

Impact of Fertilization on a Salt Marsh Food Web in Georgia

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Abstract We examined the response of a salt marsh food web to increases in nutrients at 19 coastal sites in Georgia. Fertilization increased the nitrogen content of the two dominant plants, *Spartina alterniflora* and *Juncus roemerianus*, indicating that added nutrients were available to and taken up by both species. Fertilization increased *Spartina* cover, height, and biomass and *Juncus* height, but led to decreases in *Juncus* cover and biomass. Fertilization increased abundances of herbivores (grasshoppers) and herbivore damage, but had little effect on decomposers (fungi), and no effect on detritivores (snails). In the laboratory, herbivores and detritivores did not show a feeding preference for fertilized versus control plants of either species, nor did detritivores grow more rapidly on fertilized versus control plants, suggesting that changes in herbivore abundance in the field were driven more by plant size or appearance than by plant nutritional quality.

Community patterns in control plots varied predictably among sites (i.e., 17 of 20 regression models examining variation in biological variables across sites were significant), but variation in the effects of fertilization across sites could not be easily predicted (i.e., only 6 of 20 models were significant). Natural variation among sites was typically similar or greater than impacts of fertilization when both were assessed using the coefficient of variation. Overall, these results suggest that eutrophication of salt marshes is likely to have stronger impacts on plants and herbivores than on decomposers and detritivores, and that impacts at any particular site might be hard to distinguish from natural variation among sites.

Keywords Eutrophication · Fertilization · Herbivory · *Juncus* · Salt marsh · *Spartina*

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Introduction

One of the most important current issues facing conservation biologists and ecologists is the increased loading of nitrogen to terrestrial and aquatic environments (Peierls et al. 1991, Vitousek 1994, Soulé and Orians 2001). The effects of increased nitrogen inputs include alterations to the atmospheric chemistry (Schlesinger et al. 2001), reduced water quality in aquatic systems (Paerl et al. 1998, Rabalais et al. 2002), and changes to ecological processes at the population, community, and ecosystem levels (Vitousek 1994, Heip 1995, Micheli et al. 2001).

Salt marshes may experience particularly large increases in nitrogen inputs because they occur downstream of entire watersheds, and hence potentially are exposed to nitrogen inputs in runoff, groundwater flow, and stream flow that are concentrated from large adjacent terrestrial landscapes (Peierls et al. 1991, McClelland et al. 1997, Bowen and

Valiela 2001). Because salt marshes provide many valuable ecosystem services to society (Kneib 1997, Bertness 1999, Mitsch and Gosselink 2000), it is important to understand how these nitrogen inputs may alter salt marsh function.

Early studies of nutrient effects in salt marshes focused on the performance of single plant species in monoculture, and demonstrated that salt marsh plants were primarily limited by nitrogen and not by phosphorus (Valiela and Teal 1974, Broome et al. 1975, Gallagher 1975). Recent studies of mixed stands of plants have demonstrated that increases in nitrogen may alter the composition of marsh plant communities by favoring some species that competitively suppress others (Levine et al. 1988a; Emery et al. 2001, Bertness et al. 2002, Pennings et al. 2002). In particular, the dominant low-marsh plant along the Atlantic and Gulf Coasts of the United States, *Spartina alterniflora*, usually increases in abundance with increased nutrients (Pennings et al. 2005). The response to nutrients of other marsh plants, however, appears to vary geographically or as a function of which other plant species are present in the community (Brewer 2003, Pennings et al. 2005). Pennings et al. (2002) speculated that variation in response of marsh plant communities to nutrients might be explained by variation among sites in edaphic conditions (e.g., soil salinity, redox potential, organic matter, texture, bulk density, etc.). These authors did not examine a wide enough range of different edaphic conditions, however, to rigorously test this hypothesis. To guide coastal management in the face of widespread coastal eutrophication, it is essential that we understand how greatly responses to nutrient addition will vary among sites, and what mediates this variation.

Nitrogen additions likely do not only affect primary producers, but also flow through the food web to affect other trophic levels (Vince et al. 1981, Tober et al. 1996, Rosemond et al. 2001). Although almost all trophic levels are potentially limited by nitrogen (Sterner and Elser 2002), whether particular populations actually respond to added nitrogen in the field depends on what additional factors constrain their response. For example, responses of salt marsh herbivores to nitrogen, although generally positive, have been suggested to be limited by competition, predation or life-cycle constraints (Vince et al. 1981, Stiling et al. 1991, Moon and Stiling 2002). Similar constraints might limit the responses of decomposers or detritivores to nutrient additions. A number of field studies have examined the response of salt marsh herbivores to nutrients (Vince et al. 1981, Bowdish and Stiling 1998, Levine et al. 1998b, Gratton and Denno 2003), but only one examined the response of salt marsh fungi (Newell et al. 1996) and none has examined responses by detritivores, despite extensive work on the feeding ecology of salt marsh detritivores in the laboratory (Rietsma et al. 1988, Kneib et al. 1997, Graca et al. 2000). Because many of the ecosystem services

provided by salt marshes depend on these other trophic levels, it is critical to understand how they will be affected by eutrophication, and whether these effects will vary predictably among sites.

To address these issues, we conducted fertilization experiments at 19 sites in Georgia that varied widely in edaphic conditions such as salinity, organic matter content of soils, and reduction-oxidation potential. To avoid complications arising from studying communities that differed in species composition, we focused on the border between the two most abundant plants on the Southeast and Gulf Coasts of the U.S.: *Spartina alterniflora* and *Juncus roemerianus*, and their associated herbivores, decomposer fungi, and detritivores. We tested the hypotheses that 1) effects of nutrient addition would be strongest at lower trophic levels and attenuate at higher trophic levels, and 2) effects of nutrient addition would be strongest where soil conditions were most favorable (lower salinity and bulk density; higher redox potential).

Materials and Methods

Study Sites

We worked at 19 sites on the GA coast that contained stands of monospecific *Spartina alterniflora* bordering stands of monospecific *Juncus roemerianus* (hereafter we refer to both plants generically). Ten sites were located on Sapelo Island, and nine on the mainland in McIntosh County, GA. Ten 1-m² plots with approximately equal abundance (based on percent cover) of the two plant species were established at each site in July 2000. Five plots were assigned to the fertilization treatment and five to the control treatment, alternating so that treatments were fully interspersed. Plots were placed >2 m apart to ensure fertilizer would not affect adjacent plots. Plots were fertilized three times over 1 yr (July and September 2000 and May 2001). On each occasion, each plot was fertilized with eleven 21-g tablets (Forestry Suppliers, Inc., Remke Nitroform Tablets, 20–10–5 NPK) to give an application rate (140 g N m⁻² yr⁻¹), similar to the “low dosage” rate of Vince et al. (1981). A metal corer was used to remove soil plugs to a depth of 10 cm, a tablet placed in each hole, and the soil plugs replaced. Control plots were disturbed in the same manner without the addition of the fertilizer tablet. Because salt marshes are primarily limited by N (see “Introduction”), we assume that the fertilization effects that we observed were driven by N; however, it is possible that the P and K in the fertilizer also had some effects.

