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RIBBED MUSSELS AND *SPARTINA ALTERNIFLORA* PRODUCTION IN A NEW ENGLAND SALT MARSH[1]

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Abstract. The ribbed mussel, *Geukensia demissa,* is commonly found associated with the salt marsh cordgrass, *Spartina alterniflora.* Mussels attach to the basal portion of *S. alterniflora* stems with strong proteinaceous byssal threads and deposit fecal material on the surrounding sediment as a byproduct of their filter-feeding activity. Here I demonstrate by manipulating mussel densities in the field that the presence of *G. demissa* stimulates *S. alterniflora* growth, and examine experimentally a number of potential mechanisms of this facilitation. In the natural habitat, mussel density is positively correlated with increased grass height, biomass, and flowering, and experimental removal and addition of mussels in these habitats demonstrates that mussels stimulate both aboveground and belowground *S. alterniflora* production.

In tall-form *S. alterniflora* habitat, net primary production is positively correlated with mussel density and soil nitrogen levels. Experiments in this habitat show that mussels increase soil nitrogen, and this increase in nutrients would appear to be responsible for stimulating *S. alterniflora* growth. On the seaward edge of the marsh, net primary production is strongly correlated with mussel density, but not soil nutrients. On the marsh edge, mussels are shown to bind sediments and prevent erosion and physical disturbance.

The relationship between *S. alterniflora* and *G. demissa* appears to represent a facultative mutualism that leads to increased marsh net primary production and stability. While previous research has shown that *S. alterniflora* production increases *G. demissa* growth and reproductive success, *G. demissa* also has strong stimulating effects on *S. alterniflora.* Nonconsumer plant-animal interactions such as the *G. demissa-S. alterniflora* association are potentially important determinants of marsh growth, stability, and community structure that have not been previously appreciated.

Key words: facilitation; facultative mutualism; Geukensia demissa; *primary productivity; salt marshes;* Spartina alterniflora.

INTRODUCTION

Emergent vegetation unquestionably is the primary structuring agent of salt marshes. Salt marsh communities owe their existence to the success of emergent plants, much as coral reef communities flourish due to the success of coral species. Redfield (1972) characterized salt marsh growth and development as a dynamic process where the success and expansion of emergent plants into the littoral environment is balanced by the destructive impact of erosion and physical disturbance. In addition to providing the primary framework of salt marshes, vegetation also appears to determine the distribution and abundance of many of the animals of the marsh (Bell et al. 1978, Ringold 1979, Stiven and Kuenzler 1979, Daiber 1982). The success of emergent plants, therefore, appears to dictate not only the existence and success of salt marsh communities, but also mediates the structure of marsh communities and the abundance and distribution of populations of marsh animals.

Considerable work on salt marsh dynamics has focused on the role of physical factors in influencing the primary production of marsh vegetation. Nutrient limitation, salinity, tidal fluctuation, substrate redox potentials, soil aeration, and sulfide buildup have all been suggested to affect the primary production of *Spartina alterniflora* (Teal and Kanwisher 1966, Stalter and Batson 1969, Mooring et al. 1971, Nixon and Oviatt 1973, Valiela and Teal 1974, Broome et al. 1975, Gallagher 1975, Turner 1976, Mendelssohn 1979, Gallagher et al. 1980, Smart and Barko 1980, King et al. 1982). Data supporting these contentions, however, have come primarily from correlative field data or laboratory experiments. With the exception of a few recent studies, e.g., nitrogen limitation (Valiela and Teal 1974) and water movement (King et al. 1982), these ideas have not been experimentally examined in the field.

Many of the proximate factors proposed to have an effect on primary production of marsh vegetation are potentially modified by animal activities. Animals that burrow in marsh sediment (Montague 1980), deposit-feed on marsh soils (Conner and Teal 1982), or filter-feed on marsh waters and deposit their wastes on the marsh surface (Valiela et al. 1978, Jordan and Valiela 1982) all influence sediments and may have an important impact on the primary production of marsh vegetation.

One of the most conspicuous plant-animal associations within salt marshes from Cape Cod to Florida is between the marsh-building grass *Spartina alterniflora* and the ribbed mussel *Geukensia demissa* (formerly *Modiolus demissa*). *S. alterniflora* is responsible for the

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growth of salt marshes into littoral waters throughout its range, and *G. demissa* is commonly found attached to *S. alterniflora* stems and roots. Protected marshes in southern New England and Maryland commonly have mussel densities of >1000 individuals/m^2 on the seaward edge of the marsh (M. D. Bertness, *personal observation*). Previous work has indicated that *S. alterniflora* success can be limited by physical disturbance (e.g., waves, logs, ice, etc.) which erodes and breaks up the root mat, preventing growth and colonization (Redfield 1972); low substrate oxygen levels (Howes et al. 1981); and nutrient limitation (Valiela and Teal 1974). Association with *G. demissa* could potentially alleviate all of these problems. *G. demissa* attaches to *S. alterniflora* stems and roots by strong proteinaceous byssal threads that bind the root mat together and may play a significant role in fortifying *S. alterniflora* from physical disturbance and erosion. *G. demissa* is also a filter feeder. As a result of its feeding activity, it pumps tidal water over the substrate surface (which may oxygenate the sediments), and deposits nitrogenous wastes and concentrated minerals in the form of consolidated feces and pseudofeces onto the *S. alterniflora* rootmat (Jordan and Valiela 1982). This may serve to alleviate nutrient limitation in mussel-associated *S. alterniflora* stands. Jordan and Valiela (1982) estimated that the *G. demissa* population in a small New England marsh daily filtered a volume of water in excess of the tidal volume of the entire marsh, and on a yearly basis deposited as much particulate nitrogenous material on the sediment as was exported from the marsh. If *S. alterniflora* growth is otherwise nutrient limited, association with *G. demissa* could result in a substantial benefit to marsh grass. Furthermore, if *G. demissa* positively influences the growth and persistence of *S. alterniflora,* it could also have an ameliorating effect on the expansion and stability of marshes. Marshes or portions of marshes with high *G. demissa* densities may be more productive and less prone to erosion and physical disturbance than marshes harboring smaller mussel populations. In this manner, marsh mussels may have an important role in the development, productivity, and persistence of many extant marshes.

In this paper, I examine the relationship between ribbed mussels and the marsh grass *S. alterniflora* in a southern New England salt marsh. Correlative data indicate that high mussel densities and *S. alterniflora* production are positively associated. This observation is then examined with manipulative field experiments, and a number of potential mechanisms of mussel stimulation of *S. alterniflora* production are explored. Three explicit hypotheses are examined: (1) that mussel filter feeding and movement in the sediment increases substrate oxygen levels; (2) that mussel filter feeding and the deposition of waste material on the sediment surface increases substrate nutrient supplies; and (3) that by binding sediment and root mat with byssal threads, mussels stabilize substrate and prevent substrate erosion and physical disturbance.

STUDY SITE

The marsh studied is a small, protected embayment of Smith Cove in Barrington, Rhode Island, USA, locally referred to as Rumstick Cove. The total area of emergent vegetation is ≈2 ha, while the embayment area proper is ≈0.8 ha. Rumstick Cove is connected to Smith Cove by a narrow (10 m) but unobstructed channel (1.5 m deep at mean high water). Freshwater input into the cove is small and salinity generally ranges from 10 to 15 mg/g. Rumstick Cove is characteristic of many protected New England marshes in both hydrology and vegetation (Ayers 1959). The seaward border of the marsh is characterized by a band of tall-form *S. alterniflora* ≈5 m wide. Above this zone, a band of short-form *S. alterniflora* (Valiela et al. 1978) ≈3 m wide extends to the mean high water line (Fig. 1). The marsh area dominated by the growth forms of *S. alterniflora,* therefore, represents the low marsh habitat (the area of the marsh that is regularly flooded by the tide). The seaward border of the high marsh (the marsh area that is not regularly flooded by the tide) is characterized by a *Spartina patens/Dictichlis spicata* zone (Fig. 1). *Spartina patens* is the most common grass in the high marsh as a whole, covering ≈85% of the marsh proper. *S. patens* and *D. spicata,* however, are always found growing over *S. alterniflora*-generated peat deposits, suggesting that *S. alterniflora* success is responsible for the high marsh habitat that is now dominated by *S. patens* and *D. spicata.* Aboveground grass production generally commences in April and continues into the fall (October) when temperatures drop and the aboveground portions of the halophytes die back. Ice damage to the marsh (Redfield 1972) is common at Rumstick Cove. The ribbed mussel, *Geukensia demissa,* is found in tightly packed mats of 900–2000 individuals/m^2 on the seaward edge of the marsh. Ribbed mussel density drops off markedly to 100–400 individuals/m^2 in the tall-form *S. alterniflora* band above the seaward edge of the marsh, while mussels are rare in the short-form *S. alterniflora* zone and in the high marsh areas dominated by *S. patens* and *D. spicata.*

Throughout this paper the seaward edge of the marsh (extending 1 m inland from the point where *S. alterniflora* first appears) will be referred to as the marsh edge, and the remaining low marsh area dominated by tall-form *S. alterniflora* (≈4 m wide) will be referred to as the marsh flat (Fig. 1). Unless specifically stated, both *Spartina alterniflora* and *Geukensia demissa* will be referred to by generic name.

