



Patch Size Effects on Marsh Plant Secondary Succession Mechanisms

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eters y_i , from which it follows that invertebrates would be more likely than vertebrate ectotherms, which would be more likely than endotherms, to be involved in food chain chaos; and (b) certain ranges of values of the mass ratios m_p/m_C and m_C/m_R , which affect the growth of oscillation magnitude in ways that are simple but fairly lengthy to describe explicitly (but see Yodzis and Innes [1992] for a complete discussion).

Chaos in food chains (and, surely, in other whole-system models as well) ought to be quite common when the resource productivity is sufficiently high. The obvious question, how high is sufficiently high, is particularly difficult to answer in this context, for the appropriate measure of resource carrying capacity is relative to the half saturation density of consumers in the system. There are few data available on this point, but one would expect a great deal of variation among taxa. Functional responses under field conditions, while difficult to measure, are vital for theoretical understanding.

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PATCH SIZE EFFECTS ON MARSH PLANT SECONDARY SUCCESSION MECHANISMS

Scott W. Shumway¹ and Mark D. Bertness²

The response of communities to natural disturbance has historically been of interest to ecologists (Clements 1916) and has recently received renewed attention (Pickett and White 1985). Natural disturbances are ubiquitous in nature and the frequency, intensity, and spatial scale of disturbance can greatly affect the species composition, diversity, and organization of communities. In densely packed environments such as salt marshes, old fields, and rocky intertidal and subtidal habitats where 100% of available substrate is often

occupied, disturbance releases valuable resources (space, light, nutrients), allowing expansion by clonal species and the opportunity for recruitment by fugitive species (Bazzaz 1979, Sousa 1984, Connell and Keough 1985, Bertness et al. 1992). Successional mechanisms may be influenced by competition, predation, and environmental conditions (Connell and Slatyer 1977). Moreover, the Clementsian facilitation model of succession has recently been revived by experimental studies. These studies suggest that facilitation is associated with physically stressful environments that must be modified by pioneer species before competitive dominants are able to colonize (Wood and del Moral 1987, Bertness 1991, Bertness and Shumway 1993).

New England salt marshes are physically stressful communities inhabited by a small number of stress-tolerant halophytes. These communities are subject to annual disturbance by the tidal deposition of plant debris. If this debris (wrack) remains in place it can smother underlying vegetation and create bare patches ranging from fractions of a square metre to 50 m² in size (Bertness and Ellison 1987). Solar evaporation of tidal water on the surface of bare patches drives a salinization process that renders bare patches highly stressful to plant growth (Bertness et al. 1992). Patches are initially colonized by *Salicornia europaea* and *Distichlis*

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spicata, both highly salt-tolerant species found primarily in disturbed areas. These species may ameliorate patch salinity by shading the substrate and slowing the solar-driven salinization of patch soils, thereby facilitating invasion by the less salt-tolerant, but competitively superior, species *Spartina patens* and *Juncus gerardi* (Bertness 1991, Bertness et al. 1992). This facilitation process is dependent upon high patch salinities, and under less stressful conditions facilitations are absent and competitive interactions prevail (Bertness and Shumway 1993).

Physical conditions vary with patch size, with larger patches having higher salinities due to increased exposure to solar heating (Bertness 1991). In our previous studies we identified facilitation as the mechanism of succession in patches that were 0.25 and 1 m² in area (Bertness 1991, Bertness and Shumway 1993). We hypothesized that smaller disturbance patches would have less stressful physical conditions, and thus colonization of smaller patches would be characterized exclusively by competitive interactions. Several studies have suggested that successional processes may vary after disturbances of different magnitudes and that conclusions drawn from studies of patches at one size scale may not be applicable at other scales (Sousa 1984, Pickett and White 1985, Phillips and Shure 1990). In this paper we explicitly examine the hypothesis that patch size effects mechanisms of secondary succession in salt marsh vegetation.

Methods

To study succession at different spatial scales we created bare patches 1 m² and 0.1 m² in area and monitored their colonization for 2 yr. Detailed results for the larger patches are reported elsewhere (Shumway and Bertness 1992, Bertness and Shumway 1993). All field work was conducted in a high salt marsh community at Rumstick Cove, Barrington, Rhode Island, USA. New England high marsh communities are characterized by distinct plant species zonation, with each zone dominated by a single species. *Spartina patens* (marsh hay) occupies the seaward edge of the high marsh and *Juncus gerardi* (black rush) dominates the terrestrial border of the marsh. *Distichlis spicata* (spike grass) is sparsely scattered throughout the marsh and often dominates disturbed areas. Annual (*Atriplex patula*, *Salicornia europaea*) and perennial (*Aster tenuifolius*, *Iva frutescens*, *Limonium nashii*, *Solidago sempervirens*) fugitive dicots are also found in the high marsh, often associated with bare patches (Bertness et al. 1992). We treat *Limonium nashii*, *Aster tenuifolius*, and *Solidago sempervirens* as a single group, as their seedlings are difficult to distinguish. Hereafter high marsh species will be referred to by their generic names only.