To characterize variation in edaphic conditions across sites, we measured porewater salinity and soil redox potential, organic matter content, bulk density, and texture.

Porewater salinity was measured at each site in July, August, and September 2000 and May, July, and August 2001. Five soil cores were collected between plots along the *Spartina/Juncus* border to a depth of 10 cm. The deepest 3 cm portion of each core was pooled to yield a single composite sample per site. Samples were returned to the laboratory, weighed wet, dried at 60°C for 3 d, and reweighed. A measured volume of deionized water was mixed with the soil and the salinity of the supernatant was measured after 36 h. Original soil salinity was calculated as (supernatant salinity \times ml deionized water added / soil wet–dry mass).

Soil redox conditions were measured at each site in August and September 2000 and June, July, August, and September 2001. Redox values (7 cm depth) were measured between plots at three points along the *Spartina/Juncus* border using an Orion® platinum electrode with an internal Ag–AgCl reference electrode. Areas with dense crab burrows were avoided. Uncorrected values obtained from the handheld meter are reported.

Soil organic matter content was measured in July and August 2001 for each site as loss on ignition. Three soil samples (5 cm deep) were collected between plots along the *Spartina/Juncus* border, pooled, dried, ground and weighed, ashed in triplicate at 250°C for 2 h and 500°C for 8 h, and reweighed. The proportion of organic matter in the soil was calculated as (mass lost after ignition [g]) / (initial dry mass [g]).

Bulk density of the soil at the *Spartina/Juncus* border at each site was measured on June 2001. Two soil cores (10.2 cm deep, 216.62 cm³ volume) were collected outside of plots without compacting the soil. Samples were dried and then weighed. Bulk density of each sample was calculated as (mass [g] / volume [cm³]). Soil texture (percent sand, silt, and clay) was measured on June 2002 for two samples from each site using the hydrometer method (Gee and Bauder 1986). The sum of percent silt and clay values was used as a single variable for statistical analysis because these two fractions comprised the smallest component of the soil.

Because soil organic matter, bulk density, and silt + clay content were all correlated with each other, a composite soil variable obtained from the first principle component axis of a PC ordination of these variables was used for regression analyses. This variable, hereafter called “soil”, explained 88.4% of the variance in the data, and was positively correlated with bulk density, and negatively with organic content and silt + clay.

To characterize the position of the sites within the landscape, we assigned each site values for 1) “site-score” and 2) island or mainland location. Sites were evaluated for site-score using an index ranging from 1 to 5, with 5 indicating a marsh almost completely surrounded by upland, 3 indicating a straight border between marsh and upland, and 1 indicating a marsh almost completely

surrounding a peninsula of upland. For location, a score of 0 was given to island sites and 1 to mainland sites.

Plant Variables

Percent cover of *Juncus* and *Spartina* ($n=17$ sites) and plant height ($n=19$ sites) were recorded in August 2001. Percent cover was measured using a 0.25-m² quadrat, divided by monofilament line into 100 5 \times 5 cm squares, centered within each 1 \times 1 m plot. The height of the tallest plant of each species within the 0.25 m² quadrat was also recorded. Plants were harvested after two growing seasons, in October 2001, from within a 0.5 \times 0.25 m quadrat centered in each plot with the longer side perpendicular to the vegetation border. The vegetation was sorted by species and divided into living and dead biomass. For *Juncus*, a leaf was considered dead if it was >75% brown. For *Spartina*, shoots with both live and dead leaves were stripped of their dead leaves, which were placed with the dead plant material. Plant samples were dried at 60°C for 4 d and then weighed. Leaves of live (collected July 2001) and dead (June 2001) plants were analyzed for nitrogen content (percent dry mass) using a ThermoFinnigan Flash Elemental Analyzer (1112 Series).

Consumers

We examined five consumers. The salt marsh grasshoppers *Orchelimum fidicinum* and *Paroxya clavuliger* (hereafter referred to generically) are two of the major consumers of *Spartina* and *Juncus*, respectively (Davis and Gray 1966). In salt marshes, the majority of higher plant material enters the detrital food web (Teal 1962) and is decomposed primarily by ascomycetous fungi (Newell 1993). Consumers of the standing dead plant material and fungi include the periwinkle and coffee bean snails, *Littoraria irrorata* Say and *Melampus bidentatus* Say (hereafter referred to generically) (Newell 1993; Kneib et al. 1997; Graca et al. 2000; Silliman and Newell 2003). In addition, the omnivorous marsh squareback crab *Armases cinereum* (hereafter referred to generically) includes decomposing leaves in its broad diet (Buck et al. 2003).

Densities of the salt marsh grasshoppers, *Orchelimum* and *Paroxya*, were recorded in July and August 2001 in all plots at each site, using visual counts. Damage to plants from grasshoppers was estimated in the field during the first week of August 2001 at all sites. At this time, grasshoppers were adult and actively feeding. Damage to five randomly selected plants (*Spartina*) or leaves (*Juncus*) of each species in each plot was estimated to the nearest 5%.

Fungal biomass was measured in standing-dead leaves of *Spartina* collected from each site in October 2001. The lowermost intact fully brown leaf was collected from a

single plant in each control and fertilized plot and processed following Newell (2000). Briefly, leaves were rinsed in running, cold tapwater for 15 s, and a 1-cm length was cut from the ligule end of each leaf and discarded. Another 1-cm portion was cut from the ligule end of each leaf, and the five pieces per treatment from each site were pooled and submerged in 5 ml ethanol in a screw-cap vial. The vials were placed in darkness at 4°C for storage before processing. A third 1-cm length was cut from the ligule end of each leaf, and the five pieces per treatment from each site were pooled, dried, and weighed. Dried samples were ashed for 4 h at 450°C to determine leaf organic mass. Fungal biomass was estimated using ergosterol as a proxy as in Newell (2000). Fungal biomass is reported on a per leaf basis (as microgram ergosterol per gram leaf organic mass [LOM]) and estimated on a per plot basis (as milligram ergosterol per meter square by multiplying fungal biomass per leaf [mg] × average *Spartina* litter biomass [g]).

Densities of the salt marsh snails *Melampus* and *Littoraria* were recorded in July and August 2001 in all plots at each site. Snail density was determined by counting the number of snails found on the soil surface, plant stems and in leaf furls within a 0.5×0.5 m quadrat centered in each plot. The experimental plots were too small to accurately measure fertilization effects on *Armas* densities because these crabs occurred at low densities in this marsh zone.

