore-offshore flow), the vertical flow vector (vertical flow), and the vector parallel to the shore (longshore flow). In this study system, the onshore-offshore and vertical flow components largely represent the force vectors of waves produced by wind and boats, while the longshore component can include longshore tidal currents, the wave force vector, and longshore currents that are generated when wave angles are not parallel to the shore. Although at 10 Hz the ADV takes 3000 measures for each vector in 5 min, these points are not strictly independent. Therefore, we collapsed each 5-min record into a single mean value and compared these means (after log-transformation) between bed and inter-bed locations with paired *t*-tests (a separate test was performed for each flow component). We also determined the maximum velocity as the highest value measured during each replicate 5-min interval and compared maximum velocities for each vector between locations.

The movements of standardized cobbles were used as measures of substrate stability. Experimental cobbles were randomly chosen from a large pool of cobbles of similar size (≈4 cm in diameter) and shape (≈round) and were randomly assigned to treatment locations. Each cobble was painted and individually numbered so that it could be easily relocated. Thirty cobbles were deployed along transect tapes 1.0 m above MLW at each location. The original position of each cobble was recorded and the position of each transect was marked. After two tidal cycles, the net distance of movement of each experimental cobble was determined by measuring the linear distance between its original and final location. Because the cobbles generally only moved during infrequent periods of high wind (>15–20 km/h) and wave energy (J.F. Bruno, unpublished data), to a large degree, this assay quantifies maximum disturbance events. The cobble movement assay was repeated at ten paired bed and inter-bed locations randomly selected at Haffenreffer and Prudence Island from July 1997 to July 1998. The mean of the net movement of the 30 cobbles at each pair/treatment combination was considered an independent statistical replicate and movement was compared between locations with a single paired *t*-test (i.e., *n*=10).

We performed a *S. alterniflora* removal experiment as an additional test of the null hypothesis that *S. alterniflora* has no effect on flow velocity or substrate stability. In May 1999, we trimmed 5-m-wide sections of *S. alterniflora* patches, from the upper to the lower bed borders, to a height of 1–3 cm with a "weed-whacker" (removal treatment). This height was maintained by recutting as necessary during the measurement of environmental parameters. We did not disturb the peat base beneath the shoots and the natural height of untrimmed *S. alterniflora* was 30–50 cm. A single removal plot was created within each of 12 *S. alterniflora* patches, randomly selected from Haffenreffer and Prudence Island. Each bed also contained a control plot (5 m in width) in which the *S. alterniflora* was not cut (vegetation treatment). The dissolution cylinder (one cylinder/plot) and cobble movement (ten cobbles/plot, the net movements of which were collapsed into a single mean/plot) assays described above were used to quantify average flow velocity and substrate stability directly behind the treatment plots (at 1.0 m above MLW), over a period of 10 days. Both parameters were compared between treatments with separate paired *t*-tests on log-transformed data.

Bed trait measurements

The length of 286 randomly selected *S. alterniflora* patches (from a population of >1000 and >100 km of shoreline within Narragansett Bay) was measured in July 1997. We also searched the substrate behind each of these beds for the presence of any cobble beach plant species. Three additional traits (bed width, and the elevation of the upper and lower borders of the beds) were measured at three locations along each patch, on a randomly selected subset of 100 beds. The position of the upper and lower border of each bed was measured with surveying equipment, and measurements were standardized using a computer-based tide program (Harbor Master).

Effect of bed size on habitat modification

The relationship between patch length and the ability of *S. alterniflora* to reduce wave-related physical disturbance in cobble beach habitats was determined by measuring average flow velocity (dissolution cylinder technique: one cylinder/bed) and substrate stability (cobble movement technique: 20 cobbles/bed) behind beds of varying size. Each assay was repeated at two sites: Haffenreffer (11–16 beds with an easterly exposure) and NW Prudence Island (14–17 beds with a westerly exposure). These sites were chosen because each has numerous *S. alterniflora* beds that are arrayed along a generally linear section of coastline so that fetch and direction of exposure would not be confounded with any patch traits. The dissolution block assay was performed at two tidal heights: (1) MLW, below *S. alterniflora* beds, in May and June 1999, and (2) 1.0 m above MLW, above beds, in June 1998. The below-bed assays were performed to test the null hypothesis that ambient flow is not related to *S. alterniflora* bed size. The cobble movement assay was repeated three times (June 1998, January 1999, and May 1999) behind *S. alterniflora* patches at both sites (at 1.0 m above MLW). The relationships of log bed length with log cylinder dissolution and log (cobble movement+1) were examined with linear regression analysis.

Seed addition experiment

We tested the three hypotheses that potentially explain why small *S. alterniflora* patches are unoccupied by any cobble beach plant species by adding seeds of two species behind (1) large (>100 m), occupied beds, (2) small (<25 m), unoccupied beds, and (3) small, unoccupied beds with a substrate stabilization treatment. Emergence and establishment of seedlings behind small beds without stabilization would suggest that small beds are suitable habitat, but that colonization (seed supply and/or retention) is related to bed size. If seedlings can only establish within the stabilization plots behind small beds, this would indicate that small beds do not stabilize the substrate enough to facilitate seedling emergence. Finally, if seedlings establish behind the large beds but not in either treatment type behind small beds, this would suggest that small beds are unsuitable habitat for some other reason.