METHODS

To examine the population distribution of *Geukensia* at Rumstick Cove, a series of random quadrats were sampled in May 1981. A 625-cm^2 metal quadrat was

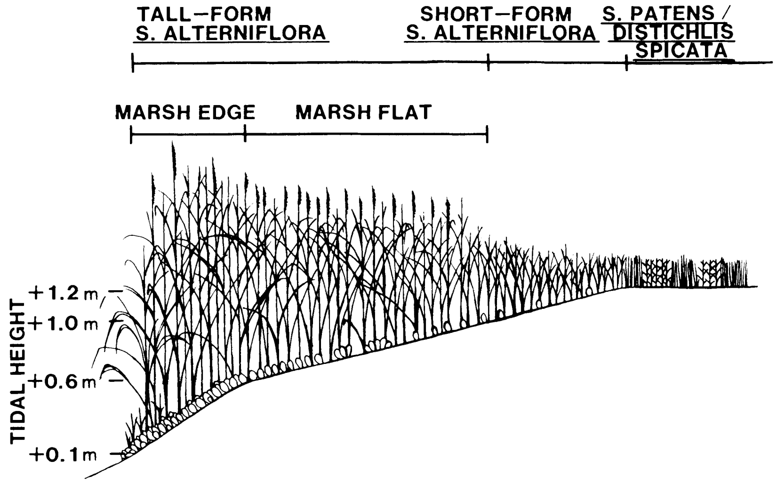


FIG. 1. Schematic drawing of the study site showing the tidal height distribution of marsh features referred to in the text.

randomly placed at 10-m intervals in the marsh edge, marsh flat, short-form *S. alterniflora*, and *S. patens/ D. spicata* zones (Fig. 1); 12–16 quadrats were sampled in each zone. Within each quadrat all mussels were removed and their lengths measured with calipers (±0.1 mm).

To examine the hypothesis that *Geukensia* influences *Spartina* production, a series of permanent quadrats was established along a 150-m stretch of the shoreline on the marsh edge and on the marsh flat in early May 1981. Ten adjacent pairs of quadrats (0.25 m^2) were marked in each zone with wooden stakes. Once the plots were established, all mussels were manually removed from one quadrat of each pair, with the second quadrat in each pair left with natural mussel densities as a control. Mussels are easily removed from their attachment to the root mat without disturbing sediment or root structures. Ten additional marsh flat and edge control quadrats were also established in May 1981 to examine correlations between mussel density and *Spartina* production at the end of the marsh grass growing season. After 16 wk (September 1981) all quadrats that could be relocated were sampled. Mussels were counted in situ, *Spartina* stems in each quadrat were cut at ground level, measured for length (±1.0 cm), scored for the presence of flowers, and then all the *Spartina* from each quadrat was dried at 50°C for 2 wk and weighed (±1.0 g). To examine potential experimental effects of the mussel manipulation experiments, five additional sets of permanent quadrats were established on the marsh flat. A set contained three quadrats (0.25 m^2). Mussels were removed from two quadrats in each set, but replaced in one of the quadrats to represent a manipulation control; the third quadrat in each set represented an unmanipulated control. The quadrats were established in May 1982 and sampled in September 1982 for aboveground grass production, using the methods described above. For sampling purposes, each quadrat was divided into four 625-cm^2 areas. Aboveground *Spartina* biomass, stem lengths, stem density, and flowering did not differ between unmanipulated ($n = 20$) and manipulated controls ($P >$ .50, t test) and the data showed no evidence of experimental effects. Mussel addition experiments provide a second control on potential experimental effects of the mussel manipulation experiments. By adding mussels, a disturbance similar to that of removing mussels is created. Results from mussel addition experiments will be presented below.

Results from the initial (1981) correlative survey and mussel removal experiments indicated that *Spartina* production was positively correlated with mussel density in the natural habitat, and that mussel removal resulted in decreased *Spartina* growth and production (see below). To examine the mechanism of the influence of *Geukensia* on *Spartina* production, in May 1982 a second series of mussel manipulation experiments was initiated. Ten pairs of new control and mussel removal quadrats were established on the marsh edge. On the marsh flat, 10 sets of three permanent quadrats were established. Each set consisted of a mussel removal quadrat, a control quadrat, and a mussel addition quadrat. For the mussel addition quadrats, mussels from edge zone mussel removal quadrats were transplanted to obtain ≈100% mussel cover (≈300 mussels). Transplanted mussels were implanted into the substrate in their natural orientation and found to attach to the root mat within 2 d with $<1\%$ mortality. In September 1982 all experimental and control quadrats initiated in May 1982 were sampled. Mussels and *Spartina* stems were sampled as described above. In addition, surface sediment (top 2 cm) and core samples were taken in each quadrat to examine the influence of mussels on sediment nutrient levels and on belowground *S. alterniflora* biomass.

From each 1982-initiated quadrat 10–30 g of surface sediment (top 3 cm) were collected in September 1982, air-dried for 3 wks, and sieved (2-mm mesh openings) to eliminate plant material. Sieved sediment samples were analyzed for total Kjeldahl nitrogen (Allen 1974); potassium, calcium, and magnesium content was determined with atomic absorption spectrophotometry (Perkin Elmer 1982) and soil phosphorus was determined colorimetrically (Naumann 1982).

All dried plant material from each quadrat in the 1982 mussel manipulation experiment was shredded in a blender and thoroughly mixed to assure representative sampling. Then the plant material was examined chemically for total Kjeldahl nitrogen (Allen 1974), calcium, magnesium, and potassium (Perkin Elmer 1982).

To assess relative oxygen availability in the experimental and control quadrats, surface (top 2 cm) and subsurface (5 cm in sediment) redox measurements were made (Howes et al. 1981, Mendelssohn et al. 1981) in all permanent quadrats before surface sediments were disturbed. An Orion 407A ionalyzer with a redox probe (Orion Research, Cambridge, Massachusetts) was used for the measurements. The probe was inserted into the substrate and allowed to equilibrate for 10 min before recording redox values (Howes et al. 1981).

A core sample was also taken in each 1982-initiated permanent quadrat in September 1982 to examine effects of mussels on belowground *Spartina* biomass. A coring device similar in design to that described by Gallagher (1974) with a 6.5 cm inside diameter was used. Core lengths varied from 20 to 30 cm. In the laboratory, cores were cut into 0–5, 5–10, 10–15, 15–20, 20–30 cm vertical sections and each section was washed and sieved through a 2-mm mesh sieve. All mussels were measured and plant material was separated into roots, rhizomes, and debris. Live and dead plant material were differentiated on the basis of rigidity and color (Barber 1984). Sorted belowground live plant material and debris was dried at 50° for 2 wk and weighed (± 0.001 g).

To examine the potential role of mussels in binding marsh sediment and influencing the vertical expansion of the marsh, level rods were installed in all 1981- and 1982-initiated permanent quadrats in May 1982. Level rods were 1.0 cm diameter steel rods that were driven vertically into the marsh surface until firmly imbedded in the clay underlying the marsh (≈ 1.5 m below the marsh surface). Each level rod was cut 5–10 cm from the marsh surface, individually labeled, and fitted with a permanent plastic cap. Height measurements of all level rods above the sediment surface were taken in May 1982 after installation, and again in September 1982, May 1983, and September 1983. To control for experimental effects of mussel manipulations and *Spartina* harvesting, mussel manipulation and control quadrats initiated in 1981 and 1982 were compared.

To examine independently the role of mussels in binding sediment and preventing erosion, two sets of 20 flower pots (15.5 cm diameter, 15 cm deep) were imbedded flush on the marsh edge in June 1982. Each pot was filled completely with ambient marsh edge substrate without live *Spartina* roots or rhizomes. Live plant material was removed by hand from the pot sediment. Twenty mussels each were placed in 20 of the pots; the mussels attached to each other and the pot edges within 1 wk. The remaining 20 sediment pots were implanted on the marsh edge without mussels present. In May 1983 the sediment pots were examined for evidence of erosion. Measurements (± 0.25 cm) were made on both the minimum and maximum extent of erosion along the lip of each pot.