Consumer Feeding Preferences

To determine whether fertilization affected palatability of leaves to herbivores, we conducted paired feeding assays with grasshoppers *Orchelimum* and *Paroxya*. Undamaged leaves of *Spartina* and *Juncus* were collected from three haphazardly chosen fertilized and control plots at each of 15 sites. Leaves were trimmed to 15 cm in length and their bases placed in a vial of tapwater. Grasshoppers (*Orchelimum* for *Spartina* assays and *Paroxya* for *Juncus* assays, $n=30$ per species) were offered a choice between a control and fertilized leaf from the same site. Each within-site paired comparison was replicated twice, for a total of 30 replicates. Individual grasshoppers were allowed to feed until >25% of either plant piece was eaten, or for a maximum of 3 d.

To determine whether fertilization affected palatability of plant litter to detritivores, we conducted similar paired feeding assays with the snail *Littoraria* and the crab *Armas*. A single standing-dead *Spartina* shoot was collected during the last week of May 2001 from each fertilized and control plot at 15 sites. Attached leaf blades were removed, and the remaining stems and surrounding sheaths were cut to 1- and 2-cm-long portions, weighed, and offered to snails and crabs, respectively. The remaining portion of each stem and surrounding sheath was weighed,

dried at 60°C for 3 d, and reweighed to calculate initial percent water content. Individual snails ($n=30$, ca. 20 mm in spire height) and crabs ($n=30$, carapace width ≥ 20 mm) were offered a choice between litter from fertilized and control plots from the same site. Each comparison ($n=15$ sites) was replicated twice, for a total of 30 replicates per consumer. Individual consumers were allowed to feed until >25% of either plant piece was eaten, or for a maximum of 40 (snails) and 30 (crabs) d, respectively. Remaining plant portions were removed, rinsed free of feces, dried at 60°C for 3 d, and weighed. The final dry weight was subtracted from the initial estimated dry weight to give the amount eaten.

Consumer Growth

To determine if fertilization affected the quality of litter for snail growth, we collected standing-dead *Juncus* and *Spartina* from all plots (one stem per species per plot) at 15 sites. Plant pieces were cut (ca. 7 cm long) at the base of the stem, and pooled within each species per treatment per site. Four of the five collected plant pieces for each treatment and species were haphazardly selected and cut to 5 cm in length. The 5-cm pieces of stem were weighed to determine wet mass. The excised 2 cm of each stem was weighed, dried at 60°C for 3 d, and reweighed to calculate initial percent water content. Small *Melampus* and *Littoraria* (<5 mm spire height, $n=120$ /species) housed individually in Nalgene bottles (125 ml) kept at room temperature were allowed to feed *ad libitum* on a single piece of standing-dead plant material. The complete experiment was replicated twice, for $n=30$ snails per snail species per plant species per treatment. Five milliliters of brackish water (15 psu) was added to each bottle to maintain humidity. Bottles were opened two times per week for ventilation, and distilled water was added as needed to replace evaporation. Snails that died during the first 3 wk were replaced. Snails that died subsequently were dropped from the analysis. Snail spire height was measured to the nearest hundredth of a millimeter at the beginning and end (after 3 mo) of the experiment.

Statistical Analysis

All proportional data were arcsine (square root) transformed and snail densities were natural log transformed to improve normality before statistical analysis. For all analyses, we used sites as the unit of replication. Thus, whenever we took data from multiple plots (e.g., redox potential), individuals (e.g., grasshopper feeding assays), or months (e.g., porewater salinity) we averaged over plots or individuals within a site, and then over months to yield a single site mean for each variable. We used four approaches to analyze results. First, effects of fertilization were compared between treatments using paired *t* tests (or, in

one case, the Wilcoxon Signed Rank test). This approach, which encompasses all variation among sites, simply asks whether there is a response to the treatment that is general across a wide range of sites. Second although we found clear treatment effects overall, there was some variation among sites in both local conditions and responses. We explored this variation using multiple regression analyses. We first examined variation in the control treatment among sites. We then calculated a “fertilization effect” by subtracting the control mean from the fertilized mean for each site, and examined variation in the “fertilization effect” among sites. For each dependent variable examined, we chose independent variables *a priori* that made the most sense biologically for input into the model. Then, results of backward elimination and forward regression (variables were included in the model at individual $P < 0.15$ level) were compared with best subsets regression analyses, and the best model was chosen by evaluating Mallows’ C_p statistic (Mallows 1973), the model adjusted R^2 , and the overall model P value. Because some data were not collected at all sites, sample sizes for regressions ranged from 15 to 19. Collinearity between variables was avoided by dropping potential predictor variables with VIF scores > 5 that made the least sense biologically. Third, we used analysis of variance (ANOVA) to examine the effects of fertilization and plant species on snail growth. Fourth, for each field measurement, we compared variation among sites (control plot means) with variation among treatments by calculating the ratio of their respective coefficients of variation.

Results

Study Sites

Averaged across dates, all edaphic values varied strongly among sites: salinity (range 30–51 psu, average 39), redox potential (range -115 to -346 mV, average -291 mV), organic matter (range 4.8–41.2%, average 17.4), silt and clay content (range 1.0–25.9%, average 13.0), bulk density (range 0.24–1.06 g cm $^{-3}$, average 0.59). We first report general results of fertilization averaged across sites and then explore variation among sites using regression.

General Effects of Fertilization

Fertilization generally favored *Spartina* at the expense of *Juncus*. The biomass of living *Spartina* was 197% greater in fertilized than control plots, whereas the biomass of living *Juncus* was 33% less in fertilized than control plots (Fig. 1a). Similarly, the biomass of standing-dead *Spartina* was 174% greater in fertilized than control plots, whereas the biomass of standing-dead *Juncus* was 31% less in

