IMPACT OF FERTILIZATION ON A SALT MARSH FOOD WEB IN GEORGIA

by

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(Under the Direction of Steven C. Pennings)

ABSTRACT

I examined the response of a salt marsh food web to nutrients, and spatial variation in this response, at 19 sites on the Georgia coast. In fertilized treatments, *Spartina alterniflora* increased at the expense of *Juncus roemerianus*. *Spartina* dominance was reduced at sites with greater upland influence, regardless of fertilization. Because fertilization changes plant quantity and quality, it could also affect consumers of plants. Fertilization positively influenced herbivores (grasshoppers), had little effect on decomposers (fungi), and no effect on detritivores (snails). The two snail species *Littoraria irrorata* and *Melampus bidentatus* were negatively correlated with each other and likely compete. Natural variation among sites was typically similar or greater than impacts of fertilization. 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 are not likely to be much greater than variation among sites.

INDEX WORDS: fertilization, salt marsh, *Spartina*, *Juncus,* fungi, snail, grasshopper, competition

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TABLE OF CONTENTS

Page

LIST OF TABLES

Page

LIST OF FIGURES

CHAPTER I

INTRODUCTION

GLOBAL CHANGES IN THE NITROGEN CYCLE

One of the most important issues facing conservation biologists and ecologists today is the rapidly-increasing rate of nutrient-loading to all environments, terrestrial and aquatic (Vitousek 1994, Soulé and Orions 2001, United Nations 2001). As the human population has soared to over 6 billion in the early 21st century (nearly tripling in the last 50 years, United Nations 2003, U.S. Census Bureau 2003), dramatic landscape alterations and increased wastes have begun to alter ecological relationships (Nichols et al. 1986, NRC 1999, Micheli et al. 2001, Valdés and Lavin 2002, Turner 2002). The nitrogen cycle has experienced particularly dramatic changes because fertilizers, legume crops, and fossil fuels have permitted the rate of anthropogenic nitrogen fixation and inorganic nitrogen application to exceed that of natural processes (Peierls et al. 1991, Vitousek 1994, United Nations 2001, Howarth et al. 2002). Moreover, fertilizer usage will likely increase as the demand for food intensifies with the growing population (Schlesinger et al. 2001, Seitzinger et al. 2002).

In addition, humans have released nitrogen from long-term storage pools by clearing land and draining wetlands (Vitousek 1994, Mitsch and Gosselink 2000). Although the effects of nitrogen additions are still largely unknown because it is a fairly recent phenomenon (natural N-fixation was surpassed by human N-inputs in the early 1980's, United Nations 2001), they include alterations to atmospheric chemistry (nitrous oxides in the troposphere, Schlesinger et al. 2001, Paerl et al. 2002, Seitzinger et al. 2002), reduced water quality in aquatic systems (Kumm 1976, Burkholder 1998, Paerl et al. 1998, Rabalais et al. 2002), and changes to ecological processes at the population and community level (Vitousek 1994, Heip 1995, Micheli et al. 2001). Because nitrogen is a limiting nutrient in many environments (e.g., coastal marine, Valiela and Teal 1974, Paerl et al. 1998, Howarth et al. 2002, Feller et al. 2003, open water marine, Redfield 1958, terrestrial grasslands, Huenneke et al. 1990, upland forests, Howarth et al. 2002, Nilsen and Abrahamsen 2003), consequences to community structure and diversity could be substantial. Impacts of nitrogen additions might not only affect primary producers, but might also flow through the food web to affect other trophic levels, positively (Tober et al. 1996, Nixon and Buckley 2002) or negatively (Deegan 2002).

Salt marshes may be one of the more susceptible environments to increased nutrients, because they receive runoff from surrounding watersheds (Peierls et al. 1991, McClelland et al. 1997, Bowen and Valiela 2001, Valiela and Bowen 2002, Bertness et al. 2002), and filter water from tidally-influenced rivers and channels (Bertness 1999, Pennings and Bertness 2001, Valiela and Cole 2002). It is vital to understand how salt marshes are affected by eutrophication because they provide many valuable ecosystem services to society. They protect the coastline from erosion by sediment accretion (Redfield 1972, Niering and Warren 1980) and buffer the effects of flooding by soil absorption (Beatley et al. 2002). They are critical to numerous commercially- and recreationally-important fisheries as nursery grounds, refuges, or food sources (Daiber 1982, Williams 1984, Kneib 1997, Minton 1999), and similarly provide feeding and nesting habitats for many birds and mammals (Daiber 1982, Bertness 1999, Boyer and Zedler 1999). Natural processes of sedimentation and denitrification in salt marshes protect coastal waters from excess nutrients that contribute to habitat loss, reduced water clarity, harmful algal blooms, and fish kills (NRC 1999, Bertness 1999, Rabalais et al. 2002, Valiela and Cole 2002, Anderson et al. 2002, Breitburg 2002). Despite their important ecological contributions, the value of salt marshes has only recently been discovered (mid-20th century, Teal 1962, Odum and de la Cruz 1967, Mitsch and Gosselink 2000) and conservation efforts are still inadequate (Beatley et al. 2002).

SALT MARSH ECOLOGY

For scientists, one of the most important aspects of salt marshes is their simplicity: they provide a useful model for community ecologists to study, and suggest theories that might also be applied to other ecosystems. Strong physical gradients occur over a short distance within salt marshes due to bidirectional flooding of the tides over an elevational gradient (Niering and Warren 1980, Wiegert and Freeman 1990, Bertness 1999). Thus, marsh plants must have the ability to cope with high soil salinity due to seawater evaporation, soil erosion due to ocean currents and tidal movement, partial to complete submersion during flooding tides, soil anoxia due to waterlogged sediments, and toxic sulfides that build up as a metabolic by-product of sulfate-reducing bacteria in the soil (Niering and Warren 1980, Wiegert and Freeman 1990, Pennings and Bertness 2001). Whereas most plants would not survive in such a harsh habitat, marsh plants have specialized physiological, metabolic, and structural adaptations that allow them to colonize this unusual niche. Physiological adaptations of plants to salt marshes include well-developed aerenchyma tissues, which are a series of air-passageways to transport oxygen from the leaves of the plant to the roots (oxygen is required for roots to take up nutrients), and salt glands in the leaves that excrete salt (Bertness 1999). Metabolic adaptations include a highly evolved anaerobic metabolic pathway (Koch et al. 1990), and the capacity to produce high concentrations of organic solutes to maintain a high osmotic potential (Cavalieri and Huang 1981, Bertness 1999, Mulholland and Otte 2001). Structural adaptations include stomatal openings that close when flooded, and an extensive root and rhizome network near the soil surface to facilitate root oxygenation (Wiegert and Freeman 1990, Bertness 1999). Because relatively few plants can inhabit salt marshes (Pennings and Bertness 2001) and because physical gradients lead to conspicuous zonation of the plants (Niering and Warren 1980), marshes are invaluable to the study of community diversity (Hacker and Gaines 1997, Hacker and Bertness 1999) and pattern (Bertness and Ellison 1987, Bertness 1991a,b, Pennings and Callaway 1992, Pennings and Moore 2001).

Salt marshes have also received attention for being among the most productive environments in the world. Net primary production in marshes dominated by *Spartina alterniflora* has been estimated to be about 3,000 g/m^2/yr, rivaling that of coral reefs and rainforests (Valiela 1995). Salt marshes are abundant along the east coast of the United States, especially where barrier islands slow water movement to allow fine sediments to accumulate on the leeward side (Bertness 1999). They occur at most latitudes, except where freezing temperatures do not allow their development or mangroves replace them in the tropics (Wiegert and Freeman 1990, Pennings and Bertness 2001). Despite a short coastline (160 km), Georgia has the most marsh area along the East Coast (almost 200,000 hectares, 33% of the total East Coast acreage) (Wiegert and Freeman 1990, Bertness 1999), and Georgia marshes may be the most productive of the entire coast (Turner 1976). The most conspicuous primary producers are the macrophytes, especially *Spartina alterniflora* (hereafter referred to as *Spartina*) and *Juncus roemerianus* (hereafter referred to as *Juncus*) which are present in expansive monotypic stands (Wiegert and Freeman 1990), although filamentous green algae, diatoms, cyanobacteria, and chemosynthetic bacteria also contribute to the carbon cycle to a variable extent (Zimba 1991, Valiela 1995, Goni and Thomas 2000).