To examine the horizontal seaward expansion of *Spartina* and mussels on the edge of the marsh, in August 1983 the position of *Spartina* and mussels was monitored in the 1982-initiated permanent edge quadrats. *Spartina* movement was measured from the seaward side of each quadrat. All 1982-initiated edge quadrats had initially been placed with their seaward side coinciding with the maximum seaward extension of *Spartina* stems, and the original position of mussels had been measured. 1981-initiated quadrats had not been precisely placed in relation to the seaward occurrence of *Spartina* or *Geukensia* and so could not be used in this analysis. Measurements of mussel seaward expansion were taken from the seaward side of control quadrats and the landward side of mussel removal quadrats. Percent cover estimates of mussels in all edge quadrats were made in August 1983 by placing a 0.25-m^2 metal frame divided into 100 0.25-cm^2 subquadrats over each permanent quadrat and counting the number of subquadrats containing mussels.

Standard error is used throughout the text to express statistical variation.

RESULTS

Distribution and abundance of Geukensia

At the study site mussel density decreased dramatically from the marsh edge to higher levels of the marsh. On the marsh edge a dense band of mussels ($\bar{x} = 352.9 \pm 22.5$ individuals/0.25 m^2, $n = 16$ quadrats), often 2–3 individuals deep, covered >90% of all exposed surfaces. Areas of the leading edge of the marsh that were not covered by dense aggregations of mussels (<5% of the marsh) appeared to have been recently disturbed by winter ice rafting (Redfield 1972). These disturbed areas were generally small (<0.5 m across) and were rapidly colonized both by recruiting juvenile *Geukensia* and the movement of adult mussels (Paine and Levin 1981). Small ice damage breaks in the leading edge of the marsh (<0.5 m across) are rendered almost undetectable within 1 yr by this process (M. D. Bertness, *personal observation*). On the marsh flat, mussel density (117.7 ± 17.1 individuals/0.25 m^2, $n = 16$ quadrats) fell to less than a third of the densities

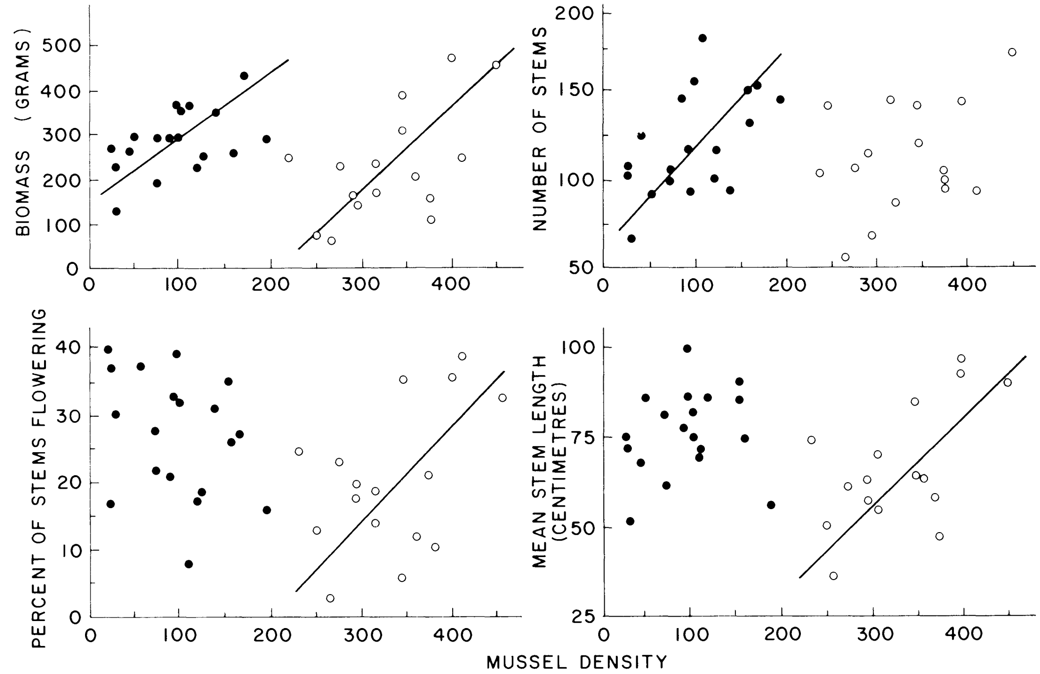


FIG. 2. Correlative relationships between aboveground *S. alterniflora* parameters and mussel density from random 0.25-m^2 quadrats on the marsh flat (●) and marsh edge (○) in September 1981. A line through the points from each habitat indicates a significant correlation ($P < .05$, ANOVA). The lines were fit by eye.

found on the marsh edge. Mussel density on the marsh flat was also more heterogeneous (coefficient of variation [CV] = 56.4%) than on the marsh edge (CV = 25.1%), ranging from areas with nearly 100% mussel surface cover (>250 mussels/0.25 m^2) to <30 mussels/0.25 m^2. Mussels were relatively rare above the marsh flat. In the short-form *S. alterniflora* zone, mussel density dropped to 15.4 ± 3.4 individuals/0.25 m^2, n = 13 quadrats, and in the *Spartina patens/Distichlis spicata* zone mussels were almost absent (0.5 ± 0.51 individuals/0.25 m^2, n = 12 quadrats).

Relationship between Spartina *parameters and mussel density*

Mussel density and *Spartina* parameters from undisturbed control quadrats are presented in Fig. 2. The mean length of *Spartina* stems from quadrats taken on the marsh flat (76.5 ± 9.6 cm, n = 19 quadrats) was significantly longer ($P < .05$, Mann-Whitney U test) than the mean length of *Spartina* stems of the marsh edge (67.7 ± 17 cm, n = 16 quadrats). Similarly, quadrats on the flat had a significantly higher proportion ($P < .05$, Mann-Whitney U test) of flowering shoots (25.8 ± 10.6%, n = 19 quadrats, $P < .05$) and significantly more ($P < .01$, Mann-Whitney U test) aboveground *Spartina* biomass (290.6 ± 74 g, n = 19 quadrats) than quadrats taken on the marsh edge (flowering 20.34 ± 10.7%, n = 16 quadrats; biomass 226.31 ± 124.7 g, n = 16 quadrats). *Spartina* production, however, clearly showed more variation on the marsh edge than on the marsh flat, both within and between the sampled quadrats. The CV of *Spartina* stem lengths within quadrats on the marsh edge ($\bar{x}$ = 66.0%) was significantly greater ($P < .02$, Mann-Whitney U test) than in quadrats taken on the marsh flat ($\bar{x}$ = 48.8%). Among quadrats, the CV of *Spartina* stem lengths on the marsh edge (25.4%) was also significantly greater (P < .05, F test) than among quadrats taken on the marsh flat (12.5%). *Spartina* growth and production thus appears to be much more variable on the edge of the marsh than on the established marsh flat, which appears to reflect the fact that the edge of the marsh is more subject to disturbance and erosion than the marsh flat (Redfield 1972). In contrast to the marsh flat, the edge of the marsh has been characterized as a mosaic of *Spartina* in differing states of recovery from physical disturbance and showing variable success in expansion below the current seaward edge of the marsh (Redfield 1972).

On the marsh edge, mussel density in the control quadrats (Fig. 2) was positively correlated with aboveground *Spartina* biomass (r = 0.60, $P < .01$, ANOVA), mean *Spartina* stem length (r = 0.55, $P < .05$, ANOVA), and the proportion of *Spartina* stems that flowered (r = 0.55, $P < .05$, ANOVA), but not with *Spartina* stem density (r = 0.36, $P > .20$, ANOVA). On the marsh flat, mussel density in the control quadrats (Fig. 2) was positively correlated with aboveground *Spartina* biomass (r = 0.52, $P < .02$, ANOVA) and *Spartina* stem density (r = 0.51, $P < .02$, ANOVA), but not with mean *Spartina* stem length ($r = 0.14$, $P > .50$, ANOVA) or the proportion of *Spartina* stems that flowered ($r = 0.43$, $P > .10$, ANOVA).

These correlations in the natural habitat between mussel density and measures of *Spartina* success may show that mussels stimulate *Spartina* growth. Correlative data, however, does not establish causation. A positive correlation between *Spartina* success and mussel density could simply indicate that mussels settle preferentially in dense stands of *Spartina,* or that areas that have been recently disturbed by ice damage (Redfield 1972) or wrack accumulation (Reidenbaugh and Banta 1980) may have reduced *Spartina* production and mussel densities.