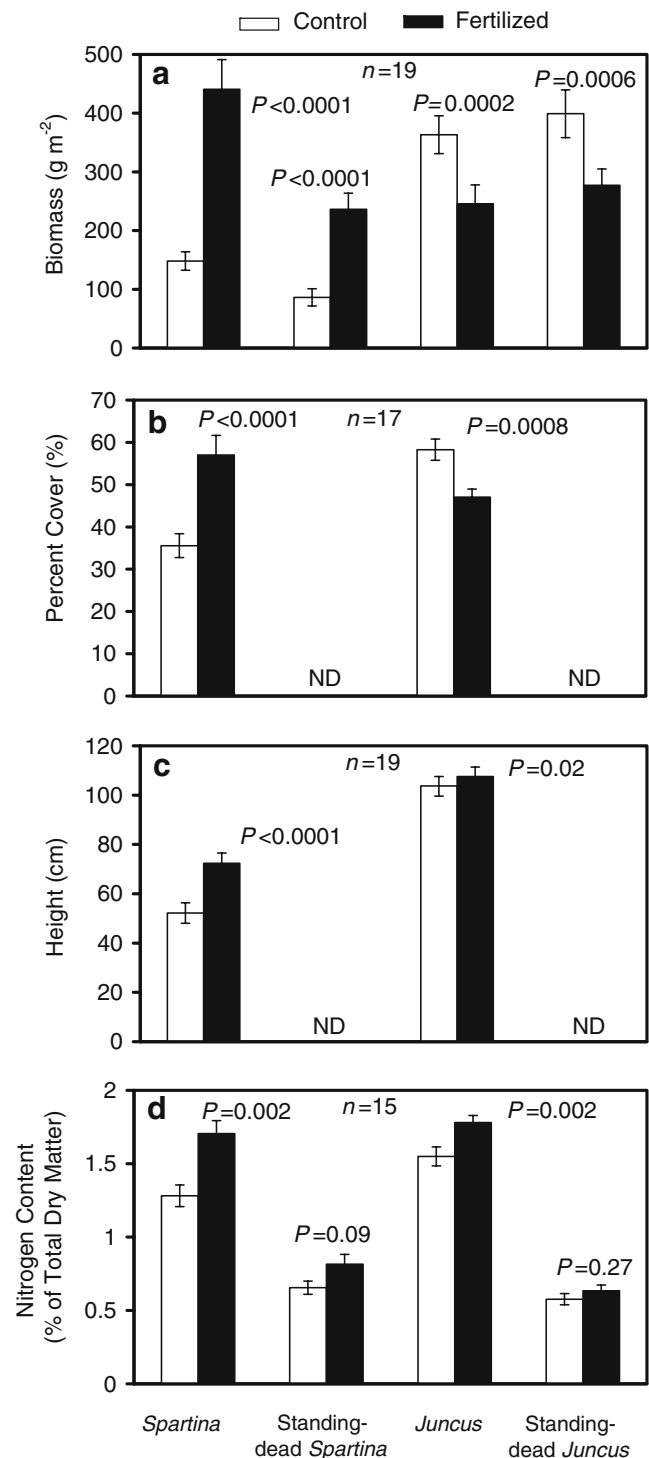


Fig. 1 Plant characteristics at Georgia sites in control and fertilized plots. **a** Above-ground biomass of live and standing-dead *Spartina alterniflora* and *Juncus roemerianus*. **b** Percent cover of live *Spartina* and *Juncus*. **c** Height of live *Spartina* and *Juncus*. **d** Nitrogen content of live and standing-dead *Spartina* and *Juncus* leaves. Data are across-site means per treatment \pm SE (the number of sites (n) is denoted within each figure). ND indicates that percent cover and height data were not collected for standing-dead material

fertilized than control plots. Changes in plant biomass could be caused by changes in percent cover and/or height. Percent cover estimates for each species mirrored live biomass results, with living *Spartina* covering 58% more ground in fertilized than control plots, and living *Juncus* covering 19% less in fertilized than control plots (Fig. 1b). Fertilization increased height of both species. Fertilized *Spartina* plants were 38% taller than control plants, and fertilized *Juncus* plants were 4% taller than controls (Fig. 1c). The nitrogen content of living *Spartina* and *Juncus* leaves was 25% and 15% greater in fertilized than control plots, respectively (Fig. 1d). In contrast, there were no significant differences in the nitrogen content of standing dead leaves of either species, although the trend for both was toward greater nitrogen content in fertilized plots.

Although all herbivores (*Orchelimum* and *Paroxya*) and detritivores (*Littoraria* and *Melampus*) tended to increase in fertilized versus control plots, only *Orchelimum* increased significantly, by 178% (Fig. 2a, c). Although *Paroxya* did not increase significantly in absolute numbers, it did increase significantly in proportion to the amount of *Juncus* present in the plots (i.e., the ratio *Paroxya*–*Juncus* increased 129%, $P=0.04$). Feeding damage by grasshoppers on *Spartina* and *Juncus* was 132% and 61% greater, respectively, in fertilized versus control plots (Fig. 2b).

Fungal biomass per gram of leaf organic matter of standing-dead *Spartina* leaves tended to increase slightly, but not significantly, in fertilized plots (Fig. 2d). However, when fungal biomass was normalized to a per plot basis (by multiplying by dead *Spartina* biomass per square meter), treatments differed significantly, with 210% more fungal biomass in fertilized than control plots. Ergosterol values per leaf reported in this study were similar to those formerly reported (Newell et al. 2000).

Neither *Orchelimum* nor *Paroxya* displayed significant feeding preferences for fertilized versus control plants (Fig. 3a). Similarly, neither *Littoraria* nor *Armas* displayed significant feeding preferences for fertilized versus control dead *Spartina* (Fig. 3b). Both *Orchelimum* and *Armas*, however, exhibited weak trends toward greater consumption of the fertilized treatment.

The growth of *Littoraria* and *Melampus* fed on a diet of senescent *Spartina* and *Juncus* did not differ among fertilization treatments (Fig. 4). Growth of *Melampus*, however, differed between plant species, with 267% better growth on *Spartina* versus *Juncus*.

Variation in Responses Among Sites

Natural (i.e., control treatment) site to site variation in the plant and consumer variables was usually (17 of 20 cases) predictable (Table 1). In contrast, only a few (6 of 20) of the calculated “fertilization effects” varied predictably among