The experimental species, *S. europaea* and *S. linearis,* are both annual forbs and two of the most common cobble beach species in Rhode Island (J.F. Bruno, unpublished data). Seeds of both species were collected in the fall of 1997 from a number of sites within Narragansett Bay and were stored in a dry, cool location over the winter. Aliquots of equal mass (≈5000 seeds) were added to the substrate within ten 0.25-m^2 plots of each treatment type in late February 1998. All plots were located in the center of patches, 1 m from the landward patch edge. The experimental *S. alterniflora* beds were located along 3 km of shoreline at Haffenreffer and 20 km of shoreline on Prudence Island. The substrate was stabilized in the stabilization treatment plots by pinning a 0.25-m^2 screen (galvanized steel hardware cloth, 1 cm mesh size) to the substrate with 20-cm nails. This manipulation was designed to stabilize the substrate in a manner that did not affect near-bottom flow velocity or restrict access to potential herbivores. Screens were placed on all 30 plots when the seeds were added, but were removed from the large-bed and small-bed treatment plots just before seedlings began to emerge in early April. Seedlings of both species in each plot were counted on 1 May and 1 June 1998. The frequency of plots containing at least one individual seedling at the first and second census (defined as seedling emergence and establishment, respectively) was compared among treatments with chi-square analysis (a separate test was performed for each species). We focused on these early life history stages because a series of previous manipulations (Bruno, in press) demonstrated that they are the stages at which the lateral distribution of cobble beach plants is restricted.

One potential artifact of our stabilization manipulation is that it could increase the retention of seeds which under natural conditions (as in the control additions) would have been washed away. Therefore, we ensured that each plot contained >100 seeds/species during the seedling emergence period, a conservative number based on previously determined germination, emergence, and establishment rates (Bruno, in press). As a conservative test of this assumption, we made five additional seed addition plots without permanent stabilization between beds and sampled them for the presence of seeds and seedlings within the soil. These five plots were constructed at the same time as the other 30 seed addition plots and their stabilization screens were removed at the same time as those from the unstabilized small- and large-bed plots. These additional plots were sampled for seeds 4 weeks after screen removal and 8 weeks after seed addition. One substrate sample (25×25 cm, 10 cm in depth) was collected from each plot and seeds were separated from the soil using a hydraulic sluice and counted under a dissecting microscope (see methods in Bruno, in press). The number of seedlings within each sample was also recorded.

Results

Habitat modification

The mass loss of dissolution cylinders placed at MLW (below beds) as a measure of ambient flow was not significantly different between treatment locations or sites (Fig. 3A; treatment, $F_{1,1}$=8.13, P>0.05; site, $F_{1,53}$=0.22, P>0.05; treatment×site, $F_{1,53}$=0.18, P>0.05). Retrospective power analysis found that this test had high power to detect a significant treatment effect even when the effect size (delta) was assumed to be relatively small (e.g., power was 0.68 at a delta of 1.5 and 0.90 at a delta of 2.0; alpha=0.05 and sigma=4.60 for both parameter estimates). In contrast to the below-bed assay, the dissolution of cylinders placed at the higher position (1.0 m above MLW) varied greatly between treatment locations (Fig. 3B; treatment, $F_{1,2}$=204.59, P<0.01) but not among sites (site, $F_{2,58}$=1.76, P>0.05; treatment×site, $F_{2,58}$=0.23, P>0.05). Additional planned contrasts using *t*-tests based

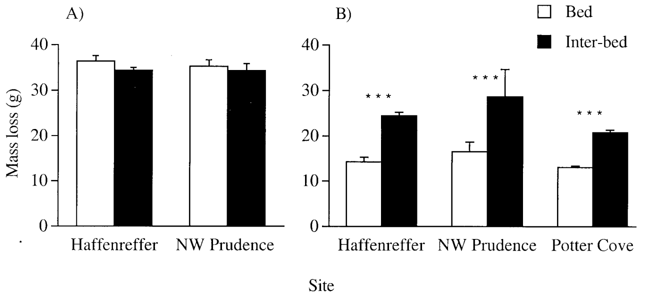

Fig. 3 Mass loss of dissolution cylinders after 10 days as a measure of average flow velocity at bed and inter-bed locations and at two tidal heights. *Bars* represent untransformed means+1 SE. ***P<0.01. **A** MLW (ambient flow; two sites, n=15 cylinders/treatment location per site). **B** At 1.0 m above MLW (modified vs unmodified flow; three sites, n=12 cylinders/treatment location per site)

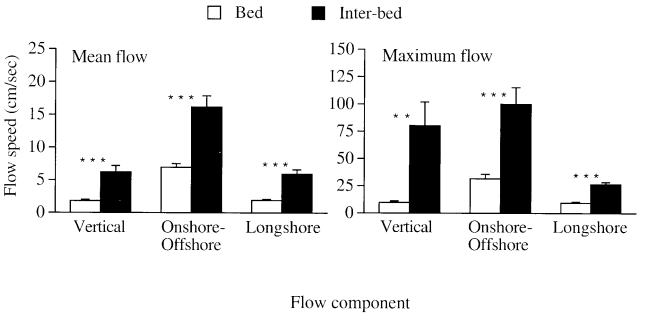

Fig. 4 Mean and maximum flow velocity of three flow components at bed and inter-bed locations. *Bars* represent untransformed means+1 SE (**P<0.01, ***P≤0.001; paired *t*-test, n=8)