FIELD MANIPULATIONS OF MUSSEL DENSITY

Effects on aboveground Spartina *production*

Results of the 1981 mussel removal experiment were dramatic (Figs. 3 and 4). On the marsh edge (Fig. 3), mussel removal resulted in a significant ($P < .01$, Scheffé test) 45% reduction in aboveground *Spartina* biomass, a significant ($P < .05$, Scheffé test) 29% reduction in mean *Spartina* stem length, and a significant ($P < .05$, Scheffé test) 41% decrease in the proportion of *Spartina* stems that flowered. Mussel removal did not significantly affect ($P > .05$, ANOVA) *Spartina* stem density when the two years were combined. Experimental removal of mussels on the marsh flat yielded less striking results than on the marsh edge ($P < .05$, ANOVA interaction for biomass and stem length comparisons). On the marsh flat (Fig. 4), mussel removal resulted in a significant ($P < .05$, Scheffé test) 26% reduction in *Spartina* biomass, and a significant ($P < .05$, Scheffé test) 38% reduction in flowering, but did not significantly influence ($P > .05$, Scheffé test) mean stem length. Results of the 1982 mussel removal experiments yielded results almost identical to the 1981 experiments (see Figs. 3 and 4 for statistics).

Addition of mussels on the marsh flat in the 1982 experiments resulted in a significant ($P < .05$, Scheffé test) 20% increase in *Spartina* biomass, but did not significantly influence ($P > .05$, Scheffé test, each case) stem density, stem length, or the proportion of stems that flowered (Fig. 4).

Effects on belowground Spartina *biomass*

Profiles of the belowground biomass of *Spartina* from all 1982 control and mussel-manipulation quadrats are presented in Figs. 5 and 6; roots and rhizomes are plotted separately. On the marsh edge (Fig. 5), mussel removal significantly reduced overall rhizome biomass ($P < .05$, biomass vs. depth ANOVA) and affected

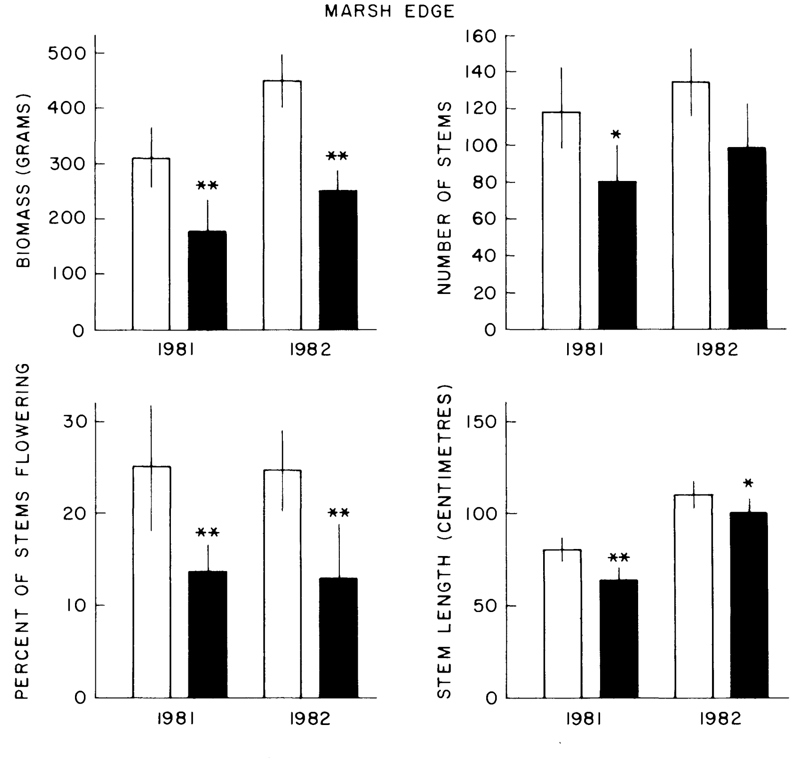


FIG. 3. Summary of aboveground *S. alterniflora* parameters in mussel manipulation experiments done on the marsh edge during the 1981 and 1982 growing seasons. ☐ control quadrats; ■ mussel removal quadrats (±SE). All data are for 0.25-m^2 quadrats. *$P < .05$, ANOVA in comparison to control within years. **$P < .01$, ANOVA in comparison to control within years.

rhizome biomass differentially at different sediment depths ($P < .05$, ANOVA interaction). The strongest rhizome response to mussel removal was recorded 10–15 cm below the surface, well below the top 5 cm of the sediment where mussels are found. On the marsh edge, mussel removal only tended ($P < .10$, ANOVA, biomass vs. depth) to reduce root biomass and did not significantly affect ($P > .20$, ANOVA interaction) the vertical distribution of roots.

On the marsh flat, mussels significantly affected ($P < .05$, biomass vs. depth ANOVA) both root and rhizome biomass (Fig. 6), and both root and rhizome biomass responses to the presence of mussels varied significantly ($P < .05$, ANOVA interaction) with sediment depth. While mussel removal on the marsh flat did not significantly affect ($P > .05$, Scheffé test) the biomass of either roots or rhizomes in comparison to control areas, addition of mussels on the marsh flat to densities similar to those naturally found on the marsh edge significantly increased root biomass ($P < .05$, Scheffé test) and showed a trend ($P < .10$, Scheffé test) towards increasing rhizome biomass.

In summary, the results of the mussel manipulation experiments demonstrate that mussels have a marked stimulating effect on both the aboveground and belowground biomass of *Spartina* and that mussel stimulation of *Spartina* biomass in the natural habitat is most pronounced on the marsh edge where mussel densities are the highest. These results suggest that the correlations documented in the natural habitat between *Spartina* biomass and mussel density are due at least in part to mussel facilitation of *Spartina* growth.

MECHANISM OF THE *GEUKENSIA-SPARTINA* FACILITATION

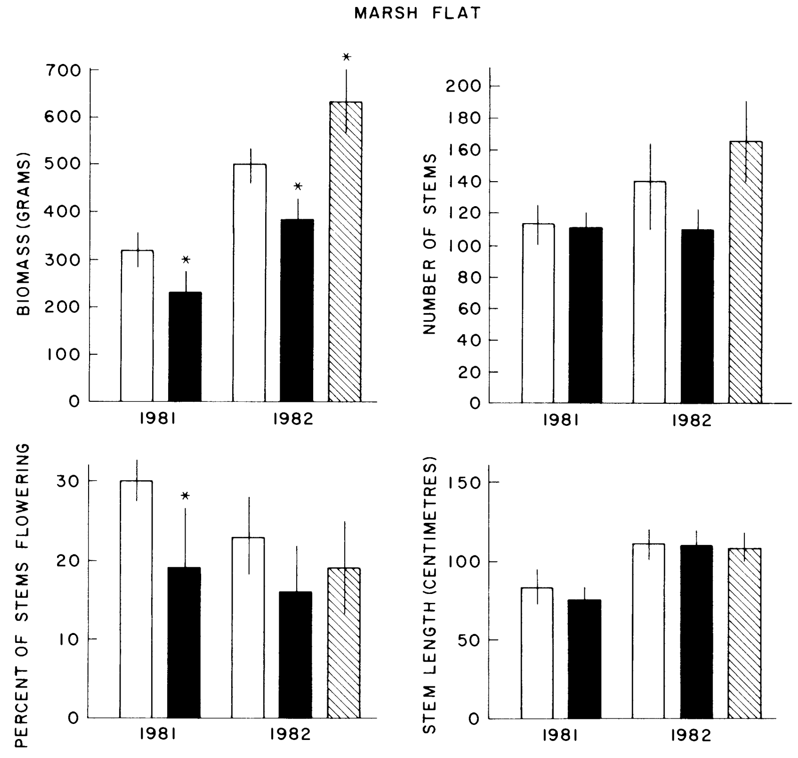
Substrate redox potential effects

A summary of surface and subsurface redox measurements taken in all 1982-initiated control and experimental areas is given in Fig. 7. As has been noted by previous workers (Howes et al. 1981, Mendelssohn et al. 1981) the readings are extremely variable.

Mussels did not significantly affect ($P > .05$, ANOVA, all cases) surface or subsurface redox levels in either the marsh flat or marsh edge habitats.

Plant and soil nutrient level effects

Analysis of plant tissue from all 1982-initiated mussel manipulation treatments (Table 1) revealed no significant effects of mussels on total Kjeldahl nitrogen, potassium, magnesium, or calcium on a dry mass basis on either the marsh edge or marsh flat ($P > .05$, ANOVA, all cases). In addition, control plant tissue



MARSH FLAT

FIG. 4. Summary of aboveground *S. alterniflora* parameters (±SE) in mussel manipulation experiments done on the marsh flat during the 1981 and 1982 growing seasons. □ control quadrats, ■ mussel removal quadrats, ▨ mussel addition quadrats. All data are for 0.25-m^2 quadrats. *$P < .05$, Scheffé test in comparison to control within years. **$P < .01$, Scheffé test in comparison to control within years.