In the summer of 1988 we simulated disturbance by creating 0.31 × 0.31 m² (0.1 m²) experimental bare patches by trenching around plots to a depth of 20 cm, spraying herbicide (Roundup; Monsanto, Saint Louis, Missouri, USA), and cutting back the resulting dead vegetation. Colonization of herbicide-generated and natural wrack-generated patches is identical (Bertness 1991). Twenty-four patches per area were created in random locations in the *Spartina* zone, the *Juncus* zone, and on the border between the *Spartina* zone and the *Juncus* zone (*Spartina*–*Juncus* border). To characterize interactions between the dominant species during patch colonization, each patch was randomly assigned to one of three different species-removal treatments. In pairwise removal experiments involving species A and B, a positive response from species B elicited by removal of species A suggests that a competitive interaction is taking place and that species A is dominant over species B. If removal of species A elicits a negative response from B, this suggests that the interaction is facilitative rather than competitive. A nonsignificant response to reciprocal removals suggests that there is little direct interaction between the two species. In the *Spartina* zone, patches were designated as *Spartina* removal, *Distichlis* removal, or unmanipulated control treatments ($N = 8$ patches/treatment). *Juncus* zone patches were designated as *Juncus* removal, *Distichlis* removal, or control treatments. Patches on the *Spartina*–*Juncus* border were designated as *Spartina* removal, *Juncus* removal, or control treatments. Species were removed by monthly weeding from May through August of 1989 and 1990. Colonization was monitored by counting all seedlings in each patch in early June and by calculating percentage vegetation cover for each species using a modified point–intercept method in late July of each year.

Soil salinity was also measured monthly during both years of the study (June–August) to characterize changes in physical conditions in experimental bare patches during succession (see Bertness et al. [1992] for methods). Salinities in these small patches were only slightly (NaCl concentration ≈ 5 g/kg) elevated over undisturbed vegetation (Bertness and Ellison 1987) and decreased over time as the patches were colonized (Bertness et al. 1992). These data are not presented.

Since the seedling and vegetation cover data were similar in both years of monitoring and for the sake of brevity we will report only results from the second year of colonization. Results were analyzed with analysis of variance, and where appropriate, Scheffé post-hoc tests. Percentage data were arcsine transformed.

Results

Seedling emergence in patches. Seedling emergence was low for all species except *Salicornia* and virtually

TABLE 1. Seedling emergence (means) in 0.1-m² bare patches located in the *Spartina* zone, on the *Spartina*-*Juncus* border, and in the *Juncus* zone in May 1990 in a high salt marsh community in Rhode Island.

	<i>Spartina</i>			<i>Spartina</i> - <i>Juncus</i> border			<i>Juncus</i>		
	Control	<i>Spartina</i> removal	<i>Distichlis</i> removal	Control	<i>Spartina</i> removal	<i>Juncus</i> removal	Control	<i>Distichlis</i> removal	<i>Juncus</i> removal
<i>Spartina</i>	0	...	0	0	...	0	0	0	0
<i>Distichlis</i>	0	0	...	0	0	0	0	...	0
<i>Juncus</i>	0	0	0	14.11	21.62	...	9.40	0	...
<i>Salicornia</i>	139.89	116.16	190.40	324.78	452.87	437.00	580.70	861.50	770.53
<i>Atriplex</i>	0.67	0.17	0.49	0	0.25	0.75	2.20	3.67	1.85
<i>Iva</i>	0.56	0	0.20	0	0.25	0	0.70	0.16	0.76
<i>Limonium</i> / <i>Aster</i> / <i>Solidago</i> *	1.11	3.60	4.70	4.11	0.12	9.75	2.40	0.33	1.46

* These species were treated as equivalent because their seedlings are difficult to distinguish.

absent for the dominant perennial species. *Salicornia* was the only species to show appreciable seedling emergence in the bare patches, with densities averaging 116–190 plants/0.1 m² in *Spartina* patches, 324–452 plants/0.1 m² in *Spartina*-*Juncus* border patches, and 580–861 plants/0.1 m² in *Juncus* patches (Table 1). *Atriplex*, *Iva*, and *Limonium*/*Aster*/*Solidago* averaged <9 seedlings/patch. Seedlings of *Spartina* and *Distichlis* were noticeably absent from all patches, regardless of zone or treatment. Seedlings of *Juncus* were absent from patches in the *Spartina* zone, but were present in densities up to 21 seedlings/patch in the *Spartina*-*Juncus* border and 9.4 seedlings/patch in the *Juncus* zone. Whereas previous research has shown that marsh plant seedling germination is dependent on bare patches (Bertness et al. 1992, Shumway and Bertness 1992), our species-removal treatments had no effect on seedling emergence in patches in any of the vegetation zones

($P > .05$, one-way ANOVA with Treatment as the main effect for each zone and each species).