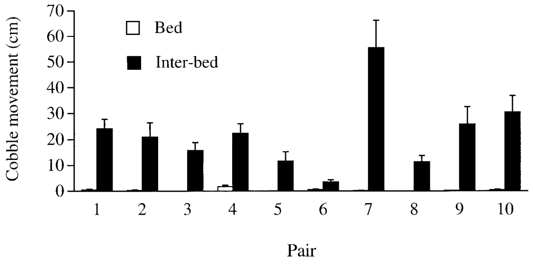

Fig. 5 Net cobble movement over two tidal cycles at bed and inter-bed locations at ten sites. *Bars* represent untransformed means+1 SE. n=30 cobbles/site

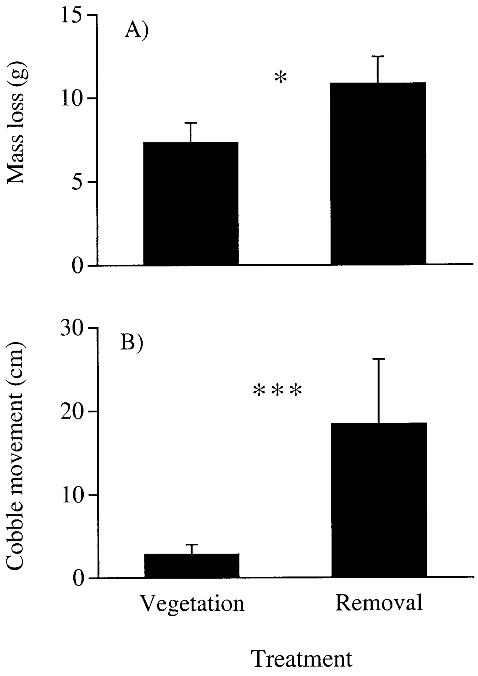

Fig. 6 Results of the *S. alterniflora* removal experiment. *Bars* represent untransformed means+1 SE (*$P<0.05$, ***$P \leq 0.001$; paired t-test, n=12). **A** Mass loss of dissolution cylinders. **B** Net cobble movement, over a period of 10 days in the vegetation and removal treatment plots

on the least-square means of the treatment effect found that mass loss was significantly greater at inter-bed than bed locations at all three sites (all $P<0.001$).

The mean and maximum velocities of all three water flow components measured with the ADV were significantly greater at inter-bed than at bed locations (Fig. 4; mean vertical flow, t=5.51, $P \leq 0.001$; mean onshore-offshore flow, t=7.96, $P<0.0001$; mean longshore flow, t=8.48, $P<0.0001$; max. vertical flow, t=4.47, $P<0.01$; max. onshore-offshore flow t=5.23, $P \leq 0.001$; max. longshore flow, t=8.07, $P<0.0001$; all df=7). Cobble movement was much greater at inter-bed locations than behind *S. alterniflora* beds (Fig. 5; t=11.42, df=9, $P<0.0001$). In the bed removal experiment, cylinder dissolution (Fig. 6A; t=2.47, df=11, $P<0.05$) and cobble movement (Fig. 6B; t=4.99, df=11, $P<0.001$) were both significantly greater in removal than in vegetation plots.

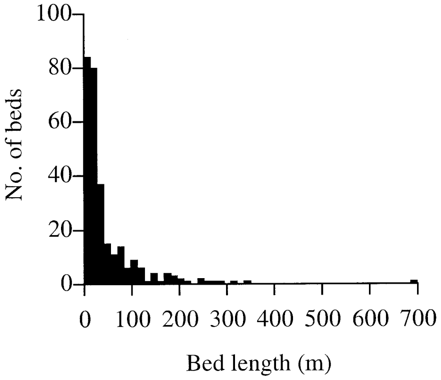

Fig. 7 Frequency distribution of *S. alterniflora* bed lengths in Narragansett Bay, R.I. (n=286)

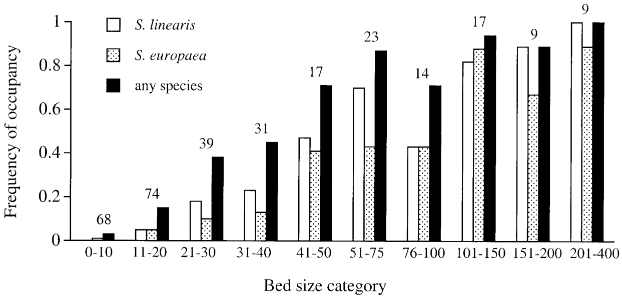

Fig. 8 Frequency of occupancy (presence of at least one adult individual) by *Suaeda linearis, Salicornia europaea* or any cobble beach plant species for different *S. alterniflora* bed size classes. Data are from 286 randomly sampled *S. alterniflora* beds in Narragansett Bay, R.I. Values above bars are sample sizes for each bed size category

Bed trait measurements

The distribution of *S. alterniflora* patch lengths was highly negatively skewed (Fig. 7) as most beds were <20 m in length. Patch length was significantly related to the presence of one or more cobble beach plant species, smaller beds being much less likely to be occupied than larger beds (Fig. 8; logistic regression; χ^2=50.45, $P<0.0001$). Although 70% of the 286 sampled patches were ≤40 m long, only 20% of these small beds were occupied and only 13% of beds <25 m were occupied. These results contrast with an occupancy rate of 87% for patches >40 m. The four measured beds traits were quite variable and were inter-correlated (Tables 1, 2). All pairwise comparisons were statistically significant (Pearson product-moment correlation analysis, $P<0.05$) except for the correlation between length and the height of the upper border. However, this correlation was nearly significant (R=0.302). In general, longer patches tended to be wider, their seaward borders extended further into the water, and their landward borders extended higher up the beach.