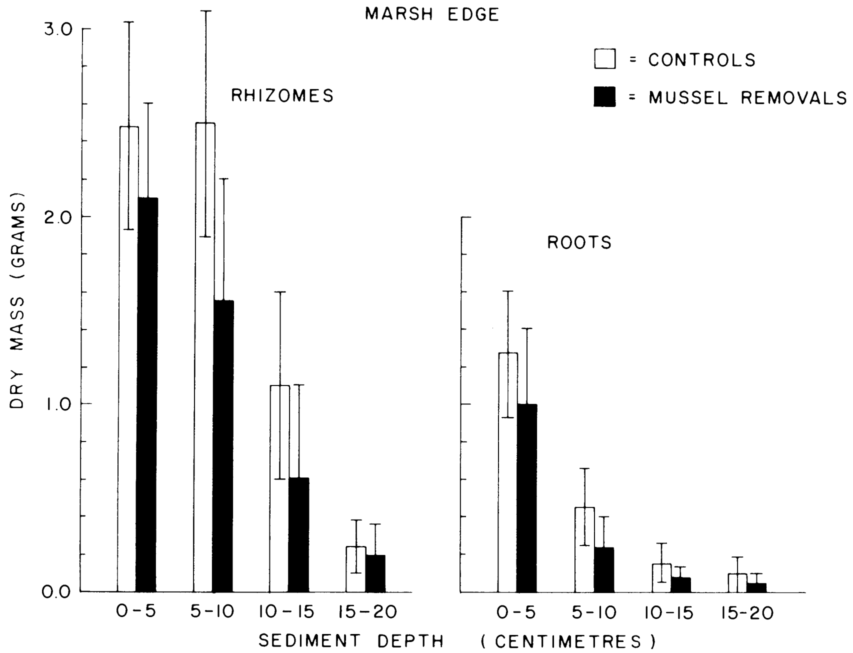


FIG. 5. *Spartina alterniflora* root and rhizome profiles (±SE) from the 1982 control (☐) and mussel removal (■) quadrats on the marsh edge.

from the marsh edge and marsh flat did not differ in concentration of total Kjeldahl nitrogen, potassium, or calcium ($P > .05$, *t* test, all cases). The only difference noted in plant tissue between marsh flat and edge control plants was in magnesium concentration ($P < .05$, *t* test).

Analysis of sediments from the 1982-initiated experimental and control quadrats (Table 2), however, indicated that the presence of mussels influenced sediment nutrient levels. On the marsh flat, mussels significantly increased the total Kjeldahl nitrogen ($P < .01$, ANOVA), potassium ($P < .02$, ANOVA) and magnesium ($P < .05$, ANOVA) in the sediments. In contrast, on the marsh edge, mussels significantly increased soil calcium, but only showed a tendency ($P < .10$, ANOVA, both cases) toward increasing soil total Kjeldahl nitrogen and magnesium.

Correlations among grass production, mussels, and soil parameters

Results presented above indicate that mussels measurably affect the nutrient levels of marsh sediments. Both soil nutrient levels (Valiela and Teal 1974) and soil redox potentials (Howes et al. 1981) have been proposed to limit *Spartina* production in New England salt marshes. To examine the relationship among soil nutrients, redox levels, and mussel density and *Spartina* biomass, correlations among these variables were determined using data from the 1982 unmanipulated control quadrats on the marsh flat ($n = 18$) and edge ($n = 10$). In addition to the 10 control quadrats from the 1982 mussel manipulation experiments, data from 8 additional control quadrats were available for the marsh flat correlations.

On the marsh flat, both mussel density ($r = 0.54$, $P < .05$, ANOVA) and total soil Kjeldahl nitrogen ($r = 0.55$, $P < .05$, ANOVA) were significantly correlated with aboveground *Spartina* biomass. Soil potassium ($r = 0.46$, $P < .10$, ANOVA), magnesium ($r = 0.47$, $P < .10$, ANOVA), and calcium ($r = 0.50$, $P < .10$, ANOVA) each showed positive correlation trends with aboveground grass biomass, while soil phosphorus ($r = 0.14$, $P > .50$, ANOVA) was not related to aboveground *Spartina* biomass. Neither surface ($r = 0$, $P > .50$, ANOVA) nor subsurface ($r = 0.17$, $P > .50$, ANOVA) redox potentials showed any correlation with aboveground *Spartina* biomass on the marsh flat. Multiple linear regression methods cannot be applied to these data to ascertain the relative contribution of each of these variables to aboveground *Spartina* biomass due to severe autocorrelation among soil nutrient levels and mussel density. On the marsh flat, natural variation in mussel density accounted for 47% ($P < .005$, ANOVA) of the variation found in total soil Kjeldahl nitrogen, and 64% ($P < .001$, ANOVA), 62% ($P < .001$, ANOVA), and 68% ($P < .001$, ANOVA) of the natural variation observed in soil potassium, magnesium, and calcium, respectively. Neither surface nor subsurface redox potentials were correlated ($r = 0$, $P > .50$, ANOVA, both cases) with mussel density in the marsh flat controls. These correlations, examined in light of the experimental results discussed above, suggest that

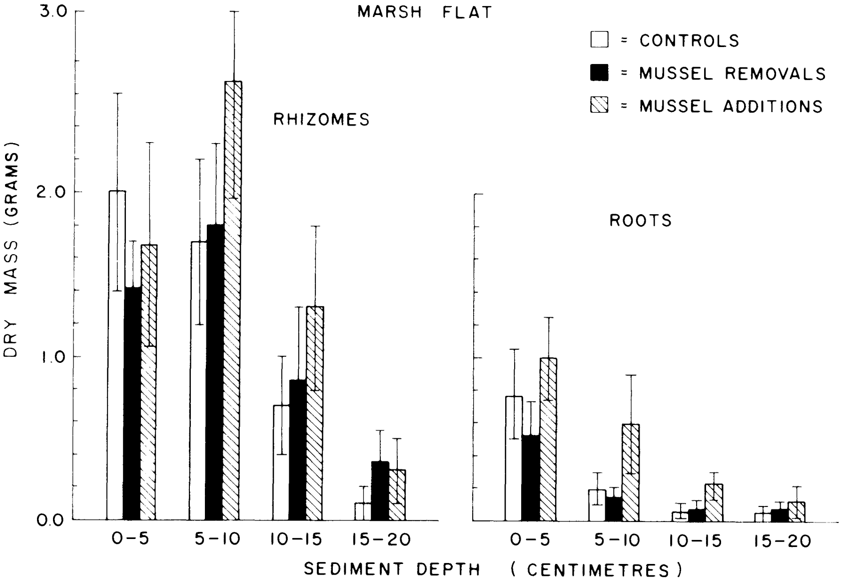


FIG. 6. *Spartina alterniflora* root and rhizome profiles (±SE) from the 1982 control (□), mussel removal (■), and mussel addition (▨) quadrats on the marsh flat.

mussels strongly influence the availability of nutrients on the marsh flat. This does not, however, appear to be the case on the marsh edge.

On the marsh edge, aboveground *Spartina* biomass was highly correlated with *Geukensia* density ($r = 0.86$, $P < .001$, ANOVA), but showed no significant correlations with total soil Kjeldahl nitrogen ($r = 0.40$, $P > .50$, ANOVA), soil phosphorus ($r = 0.65$, $P > .10$, ANOVA), soil potassium ($r = 0.24$, $P > .50$, ANOVA), soil magnesium ($r = 0.70$, $P > .20$, ANOVA), soil calcium ($r = 0.40$, $P > .50$, ANOVA), or either surface ($r = 0.0$, $P > .50$, ANOVA) or subsurface ($r = 0.20$, $P > .50$, ANOVA) redox potentials. In addition, mussel density on the marsh edge was not significantly correlated with soil nitrogen, phosphorus, potassium, magnesium, or surface or subsurface redox potentials ($r = 0.30$, $P > .50$, ANOVA, all cases). Soil calcium ($r = 0.70$, $P < .05$, ANOVA) was the only soil nutrient analyzed that showed a significant correlation with mussel density on the marsh edge. These results suggest that the strong effect of mussels on the production of *Spartina* on the marsh edge is not primarily due to either nutrient enrichment or effects on substrate redox potentials.