Species interactions and vegetation cover in patches. Reciprocal removals of the dominant species suggest that competition among clonal invaders *Spartina*, *Distichlis*, and *Juncus* strongly influences vegetation cover in small bare patches recovering from disturbance. The percentage cover of fugitive species was not affected by removals of clonal dominants and, with the exception of *Salicornia*, made up a small fraction of vegetation cover (Fig. 1).

In the *Spartina* zone *Distichlis* colonization was suppressed by *Spartina*, and in patches where *Spartina* was removed *Distichlis* cover was double that of unmanipulated controls ($P = .0002$ one-way ANOVA; Fig. 1). Conversely, the presence of *Distichlis* had no significant effect on colonization by *Spartina* ($P = .63$). *Juncus* occupied only a small percentage (<4%) of patch cover in *Spartina* patches and was not affected by species-removal treatments ($P = .30$). The fugitives *Iva*, *Solidago*, and *Aster* each contributed <3% cover and were not affected by removals ($P > .30$ for each species).

On the *Spartina*-*Juncus* border *Spartina* invasion was sharply curtailed by the presence of *Juncus* ($P < .008$) and *Spartina* cover was 33% higher in *Juncus*-removal patches than in control patches (Fig. 1). The presence of *Spartina* had no effect on *Juncus* cover ($P = .32$). Similarly *Juncus* had no effect on *Distichlis* cover ($P = .30$). *Salicornia* exhibited a rise in percentage cover in *Spartina*-removal patches but was not significantly affected by the removal of either *Spartina* or *Juncus* ($P = .08$). The fugitives *Iva*, *Limonium*, *Aster*, and *Solidago* did not respond to removal treatments ($P > .44$ for each species) and averaged <5% cover each.

In *Juncus* zone patches, *Distichlis* cover was inhibited by the presence of *Juncus* ($P = .01$). *Distichlis* cover in *Juncus*-removal treatments was 32% higher than in control patches (Fig. 1). However, *Distichlis* removal

TABLE 2. Species comparisons (by percentage cover, mean \pm 1 SE) in large and small disturbance patches after 2 yr of recovery.*

Treatment	1-m ² patches		0.1-m ² patches
	Control	Watered	Control
<i>Spartina</i> zone			
<i>Spartina</i> removal	48 \pm 2	55 \pm 2	68 \pm 5
<i>Distichlis</i> removal	30 \pm 3	25 \pm 5	30 \pm 3
<i>Spartina</i> - <i>Juncus</i> border			
<i>Spartina</i> removal	40 \pm 1	30 \pm 4	53 \pm 6
<i>Juncus</i> removal	18 \pm 2	60 \pm 5	71 \pm 6
<i>Juncus</i> zone			
<i>Distichlis</i> removal	50 \pm 5	35 \pm 3	44 \pm 6
<i>Juncus</i> removal	45 \pm 5	75 \pm 5	57 \pm 4

* The relative proportions of competitive dominants and subordinates in small patches resemble those of large patches in which soil salinities were artificially lowered by watering with freshwater. Large-patch data are from Bertness and Shumway (1993).

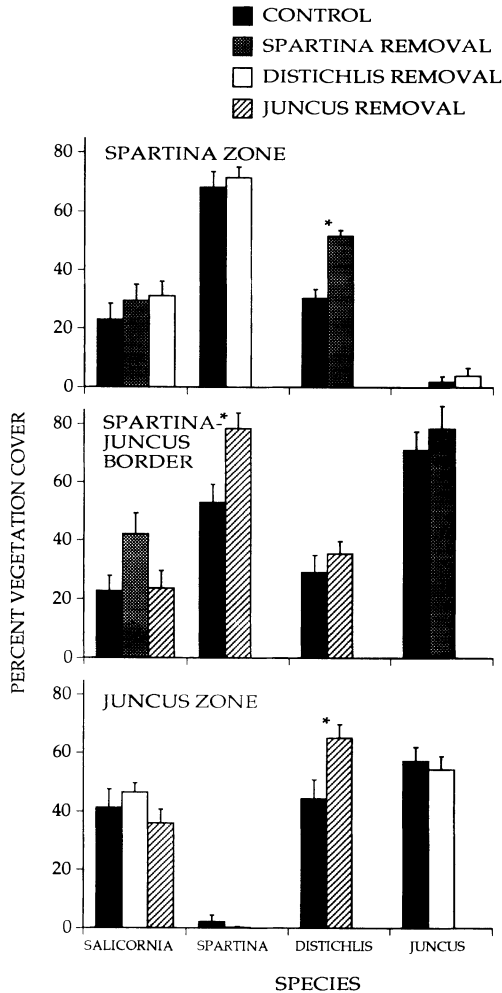


FIG. 1. Percentage cover (mean and 1 SE) of *Salicornia*, *Spartina*, *Distichlis*, and *Juncus* in experimental 0.1-m² patches in the *Spartina* zone, on the *Spartina*-*Juncus* border, and in the *Juncus* zone in July 1990. * $P < .05$, ANOVA.