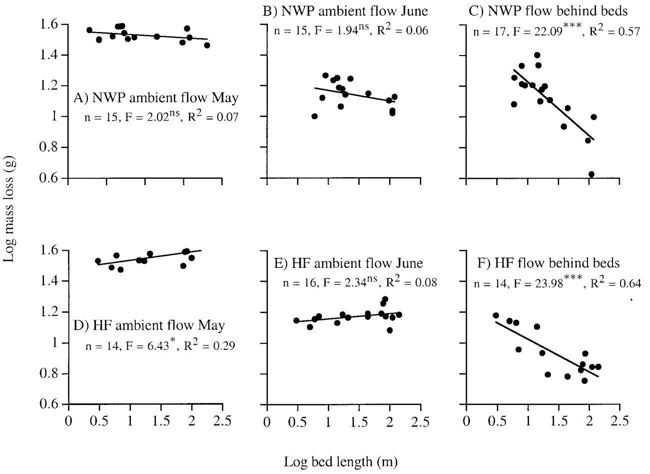

Fig. 9 Linear relationships between the length of *S. alterniflora* beds and the mass loss of dissolution cylinders at two large sites in Narragansett Bay, RI (*NWP* NW Prudence Island, *HF* Haffenreffer). Measurements were made at two tidal elevations: at MLW, below beds, as a measure of ambient flow (**A,B,D,E**) and at 1.0 m above MLW, behind beds, as a measure of the extent of flow modification (**C,F**) (R^2=adjusted R^2; *$P<0.05$, ***$P \leq 0.001$, *ns* not significant)

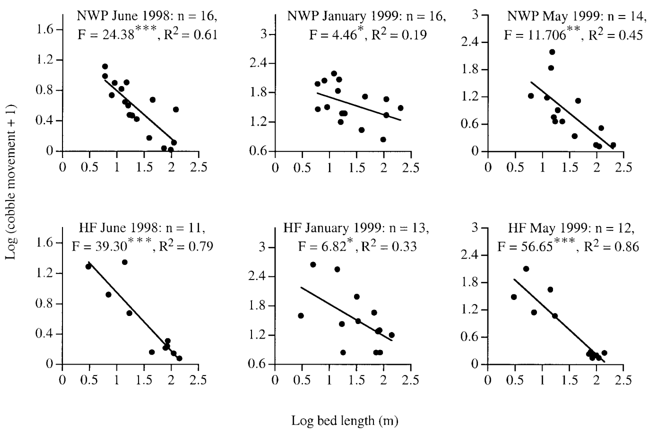

Fig. 10 Linear relationships between the length of *S. alterniflora* beds and substrate stability (net cobble movement) behind beds (at 1.0 m above MLW) at two sites in Narragansett Bay, R.I. (*NWP* NW Prudence Island, *HF* Haffenreffer). Note difference in scales of *y*-axis (R^2=adjusted R^2; *$P<0.05$, **$P<0.01$, ***$P \leq 0.001$)

Table 1 Traits of *S. alterniflora* beds on cobble beaches in Narragansett Bay, R.I. (*MLW* mean low water)

Trait	*n*	Mean	SD	Range
Length (m)	286	47.5	68.7	3–688
Width (m)	100	5.9	2.3	2.0–11.7
Upper border (m above MLW)	100	0.97	0.22	0.23–1.35
Lower border (m above MLW)	100	0.47	0.19	0.09–0.97

Table 2 Matrix of Pearson product-moment correlations among four measured *S. alterniflora* bed traits. All are significant at $P<0.05$ except for the bed length-upper border correlation. n=90

Trait	Length	Width	Upper border
Width	0.498		
Upper border	0.302	0.378	
Lower border	–0.329	–0.368	0.450

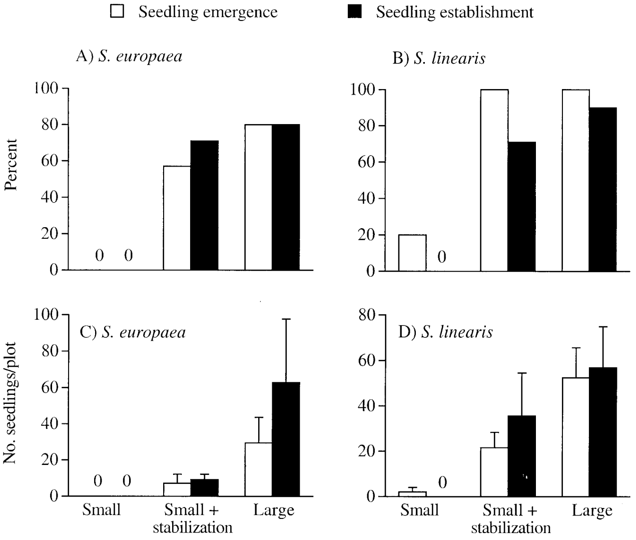

Fig. 11 Emergence and establishment of *S. europaea* (**A,C**) and *S. linearis* (**B,D**) seedlings within each type of treatment plot. Bars are the frequency of the plots of each treatment that contained one or more seedlings (**A,B**) or represent untransformed means (+1 SE) of seedling abundances (**C,D**)