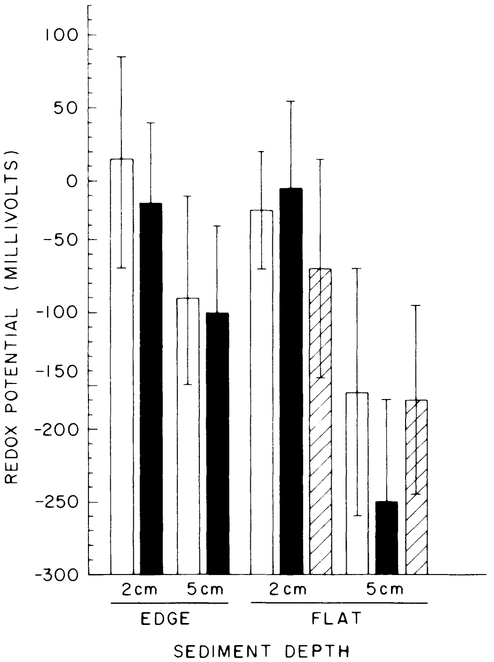


FIG. 7. Redox potentials (E_n) from control (□, $n = 10$), mussel removal (■, $n = 10$), and mussel addition (▨, $n = 10$) quadrats initiated in May 1982 (±SE). All measurements were made in September 1982. Data are given for quadrats on the marsh edge and marsh flat at 2 and 5 cm below the marsh surface.

Mussel effects on marsh erosion and stability

Cumulative changes in the relative tidal heights of experimental and control quadrats over a 17-mo period are summarized in Fig. 8. Comparisons between the mussel-removal and control quadrats initiated in May 1981, 1 yr before the level rods were installed, and the quadrats (1982-initiated) that were established immediately after the mussel manipulations revealed that the experimental disturbance associated with removing mussels did not significantly affect marsh height ($P > .50$, ANOVA). All other statistical comparisons on the marsh height data were therefore done on data pooled by treatment and habitat.

Both habitat and the presence of mussels had a significant effect ($P < .001$, ANOVA) on changes in marsh height over the experimental period. Control quadrats with natural mussel densities on the marsh edge differed markedly ($P < .001$, Scheffé test) from marsh-edge mussel-removal quadrats after only 17 mo. In the control marsh-edge quadrats, marsh height measurably increased, while after mussel removal marsh height decreased dramatically (Fig. 8). After mussels had been removed for 17 mo, control and mussel-removal quadrats on the marsh edge were also very different visually. In control areas, *Spartina* roots and rhizomes were buried in sediment and the byssal threads of *Geukensia,* while in mussel-removal quadrats, both live and dead *Spartina* roots and rhizomes were exposed on the surface, without sediment cover.

On the marsh flat, control quadrats showed measurable vertical accretion (Fig. 8), but this accretion was significantly less ($P < .05$, Scheffé test) than the vertical expansion of the marsh-edge control quadrats. The presence of mussels on the marsh flat also had an effect on vertical marsh expansion (Fig. 8). Mussel removal significantly reduced ($P < .01$, Scheffé test) vertical growth on the flat relative to the control quadrats, and the addition of mussels on the marsh flat resulted in vertical marsh growth that did not differ ($P > .50$, Scheffé test) from that on the leading edge of the marsh.

The marsh height data (Fig. 8) also showed that vertical marsh expansion occurs primarily in the summer months, while in the winter months, erosion of surface sediment from ice scouring (Redfield 1972) would appear to prevent vertical marsh expansion ($P < .001$, ANOVA; considering height changes between sampling dates).

The seaward horizontal expansion of *Spartina* tillers and mussels from experimental quadrats on the marsh edge is presented in Table 3. In control quadrats with natural mussel densities, *Spartina* tillers were found to have moved seaward from the initial edge of *Spartina* shoots ($P < 0.05$, *t* test). In the edge mussel-removal plots, however, the leading seaward edge of *Spartina* tillers showed significant landward movement ($P < .05$, *t* test). This suggests that mussels on the leading edge of the marsh facilitate the seaward expansion of *Spartina.*

Mussels also showed significant seaward expansion in both the marsh-edge control and mussel-removal plots ($P < .05$, *t* test, both cases). Seaward expansion of mussels on the edge of the marsh did not differ significantly ($P > .05$, *t* test) between control and removal plots, ruling out the possibility that the observed mussel movement was the result of the disturbance caused by manipulating mussel density. In addition, the 1981 mussel-removal quadrats had significantly more ($P < .05$, *t* test) mussel cover than the 1982 mussel quadrats in 1983, suggesting that the seaward expansion of mussels on the marsh edge is a continuous process. Of the mussels that moved into the removal quadrats, >90% were adult mussels >3 yr old, and not recruiting juveniles (M. D. Bertness, *personal observation*). Seaward mussel movement on the marsh edge appears to be the passive byproduct of individual mussel crowding and growth, which pushes mussels into unoccupied space (M. D. Bertness, *personal observation*). These results suggest that mussels facilitate both the vertical and seaward expansion of the marsh on its seaward edge and also accelerate vertical marsh accretion on the marsh flat. While mussel stimulation of belowground *Spartina* biomass (Figs. 5 and 6) must contribute to increases in marsh height and the binding of sediments, mussels themselves appear to play a role in binding marsh sediments and stabilizing substrate against erosion. In the natural marsh habitat, in areas of high mussel density the byssal threads of mussels are a major component of the sediment surface; they appear to both bind and trap sediments. In sediment pots placed in the marsh without mussels, over a 1-yr period minimum change in sediment height per replicate measured −1.90 ± 1.36 cm ($n = 20$ pots), while maximum sediment-level change per replicate was −5.45 ± 2.01 cm ($n = 20$ pots). In sediment pots with mussels at normal field densities, minimum sediment erosion per replicate was zero (0 ± 0 cm, $n = 20$ pots) and maximum sediment erosion per replicate (−1.95 ±

TABLE 1. Nutrient concentrations in *Spartina alterniflora* tissue from control and mussel-manipulation plots on the marsh edge and marsh flat. All values are means ±SE. Sample size is 10 for each. Values that are significantly different ($P < .05$, ANOVA) between edge and flat habitats in the control treatments are indicated by a superscript *a*. The presence of mussels did not significantly affect ($P > .05$, ANOVA) any variable examined.

Habitat treatment	Nitrogen* (% of dry mass)	Potassium† (g/kg)	Magnesium† (g/kg)	Calcium† (g/kg)
Marsh flat				
Controls	1.14 ± 0.43	9500 ± 1878	4134 ± 302[a]	2129 ± 612
Mussel removals	1.04 ± 0.14	9346 ± 1182	4492 ± 400	2192 ± 363
Mussel additions	1.02 ± 0.13	9303 ± 1992	4315 ± 319	2483 ± 644
Marsh edge				
Controls	0.90 ± 0.03	8391 ± 1218	5138 ± 500[a]	2136 ± 378
Mussel removals	1.10 ± 0.12	7828 ± 1159	5237 ± 575	2403 ± 618

* Total nitrogen, Kjeldahl method.

† Colorimetric determination.

TABLE 2. Nutrient concentrations of dried sediment samples collected from quadrats on the marsh edge and flat. All values are means ±SE. Sample size is 10 replicate quadrats for each treatment. For within-habitat comparisons, values different from the controls are indicated with a superscript *a* ($P < .05$, Scheffé test) or *b* ($P < .10$, Scheffé test).

Habitat treatment	Nitrogen* (% of dry mass)	Potassium (g/kg)	Magnesium (g/kg)	Calcium (g/kg)	Phosphorus (g/kg)
Marsh flat					
Controls	0.93 ± 0.07	1350.0 ± 74	3218.0 ± 121	2770.2 ± 140	71.5 ± 9
Mussel removals	0.76 ± 0.09^a	1301.0 ± 58	3243.6 ± 142	3154.4 ± 215	62.5 ± 8
Mussel additions	1.08 ± 0.04	1477.2 ± 35^a	3659.3 ± 160^a	2983.0 ± 163	64.5 ± 10
Marsh edge					
Controls	0.93 ± 0.06	1503.0 ± 80	4023.4 ± 130	4097.3 ± 186	28.2 ± 6
Mussel removals	0.75 ± 0.10^b	1412.5 ± 67	3598.8 ± 191^b	3784.1 ± 166^a	34.0 ± 9

* Total nitrogen, Kjeldahl method.

0.85 cm, $n = 20$ pots) was less than half that of pots without mussels ($P < .001$, *t* test). These data examined in relation to the extremely high density of mussels found in some marsh habitats strongly suggest that mussels can play a major role in stabilizing marsh sediments against erosion.