BOTTOM-UP CONTROLS ON SALT MARSH PRODUCTION AND THE NITROGEN PARADOX

Early studies sought to determine controls on salt marsh primary production, as marsh plants were long suspected to contribute to secondary productivity both within and outside of the marsh (Teal 1962, Odum and de la Cruz 1967). Teal estimated that as much as 40% of production in Georgia marshes was exported to surrounding marine environments (1962), although subsequent studies found that marshes vary in exportation (Odum 1980, Nixon 1981). Most studies have focused on bottom-up controls on primary productivity, that is, the supply of resources such as nutrients that regulate growth performance of producers at the base of the food web (Bertness 1999). Numerous studies have confirmed nitrogen to be the most limiting nutrient to marsh plant production (Valiela and Teal 1974, Gallagher 1975, Valiela et al. 1975, Haines and Dunn 1976, Jeffries 1977, Mendelssohn 1979), as it is for other marine primary producers (Ryther and Dunstan 1971, Valiela 1995, Weiss et al. 2002), but its effects are masked. For example, many plant species (most notably, *Spartina*, but also *Iva frutescens*, *Juncus roemerianus*, and *Borrichia frutescens*) exhibit marked differences in height forms across the elevational gradient (Valiela et al. 1978, Mendelssohn 1979, Howes et al. 1986, Seliskar 1985, Pennings and Richards 1998, Bertness 1999). *Spartina* is tallest at the creekbank (up to 2 meters) and shortest in the mid- to high-marsh (less than 30 cm) (Valiela et al. 1978, Mendelssohn 1979, Bertness 1999), despite lower soil nitrogen (ammonium) in the low marsh than in higher marsh areas (Mendelssohn 1979). If nitrogen were the most limiting nutrient, production would be expected to be greatest where the nitrogen concentration is highest, yet this is not so. At the same time, nitrogen fertilization boosted high-marsh *Spartina* production (height) to levels of that near the creekbank, but did not further increase creekbank production (Gallagher 1975, Valiela et al. 1978, Mendelssohn 1979). Why, then, did added nitrogen increase production where it did not appear to be limiting?

The answer to this paradox lies in the fact that adaptations to the physical conditions in the high marsh are energetically costly. Most evidence suggests that lowered production of *Spartina* at high elevations is in response to unfavorable edaphic conditions (Haines and Dunn 1976, Anderson and Treshow 1980, Howes et al. 1986, Mendelssohn and Morris 2000), rather than being due to genetic differences within plant species (Shea et al. 1975, but see Mooring et al. 1971, and Gallagher et al. 1988). Creekbank soils are well drained and less saline due to frequent tidal flushing and coarser sediments of the elevated levees, whereas sediments further inland are finer, poorly drained, and increasingly more saline due to increased evaporative time between flooding tides (Pennings and Bertness 2001). At the border with terrestrial vegetation, where tides are infrequent and freshwater runoff from surrounding upland becomes more important, salinity drops again (Pennings and Bertness 1999). Salinity limits production of marsh plants due to water stress, salt toxicity, and competitive inhibition by sodium for the uptake of important cations, namely ammonium and potassium (Phleger 1971, Levitt 1972, Haines and Dunn 1976, Mendelssohn and Morris 2000). Moreover, increasing salinity causes some plants to use available nitrogen for the production of osmoregulatory compounds, such as proline and glycinebetaine, rather than for growth (Cavalieri and Huang 1981, Mulholland and Otte 2001).

In addition, where soil is poorly drained (anaerobic), sulfides build up due to microbial sulfate reduction and suppress plant growth (Howes et al. 1981, 1986, King et al. 1982, but see Hines et al. 1989). Plant biomass (height, leaves, stems, and root system) has been shown to decrease with increasing sulfides above 0.5 mM, and no growth occurs at all at concentrations above 2.0 mM in solution for *Spartina* and *Borrichia* (DeLaune et al. 1983, Bradley and Dunn 1989). Mechanisms by which sulfides lead to decreased plant biomass include sulfide toxicity (Allam and Hollis 1972) and inhibitory effects to root metabolism (Mendelssohn and Morris 2000). Sulfides negatively affect root metabolism at concentrations as low as 0.5 mM by reducing activity of alcohol dehydrogenase (ADH), the enzyme responsible for alcoholic fermentation in highly reduced anaerobic soils, thus reducing carbon production by the plant (Koch et al. 1990). Additionally, sulfides and low oxygen concurrently reduce uptake of important nutrients, especially nitrogen (Howes et al. 1986). Bradley and Morris showed that reduced oxygen alone lowered the V_{max} and increased the K_m of nitrogen uptake (Michaelis-Menton parameters), but that in the presence of a low concentration of sulfide, V_{max} decreased and K_m increased subsequently (1990). Furthermore, ammonium uptake was almost completely inhibited at a concentration of 2.0 mM sulfide and anoxia (Bradley and Morris 1990). Changes in the nitrogen-uptake efficiency imply that there will be changes in growth following nitrogen additions (Bradley and Morris 1990). Thus the nitrogen paradox can be explained by physical gradients that complicate plant nitrogen metabolism. Although nitrogen is more abundant in the soil in the high marsh than in the low marsh, bioavailability is lower in the high marsh and plant requirements are higher. Thus, *Spartina alterniflora* plants are actually more nitrogen-limited in high versus low marsh habitats.

BIOTIC CONTROLS ON SALT MARSH PLANTS: PLANT-PLANT INTERACTIONS

Although physical gradients may explain growth performance of a species in monoculture, they alone cannot explain community patterns (Callaway and Walker 1997, Huckle et al. 2000, Greiner La Peyre 2001, Pennings and Bertness 2001). Biotic controls, particularly plant-plant and animal-plant interactions, also facilitate or inhibit production, influencing success and diversity of plants in the community (Pennings and Bertness 2001). Important plant-plant interactions in the marsh include parasitism, facilitation, and competition. Epiphytic parasitism has received more attention in terrestrial environments than in salt marshes (Press and Graves 1995), but one study in a California marsh showed that plant diversity increased in the presence of the parasite *Cuscuta salina* because non-preferred plants had greater success when the typically-dominant plant *Salicornia virginica* was heavily parasitized (Pennings and Callaway 1996). Parasitic plants, however, are rare in salt marshes on the East Coast of the U.S., and do not occur in Georgia salt marshes (Pennings, *pers. comm.*).

Facilitation occurs when fugitive plants colonize stressful bare patches in the marsh following disturbance events that kill dominant vegetation (such as ice scours, wrack deposits, consumer eat-outs, fires, and sedimentation) and facilitate regrowth of zonal dominants by ameliorating high soil salinity through shading, or by stabilizing or oxygenating sediments (Bertness and Callaway 1994, Bertness 1999, Pennings and Bertness 2001). Similar positive interactions also occur between established zonal neighbors (Bertness and Hacker 1994). Although facilitation and positive associations between plants may be important to northern Atlantic coast marshes (Bertness and Ellison 1987, Bertness 1991a, Bertness and Hacker 1994, Bertness 1999), they appear to be less prevalent in southern Atlantic marshes where species have greater salt tolerances, and thus are unlikely to benefit from neighboring plants (Pennings et al. 2003). Further, although parasitism and facilitation may be restricted to certain marshes and latitudinal locations, respectively, competition appears to be universal to all marshes and may be most important in structuring communities.

Competition is a major factor determining productivity and distribution patterns of marine invertebrates (Connell 1961, Paine 1974, Menge 1976), and plants (Harper 1977, Grime 1979, Tilman 1982, Keddy 2001). Demand for limiting resources such as nutrients, light, water, and space leads to competition within and between plant species (Grime 1979). Both intra- and interspecific competition decrease seed germination, survival, and growth (Bertness and Ellison 1987, Bertness 1991b, Bertness and Yeh 1994), and plants that survive through germination may have lowered biomass, reduced leaf production, and thinner stems (Harley and Bertness 1996). Intraspecific competition is easily seen in productive monocultures: as plant density increases, the amount of resources available per individual decreases, and the size of the individual plants becomes smaller (Keddy 2001). Interspecific competition restricts some plant species to metabolically-costly, suboptimal habitats (Keddy 2001), despite better growth in nearby less stressful habitats (Grime 1979, Grace and Wetzel 1981, Tilman 1982, 1988, Wilson and Keddy 1985, Bertness and Ellison 1987).

Marsh plant zonation patterns cannot be fully explained by differential adaptations to abiotic factors between species, since some plants often perform better outside their natural zonation range. *Spartina patens* and *Distichlis spicata*, for example, grow equally well or better higher in the marsh (the *Juncus* zone) if transplanted without neighbors in experimental plots (Bertness 1991a), or if they naturally colonize a bare patch in the upper marsh following disturbance (Bertness and Ellison 1987), but do not perform well with neighboring *Juncus*, suggesting that they are excluded from this zone by competition (Bertness 1991a). On the other hand, *Juncus* died with or without neighbors when transplanted into the *Spartina patens* zone, suggesting that it is excluded from this zone by physical stress (Bertness 1991a). These studies have generally found that abiotic factors control lower limits of marsh plants, while competition sets upper limits (Bertness and Ellison 1987, Bertness 1992, Pennings and Moore

2001), although zonation is more complicated in the mid-marsh at lower latitudes since along with frequent flooding, soils are hypersaline due to greater solar radiation (Pennings and Bertness 2001). Because the mid-marsh is more stressful than higher or lower marsh zones in low-latitude sites, zonation is likely mediated by a combination of competition and physical restraints for both lower and upper growth limits (Pennings and Callaway 1992).