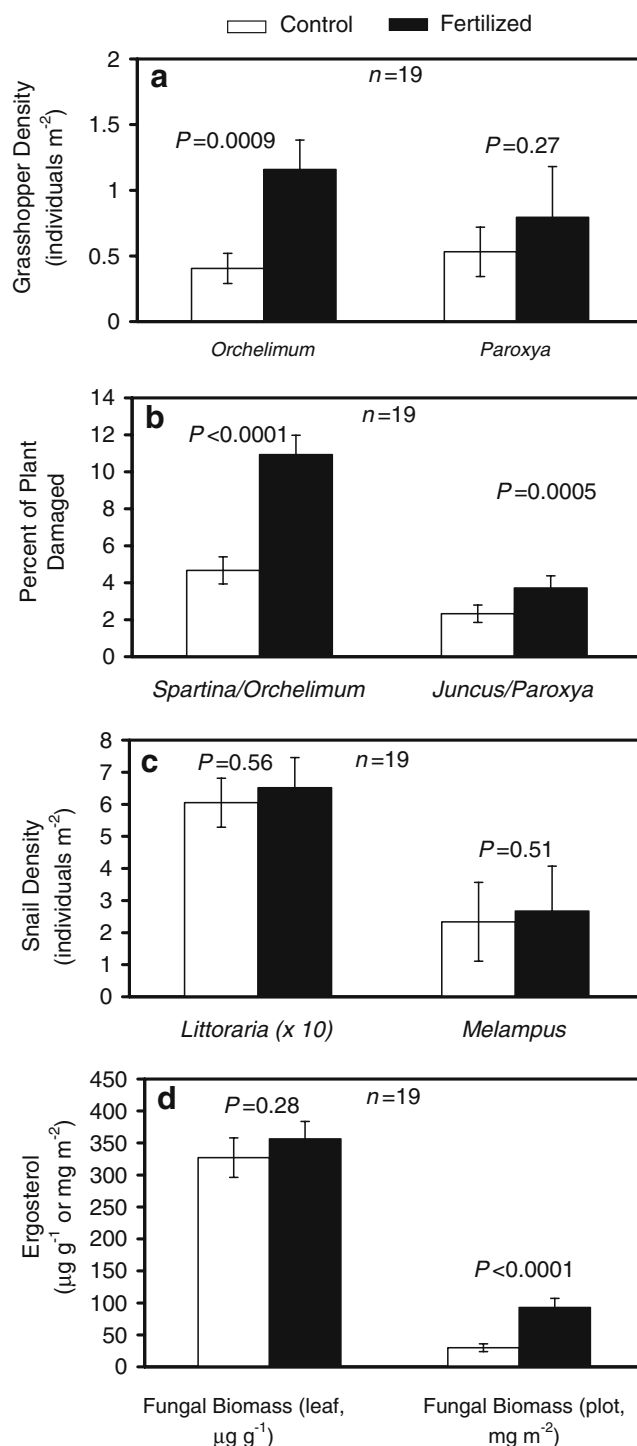


Fig. 2 Herbivore, detritivore, and fungal density in control and fertilized plots. **a** Density of the grasshoppers *Orchelimum fidicinum* and *Paroxya clavuliger*. **b** Grazing damage by grasshoppers to *Spartina alterniflora* and *Juncus roemerianus*. **c** Density of the snails *Melampus bidentatus* and *Littoraria irrorata* (values scaled for clarity of presentation). **d** Fungal biomass on leaves of standing-dead *Spartina* reported as ergosterol on a per leaf (g LOM) and per plot basis. Data are across-site means per treatment \pm SE ($n=19$ sites)

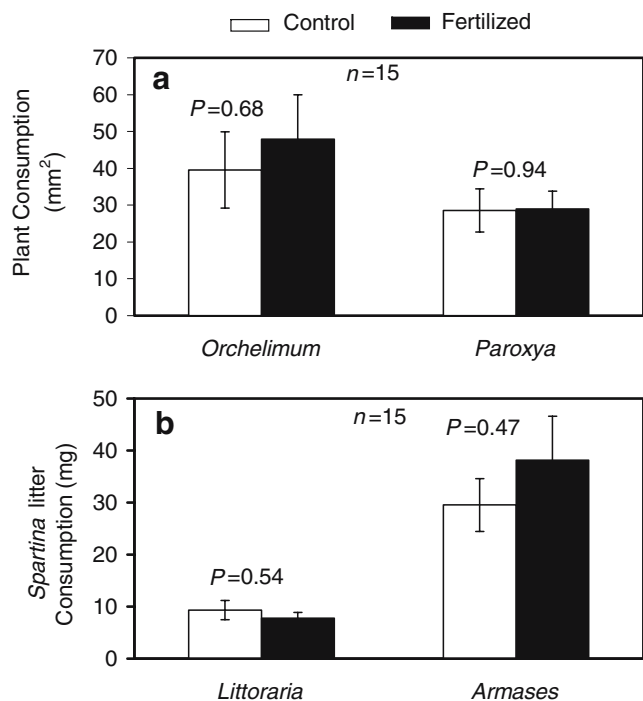


Fig. 3 Herbivores and detritivores, plant consumption. (a) Consumption of *Spartina* leaves by *Orchelimum fidicinum*, and *Juncus roemerianus* leaves by *Paroxya clavuliger*, in two-choice feeding assays. (b) Consumption of *Spartina alterniflora* litter by *Littoraria irrorata* and *Armases cinereum* in two-choice feeding assays. Data are across-site means per treatment ± SE (n=15 sites)

sites. In both cases, the regression models were often complicated, and given that we had a modest number of sites and a large number of potential predictor variables, some relationships might be because of chance. Nevertheless, a high proportion of the relationships made sense biologically. We emphasize these most interesting and biologically reasonable relationships in the discussion.

Discussion

We found striking effects of fertilization on the salt marsh food web. Many of these effects were consistent with previously published results, but by examining multiple variables in a single study we were able to compare the relative impact of nutrients on different aspects of the food web.

Plant Community Responses

In salt marshes on the Atlantic and Gulf coasts of the United States, *Spartina alterniflora* typically dominates lower marsh zones and *Juncus* species (*J. gerardii* at high latitudes and *J. roemerianus* at low latitudes) higher marsh zones. Past work has shown that *S. alterniflora* increases in height, cover, and biomass with nutrient additions (Levine

et al. 1998a; Emery et al. 2001; Pennings et al. 2002), as reported here. On the Atlantic Coast, this increase typically comes at the expense of *Juncus* spp., probably because of competition from *Spartina*, but studies on the Gulf Coast report little change in *Juncus* biomass despite increases in *S. alterniflora* (Pennings et al. 2002; Brewer 2003). We also found that *Juncus* decreased in cover and biomass in GA, but parallel studies in three MS sites (Brewer, unpublished data) found that *Juncus* tended to increase in biomass (by 57%) in fertilized plots (fertilized 353 g m⁻² + 232 SD; control 225 + 119, n=3, P=0.22) rather than decrease. *Spartina* biomass, however, increased by 247% (fertilized 468 g m⁻² + 47; control 135 + 11, P=0.01), so fertilization still shifted plots toward proportional dominance by *Spartina*. *Juncus* also increased in biomass with fertilization at two of the 19 GA sites, but we were unable to identify anything unique about these sites that would explain this variation. We suspect that the increase in *Juncus* in MS is a transient phenomenon, because the results of Brewer (2003) in MS suggest that over the long term, N enrichment would lead to displacement of *Juncus* by *Spartina* because of the latter's superior ability to compete for space when N availability is high. Thus, we speculate that the competitive dynamics in MS (and two of the GA sites) are slower than at most GA sites, but that the ultimate outcome of N enrichment would be the same: displacement of *Juncus* by *Spartina*.

Although we could not predict site to site variation in fertilization effects, variation among sites in control plots was highly predictable (Table 1). Most notably, percent cover of both plants was correlated with “mainland” (positively for *Juncus* and negatively for *Spartina*) and negatively correlated with grazing damage to each species. Height of both plants was negatively correlated with “soil” (as was percent cover of *Spartina* and biomass of *Juncus*) and salinity, and positively correlated with site-score.