DISCUSSION

Results presented in this paper demonstrate that the ribbed mussel, *Geukensia,* plays a major role in dictating the production of *Spartina* in habitats where mussels are common. Marshes where mussels densely populate the leading edge of *Spartina*-dominated habitats, e.g., Rumstick Cove, are common in protected littoral areas in southern New England (M. D. Bertness, *personal observation*). In these areas mussels appear to be a potent mediator of *Spartina* production and ultimately marsh development and stability.

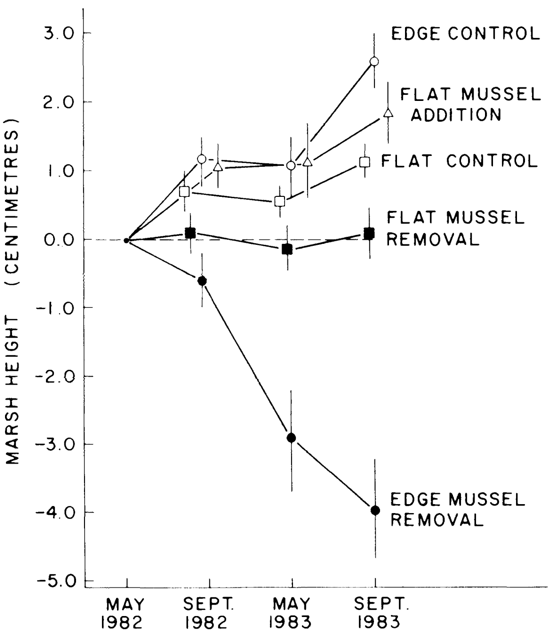


FIG. 8. Cumulative elevation changes in the tidal height of all 1981- and 1982-initiated permanent quadrats over time, in centimetres. All data are from level rods installed in the quadrats in April 1982. ○ = marsh edge control quadrats, ● = marsh edge mussel-removal quadrats, □ = marsh flat control quadrats, ■ = marsh flat mussel-removal quadrats, and △ = marsh flat mussel-addition quadrats. Error bars are ±1 SE.

The relationship between *Geukensia* and *Spartina* appears to fit the definition of a facultative mutualism. Neither species is an obligate dependent on the other, but their association benefits both. The positive influence of mussels on *Spartina* success is documented in this paper, and previous research (Stiven and Kuenzler 1979) has demonstrated that increased *Spartina* production increases both individual and population growth of *Geukensia.* Both species, however, do well on their own. In southern New England marshes, the common association between mussels and *Spartina* appears to result from the gregarious settlement of juvenile mussels near conspecifics in conjunction with increased survivorship of mussels associated with *Spartina.* Mussels do not preferentially settle on or near *Spartina* (M. D. Bertness, *personal observation*).

Mechanism of the Spartina-Geukensis *facilitation*

The mechanism of the positive influence of mussels on *Spartina* appears not to be attributable to a single proximate factor and to vary between marsh habitats. The initial hypothesis that the filter feeding and movement of *Geukensia* in the substrate increases soil oxygen levels and thereby stimulates *Spartina* growth (Howes et al. 1981) is rejected. In both the marsh edge and flat habitats, mussels are experimentally shown to have no marked effects on substrate redox (Fig. 7), and substrate redox does not correlate with variation in aboveground *Spartina* biomass in either habitat.

The second initially hypothesized mechanism whereby mussels could stimulate *Spartina* production is by influencing soil nutrient levels. As a filter feeder, *Geukensia* filters and processes a large portion of the tidal water volume during each tidal cycle, and the result of this activity is that particulate matter and metabolic waste products in the form of consolidated feces and pseudofeces are deposited on the marsh sediment (Jordan and Valiela 1982). In addition, *Geukensia* continually produces proteinaceous byssal threads for attachment and movement; these can potentially decompose and further augment soil nutrient supply. In either case, the presence of mussels could transfer and concentrate nutrients from the water column to the sediment surface, and by increasing sediment nutrient levels facilitate *Spartina* production. Experimental and correlative evidence presented in this paper support this mechanism. On the marsh flat, substrate nutrient levels, especially nitrogen, show a strong positive correlation with mussel abundance, and mussel density predicted *Spartina* biomass as well as the supply of any soil nutrient. Most important, manipulative field experiments clearly demonstrate the role of mussels in supplementing the supply of soil nutrients (Table 2) and increasing *Spartina* production (Fig. 4) on the marsh flat. Nutrient augmentation appears to be the primary mechanism of the positive influence of mussels on cordgrass production on the marsh flat, but appears to be of lesser importance in mediating *Spartina* production on the marsh edge.

The final mechanism among the hypotheses regarding the *Geukensia-Spartina* interaction was the role of substrate stabilization and sediment binding by *Geukensia.* The seaward expansion of *Spartina* stands and marshes in general is considered to represent a balance between the growth and expansion of *Spartina* to lower intertidal levels and the destructive physical forces of soil erosion and physical disturbance caused by storms and winter ice (Redfield 1972, Delaune et al. 1978). When mussel densities are great on the edge of marshes, mussels may serve to prevent soil erosion and physical disturbance. Mussels attach to the marsh root mat with strong byssal threads, and when mussel densities are high, substrate binding by the byssal thread network is evident. Mussel removal from the marsh edge at Rumstick Cove reduced the biomass of *Spartina* roots and rhizomes (Figs. 5 and 6) which normally bind edge sediments and allow for marsh expansion (Redfield 1972), and resulted in marked vertical and horizontal erosion of the edge of the marsh in <18 mo (Fig. 8). Conversely, addition of mussels to the marsh flat to mimic the density of mussels naturally found on the marsh edge resulted in increased marsh accretion (Fig. 8).

While mussel abundance on the marsh flat was strongly correlated with nutrient levels and *Spartina* biomass, on the marsh edge aboveground *Spartina* biomass was highly correlated with mussel abundance, but not with sediment nutrient levels. Mussel manipulations on the marsh edge strongly influenced *Spartina* biomass but did not markedly influence soil nutrients. This strongly suggests that the role of mussels on the marsh edge is primarily due to substrate stabilization.

Mussels, Spartina *productivity, and marsh growth and stability*

The factors that dictate the productivity and expansion of salt marshes are complex, and the role of mussels in influencing *Spartina* production appears to differ in the marsh edge and marsh flat habitats. In Fig. 9 I have outlined a simple conceptual model of the interaction of some of the variables that dictate marsh development. Facultative mutualism between *Spartina* and *Geukensia* is central to marsh development in the model, which is intended to reflect marsh development in areas with large populations of mussels, such as Rumstick Cove. By increasing *Spartina* primary production, preventing erosion by binding *Spartina* rootmat, accelerating sedimentation, and stabilizing the root mat from possible physical disturbance, *Geukensia* is proposed to accelerate and stabilize marsh growth. Conversely, by increasing the growth rate of *Geukensia* (Stiven and Kuenzler 1979) and decreasing mussel mortality (M. D. Bertness, *personal observation*), *Spartina* ameliorates the success of *Geukensia.* The role of *Spartina* in marsh growth is partitioned into the roles of slowing water currents, and thereby increasing sedimentation rates, and binding of marsh sediment by the root mat (Gibbs 1902, Redfield 1972). Both of these processes are accelerated by increased *Spartina* production. Erosion of the marsh and physical disturbance act as destructive forces that prevent marsh expansion. While this model is designed to account for factors influencing the expansion of protected New England marshes, which are subject to heavy annual winter disturbance and harbor large mussel pop-

TABLE 3. Movement of *Spartina alterniflora* and *Geukensia demissa* in permanent quadrats on the edge of the marsh ($\bar{x} \pm 1$ SE). All data were taken in September 1983 on quadrats that had been established one (1982 quadrats) and two (1981 quadrats) years before monitoring. Positive *S. alterniflora* and *G. demissa* movement indicates net seaward migration; negative movement indicates net landward migration. *S. alterniflora* and *G. demissa* horizontal movement data were not available from the 1981 quadrats. A superscript *a* indicates a significant difference ($P < .001$, *t* test) between control and mussel-removal quadrats; superscript *b* indicates a significant difference ($P < .002$, *t* test) between 1981- and 1982-initiated quadrats.