Competition can form competitive hierarchies within plant communities, creating patterns where competitive-dominants, that suppress all other species in their community, occupy optimal habitats, and competitive-subordinates, that are suppressed by all other species in their community, occupy sub-optimal habitats (Keddy 2001). In the salt marsh, competitive dominance may largely be a function of a plant's growth morphology (Bertness 1999), though other factors such as growth rate, phenology, storage organs, and the ability to overcome stressors and disturbances also affect the fitness of the species (Grime 1979). For example, *Juncus* grows as a dense turf with extensive roots, rhizomes, and tillers, whereas *Distichlis* grows diffusely along rhizomes, and invests less into root biomass (Bertness 1999). The two growth forms, termed Phalanx and Guerilla, respectively, (Harper 1977), vary in their abilities to access belowground nutrients and space. In particular, *Juncus* is successful in competing for nutrients and space under ambient conditions due to its complex root system and dense clonal morphology, but *Distichlis* can rapidly expand along runners and colonize extensive areas of the marsh under disturbed or unusually-stressful conditions (Bertness 1999). Other studies have suggested that clonal plants have an advantage over solitary plants, especially in colonizing disturbed marsh habitats (Shumway 1995), though this does not necessarily infer a competitive advantage over plants that are already established (Pennings and Callaway 2000, but see Hartnett and Bazzaz 1985). Because competition is such an important determinant in plant growth, it is important to understand the competitive hierarchy of the plant community of interest and its dynamics under variable environmental conditions (Goldberg and Barton 1992, and sources therein, Bart and Hartman 2000, Huckle et al. 2000, Greiner La Peyre et al. 2001).

Several studies have pointed to an inverse relationship between abiotic factors and competition (Bertness and Ellison 1987, Bertness and Hacker 1994, Bertness and Callaway 1994, Callaway and Walker 1997, Greiner La Peyre 2001): as physical environments become more harsh, competition is less important in regulating the abundance of species (Grime 1979, Keddy 2001). Understanding this relationship is important in order to predict competitive outcomes (i.e. “winners” and ”losers”) among vegetation in various habitats. Grime described three strategies plants have for dealing with environmental conditions: “competitors (C), which exploit conditions of low stress and low disturbance, stress-tolerators (S) (high stress-low disturbance), and ruderals (R) (low stress-high disturbance)”, and argued that no plant life can exist in high stress and high disturbance areas (Grime 1979). The C-S-R model depicts each strategy at its extreme at the apices of an equilateral triangle, such that for any one strategy, the relative importance of competition, stress, or disturbance is 100%, respectively (Grime 1974, 1977, 1979). Secondary plant strategies are located within the triangle for habitats experiencing intermediate competition, stress, and disturbance intensities, but a plant cannot be both a dominant competitor and strong stress-tolerator in the C-S-R model, supporting the inverse relationship between abiotic stress and importance of competition (Grime 1979, Hodgson et al. 1999). In sum, theories of plant competition predict that altering nutrient cycles may change plant dominance patterns. In particular, adding nitrogen will tend to reduce “stress” at a site, which should favor different plant species better adapted to the new conditions (Tilman 1988, Wisheu et al. 1991). A wide variety of experimental studies have in fact demonstrated that increasing nutrient supplies produce changes in plant community composition in a wide variety of community types (Austin and Austin 1980, Tilman 1987, Huenneke et al. 1990, Bobbink 1991, Goldberg and Barton 1992, Emery et al. 2001).

Biotic Controls on Salt Marsh Plants: Animal-Plant Interactions

Animals can also control plant growth and vice versa, both positively and negatively. Some of the most conspicuous marsh residents are bivalve filter feeders, burrowing crabs, snails, and insects (Daiber 1982). Many of the animal-plant interactions in the marsh are important facultative symbioses (Long and Mason 1983, Adam 1990, Bertness 1999). Burrowing crabs, such as *Uca* and *Sesarma*, facilitate plant growth by aerating the soil, aid belowground decomposition and mineralization by reworking the soil, and add nutrients (i.e. nitrogen) to soil in their wastes (Montague 1980, Bertness 1985); however, the level of facilitation to plants may change across abiotic environments (Nomann and Pennings 1998). Similarly, bivalves like *Geukensia demissa* (ribbed mussel) and *Crassostraea virginica* (eastern oyster) stabilize soil against erosion and move nutrients from the water column to the soil (Jordan and Valiela 1982, Bertness and Grosholz 1985, Dame 1996, Pennings and Bertness 2001). Reciprocally, plants provide invertebrates with stable substrate through their extensive root systems (Bertness 1984b), food (mainly as detritus, Newell and Porter 2000), habitat and refuge from predators (Diaber 1982, Kneib 1997, Nomann and Pennnings 1998, Lewis and Eby 2002).

Although it has been estimated that herbivores only remove approximately 10% or less of living marsh biomass (Smalley 1960, Teal 1962, Nixon and Oviatt 1973, Pfeiffer and Wiegert 1981, Montague and Wiegert 1990), they may be important in mediating plant community structure (Gough and Grace 1998), especially in the case of rarer plant species (Rand 1999). Larger mammals and birds may be capable of removing larger portions of biomass (Furbish and Albano 1994, van der Wal et al. 1998, Smith and Odum 1981, Kerbes et al. 1990, Ford and Grace 1998), but insects such as grasshoppers and beetles may also be more important than once thought. Because herbivores tend to focus on particular, preferred plant species, and particular plant qualities, they promote the success of less-preferred plants (Ellison 1987, Foster 1984, Rand 2000, 2002). Herbivore preferences are mediated by plant chemistry, toughness, and nitrogen concentration (Pennings et al 1998, Pennings et al. 2001, Goranson and Pennings, unpublished manuscript). Many plants produce a variety of compounds that deter herbivory, such as ferulic and coumaric acid, which are found in *Spartina* (Buchsbaum et al.

1984). Additionally plants may deter feeding by being tough or salty, or by containing silica (Pennings et al. 1998). Although foliar nitrogen content usually does not predict herbivore preference rankings among plant species (Buchsbaum et al. 1984, Pennings et al. 1998), many studies have reported that it does affect herbivore choices within a plant species (Vince et al. 1981, Denno et al. 1986, Bowdish and Stiling 1998, Gratton and Denno 2003). Thus, eutrophication is likely to alter relationships between a plant and its herbivores by making the plant more palatable to consumers.

An extensive study by Vince et al. (1981) found that 5 families of salt marsh herbivores from 2 distinct feeding types (piercing and sucking, and chewing) increased in fertilized plots of 3 plant species (*Spartina alterniflora, Spartina patens, and Distichlis spicata*) in both the low and high marsh, especially where both foliar nitrogen and biomass were greatest. They suggest that herbivore responses were due to increased survivorship and fecundity, but were limited by predation and annual generations (Vince et al. 1981). In other cases, increased herbivory on fertilized plants was not directly limited by predation (Moon and Stiling 2002, Bowdish and Stiling 1998), but was limited by the presence of other insects, possibly through egg-predation, reductions to host-plant palatability, or decreased host plant biomass (Moon and Stiling 2002). Densities of the delphacid planthopper, *Prokelisia*, were shown to decrease in fertilized plots at sites with high grasshopper density, but continued to increase at sites with low grasshopper density, likely due to asymmetrical competition for resources (Stiling et al. 1991). Competition for food resources has also been documented between geese and hares in salt marshes in The Netherlands (van der Wal et al. 1998). Nevertheless, fertilization appears to have an overall positive effect on herbivore biomass, by increasing both the quality (nitrogen content) and quantity of plants (Onuf et al. 1977, Lightfoot and Whitford 1987, Levine et al. 1998b, Gratton and Denno 2003).

The salt marsh grasshoppers *Orchelimum fidicinum* and *Paroxya clavuliger* (hereafter referred to generically) are known to correlate their greatest seasonal abundance with the maximum development of host plant biomass (Davis and Gray 1966). Grasshoppers can locate food visually, possibly by responding to larger clumps of vegetation, vertical stripes (i.e. taller plants), or color (Chapman and Joern 1990), all of which are influenced by fertilization. Further, of 71 studies compiled by Waring and Cobb (1992), 60% of chewing insects such as grasshoppers responded positively to nitrogen fertilization, over 20% had no response or a nonlinear response, and less than 10% responded negatively. However, it is not clear which mechanism of fertilization grasshoppers respond to, increased biomass or plant quality, since both increase with fertilization (Vince et al. 1981, Waring and Cobb 1992). Grasshoppers are likely to be nitrogen-limited, as indicated by stoichiometric analyses (Vince et al. 1981), yet the highest biomass of salt marsh grasshoppers occurs at a time of high plant biomass but seasonally low protein levels (i.e. when grasses are more mature, Bernays and Barbehenn 1987, Davis and Gray 1966). Thus, life histories of *Orchelimum* and *Paroxya* suggest that they may be most influenced by biomass.

THE DETRITAL FOOD WEB

In salt marshes, the majority of higher plant material enters the detrital food web (Teal 1962, Odum and de la Cruz 1967), following senescence and colonization by microbes (Newell et al. 1989, Newell 1993). In southeast marshes, the dominant plants *Spartina* and *Juncus* decay in a standing position (Newell et al. 1989, Newell 2001a), which creates a unique micro-ecosystem for specialized fungal colonizers (Newell 1996). Environmental conditions such as access to light, water (dew and tides), and organic and inorganic nutrients, the influence of consumer activity, and exposure to toxic fermentation products and/or anaerobic zones, vary between plants decaying in the canopy versus the soil surface (Newell et al. 1989, 1991, 1998, Newell 1993, 1996, Newell and Porter 1999, Graca et al. 2000), thus influencing the composition of the dominant decomposers in the system.