Effect of bed size on habitat modification

At NW Prudence there was no significant linear relationship between mass loss of cylinders placed below patches (as a measure of ambient flow) and bed length for either assay (Fig. 9A,B). At Haffenreffer in May 1999, below-bed cylinder dissolution was significantly positively related to patch length, indicating that ambient flow was higher below longer beds (Fig. 9D). Although, the results of the second Haffenreffer ambient flow assay in June were similar, this regression was not significant (Fig. 9E). In contrast to the four ambient flow assays below beds, behind *S. alterniflora*, there was a highly significant inverse relationship between patch length and average flow (Fig. 9C,F). There was also a strong inverse logarithmic relationship between patch length and cobble movement at both sites each time this assay was performed (Fig. 10).

Seed addition experiment

Three of the ten stabilization plots were destroyed by a storm in March. *S. europaea* and *S. linearis* seedlings emerged and established in most of the large-bed and stabilization treatment plots (Fig. 11A,B). In contrast, *S. europaea* seedlings did not emerge in any of the ten small-bed plots without stabilization and *S. linearis* seedlings emerged in only two of these plots. At the second census (1 June), there were no seedlings in any of the small-bed plots. Frequencies of seedling emergence and seedling establishment, defined as the frequency of plots that contained at least one seedling at the 1 May and 1 June censuses, respectively, varied significantly among the three treatments (emergence: *S. europaea*, $\chi^2=13.58$, $P<0.01$; *S. linearis*, $\chi^2=19.33$, $P<0.0001$; establishment: *S. europaea*, $\chi^2=14.87$, $P<0.001$; *S. linearis*, $\chi^2=23.27$, $P<0.0001$). Additional planned comparisons demonstrated that for both species, frequencies of emergence and establishment varied significantly between the small-bed and the other two treatments (chi-square analysis, all $P<0.05$), but not between the large-bed and small-bed+stabilization treatments (all $P>0.05$). The number of seedlings that emerged and became established did not differ significantly between the large-bed and small-bed+stabilization treatments (Fig. 11C,D; emergence: *S. europaea*, $t=1.58$; *S. linearis*, $t=1.81$; establishment: *S. europaea*, $t=1.37$; *S. linearis*, $t=1.18$; all $P>0.05$, $df=15$). The small-bed plots were not included in analyses of seedling density because only two replicates of this treatment contained any seedlings. A substantial number of seeds and seedlings were found in the five extra seed addition plots (*S. linearis* seeds=1144±640; *S. europaea* seeds=2896±1,200; combined seedlings =132±70.4; mean number/plot±1 SE).

Discussion

Our results indicate that beds of *Spartina alterniflora* can modify estuarine cobble beaches by substantially reducing wave-related physical disturbance. This habitat modification was mediated by patch size: flow velocity and substrate instability behind beds were inversely related to bed length. In addition, the results of the seed addition experiment suggest that substrate instability prevents seedlings of cobble beach forbs from emerging and surviving behind small *S. alterniflora* beds. This in turn appears to generate a pattern of patchy yet predictable population and community distribution at a landscape spatial scale.

We measured three distinct parameters in a comparative manner at locations of the shoreline with and without *S. alterniflora* beds. The dissolution cylinder technique provided an indirect, yet sensitive and integrated measure of flow velocity. The dissolution of cylinders placed below beds did not vary significantly between treatment locations. Furthermore, retrospective power analysis indicated that there was ample statistical power to detect even relatively small (i.e., 1.5–2.0 g or 4–6%) differences in net mass loss between treatment locations. Moreover, there was a slight, but nonsignificant trend for ambient flow to be higher in front of beds than at the low inter-bed locations. Therefore, at our study sites, *S. alterniflora* patches were not positioned at locations of low ambient flow; had they been so, this would have confounded the interpretation of our comparative measurements. In general, average ambient flow varied little within or between Haffenreffer and NW Prudence, which is not surprising since these sites were specifically chosen to minimize the potentially confounding effect of variable ambient flow. In contrast to the results of the ambient flow assay, at the higher tidal elevation (i.e., at 1.0 m above MLW), average flow velocity was significantly greater between than behind beds. These results suggest that, on average, *S. alterniflora* reduces mean flow by ≈40% (range of flow reduction among sites: 37–44%). This is roughly concordant with our shorter-term, yet more precise measurements of flow velocity using an ADV, as the mean velocity of all three flow components was 50–60% lower behind than between patches. The difference in maximum flow between bed and inter-bed locations was somewhat greater, and for some pairs, the difference was more than an order of magnitude. Maximum onshore-offshore velocity between patches was often greater than 100 cm/s. However, behind *S. alterniflora*, the maximum velocity was usually below 35 cm/s for the onshore-offshore flow component and did not exceed 20 cm/s for the other two components.