	Spartina alterniflora movement (cm)	*Geukensia demissa* movement (cm)	*Geukensia demissa* cover (%)
1982 control quadrats	+12.78 ± 1.87	+15.00 ± 2.09	100 ± 0
1982 mussel-removal quadrats	-9.78 ± 4.62^{a}	+11.44 ± 1.72	20.78 ± 2.13^{b}
1981 control quadrats	...	...	96.0 ± 3.21
1981 mussel-removal quadrats	...	...	30.25 ± 1.94^{b}

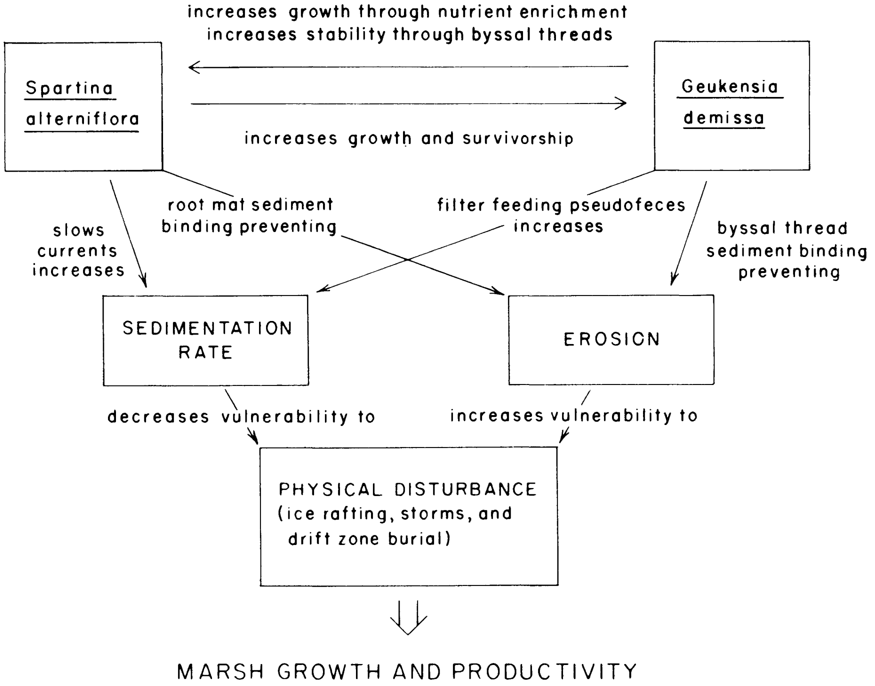


FIG. 9. Conceptual model of potential interactions influencing marsh growth.

ulations, its major components are generally applicable to the development of all marsh systems. It stresses the dynamic aspect of marsh systems and emphasizes that any factor (biotic or physical) that influences the success of marsh grasses potentially influences the development, size, and stability of marshes.

The role of plant-animal interactions in mediating marsh productivity and growth is virtually unexplored. While the *Geukensia-Spartina* interaction may be important in other marsh habitats, other nonconsumer plant-animal interactions may be equally important in salt marsh systems. All filter-feeding, burrowing, and deposit-feeding animals of salt marshes potentially have important habitat-modifying effects that may influence marsh grass productivity, and ultimately, marsh growth. Since the effect of plant-animal interactions on marsh grass productivity may be mediated by a complex interaction of proximate mechanisms, e.g., influences on soil nutrients, soil aeration and soil stability, the actual role of these animals in salt marshes cannot be assessed inferentially (see Paine 1977). Correlative studies among New England salt marshes have not suggested relationships between animal abundance and *Spartina* production (Nixon and Oviatt 1973, Oviatt et al. 1977). Elucidation of the role of habitat-modifying animals on marsh dynamics will require carefully controlled manipulative field experimentation designed to test explicit hypotheses.

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LITERATURE CITED

Allen, Stewart E., editor. 1974. Chemical analysis of ecological materials. Wiley and Sons, New York, New York, USA.

Ayers, J. C. 1959. The hydrography of Barnstable Harbor, Massachusetts. Limnology and Oceanography **4**:448–462.

Barber, M. C. 1984, *in press*. Below-ground interactions among three salt marsh plants: *Spartina alterniflora, Spartina patens,* and *Junius roemerianus*. I. Rhizome distribution and morphology. Journal of Ecology.

Bell, S. S., M. C. Watzin, and B. C. Coull. 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. Journal of experimental Marine Biology and Ecology **35**:99–107.

Broome, S. W., W. W. Woodhouse, and E. D. Seneca. 1975. The relation of mineral nutrients to growth of *Spartina alterniflora* in North Carolina. I. Nutrient status of plants and soils in natural stands. Proceedings of the Soil Science Society of America **39**:295–301.

Connor, M. S., and J. M. Teal. 1982. The effect of feeding by mud snails, *Ilyanassa obsoleta,* on the structure and metabolism of a laboratory benthic algal community. Journal of Experimental Marine Biology and Ecology **65**:29–45.

Daiber, F. C. 1982. Animals of the tidal marsh. Van Nostrand Reinhold, New York, New York, USA.

Delaune, R. D., W. H. Patrick, and R. J. Buresh. 1978. Sedimentation rates determined by ^{137}Cs. Nature **275**:532–533.

Gallagher, J. L. 1974. Sampling macro-organic matter profiles in salt marsh plant root zones. Proceedings of the Soil Science Society of America **38**:154–155.

———. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus.* American Journal of Botany **62**:644–648.

Gallagher, J. L., R. J. Reimold, R. A. Linthurst, and W. J. Pfeiffer. 1980. Aerial production, mortality, and mineral accumulation-export dynamics in *Spartina alterniflora* and *Juncus roemerianus* stands in a Georgia salt marsh. Ecology **61**:303–312.

Gibbs, R. E. 1902. *Phyllospadix* as a beach builder. American Naturalist **36**:101–109.

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

Jordan, T. E., and I. Valiela. 1982. The nitrogen budget of the ribbed mussel, *Geukensia demissa,* and its significance in nitrogen flow in a New England salt marsh. Limnology and Oceanography **27**:75–90.

King, G. M., M. J. Klug, R. G. Wiegert, and A. G. Chalmers. 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia salt marsh. Science **218**:61–63.

Mendelssohn, I. A. 1979. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. Ecology **60**:574–584.

Mendelssohn, I. A., K. L. McKee, and W. H. Patrick. 1981. Oxygen deficiency in *Spartina alterniflora* roots; metabolic adaptation to anoxia. Science **214**:439–441.

Montague, C. L. 1980. A natural history of temperate Western Atlantic fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. Contributions in Marine Science **23**:25–55.

Mooring, M. T., A. W. Cooper, and E. D. Seneca. 1971. Seed germination response and evidence for height ecophenes in *Spartina alterniflora* from North Carolina. American Journal of Botany **58**:48–55.

Naumann, P. C. 1982. Chemical soil test procedures. Soil Resource Series 8, University of Rhode Island, Kingston, Rhode Island, USA.

Nixon, S. W., and C. A. Oviatt. 1973. Analysis of local variation in the standing crop of *Spartina alterniflora.* Botanica Marina **16**:103–109.

Oviatt, C. A., S. W. Nixon, and J. Garber. 1977. Variation and evaluation of coastal salt marshes. Environmental Management **1**:201–211.

Paine, R. T. 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Proceedings of the National Academy of Sciences (USA) Special Publication **12**:245–270.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145–178.

Perkin Elmer. 1982. Analytical methods for atomic absorption spectrophotometry. Perkin Elmer Corporation, Norwalk, Connecticut, USA.

Redfield, A. C. 1972. Development of a New England salt marsh. Ecological Monographs **42**:201–237.

Reidenbaugh, T. G., and W. C. Banta. 1980. Origin and effects of tidal wrack in a Virginia salt marsh. Gulf Research Reports **6**:393–401.

Ringold, P. 1979. Burrowing, root mat density, and the distribution of fiddler crabs in the Eastern United States. Journal of Experimental Marine Biology and Ecology **36**: 11–21.

Smart, R. M., and J. W. Barko. 1980. Nitrogen nutrition and salinity tolerance of *Distichlis spicata* and *Spartina alterniflora.* Ecology **61**:630–638.

Stalter, R., and W. T. Batson. 1969. Transplantation of salt marsh vegetation, Georgetown, South Carolina. Ecology **50**: 1087–1089.

Stiven, A. E., and E. J. Kuenzler. 1979. The response of two salt marsh molluscs, *Littorina irrorata* and *Geukensia demissa,* to field manipulations of density and *Spartina* litter. Ecological Monographs **49**:151–171.

Teal, J. M., and J. W. Kanwisher. 1966. Gas transport in the marsh grass, *Spartina alterniflora.* Journal of Experimental Botany **17**:355–361.

Turner, R. E. 1976. Geographic variations in salt marsh macrophyte production: a review. Contributions in Marine Science **20**:47–68.

Valiela, I., and J. M. Teal. 1974. Nutrient limitation in salt marsh vegetation. Pages 547–563 *in* R. J. Reimold and W. H. Queen, editors. Ecology of halophytes. Academic Press, New York, New York, USA.

Valiela, I., J. M. Teal, and W. G. Deuser. 1978. The nature of growth forms in the salt marsh grass, *Spartina alterniflora.* American Naturalist **112**:461–470.