Ascomycetous fungi are the major decomposers of standing dead *Spartina*, making up 98 percent of the microbial standing crop on leaves (Newell 1989). They are able to rapidly scavenge plant nitrogen and break down plant organic matter within plant cells (Bergbauer and Newell 1992, Newell 1993, 1996, Newell et al. 1996a, Newell and Porter 1999). Further, these fungi appear to be nitrogen-limited, as fertilization increases their biomass significantly (Newell 1996b). Specialized consumers of standing dead material and fungi are the periwinkle and coffee bean snails, *Littoraria irrorata* Say and *Melampus bidentatus* Say, and the amphipod *Ulorchestia spartinophila* (Newell 1993, Graca et al. 2000, Kneib et al. 1997). Though several laboratory studies have pointed to increased detritivore growth, reproduction, and/or food palatability with increased fungal biomass of detrital food (Rietsma et al. 1988, Bärlocher et al. 1989b, Newell and Bärlocher 1993, Bärlocher and Newell 1994, Kneib et al. 1997,Graca et al. 2000,), no studies have investigated how increases in nutrients available to plants might ultimately affect these detritivores in the field.

BOTTOM-UP EFFECTS ON COMPETITION AMONG MARSH PLANTS

Though most studies of nutrient effects in salt marshes have focused on the performance of single species in monoculture (Valiela and Teal 1974, Gallagher 1975, Haines and Dunn 1976, Mendelssohn 1979), a few studies have examined how nitrogen causes plant community dynamics to change. Levine et al. (1988) assessed fertilization effects along four natural zonal borders in New England made up of *Distichlis spicata*, *Spartina* (*alterniflora* and *patens*), and *Juncus gerardi*, and found a complete reversal in the competitive hierarchy in fertilized plots; that is, the inferior plants increased in abundance (especially *Spartina alterniflora*), while the zonal dominants decreased in abundance, with the degree of displacement mirrored by the amount of height increase of the inferior competitor following fertilization (i.e. the taller the inferior, the more it displaced the zonal dominant). Moreover, Emery et al. (2001) showed that, when nutrient stress was alleviated with fertilization, competitive interactions switched from belowground to aboveground, allowing inferior plants to increase in height and creating light-limitation for plants dominant under ambient conditions. In these studies, the typical stress-tolerators became the dominant competitors under fertilized conditions, regardless of their location along the tidal gradient. That is, stress-tolerators were able to not only outcompete neighbors at naturally occurring borders, but also unnatural neighbors adjacent to them when transplanted and fertilized in new zones, indicating that species shifts under eutrophied conditions can be quite substantial (Emery 2001).

To test whether results from the New England studies could be generalized to other regions with different abiotic conditions, Pennings et al. (2002) conducted a similar study along the southeast and gulf coasts, and also found that adding nutrients shifted species composition to the advantage of the inferior competitor, the low-marsh species *Spartina alterniflora*, regardless of the physical characteristics of the marsh (2002). Their conclusions, however, came with the caveat that the extent of *Spartina* dominance might be influenced by soil salinity, with its advantage over other zonal dominants decreasing at more saline sites, in accordance with Greiner La Peyre's study (2002) that showed reduced competition (at the individual species level) in higher salinities. Not enough different salinity conditions were examined, however, to rigorously test this hypothesis.

Generalizations from fertilization studies on community composition are essential to coastal management decisions because nutrient enhancement is now a common phenomenon, as more and more people live near the coast and contribute to eutrophication of local watersheds (Osmond et al. 1995, McClelland and Valiela 1998, Bowen and Valiela 2000,). Bertness et al. (2002) compared pristine marshes to those abutting developed areas in New England (i.e. farms, roads, lawns, golf courses, or other human developments), and found that the developed marshes had more available nitrogen leading to *Spartina* encroachment into higher elevations, and invasion of the reed *Phragmites* from the terrestrial border into lower marsh habitats. Their results show that anthropogenic inputs to the marsh may ultimately lead to a loss of diversity, as *Spartina* and *Phragmites* outcompete other marsh plants (Bertness et al. 2002). Similarly, as marsh mitigation and restoration are becoming common practice due to Clinton's "No Net Loss Policy" (Dionne et al. 1999, Beatley et al. 2002), understanding nutrient impacts will be critical to evaluating marsh function at restoration sites (Langis 1991, Minton 1999). For example, in California where marshes have been restored for nesting habitat of the endangered light-footed clapper rail, fertilization compromises this function by leading to competitive dominance of plants other than *Spartina foliosa*, the rail's preferred nesting habitat (Boyer and Zedler 1999). Finally, because marshes are ultimately linked to productivity of commercially important species (Teal 1962, Kneib 1997, Silliman and Bertness 2002), understanding outcomes of trophic interactions under high-nutrient scenarios may ultimately be essential to sustaining fisheries.

Competition and Trophic Dynamics Across Environmental Gradients

Despite the major consensus that competition and abiotic stress are inversely related (Grime 1979, Bertness and Ellison 1987, Bertness and Hacker 1994, Bertness and Callaway 1997, Huckle et al. 2000, Greiner La Peyre 2001), it is unclear whether resource availability (i.e. nutrients) can alter this relationship (but see Brewer 2003). To explore the relationship between competition and stress-tolerance, I examined the responses of marsh plants to nutrient additions at sites across a range of abiotic conditions. To avoid complications arising from studying different plant species I focused on the interactions of two plant species, *Spartina alterniflora* and *Juncus roemerianus*. These two species abut each other in an abrupt border across a wide range of edaphic conditions. I tested the hypothesis that *Spartina* would outcompete *Juncus* regardless of site edaphics (as nutrients reversed the normal competitive hierarchy to favor *Spartina* more than *Juncus* in previous studies), but that the extent of *Spartina* dominance would depend on edaphic conditions, i.e. *Juncus* would be a better competitor at lower abiotic stress.

Only a handful of studies have examined numerical responses of salt marsh herbivores to nutrient changes (Vince et al. 1981, Levine et al. 1998b, Gratton and Denno 2003), only one has looked at the response of salt marsh fungi (Newell 1996) and none have examined numerical responses by detritivores. In my experiments, I examined the numerical response of all three guilds to nutrient enhancements across a range of edaphic conditions in the field. In order to examine whether the responses in the field were due to plant quality (i.e. greater tissue N-content with fertilization) alone, I examined the laboratory feeding choices of herbivores and detritivores between control and fertilized plants. I hypothesized that shifts in plant community composition would also shift the abundance and/or composition of all three guilds of consumers. I expected that herbivore (grasshopper) abundances would decrease or increase with decreases or increases in their plant food source (rather than due to plant quality alone), but that detritivores would be less responsive because the common salt marsh detritivores are less mobile and more generalized in feeding habitats than the herbivores (plant quantity and quality would not strongly affect their responses).

Lastly, although it has been shown that additional nitrogen influences herbivore growth by increasing plant quality (Bernays and Barbehenn 1987), few studies have examined whether detritivores also grow better on detritus from plants grown under high-nitrogen conditions. Rietsma et al. found no effect of nitrogen fertilization on the growth of the salt marsh snail *Melampus* (1988); but two studies in freshwater habitats found positive detritivore growth results under high nitrogen conditions (Friberg and Jacobsen 2001) and under high phosphorus conditions (Rosemond et al. 2001). To assess detritivore response to litter quality, I examined growth of salt marsh detritivores on plant litter from fertilized versus natural conditions. Because plants resorb nutrients from senescing stems and leaves, litter quality may not change as much as living biomass following nutrient increases, and thus I expected there to be little difference in detritivore growth on the different litter types.

CHAPTER II

METHODS

EXPERIMENTAL SETUP

Site Selection

Nineteen sites were selected on the GA coast that contained stands of monospecific *Spartina alterniflora* bordering stands of monospecific *Juncus roemerianus* (hereafter referred to generically). Sites were chosen to span as wide a range of salinity as possible, while still containing these two plant species. Ten sites were located on Sapelo Island, and nine on the mainland in McIntosh County, Georgia (Fig. 2.1).

Plot Set-up

Plots were established at the sites in July 2000. Plots were initially set up and maintained by Tracy Buck (Pennings laboratory technician) until I began my field work in May 2001. Ten 1m^2 plots were established at each site. A 1m^2 PVC quadrat was laid over the border between *Juncus* and *Spartina* to delineate a plot with a 1:1 mixture of the two species. Areas where the border was poorly defined (mixing of species) were avoided if possible. A wooden stake was placed at each corner to designate the plot boundaries. Areas of sparse vegetation, obvious physical disturbance (wrack, pigs, cows, etc.), or species other than *Juncus* and *Spartina* were avoided if possible. Five plots were designated as fertilized plots while the remaining five were designated as control plots. The two treatments were assigned to alternate plots so that treatments were fully interspersed. Plots were placed at least 2 m apart to ensure fertilizer would not affect neighboring control plots.