We utilized the cobble movement assay as a measure of relative substrate stability, and found the substrate to be substantially more stable behind than between *S. alterniflora* patches. When this assay was performed on very windy days (wind speed>40 km/h), most of the inter-bed cobbles were dispersed so far that they could not be relocated. Even on such days, however, the bed cobbles generally moved <3 cm, suggesting that *S. alterniflora* greatly increases the stability of the substrate across a range of flow conditions. Although mean flow only varied by ≈40–60% between treatment locations, cobble movement varied by more than an order of magnitude at most sampled sites. This could be due to the non-linear scaling of mean and maximum flow velocities (Gaines and Denny 1993) or to thresholds in the velocity necessary to dislodge and move cobbles of the size used in our assay.

The results of our comparative measurements are corroborated by the *S. alterniflora* removal experiment. Shoot removal resulted in a 33% increase in average flow velocity and an 85% increase in substrate instability in comparison to control areas. Because a small portion of the aboveground shoots and all of the peat base beneath were not removed, the manipulation was not a complete patch removal and the removal treatments are not the equivalent of natural inter-bed locations. This is presumably why differences in flow and substrate stability between the removal and vegetation treatment plots were not as great as those between locations with and without *S. alterniflora*. The results of this manipulation also indicate that the flexible grass shoots and the peat base beneath them (which can extend 10–200 cm above the substrate) act synergistically to reduce levels of physical disturbance. The three trials of the cobble movement assay performed in the winter (after most of the shoot tissue had senesced and was removed by wave action; Fig. 5, pairs 8–10; Fig. 10) also support this conclusion.

When considered together, our comparative and experimental results strongly indicate that the presence of *S. alterniflora* is responsible for the measured reduction of physical disturbance behind beds. This interpretation is supported by numerous other studies that have demonstrated the large effect that aquatic macrophytes including freshwater angiosperms (Madsen and Warncke 1983), marine grasses (Orth 1977; Fonseca et al. 1982; Peterson et al. 1984; Ward et al. 1984), and overstory (Jackson and Winant 1983) and understory (Eckman et al. 1989) kelps can have on characteristics of the local flow environment. Additionally, *S. alterniflora* performs a similar function in salt marsh habitats by reducing flow velocity and damping wave energy (Knutson et al. 1982; Leonard and Luther 1995). In general, the array of vertical, flexible tube-like structures created by macrophytes can reduce local flow velocity and sheer force at the fluid-substrate interface by absorbing a large portion of fluid momentum (Eckman 1987). This in turn can reduce substrate particle size and can increase substrate stability (Ginsburg and Lowenstam 1958; Orth 1977), sedimentation rates (Ward et al. 1984; Eckman et al. 1989; Eckman and Duggins 1991), and the quantity of organic matter and nutrients in the substrate (Ginsburg and Lowenstam 1958). However, characteristics of the structures generated by macrophytes largely mediate the effect that these and other habitat-modifying organisms have on the environment (Peterson 1982; Leonard and Luther 1995). For example, when the density of sea grasses (Fonseca et al. 1982), subtidal kelp (Jackson and Winant 1983), and intertidal grasses including *S. alterniflora* (Gleason et al. 1979; Leonard and Luther 1995) is higher, flow reduction is usually greater (Eckman et al. 1981; Eckman 1983). This in turn can have cascading effects on other environmental parameters (Gleason et al. 1979), the fitness and population densities of dependent organisms (Peterson 1982; Eckman 1983, 1987) and ultimately on community composition (Orth 1977).

In this study, we found that smaller *S. alterniflora* patches did not reduce average water velocity or stabilize the substrate to the same degree as larger patches. For both the dissolution block assay and all three cobble movement assays above beds, there was a strong negative logarithmic relationship between bed length and physical disturbance. However, not surprisingly, the length-movement relationship was the weakest (though still significant) in January when a majority of above-peat biomass of *S. alterniflora* has naturally senesced. Our measurements of ambient flow below patches during both months and at both sites indicate that ambient flow is not negatively related to bed size. In fact, at Haffenreffer, there was a significant *positive* relationship between patch length and ambient flow. Waves refract around the ends of patches at high tide (J.F. Bruno, personal observation) and substrate stability increases with distance from the ends toward the center of patches (J.F. Bruno, unpublished data) suggesting that the relationship between patch length and substrate stability could be due to edge effects (Madsen and Warncke 1983; Leonard and Luther 1995). However, bed length was significantly correlated with width and the height of seaward border, and nearly significantly related to the height of the landward border. These as well as other traits such as shoot density and morphology (Leonard and Luther 1995) might also affect flow velocity and substrate instability. Thus it is likely that the multicharacter changes that take place as beds grow enable them to further reduce these measures of wave-related disturbance.