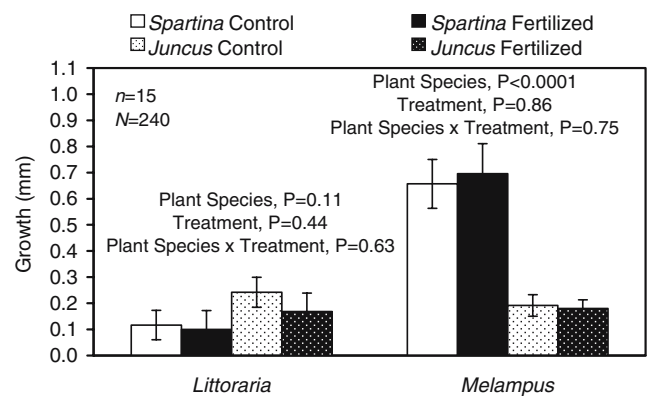


Fig. 4 Snail Growth. Growth of *Littoraria irrorata* and *Melampus bidentatus* fed either a control or fertilized stem of standing-dead *Spartina alterniflora* or leaf of standing-dead *Juncus roemerianus*. Data are across-site means per treatment ± SE (n=15 sites)

Table 1 Summary of results of multiple regression models describing variation in variables across sites (control plots only) and variation across sites in fertilization effect (fertilized mean-control mean)

Variable	Control	Fertilization effect	
Percent Cover	<i>Spartina</i>	–S*, –ML*, –SAL**, –GS** adjusted $R^2=0.72$, $P=0.0004$, $n=17$	NS, $n=17$
	<i>Juncus</i>	+ML*, +R**, –SS*, –GJ*, +JLN*, +P* adjusted $R^2=0.72$, $P=0.008$, $n=15$	NS, $n=17$
Height	<i>Spartina</i>	–S***, –ML, –SAL**, +SS*, –GS***, –SLN adjusted $R^2=0.91$, $P=0.0001$, $n=15$	NS, $n=19$
	<i>Juncus</i>	–S***, –SAL, +SS**, –P adjusted $R^2=0.83$, $P<0.0001$, $n=19$	NS, $n=19$
Biomass	<i>Spartina</i>	–R**, +SLN* adjusted $R^2=0.61$, $P=0.001$, $n=15$	NS, $n=19$
	<i>Juncus</i>	–S, –ML, +SS**, +JLN* adjusted $R^2=0.52$, $P=0.02$, $n=15$	NS, $n=19$
	<i>Spartina</i> litter	–R**, –SS* adjusted $R^2=0.40$, $P=0.006$, $n=19$	+S*, –R*, +SLB* adjusted $R^2=0.47$, $P=0.005$, $n=19$
	<i>Juncus</i> litter	+JLB*** adjusted $R^2=0.61$, $P<0.0001$, $n=19$	+R* adjusted $R^2=0.24$, $P=0.02$, $n=19$
Nitrogen content	<i>Spartina</i>	–S*, +JLB*, –JLN*** adjusted $R^2=0.62$, $P=0.003$, $n=15$	+ML**, +R**, –SS**, –SLBE*, –JLBE, –LE* adjusted $R^2=0.70$, $P=0.01$, $n=15$
	<i>Juncus</i>	–R*, –SLB, +JLB**, –SLN* adjusted $R^2=0.75$, $P=0.0009$, $n=15$	NS, $n=15$
	<i>Spartina</i> litter	–ML, –SAL** adjusted $R^2=0.46$, $P=0.01$, $n=15$	NS, $n=15$
	<i>Juncus</i> litter	+JLN** adjusted $R^2=0.39$, $P=0.008$, $n=15$	+ML, –LE*, –SLNE**, +JLNE adjusted $R^2=0.56$, $P=0.01$, $n=15$
	<i>Orchelimum</i>	–L***, +SS* adjusted $R^2=0.48$, $P=0.002$, $n=19$	NS, $n=19$
Herbivores	<i>Paroxya</i>	+JLN**, +L***, +M***, –SS adjusted $R^2=0.79$, $P=0.0004$, $n=15$	NS, $n=19$
	<i>Spartina</i>	NS, $n=19$	+OE** adjusted $R^2=0.4$, $P=0.001$, $n=19$
Grazing Damage	<i>Juncus</i>	NS, $n=19$	NS, $n=19$
	Fungi (mg/plot)	–R***, –SS* adjusted $R^2=0.53$, $P=0.0009$, $n=19$	+S*, –R* adjusted $R^2=0.31$, $P=0.02$, $n=19$
Decomposers	Fungi ($\mu\text{g}/\text{leaf}$)	NS, $n=19$	NS, $n=19$
	<i>Littoraria</i>	–JLN, –M***, –O*, +GS** adjusted $R^2=0.89$, $P<0.0001$, $n=15$	NS, $n=19$
Detritivores	<i>Melampus</i>	–JLN**, –L***, +P*** adjusted $R^2=0.90$, $P<<0.0001$, $n=15$	NS, $n=19$

Symbols *, **, and *** indicate $P<0.05$, <0.01 , and <0.001 , respectively, and no asterisks for $0.15>P>0.05$ indicate significance of individual terms in the model. Overall model adjusted R^2 , P values, and sample size (n) are given beneath the list of terms.

No significant models were found for grasshopper, snail and crab feeding preferences (not shown).

Abbreviations: *GJ* grazing damage to *Juncus*, *GS* grazing damage to *Spartina*, *JLB* live *Juncus* biomass, *JLBE* live *Juncus* biomass effect, *JLN* nitrogen content of live *Juncus*, *JLNE* nitrogen content of live *Juncus* effect, *L* *Littoraria* density, *LE* *Littoraria* density effect, *M* *Melampus* density, *ML* island or mainland, *NS* not significant, *O* *Orchelimum* density, *OE* *Orchelimum* density effect, *P* *Paroxya* density, *S* soil, *SAL* salinity, *SLB* live *Spartina* biomass, *SLBE* live *Spartina* biomass effect, *SLN* nitrogen content of live *Spartina*, *SLNE* nitrogen content of live *Spartina* effect, *SS* site score, *R* redox.

Biomass of both plants was positively correlated with their own nitrogen content. We speculate that the “mainland” effect might reflect greater groundwater discharge (deeper in the soil than our salinity cores, and hence not reflected in the salinity data) from the contiguous mainland versus the barrier islands, which would favor *Juncus* over *Spartina*. A

negative correlation between grazing damage and percent cover is self-explanatory, although it suggests a greater role for herbivory in structuring marsh plant communities than is usually allowed (but see Pennings and Bertness 2001, Silliman and Zieman 2001). The negative relationship between “soil” and various growth parameters of both

plants indicates greater growth where bulk density was low, and organic matter content and proportion silt + clay content were high. Greater organic matter in the soil likely benefits plants by providing a suite of nutrients including nitrogen and phosphorous (Padgett and Brown 1999, McLaughlin et al. 2000). Similarly, silt and clay hold nutrients better than sand (Eleuterius and Caldwell 1985). Previous studies have repeatedly shown that salinity negatively influences marsh plant height and productivity (Smart and Barko 1980; Howes et al. 1986). Site score is an index of how much upland surrounds the marsh, and again might reflect groundwater input at levels deeper than sampled by our salinity measurements. If so, reduced salinities might increase height of both species, but disproportionately favor biomass of *Juncus*, which is less salt-tolerant than *Spartina* (Pennings et al. 2005). Finally, the positive relationship between nitrogen content and biomass of both plant species likely simply reflects better growth of plants with better mineral nutrition.