Fertilization

Plots were fertilized 3 times over a period of 1 year (July 2000, September 2000, May 2001). On each occasion, each plot was fertilized with 11 planting tablets (Forestry Suppliers, Inc., Remke Nitroform Tablets, 20-10-5 (N-P-K), 21g per tablet, total=140 g N/plot/year, similar to the yearly "high dosage" fertilization rate applied by Vince et al. 1981). To fertilize plots, a metal corer was used to remove 11 soil plugs to a depth of 10 cm. A tablet was placed in each hole and the soil plugs were replaced. Control plots were disturbed in the same manner as the fertilized plots without the addition of the fertilizer tablet.

Salinity

Porewater salinity was measured monthly at each of the 19 sites during July – September 2000 and May and July-August 2001. On each occasion, five soil cores were collected per site between experimental plots along the *Spartina*/*Juncus* border using a metal corer (approximately 2 cm diameter) to a depth of 7-10 cm. A 2-3 cm soil sample from the deepest portion of each of the five cores was pooled to yield a single composite sample/site. Samples were placed in plastic cups of known weights, capped tightly to minimize water loss, and returned to the laboratory. Soil samples were weighed wet, dried at 60^{O}C for 3 days, and weighed dry. A measured volume of deionized water (typically 40 ml, enough to saturate the sample) was then added to rehydrate the soil, mixed well with the soil, and the salinity of the supernatant was measured with a refractometer after 36 hours. Original soil salinity was calculated as (supernatant salinity in psu)(ml deionized water added)/(soil wet weight (g) – soil dry weight (g)). The six monthly measurements were averaged to yield a single overall porewater salinity value for each site.

Redox Conditions

Soil redox measurements were taken monthly at each of the 19 sites during August-September 2000 and June-September 2001. Soil redox was measured at a depth of 7cm using a handheld probe Orion® platinum electrode at three points along the *Spartina*/*Juncus* border between experimental plots. Areas with dense crab burrows were avoided. The triplicate readings for each site were averaged to yield a single monthly mean. The six monthly means were averaged to yield a single overall redox value for each site and recorded as millivolts (mV).

Organic Matter

Soil organic matter content was analyzed in July and August 2001 for each of the 19 marsh sites using the "Loss on Ignition" method (Craft et al. 1991). Three soil subsamples per site were collected between plots along the *Spartina/Juncus* border using a metal corer (2 cm diameter) to a depth of 5 cm. The three subsamples were pooled by site, dried, and ground in a mortar and pestle. A known weight of soil was added to three replicate crucibles per site, burned at 250ºC for 2 hours, then at 500ºC for 8 hours, and reweighed. The proportion of organic matter in the soil was calculated as (mass lost after ignition (g))/ (initial dry mass(g)). The triplicate values for each site were averaged to yield a single monthly mean. The two monthly means were averaged to yield a single overall percent organic matter value for each site. Because these data were proportions, they were arcsine (square root) transformed before analysis.

Bulk Density

Bulk density of the soil was measured on June 2001 for each of the 19 marsh sites (using a similar method to Craft and Casey 2000). Two replicate soil samples were collected at each site along the *Spartina/Juncus* border. A metal corer of known volume (216.62 cm^3) with a beveled edge was pushed into the soil to a depth of 10.2 cm (the height of the corer). The soil was leveled off on either end of the corer to ensure that only the volume of the core was collected. Soil samples were dried, then weighed. Bulk density of each sample was calculated as (dry weight of soil sample (g)/volume of soil in the corer (cm^3)). The two replicates were averaged to yield a single overall bulk density value for each site.

Soil Texture Composition

Soil texture composition was measured on June 2002 for each of the 19 marsh sites to determine the percent sand, silt, and clay content using the hydrometer method (Gee and Bauder, 1986). Soil collected for the bulk density analysis was used to analyze soil texture. Because soil had already been oven-dried, we did not use the moisture correction factor (MCF).

Soil was pulverized using a mortar and pestle to obtain a sample of 100 or 50 grams, depending on whether the soil was medium-textured, sandy, and low in organic matter, or clayey and organic-rich, respectively. If the bulk density was greater than 0.75 g/cm^3 and the organic matter content was low compared to other sites (typically <7%, with one exception, North Cabretta, having 16% organic matter content, but a high bulk density), the soil was categorized as sandy (7/19 sites were categorized as having sandy soil).

Two replicates for each site were run (one from each replicate bulk density sample), and four blank replicates were run every 10 and 9 samples. Blank replicates contained no soil and were used correct hydrometer readings. The percent sand, clay, and silt were determined using the following equations:

1) % Sand (2 to 0.05 mm) = [oven dry weight – $CO_{40\ secs}$]/oven dry weight * 100,
   where $CO_{40\ secs}$ = hydrometer reading of sample at 40 seconds minus blank reading at 40 seconds.
2) % Clay (< 0.002 mm) = $CO_{2\ hours}$/oven dry weight * 100,
   where $CO_{2\ hours}$= hydrometer reading of sample at 2 hours minus blank reading at 2 hours.
3) % Silt (0.002 to 0.05 mm) = 100% - % Sand - % Clay.

The duplicate replicates were averaged to yield a single overall percent sand, silt, and clay content value for each site. The sum of percent silt and clay values was used as a single variable for statistical analysis (since these comprised the two smallest fractions of total soil composition). Because these data were proportions, they were arcsine (square root) transformed before analysis.

Site Landscape Location

To characterize the position of the sites within the landscape, we assigned each site two scores for 1) upland influence and 2) whether the site was on an island or mainland. First, sites were scored for upland influence using an index ranging from 1 to 5, with 5 being a marsh site with the most upland influence (i.e. the marsh almost completely surrounded by upland, a peninsular marsh shape), 3 being a straight marsh to upland border, and 1 being a site least influenced by upland (i.e. the marsh almost completely surrounded the upland, a peninsular upland shape). Second, to see if differences existed based on whether the site was located on Sapelo Island or on the mainland in McIntosh County, a score of 0 was given to island sites and 1 to mainland sites.

PLANT GROWTH AND NUTRITIVE QUALITY

Percent Cover and Height

To determine whether fertilization affected plant growth and dominance, percent cover of *Juncus* and *Spartina* (n=17 sites, all but Sapelo Golf Course and I-95) and the height of tallest plant of each species (n=19 sites) were recorded for each plot in August 2001. Percent cover was measured using a 0.25 m^2 quadrat, separated by fishing line into 100-5x5 cm squares. The quadrat was placed in the center of the plot, and the number of individual squares in which each species was present and the height of the tallest plant within the quadrat was recorded. The percent cover and height measurements taken at each plot were averaged to yield an overall site mean for each treatment.

Biomass

To determine whether fertilization affected plant biomass and dominance, plants were harvested from each plot in October 2001. A 0.5-m x 0.25-m quadrat was placed through the center of each plot with the longest side perpendicular to the vegetation border, and all vegetation within the quadrat was clipped at the base. The vegetation was sorted by species and *Juncus* and *Spartina* were further divided into living and dead plant material. 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. Dead leaves were placed with the dead plant material while the remaining green stem and leaves were placed with the living plant material. Plant material was dried at 60°C for 4 days and then weighed to the nearest hundredth of a gram. The sorted vegetation collected from each plot was multiplied by 8 to estimate total plot biomass for each plant type (live or litter) and species, then were averaged to yield an overall site mean for each treatment.

Plant Quality

To determine whether fertilization affected plant quality, leaves of living and litter portions of *Spartina* and *Juncus* were analyzed for nitrogen content (% dry mass). Leaves were collected in June (litter) and July (living) 2001, as subsamples from material used in feeding experiments described below (*n*=15 sites, denoted by asterisks in Table 3.1), then freeze dried. Samples were ground to a powder by Tracy Buck, weighed to approximately 35 mg on a microbalance and placed in tin foil cups by me, and analyzed using a CHN autoanalyzer operated by Monica Palta. An amino acid standard was run every 13 samples, and a blank daily.

CONSUMER ABUNDANCE

Fungal Biomass

To determine whether fertilization affected fungal biomass in *Spartina* litter, standing dead leaves of *Spartina* were collected from each site in October 2001 (*n*=19 sites). The lower-most intact fully-brown leaf was collected from each control and fertilized plot (*n*=10 leaves per site) and preparation of leaves for fungal biomass analyses was performed by Steve Newell (following protocol from Newell 2001). Briefly, leaves were rinsed in running, cold tapwater for 15 seconds, 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 site x treatment were pooled and submerged in 5 ml ethanol in a screw-cap vial. The vials were placed in darkness at 4ºC for storage prior to processing. Another 1-cm length was cut from the ligule end of each leaf, and the five pieces per site x treatment were pooled in small glass drying pans, dried in a microwave (1000W, as in Newell 2001) and weighed. Samples were then placed in a muffle furnace in aluminum tares for 4 hours at 450ºC and reweighed for determination of leaf organic mass through loss on ignition. Fungal biomass was estimated using the ergosterol method following the methods described by Newell (2000). Fungal biomass was calculated on a per leaf basis (as µg ergosterol/g leaf organic mass (LOM)) for each treatment. To also estimate fungal biomass on a per plot basis (as mg ergosterol/m^2), I multiplied fungal biomass per leaf (mg) x average *Spartina* litter biomass (g) to obtain a single site value for each treatment.