The bed-size specific habitat modification we documented apparently generates predictable species distributional patterns at spatial scales of tens to hundreds of kilometers. Most beds in Narragansett Bay, R.I., were small (<25 m in length) and were not occupied by any plant species. The results of the seed addition experiment suggest that small beds are usually unoccupied because they do not stabilize the cobble substrate to a degree that meets the establishment requirements of seedlings of cobble beach plants. Seedlings of both experimental species were able to emerge and become established behind small beds only when the substrate was artificially stabilized. Overall frequencies of emergence and establishment did not differ between the small-bed+stabilization plots and the large-bed plots, although there was a nonsignificant trend for seedling densities to be higher behind large beds.

The inability of seedlings to emerge behind small beds (to which large numbers of seeds were added and evidently retained) without stabilization suggests that seed supply is not a factor restricting adult plants from small beds. A previous seed sampling study indicated that seeds arrive in high numbers in locations on the shoreline where large *S. alterniflora* patches or populations of cobble beach plants are not present (Bruno, in press). For example, natural *S. linearis* seed supply between patches at Haffenreffer was estimated to be 253 seeds/m^2. Additionally, relatively high numbers of forb seedlings (range among three sites 105–185/m^2) were found buried below the substrate surface between beds during the period when seedlings were emerging behind beds (Bruno, in press). If the seeds of cobble beach plants are able to arrive, persist, and germinate between patches, it seems highly likely that they can also do so behind small beds where flow velocity and substrate instability are relatively lower.

It is plausible that an artifact of the stabilization manipulation was an effect on soil quality, which could have contributed to the higher emergence and establishment rates in the stabilization plots compared to the unstabilized small-bed plots. However, this is unlikely for several reasons. First, measurements of average water velocity 1 cm above the surface of identical stabilization screens indicated that this manipulation had no detectable effect on near-bottom flow (Bruno, in press). Consequently, it is unlikely that sedimentation, and hence soil quality, was affected by the stabilization manipulation. Second, the substrate in all three treatments was originally stabilized and the screens were not removed from the unstabilized small- and large-bed treatments until less than 2 weeks before seedlings began to emerge. This was done to further ensure that there was not a soil quality artifact. Third, in a series of greenhouse experiments, seeds of *S. linearis* and other cobble beach plants added to soil collected between beds and behind small beds, produce adults plants equal in fitness to those grown in soil from large beds (Bruno, in press; J.F. Bruno, unpublished data). This result suggests that the lateral distribution of cobble beach plants is not limited by soil quality.

In Narragansett Bay, there appears to be a minimum threshold of critical *S. alterniflora* bed length of approximately 40–50 m for predictable occupancy by at least one cobble beach plant species. However, this value undoubtedly is context specific, and likely increases with ambient levels of wave-related physical disturbance. Even when this minimum size has been exceeded, patch size could still have a significant impact on population dynamics and community structure. For example, 50% of the variance in plant diversity among occupied beds is explained by patch length and the rarest cobble beach plant species are only found behind the longest beds (J.F. Bruno, unpublished data). If seed supply and retention are related to bed length, then rates of colonization should increase with patch size which could in turn affect patterns of local species diversity and large-scale abundance. Moreover, population sizes appear to be directly related to bed length (J.F. Bruno, unpublished data), and hence local extinction rates are probably lower behind larger *S. alterniflora* patches. However, it is also possible that species-specific stabilization requirements restrict the establishment of rare species to the largest beds. Whatever the mechanism, *S. alterniflora* patch size is clearly an important parameter that needs to be taken into account to understand landscape-scale patterns in cobble beach plant communities.

The presence of habitat-forming species is crucial to habitat preservation (Caughley and Gunn 1996). However, simply protecting a habitat modifier may not be sufficient if its ability to facilitate associated species is strongly dependent on its age, size, population density, or other trait(s). This relationship becomes even more complex if such trait-dependent facilitation is also species specific or is affected by spatial or temporal variation in ambient stress levels. In light of these potential complexities, we advocate a more comprehensive approach to studying the role of habitat modifiers that considers the conditionality of facilitative interactions (Bertness et al. 1999). Such investigations will provide critical information that can form the foundation of an informed, whole-habitat approach to the preservation of marine communities.

Acknowledgements We thank M. Bertness, N. Emery, A. Melendy, D. Morse, G. Polis, T. Rand, G. Trussell, and J. Witman for their comments on earlier drafts of this manuscript and also for their general encouragement and S. Grace and R. Tavani for their help in the field. A. Beck, the director of the Narragansett Bay National Estuarine Research Reserve, provided logistic support and access to our Prudence Island field sites. This research was funded in part by a National Oceanic and Atmospheric Administration/Office of Ocean and Coastal Resource Management graduate research fellowship to JFB (No. NA77OR0218), a National Science Foundation dissertation improvement award to JFB (No. DEB98-01422), the Andrew W. Mellon Foundation, and the Quebec-Labrador Foundation's Atlantic Center for the Environment.