Plant Nitrogen Content

Both plant species increased in nitrogen content when fertilized, as found in previous studies (Vince et al. 1981; Gratton and Denno 2003), and demonstrating that the nitrogen that we added was available to and taken up by the plants. Dead plant material, however, did not differ in nitrogen content between treatments, although there was a trend toward higher nitrogen content in fertilized plots, as found previously (Valiela et al. 1984, 1985). The lack of a treatment effect on nitrogen content of dead material may have occurred because nutrients were resorbed to living portions before leaves and stems senesced (Hopkinson and Schubauer 1984; Kemp et al. 1990), leached during tidal submergence or periods of high rainfall (Valiela et al. 1985), and/or lost to the fungal-detritivore food web (Valiela et al. 1985; Newell 1993; Newell et al. 1996; Graca et al. 2000). It is also possible that, despite attempts to standardize the collection protocol, the dead plant material was in a range of different decay stages, which would have increased variability and reduced statistical power (Rice and Tenore 1981; Valiela et al. 1984, 1985; Newell et al. 1996).

In control plots, the nitrogen content of each plant species was negatively correlated with the nitrogen content of the other species, suggesting belowground competition for nutrients (Table 1). Interestingly, in fertilized plots, this relationship was reversed, and the nitrogen content of *Juncus* was positively correlated with the nitrogen content of *Spartina* (adjusted $R^2=0.25$, $n=15$, $P=0.03$), suggesting that nitrogen was available in excess for both species in the fertilized plots. This scenario is consistent with the theory that competitive interactions among marsh plants shift from belowground under ambient conditions to aboveground

when nutrients are highly available (Levine et al. 1988a; Emery et al. 2001; but see Brewer 2003).

The effect of fertilization on the nitrogen content of *Spartina* was negatively correlated with the biomass effect of both plant species, indicating that nitrogen content increased less when biomass (of either species) increased more (Table 1). One explanation for this result would be that nitrogen was used for biomass production when conditions favored rapid growth, but accumulated in tissues if any factor other than nitrogen availability limited growth. This effect would be more likely to occur for *Spartina* than for *Juncus* because *Spartina* has a guerilla morphology (Harper 1977) and is capable of rapid growth under favorable conditions, whereas *Juncus* has a phalanx morphology, conserves nutrients (Kruczynski et al. 1978; Christian et al. 1990) and is less capable of rapid growth.

Herbivore Density and Food Selection

Most studies that have examined fertilization effects on herbivores have found that herbivore densities are elevated in plots with increased plant biomass and nitrogen content (Vince et al. 1981, Denno et al. 2002, Gratton and Denno 2003), likely because herbivores face a general problem of inadequate nitrogen in their food plants (White 1993). In this study, *Orchelimum* increased significantly in fertilized plots, corroborating results of an earlier experiment with the same species (Stiling et al. 1991), but *Paroxya* did not increase. However, *Paroxya* density increased in proportion to its food plant (because *Paroxya* density changed little, whereas that of *Juncus* decreased), suggesting that *Paroxya* did respond positively to fertilization. In a similar manner, grazing damage was significantly greater on both species of plants in the fertilized versus control plots. It is surprising, however, that laboratory studies indicated that grasshoppers did not preferentially feed on fertilized plants. This suggests that increases in herbivore abundance and damage in the field were driven primarily by increases in plant biomass and/or height, rather than nutritional quality. Previous studies have found that some grasshoppers use plant biomass (Chapman and Joern 1990), color (Bernays and Wrubel 1985) or shape (Mulkern 1967) as feeding cues, which ultimately would lead to feeding on higher quality plants, without herbivores necessarily responding to plant nutritional quality *per se*.

Across sites, densities of both grasshoppers were correlated with *Littoraria* density (Table 1). *Orchelimum* was negatively correlated with *Littoraria*, likely because the snails wound plants and promote invasion by ascomycete decomposers, hastening plant death (Silliman and Zieman 2001; Silliman and Bertness 2002; Silliman and Newell 2003). Thus, it is possible that *Littoraria* competes with *Orchelimum* for *Spartina*. In contrast, *Melampus* does

not damage *Spartina* (Pennings and Silliman 2005) and was not negatively correlated with *Orchelimum*. *Paroxya* density was positively correlated with *Littoraria* and *Melampus* densities, likely reflecting a common response to some unmeasured variable as it is difficult to imagine a mechanism by which the snails would facilitate the grasshopper. Because the two species of grasshopper feed on different plants, it is not likely that they would directly compete with each other, and in fact, neither species was a significant predictor of the others' density. Finally, the grazing effect on *Spartina* was positively correlated with the density effect of *Orchelimum*, reflecting the intuitive relationship between increased herbivore density and increased grazing damage.

Decomposers

Previous studies found a positive effect of fertilization on fungal content per gram of standing-dead *Spartina* leaf (Newell et al. 1996, 1998). This study found no effect of fertilization on fungal biomass (microgram ergosterol per gram LOM) perhaps because the fertilization treatment did not strongly increase the nitrogen content of standing-dead leaves, and/or because increased fungal production was cropped by detritivores. The trend, however, was toward greater fungal biomass in leaves in fertilized plots, as would be expected. In contrast, if fungal biomass is examined on the scale of the plot (taking into account the increase in standing-dead *Spartina* biomass with fertilization), fungal biomass (milligram ergosterol per meter square of *Spartina* litter) was much greater in fertilized plots.

Multiple regression analyses suggested that variation in fungal biomass per plot between sites was caused by a negative relationship with redox and site score (Table 1), presumably because these same variables affected *Spartina* standing-dead biomass (no significant model was found for fungal biomass per LOM). In a similar manner, the fertilization effect of fungal biomass per plot was predicted by the same variables that predicted the fertilization effect of *Spartina* standing-dead biomass per plot.

Detritivore Density, Food Selection, and Growth Rate

Our density estimates of *Littoraria* and *Melampus* are very similar to literature values for the high marsh zone of nearby sites (Lee and Silliman 2006). Previous studies have found that *Littoraria* and *Melampus* densities are affected by live and standing-dead *Spartina* biomass (Stiven and Kuenzler 1979; Fierstien and Rollins 1987; Lee and Silliman 2006). Thus, it would have been reasonable to expect that the increase in *Spartina* biomass (both live and standing dead) in fertilized plots would have been followed by an increase in snail densities. There were, however, no significant treatment effects on the density of either snail,

despite slight trends toward greater numbers in fertilized plots. It is possible that we did not see a response because the snails respond primarily to litter quality (nitrogen content and fungal biomass), neither of which differed significantly between treatments. Alternatively, snails may not have been capable of aggregating in response to habitat variation at this fairly small spatial scale.