Snail Density

Densities of the salt marsh snails *Melampus bidentatus* and *Littoraria irrorata* (hereafter referred to generically) were recorded in July and August 2001 in each of the 10 plots within the 19 sites. A 0.5-m x 0.5-m quadrat was laid in the center of each plot, and the total number of each snail species was counted. Care was taken to look within leaf furls for small snails and near the bases of plants along the marsh surface where snails often reside during low tide. The density of each species within the 0.5-m x 0.5-m quadrat was multiplied by 4 to estimate the density in the 1-m x 1-m plot. Snail densities were averaged across plots within each treatment and site to yield single monthly means per site, and monthly means were averaged for an overall site mean for each treatment. Snail densities were natural log transformed to improve normality before statistical analysis.

Grasshopper Density

Densities of the salt marsh grasshoppers, *Orchelimum fidicinum* and *Paroxya clavuliger* (hereafter referred to generically), were recorded in July and August 2001 in each of the 10 plots within the 19 sites. A pvc pipe was used to carefully brush through vegetation within the entire plot, and the number of each grasshopper species was counted as they jumped from the plot. Care was taken to ensure that grasshoppers were not counted twice if they jumped from and landed within plots again. Grasshopper densities were averaged to yield single monthly means per site, and monthly means were averaged for an overall site mean for each treatment. Further, the ratio of each grasshopper species to their food plant (*Orchelimum* eats *Spartina*, *Paroxya* eats *Juncus*, Davis and Gray 1966) in control and fertilized plots at each site was calculated to test whether this ratio varied among treatments.

CONSUMER FOOD SELECTION

Detritivore Choice Experiment

To determine whether fertilization affected palatability of plant litter to detritivores, I conducted paired feeding assays with the snail *Littoraria irrorata* and the crab *Armases cinereum* (hereafter referred to generically). A single standing-dead *Spartina* shoot was collected during the last week of May 2001 from each fertilized and control plot at 15 sites (9 island and 6 mainland sites, denoted by asterisks in Table 3.1). Attached leaf blades were removed to correct for variability in blade occurrence among shoots, and thus potential consumer choice bias among food (as detritivores often prefer softer blade material over tougher stem and sheath material, Graca et al. 2000). The collected plant samples were then pooled across plots within each treatment and site. Thirty *Littoraria* (approximately 20 mm in spire height) and 30 *Armases* (carapace width≥20mm) were collected from Dean Creek and Cabretta Island, respectively.

In the lab, one inch of each stem and surrounding sheath was cut, pooled within site and treatment, and frozen for Carbon:Nitrogen (C:N) analysis. Then stems and surrounding sheaths were cut to 1 and 2 cm in length, weighed, and used as food for snails and crabs, respectively, in the detritivore choice experiments. The remaining portion of each stem and surrounding sheath was also weighed, dried at 60ºC for 3 days, and reweighed to calculate initial percent water content (calculated as 100 – [(dry weight (g) of stem / wet weight (g) of stem) x 100].

Snails and crabs 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. One snail or one crab was placed into a pint jar or plastic bucket respectively, with two plant pieces, one control and one fertilized. Plant pieces were labeled with colored pushpins to denote treatment. A small amount of brackish water (15 ppt) was added to maintain humidity. Jars were capped with mesh and buckets had mesh windows to allow air circulation.

Assays were checked once daily. Individual replicates of snails and crabs were allowed to feed until $\geq$ 25% of either plant piece was eaten, or for a maximum of 40 and 30 days, respectively. Then plants were removed, rinsed free of feces, dried at 60ºC for 3 days, and weighed. The final dry weight was subtracted from the initial estimated dry weight (calculated as [initial weight of stem and surrounding sheath – (percent water x initial weight of stem and surrounding sheath)]) to give the amount eaten. The duplicate replicates per site were averaged for an overall mean for each site. For multiple regression analysis, effects of fertilization on preference were calculated as (fertilized plant consumption (mg) – control plant consumption (mg)).

Herbivore Choice Experiment

To determine whether fertilization affected palatability of leaves to herbivores, we conducted paired feeding assays with grasshoppers *Orchelimum fidicinum* and *Paroxya clavuliger* (hereafter referred to generically). Fresh, undamaged leaves of *Spartina* and *Juncus* were collected from 15 sites (9 island and 6 mainland sites, denoted by asterisks in Table 3.1) from 3 randomly chosen fertilized and control plots each (total *n*=90/species). Leaves were pooled within treatments at each site. Grasshoppers (*Orchelimum* and *Paroxya*, *n*=30 each) were collected from a site that was not one of the experimental sites.

In the lab, one inch of each leaf per plant species per site was cut, pooled within sites and treatments, and frozen for Carbon:Nitrogen (C:N) analysis as described earlier. The remaining leaves were trimmed to 150 mm in length, marked at the base to indicate treatment, and used in the herbivore choice experiments.

Grasshoppers were offered a choice between a control and fertilized leaf from the same site (*n*=15 sites). Each comparison was replicated twice, for a total of 30 replicates. A single grasshopper (*Orchelimum* for *Spartina* assays and *Paroxya* for *Juncus* assays) was placed inside a mesh cage with the two plant pieces oriented upright in a 5-ml vial filled with distilled water.

Assays were checked twice daily. Individual replicates of grasshoppers were allowed to feed until $\geq$ 25% of either plant piece was eaten, or for a maximum of 3 days. The leaf area eaten was estimated using a 1-mm x 1-mm mesh grid laid over the leaves. The duplicate replicates per site were averaged for an overall mean for each site. For multiple regression analysis, effects of fertilization were calculated as (fertilized plant consumption (mm^2) – control plant consumption (mm^2)).

Grazing Damage

To determine if fertilization affected the amount of damage that plants received from grasshoppers, I estimated damage to plants in the field during the first week of August 2001 (*n*=19 sites). At this time, grasshoppers were large and actively feeding. A 1 m-long pvc pipe was marked at 10, 30, 50, 70, and 90 centimeters. At each plot, the pvc pipe was placed parallel to the vegetation border, first through the center of the *Juncus* stand and then through the center of the *Spartina* stand. In each stand, the plant closest to each mark on the pvc pipe was scored for damage by grasshoppers using standardized scores that ranged from 0-50% damage in 5% increments (Table 2.1). Damage to individual plants was averaged for each plot, and plot means were averaged to yield an overall site mean for each treatment.

CONSUMER GROWTH

To determine if fertilization affected snail growth, we conducted a laboratory growth experiment. Two species of snails, *Melampus* and *Littoraria*, were collected from the Chocolate and Meridian, and Dean Creek, sites respectively. The spire height of all snails (*n*=120/species) was measured to the nearest hundreth of a millimeter. To allow potential for rapid growth, only small snails (< 5 mm in length) were used (Bingham 1972).

Snails were fed standing dead *Juncus* or *Spartina* collected from control or fertilized plots. Standing dead leaves (*Juncus*) or stems (*Spartina*) were cut (approx. 7cm length) as close as possible to the base of the stem from each of the five fertilized and five control plots (1 stem/plot) at each of fifteen of the experimental sites (9 island and 6 mainland sites, denoted by asterisks in Table 2). The 5 stem pieces of each species from each treatment were pooled within a site. A total of 300 (5 plots * 2 treatments * 2 plant species* 15 sites) dead stem pieces were collected.

Because the *Spartina* stems were in varying states of decay, loose leaf and sheath material was removed from some stems to create standardized stem pieces lacking leaf material. Four of the five collected plant pieces for each treatment and species were haphazardly selected and cut to 5 cm in length. The fifth plant piece was stored in the freezer as a replacement for samples if needed during the experiment. The 5 cm pieces of stem were weighed on an analytical balance to determine wet mass. The excised 2 cm of each stem was also weighed, dried at 60° C for 3 days, and reweighed to calculate initial percent water content (calculated as in the Detritivore Choice Experiment).

Snails were housed individually in Nalgene vials (125 mL), kept at room temperature, and placed in indirect light in a location that experienced a natural light and dark cycle, but was out of direct sunlight. Five mL of brackish (15 ppt) water (a mixture of seawater collected from a tidal creek and deionized water) was added to each of the vials. The 5 cm dead plant shoots were added to each vial in an upright position.

The growth experiment ran for 3 months and food was not replaced. Vials were opened 2 times/week for ventilation, and distilled water was added if needed to replace evaporation. Snails that died during the first 3 weeks were replaced (these replicates ran to a later date than the others to allow a total of 3 months of growth). Snails that died subsequently were dropped from the analysis.

To determine snail growth, snails were re-measured. The duplicate replicates per snail species x plant species x treatment combination were averaged to yield a single replicate value for each treatment at each site.

STATISTICAL ANALYSIS

For all analyses, sites were the unit of replication. Whenever multiple data points were obtained for a treatment within a site, these were averaged to yield a single value for each treatment at each site.