References

Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge, UK

Bertness MD (1992) The ecology of a New England salt marsh. Am Sci 80:260–268

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989

Bertness MD, Gough L, Shumway SW (1992) Salt tolerances and the distribution of fugitive salt marsh plants. Ecology 73: 1842–1851

Bertness MD, Leonard GH, Levine JM, Bruno JF (1999) Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. Oecologia 120:446–450

Bertness MD, Leonard GH, Levine JM, Schmidt PR, Ingraham AO (in press) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80

Bond WJ (1993) Keystone species. In: Schulze ED, Mooney HA (eds) Ecosystem function and biodiversity. Springer, Berlin Heidelberg New York, pp 237–253

Bruno JF (in press) Whole-community facilitation through substrate stabilization by the intertidal grass *Spartina alterniflora*. Ecology 81

Callaway RM (1995) Positive interactions among plants. Bot Rev 61:306–349

Caughley G, Gunn A (1996) Conservation biology in theory and practice. Blackwell, Cambridge, UK

Chmura GL, Chase P, Bercovitch J (1997) Climatic controls of the middle marsh zone in the Bay of Fundy. Estuaries 20:689–699

Dayton PK (1972) Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica. In: Parker BC (ed) Proceedings of the colloquium on conservation problems in Antarctica. Allen, Lawrence, Kans, pp 81–95

Eckman JE (1983) Hydrodynamic processes affecting benthic recruitment. Limnol Oceangr 28:241–257

Eckman JE (1985) Flow disruption by an animal-tube mimic affects sediment bacterial colonization. J Mar Res 43:419–435

Eckman JE (1987) The role of hydrodynamics in recruitment, growth, and survival of *Agropecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. J Exp Mar Biol Ecol 106:165–191

Eckman JE, Duggins DO (1991) Life and death beneath macrophyte canopies: effects of understory kelps on growth rates and survival of marine, benthic suspension feeders. Oecologia 87:473–487

Eckman JE, Nowell ARM, Jumars PA (1981) Sediment destabilization by animal tubes. J Mar Res 39:365–374

Eckman JE, Duggins DO, Sewall AT (1989) Ecology of understory kelp environments. I. Effects of kelps on flow and particle transport near the bottom. J Exp Mar Biol Ecol 129:173–187

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060

Fonseca MS, Fisher JS, Zieman JC, Thayer GW (1982) Influence of the seagrass, *Zostera marina* L., on current flow. Estuarine Coastal Shelf Sci 15:351–364

Gaines SD, Denny MW (1993) The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. Ecology 74: 1677–1692

Ginsburg RN, Lowenstam HA (1958) The influence of marine bottom communities on the depositional environment of sediments. J Geol 66:310–318

Gleason ML, Elmer DA, Pien NC, Fisher JS (1979) Effects of stem density upon sediment retention by salt marsh cord grass, *Spartina alterniflora* Loisel. Estuaries 2:271–273

Goreau TF, Goreau NI, Goreau TF (1979) Corals and coral reefs. Sci Am 241:124–136

Hunter AF, Aarssen LW (1988) Plants helping plants. BioScience 38:34–40

Irlandi EA, Peterson CH (1991) Modification of an animal habitat by large plants: mechanisms by which seagrasses influence clam growth. Oecologia 87:307–318

Jackson GA, Winant CD (1983) Effects of a kelp forest on coastal currents. Cont Shelf Res 2:75-80

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Knutson PL, Brochu RA, Seelig WN, Inskeep M (1982) Wave damping in *Spartina alterniflora* marshes. Wetlands 2:87–104

Leonard GH (1999) Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles. Mar Ecol Prog Ser 178:241–249

Leonard LA, Luther ME (1995) Flow hydrodynamics in tidal marsh canopies. Limnol Oceanogr 40:1474–1484

Lohse DP (1993) The importance of secondary substratum in a rocky intertidal community. J Exp Mar Biol Ecol 166:1–17

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

Madsen TV, Warncke E (1983) Velocities of currents around and within submerged aquatic vegetation. Arch Hydrobiol 97:389–394

Orth RJ (1977) The importance of sediment stability in seagrass communities. In: Coul BC (ed) Ecology of marine benthos. University of South Carolina Press, Columbia, pp 281–300

Peterson CH (1982) Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Mar Biol 66:159–170

Peterson CH, Summerson HC, Duncan PB (1984) The influence of seagrass cover on population structure and individual growth of a suspension-feeding bivalve, *Mercenaria mercenaria*. J Mar Res 42:123–138

Reaka-Kudla M (1997) The global biodiversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla M, Wilson DE, Wilson EO (eds) Biodiversity II. Henry, Washington, DC, pp 83–108

Seed R (1996) Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. J Mar Biol Assoc UK 76:203–210

Suchanek TH (1979) The *Mytilus californianus* community: studies on the composition, structure, organization, and dynamics of a mussel bed. PhD thesis, University of Washington, Seattle

Suchanek TH (1985) Mussels and their role in structuring rocky shore communities. In: Moore PG, Seed R (eds) The ecology of rocky coasts. Hodder Stoughton, London, pp 70–96

Thompson RC, Wilson BJ, Tobin ML, Hill AS, Hawkins SJ (1996) Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. J Exp Mar Biol Ecol 202:73–84

Thompson TL, Glen EP (1994) Plaster standards to measure water motion. Limnol Oceanogr 39:1768–1779

Ungar IA (1987) Population ecology of halophyte seeds. Bot Rev 53:301–334

Ward LG, Kemp WM, Boynton WR (1984) The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. Mar Geol 59:85–103

Wilson JB, Agnew ADQ (1992) Positive feedback switches in plant communities. Adv Ecol Res 23:263–336

Witman JD (1985) Refuges, biological disturbance, and rocky subtidal community structure in New England. Ecol Monogr 55:421–445