had no effect on *Juncus* percentage cover ($P = .60$). *Spartina* represented only a small percentage of patch cover in the *Juncus* zone and was not influenced by removal of either *Juncus* or *Distichlis* ($P = .26$). *Salicornia* occupied 40% of patch cover in all treatments and was not affected by removals ($P = .46$). *Iva*, *Limonium*, *Aster*, and *Atriplex* covered <9% of patch area each and were not influenced by species removals ($P > .13$ for each species).

Discussion

Our results show that, in contrast to the colonization of large bare patches, the secondary succession of small bare patches is driven entirely by competitive interactions. In large patches with high soil salinities, initial colonization and amelioration of soil salinization by salt-tolerant species facilitates colonization by the

competitively dominant species. Small patches, however, do not exhibit the hypersaline soil conditions found in large patches (Bertness 1991, Bertness et al. 1992), and thus, as hypothesized, small patches did not exhibit facilitation during succession (Table 2).

Patch size may also have important effects on sexual recruitment to patches during succession. Small patch seedling densities predicted from comparable large patches (data from Shumway and Bertness [1992]) were 1.5–5 times higher than the seedling densities observed in small patches. Studies of different-sized bare patches in other communities have also found greater seedling emergence and diversity in larger patches due to a greater release of resources (Bazzaz 1979, Phillips and Shure 1990). Our results also suggest that patch size may influence the differential success of vegetative growth strategies. For example, the relative proportions of species in large and small patches (Table 2) suggests that the runner morphology of *Distichlis* is more effective for the rapid colonization of large open areas, but that the turf morphologies of *Spartina* and *Juncus* are more effective for the colonization of small disturbance patches.

Together our results suggest that secondary succession dynamics may be strongly influenced by patch size considerations. The rates at which different species invade disturbance patches are dependent upon individual stress physiologies, growth morphologies, and life history strategies. Interactions of these species traits with patch traits, such as size, resource availability, and physical stress, must be considered when making predictions about processes of succession following disturbance. Our results demonstrate that models for succession are specific to the size scale of disturbance and warn that extrapolating the results of experiments conducted at small size scales to larger size scales may be misleading.

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FRACTIONAL RESOURCE ALLOCATION INTO FEW EGGS: DAPHNIA AS AN EXAMPLE

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Most of our understanding of environmental effects on life history traits is based on models of continuous quantitative traits like age and body size. This approach has problems when discretely varying traits like clutch size or the number of broods in a breeding season are considered. For example, if total investment in a clutch is not some whole number multiple of the optimal egg size, production of either the next highest whole number of smaller than optimal eggs, or the next lowest whole number of larger than optimal eggs, is possible. This effect is particularly strong for small clutches. For a given reproductive investment, changing clutch size from one to two eggs is accompanied by a 50% decrease in investment per egg, while increasing a four-egg clutch by one egg reduces investment per egg only by 20%. Although species with small clutches are found in all groups of organisms, fractional

resource allocation into few eggs has been discussed only for birds and reptiles (Ricklefs 1968, Nussbaum 1981).

The Model

Offspring fitness is described by a positive convex function with zero fitness below a minimum offspring size (Fig. 1; Smith and Fretwell 1974). Under the assumption that a trade-off between offspring size and can be found that maximizes total clutch-fitness (product of offspring number and fitness). This level of investment can be found using the marginal value approach (Appendix: Part 1), here called marginal value solution (MVS). Since for most organisms resources invested into reproduction increase with environmental quality, I use reproductive investment as a measure of environmental quality.

Calculating the MVS implies that non-integer clutch sizes are possible. Since this is unrealistic, an alternative method is needed to find the offspring size and number which maximizes fitness. For any given clutch size, clutch fitness increases asymptotically as more resources are invested into each offspring (Fig. 1). Fig. 1 shows that the clutch size with the highest fitness for a given reproductive investment is the one that maximizes fitness (Appendix: Part 3). Dividing the reproductive investment by this fitness maximizing clutch size results in the corresponding “realizable offspring size” (ROS). Due to the discrete nature of clutch size, the ROS is sometimes larger and sometimes smaller than the MVS for the same amount of reproductive investment (Fig. 2a). The largest size differences can be found for the smallest levels of reproductive investment. From Figs. 1 and 2a it becomes clear that

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