Because soil organic matter, bulk density, and silt + clay content were all correlated to one another, I used a composite soil variable obtained from the first principle component axis of a PC ordination of these variables for regression analyses. PCA1, hereafter called “soil”, explained 88.4 percent of the variance in the data, and was positively correlated with bulk density, and negatively with organic content and silt + clay.

I used 4 general approaches to analyze results. First, effects of fertilization were compared between treatments using paired t-tests (H_a: difference <>0). In one case, the non-parametric Wilcoxon Signed Rank test was used because it was more powerful given the distribution of the data. Second, I explored variation among site responses to fertilization using multiple regression analyses. For each site response, 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 Mallow’s C_p statistic (Mallows 1973), model adjusted R^2, and the overall model *P*-value. Because some data were not collected at all sites, sample sizes for selected regressions range from 15 to 19. Collinearity between variables was avoided by dropping potential predictor variables with VIF scores>5 that made the least sense biologically. When the N-content of litter of either plant species was the dependent variable, the N-content of the live portions of that species was initially forced into the model, and later removed only if it had $P<0.15$ in the best resulting model. Third, I used ANOVA to examine the effects of fertilization and plant species on snail growth. Finally, for each field measurement, I compared natural site variation to treatment variation by analyzing the ratio of the coefficients of variation in control plots at 19 sites versus the coefficient of variation among treatments.

Table 2.1. Criteria for scoring grasshopper damage.

Observed Grazing	Percent Damage Assigned
None	0
Tips of plant removed or evidence of chewing along sides of plant	5 if 1-2 tips or chewing-marks observed 10 if 3-5 tips or chewing-marks observed
More than 5 chewing-marks observed (+/- tips removed)	15-30, depending on extent of damage
Large portions of plant removed or less than half of leaves removed (*Spartina* only)	35-45, depending on extent of damage
Complete top portion of plant removed or half of leaves removed (*Spartina* only)	50

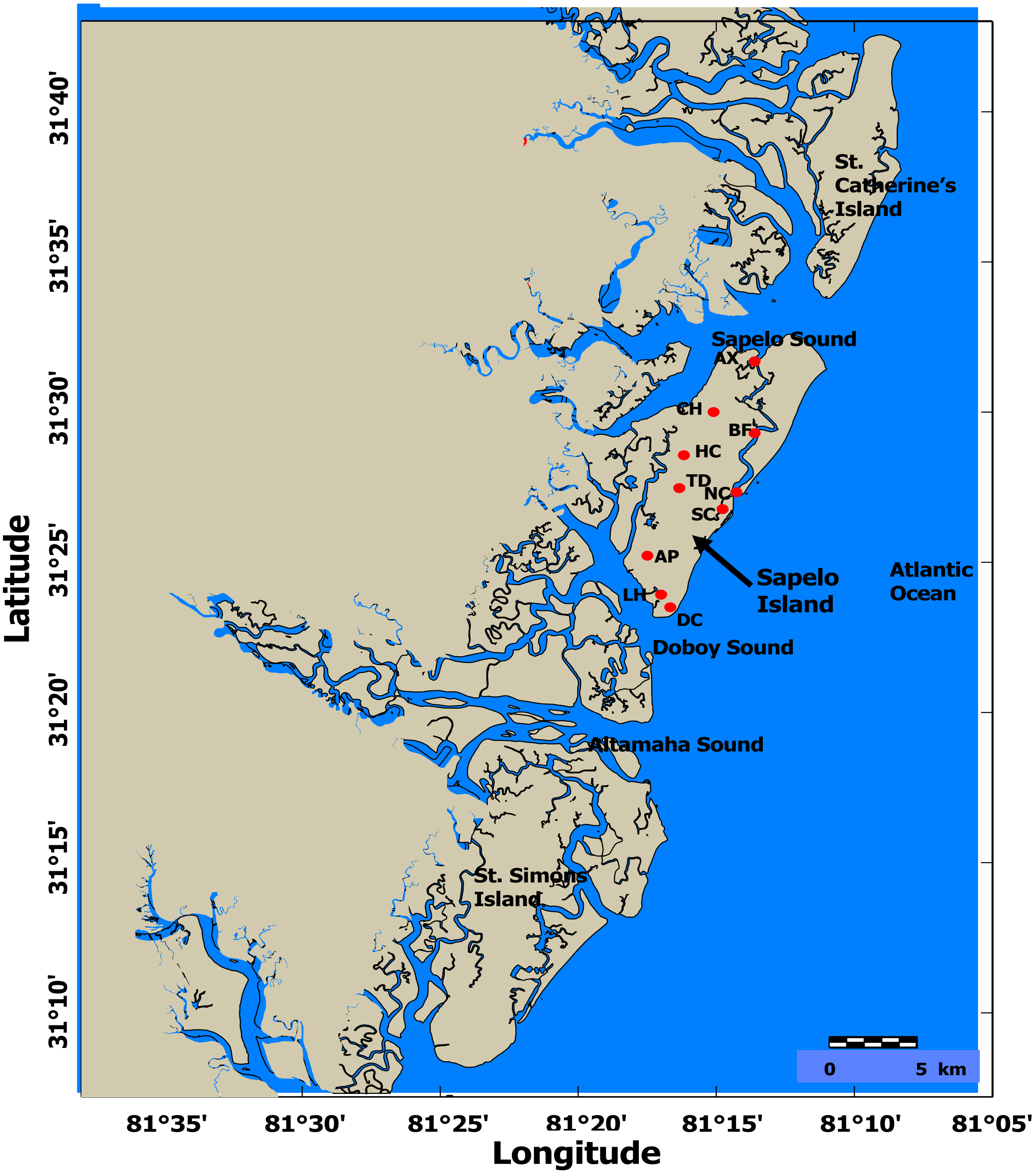

Figure 2.1. Map of study sites. Ten sites were located on Sapelo Island, Georgia, and nine sites were located on the mainland in McIntosh County, Georgia. Site codes are: AP=Airport, AX=Apex, BB=Belle Bluff, BF=Bourbon Field, BH=Buck Hill Swamp, CH=Chocolate, DC=Dean Creek, HC=Hunt Camp, I-95=Interstate 95, LH=Lighthouse, ME=Meridian, NC=North Cabretta, PH=Pine Harbor, RV=Newport RV Park, SC=South Cabretta, SG=Sapelo Golf Course, TD=Timber Dock, VA=Valona, and YM=Young Man

CHAPTER III

RESULTS

GENERAL EFFECTS OF FERTILIZATION

Plant Growth and Dominance

Fertilization altered the border between *Spartina* and *Juncus* at a majority of the 19 sites, typically increasing *Spartina* dominance within plots. Averaged across all sites, the biomass of living *Spartina* was 197% greater in fertilized than control plots, while biomass of living *Juncus* was 33% less in fertilized than control plots (Fig. 3.1). Similarly, the biomass of standing dead (litter) *Spartina* was 174% greater in fertilized than control plots, while the biomass of standing dead (litter) *Juncus* was 31% less in fertilized than control plots (Fig. 3.1). The pattern of increasing living and standing dead (litter) *Spartina* biomass occurred at 18 of 19 sites each, while the pattern of decreasing living and standing dead (litter) *Juncus* occurred at 17 and 16 of 19 sites, respectively. Changes in biomass of live plant species can be caused by changes in either 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. 3.2). The pattern of increasing ground cover by *Spartina* in fertilized plots held at 15 of 17 sites, and the pattern of decreasing ground cover by *Juncus* in fertilized plots held at 13 of 17 sites. Fertilization significantly boosted heights of both plant species, although *Spartina* experienced the greatest benefit with fertilized plants 38% taller than control plants, compared to fertilized *Juncus* plants which were only 4% taller than controls (Fig. 3.3). The trend towards taller plants in fertilized plots held at 18 of 19 sites for *Spartina* and 16 of 19 for *Juncus*.

Plant Nutritive Quality

Averaged across all sites, the nitrogen content of living *Spartina* and *Juncus* leaves was 25% and 15% greater in fertilized than control plots, respectively (Fig. 3.4). This pattern held at 12 of 15 sites for *Spartina* and 13 of 15 sites for *Juncus*. In contrast, there were no significant differencea in the nitrogen content of standing dead leaves of either species, although the trend was toward greater nitrogen content in fertilized plots (Fig. 3.4).

Herbivore and Detritivore Density

Although the trend for all herbivores (*Orchelimum* and *Paroxya*) and detritivores (*Littoraria* and *Melampus*) was toward greater abundance in fertilized than control plots, only *Orchelimum* increased significantly, with 178% more individuals in fertilized than control plots (Fig. 3.5, 3.6), suggesting that herbivores may be more responsive than detritivores to increased plant-nutrient status and biomass. The ratio of grasshopper abundance:host plant biomass was significantly greater in fertilized plots for *Paroxya*, suggesting that they responded to plant quality because *Juncus* biomass actually decreased in fertilized plots. Although the ratio of *Orchelimum* to *Spartina* was not significantly greater, there was a trend toward higher values in fertilized plots, hinting that they may also be responding to changes in plant quality in addition to plant quantity (Fig. 3.7).