Densities of the two snail species were negatively correlated across sites (Table 1), and similar negative correlations between the two snails were documented in Georgia Coastal Ecosystems LTER monitoring data (mollusc population abundance monitoring at nine sites with both species present; dataset fall 2000: $n=28$ mid-marsh plots, $R^2=0.38$, $P=0.0007$; dataset fall 2001: $n=31$ mid-marsh plots, $R^2=0.30$, $P=0.001$). These distributional patterns support previous results indicating that the two snail species compete with each other (Lee and Silliman 2006). The negative correlation between *Littoraria* and *Orchelimum* (Table 1) also occurred in *Orchelimum* density models, and is most likely because of *Littoraria* having negative effects on *Orchelimum* rather than the reverse, because *Littoraria* induces plant senescence and increases fungal biomass (Kemp et al. 1990, Silliman and Ziemann 2001, Silliman and Bertness 2002), which would not be advantageous to an herbivore. In contrast, *Littoraria* densities were positively correlated with grazing damage to *Spartina*, likely because grazing would damage plants, induce fungal growth, and thereby increase the flow of material into the detrital food web.

Laboratory feeding experiments indicated that fertilization did not change the quality of standing-dead stems enough to influence consumption by *Littoraria* or the omnivorous crab *Armases*, perhaps because fertilization did not markedly alter nitrogen content or fungal biomass of dead material. Laboratory growth experiments similarly indicated that fertilization did not change the quality of *Juncus* and *Spartina* standing-dead material enough to alter growth rates of juvenile *Littoraria* or *Melampus*. Again, this likely occurred because nitrogen content and fungal loads did not differ significantly between treatments. *Melampus* grew >200% better on a diet of *Spartina* than *Juncus*, supporting a previous study that also found better growth of *Melampus* on *Spartina* versus *Juncus* (Lee and Silliman 2006). Although the physiological mechanisms underlying this pattern are unknown, *Melampus* is rare in low-elevation habitats of low latitude marshes because of competition from *Littoraria*, not because of dietary constraints (Lee and Silliman 2006).

Natural Variation versus Treatment Effects

The determination of how important processes are is not only by statistical significance, but also by how much

variation they explain in nature relative to other processes (Welden and Slauson 1986). One way to assess this for our data is to compare variation between treatments (importance of nutrients) to variation among sites (importance of other sources of variation at a landscape scale), using the coefficient of variation as an index of variation (Table 2). For *Spartina*, fertilization had a very large relative effect on live and standing-dead biomass and live nitrogen content (i.e., variation among treatments was as great as, or greater than, variation across space). In comparison, fertilization had less of an effect on *Juncus* parameters, supporting previous work that *Spartina* is more limited by nitrogen than is *Juncus* (Gallagher 1975). Although fertilization did not have as large effects on standing-dead litter nitrogen contents of either species as it did on live nitrogen contents, standing-dead *Spartina* was more responsive to fertilization than was standing-dead *Juncus*.

The strong effects of fertilization on live *Spartina* were transmitted to herbivores, inducing greater grazing damage, which almost equaled variation in grazing over space. In contrast, fertilization had a relatively smaller effect on grazing damage to *Juncus*. These findings were paralleled by herbivore density ratios, where the density of *Orchelimum* (which eats *Spartina*) was much more influenced by fertilization than was the density of *Paroxya* (which eats *Juncus*).

Table 2 Summary of coefficients of variation (CV) of natural variation across sites (control plots, $n=19$ sites) and of treatments (mean of fertilized plots and control plots across sites, $n=2$ treatments)

	Natural Site Variation	Treatment Variation	Ratio of Site: Treatment Variation
<i>Spartina</i> Biomass	46.6	70.3	0.66
<i>Juncus</i> Biomass	38.5	27.3	1.41
Standing Dead	73.7	65.8	1.12
<i>Spartina</i> Biomass Standing Dead	44.5	25.5	1.75
<i>Juncus</i> Biomass			
<i>Spartina</i> N-Content	22.3	20.1	1.11
<i>Juncus</i> N-Content	16.2	9.8	1.65
Standing Dead	26.8	15.4	1.74
<i>Spartina</i> N-Content Standing Dead	25.7	6.7	3.84
<i>Juncus</i> N-Content			
<i>Orchelimum</i> Density	124.1	68.1	1.82
<i>Paroxya</i> Density	154.2	28.1	5.49
Grazing Damage to <i>Spartina</i>	68.5	57.5	1.19
Grazing Damage to <i>Juncus</i>	88.2	32.6	2.71
Fungal Biomass ($\mu\text{g/g}$ LOM)	41.1	6.1	6.74
<i>Littoraria</i> Density	110.4	5.2	21.23
<i>Melampus</i> Density	228.9	9.5	24.09

For fungal biomass, treatment variation was smaller than variation across space, likely because litter quality was not strongly enhanced by fertilization. Lastly, for snail densities, treatment variation was much smaller than variation across space likely because treatment did not markedly alter litter quality, but also because variation in snail densities at the site scale is strongly mediated by variation in recruitment, competition, and predation.

Because natural variation among sites in most variables measured was high, often quite a bit greater than variation between control and fertilized treatments, it may be difficult to detect impacts of eutrophication on sites by casual observation, especially if the degree of eutrophication is modest. The strongest indicators of increased nutrient supply in this study were the variables with the highest signal–noise ratio: *Spartina* biomass and nitrogen content. Our results suggest that evaluation of these two indicators at sites carefully matched for other edaphic variables will be the most powerful way to detect impacts of eutrophication in the Southeastern US.

Conclusions

In sum, the impacts of fertilization were strongest for the plant community, moderate for herbivores, and almost undetectable for the decomposer/detritivore food web, suggesting that impacts of anthropogenic eutrophication will affect marsh plant and herbivore trophic levels more than decomposers and detritivores. We rejected the hypothesis that effects of fertilization are stronger where soil conditions were most favorable (lower salinity and bulk density; higher redox potential). We sampled as wide a range of *Juncus/Spartina* marshes within coastal GA as we could find, and the different variables that we measured varied predictably in control plots across these sites, but the impacts of fertilization (Table 1, “fertilization effect”) were nevertheless generally consistent across the coastal landscape. Thus, the impacts of anthropogenic eutrophication on salt marsh communities (e.g., Bertness et al. 2002) are likely to be similar at a variety of sites, at least within a single geographic region. In particular, the results of this study, in combination with previous work (Levine et al. 1998a; Emery et al. 2001; Pennings et al. 2002; Bertness et al. 2002) indicate that eutrophication is likely to lead to increases in the abundance of *Spartina alterniflora* at the expense of *Juncus* spp. at a wide range of sites along the Atlantic Coast of the US.

Although *Spartina alterniflora* usually increases in response to increased nutrients, other responses of marsh plant communities may differ geographically (Pennings et al. 2005). In New England, where coastal development and eutrophication are intense, the increase in *S. alterniflora*

with eutrophication is paralleled by an increase in the high-marsh grass *Phragmites australis* (Bertness et al. 2002). In addition, although *S. alterniflora* increases with fertilization at Gulf Coast sites, *Juncus* does not decrease in response as it does on the Atlantic Coast (Pennings et al. 2002; Brewer 2003; this paper). These differences in community response caution against uncritical extrapolation of every aspect of our results to new geographic regions.

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