Decomposer Biomass

When fungal biomass was estimated on a per gram of LOM basis, the trend was toward greater fungal biomass in standing dead *Spartina* leaves in fertilized plots, but the difference was not significant (Fig. 3.8). However, when the fungal biomass was normalized to fungal biomass m^{-2} by multiplying by dead *Spartina* biomass m^{-2} (per plot basis), treatments differed significantly, with 210% more fungal biomass in fertilized than control plots, and 14 of 19 sites exhibiting this pattern (Fig. 3.8). Thus, fertilization did not affect fungal biomass on a per leaf basis, though it could be that fungal activity and sexual output were higher with fertilization (Newell et al. 1996b), this was not examined, but significantly affected fungal biomass when it was considered on a per plot basis to include increases in biomass of dead *Spartina*. Ergosterol values per leaf reported in this study were similar to those formerly reported by Newell et al. (2000).

Consumer Food Selection

Feeding damage by grasshoppers on fertilized plants of *Juncus* and *Spartina* was 61% and 132% greater, respectively, than control values (Fig. 3.9). This trend held at 18 of 19 sites for *Spartina* and 15 of 19 sites for *Juncus*. Although these data suggest that grasshoppers were preferentially consuming fertilized plants, consumption of *Spartina* and/or *Juncus* by detritivores and herbivores during paired feeding assays in the lab did not indicate that fertilization influenced feeding choices. Consumption of fresh plant material by *Orchelimum* and *Paroxya* did not significantly differ between treatments (Fig. 3.10), nor did consumption of dead *Spartina* by *Littoraria* and *Armases*, although *Armases* exhibited a trend toward greater consumption of the fertilized treatment at 11 of 15 sites (Fig. 3.11).

Consumer Growth

Growth of *Littoraria* and *Melampus* feeding on dead *Spartina* and *Juncus* did not differ among fertilization treatments (Fig. 3.12). Growth of *Melampus*, however, differed between the plant species, with 267% better growth on *Spartina* versus *Juncus*. *Littoraria* growth did not differ between plant species.

VARIATION IN RESPONSES AMONG SITES

Site Characteristics

Sites varied in salinity, redox potential, sediment organic matter content, sediment silt and clay content, sediment bulk density, and upland influence (Table 3.1). Comparisons of coefficients of variation (CV) indicates that organic matter content varied most, followed by bulk density, silt and clay content, redox potential, and salinity (Table 3.2). However, all site edaphics were quite variable (i.e. all CVs > 15).

Plant Growth Responses

Plant growth, as determined by percent cover, height, and biomass, was correlated with both physical characteristics and biological factors at each site (Table 3.3). Three of 4 models for percent cover were significant, with the most common predictors being mainland score, grazing damage, N-content, and herbivore densities, each significant at $P<0.05$ in the models, except for *Orchelimum* density. Mainland score was negatively correlated to control *Spartina* and positively correlated to control *Juncus* (i.e. more *Juncus* and less *Spartina* on mainland versus island sites), grazing damage was negatively correlated with plant cover in control plots, N-content of fertilized *Spartina* was negatively correlated to its percent cover while the N-content of control *Juncus* was positively correlated to its percent cover, and densities of the herbivores *Orchelimum* and *Paroxya* were positively correlated to fertilized *Spartina* and control *Juncus*, respectively. Salinity was only an important predictor in the control *Spartina* model, but it had a strong inverse relationship to *Spartina* cover ($P<0.01$).

Salinity was the most important correlate of height for *Spartina* and *Juncus*, negatively predicting height in each case, with a significant relationship in 3 of 4 full models ($P<0.01$, Table 3.3). In a univariate regression, it significantly explained over 40% of the variation in height for both species in both treatments ($P<0.01$ each, Fig. 3.13). Soil, sitescore, and either grazing damage or herbivore density each occurred as predictor variables in 3 of 4 models, with soil and grazing damage negatively related and sitescore positively related to height.

Sitescore, a measure of upland influence, was the dominant variable in 4 of 6 significant models for biomass of each species and treatment. Sitescore was negatively correlated with fertilized *Spartina* and control *Spartina* litter (indicating reduced *Spartina* where there was greater upland influence), and positively correlated with live and litter portions of control *Juncus* (indicating increased *Juncus* where there was greater upland influence). Thus, sitescore was the most important determinant of biomass, especially in control plots (occurring in 3 of 4 significant control models), and having opposite correlations to each plant species. In 3 of the 4 significant models for *Spartina* biomass, redox was also an important predictor, with control live and litter portions having a negative and fertilized live *Spartina* a positive relationship to redox potential. Live biomass of *Spartina* was further explained by its own N-content, with a positive relationship in the control model and a negative relationship in the fertilized model. In addition to sitescore, the only other common predictor of *Juncus* biomass was soil, which was negatively correlated with live and dead *Juncus* biomass in the control treatment.

Over all 3 plant size variables (percent cover, height, and biomass), the most common predator variable was sitescore, which occurred in over half of the significant models (8/13), with a majority of those relationships being significant. Sitescore was in every significant model predicting *Juncus* growth parameters (5/5) and in 3 of 8 of the models predicting *Spartina* growth parameters, with a positive relationship in all but one *Juncus* model (percent cover) and a negative relationship in all but one *Spartina* model (height).

Plant Quality Responses

The most common variable predicting the N-content of living plants was the N-content of the other plant species (Table 3.4). This result occurred in a majority (3/4) of the models predicting live N-content, with a negative relationship in both control models and a positive relationship in the *Juncus* fertilized model. Furthermore, in a univariate regression, N-content of the other plant significantly explained over 30% of the variation in N-content of control plants (*P*=0.03 each, Figs. 3.14, 3.15). Live *Spartina* N-content was correlated with different factors in the two treatments, but a majority of the factors (4/5, mainland, redox, sitescore, and grazing damage) that were correlated with N-content in the fertilized treatment were also important in fertilized *Spartina* biomass models, with the same relationships. Additionally, there was a correlation between the N-content of each species and biomass in 3 of 4 models, with *Spartina* biomass always negatively related to live N-content and *Juncus* biomass always positively related to live N-content, regardless of species or treatment.

Although mainland, salinity, and *Juncus* N-content occurred in a majority of the significant models (2/3) predicting litter N-content for each species, only salinity had both a consistent relationship (negative) and a high significance level ($P<0.01$). N-content of *Juncus* litter was best predicted by live *Juncus* N-content, but the relationship was positive in the control model and negative in the fertilized model.

Herbivore Densities

The density of *Orchelimum* was negatively correlated with *Littoraria* density, whereas the density of *Paroxya* was positively correlated with *Littoraria* density in all 4 models, regardless of treatment ($P \leq 0.05$ each, Table 3.5). However, in a univariate regression, only *Orchelimum* density in the fertilized treatment was significantly ($P=0.003$) and tightly correlated with *Littoraria* density, which explained 42% of *Orchelimum* density variation in fertilized plots, but only 18% in control plots (Fig. 3.16). *Paroxya* density, on the other hand, was not significantly explained by *Littoraria* density in either treatment in univariate regressions and had weak R^2 values of 0.10 and 0.15, respectively, for control and fertilized treatments (not shown). Grasshopper densities in control plots were further predicted by sitescore in the full models, which was positively related to *Orchelimum* density and negatively related to *Paroxya* density. *Paroxya* density was positively related to *Melampus* density in the control plot model, whereas *Orchelimum* density was negatively related to *Melampus* density in the fertilized plot model.

Decomposer Biomass Responses

Fungal abundance on a per plot and per leaf basis was consistently negatively correlated with redox in the 3 significant models, but the strength of the relationship was strongest on a per plot basis ($P<0.01$), likely due to the strong negative relationship between redox and dead *Spartina* biomass (Tables 3.5 and 3.3). In a univariate regression, redox significantly explained 39% and 22% of the variation in fungal biomass per plot in control and fertilized plots, respectively ($P \leq 0.05$ each, Fig. 3.17). Sitescore also consistently occurred in models of fungi per plot with a negative relationship, regardless of treatment. When examined on a per leaf basis, variation in fungal density was predictable only in fertilized plot models, in which it was negatively correlated with redox and positively with dead *Spartina* biomass.

Detritivore Density Responses

Littoraria and *Melampus* densities were best predicted by a strong negative relationship between the two species in all 4 models ($P < 0.001$ each, Table 3.5). In a univariate regression, the inverse relationship between the two snails significantly explains 47% and 37% of the variation in their densities in control and fertilized plots, respectively ($P < 0.01$ each, Fig. 3.18). Other variables were also included in the models, but were not consistently significant or as common throughout. Most notable, herbivore densities were important in 3 of 4 models, with *Littoraria* density negatively correlated with *Orchelimum* in each treatment and *Melampus* density positively correlated with *Paroxya* in the control treatment. Further, densities of both snails were negatively related to N-content of live *Juncus* in control plots, although the relationship was strong ($P < 0.01$) only in the *Melampus* model.

Consumer Food Selection Responses

Damage to plants in fertilized plots was significantly predicted by herbivore densities, with *Orchelimum* and *Paroxya* densities positively related to and explaining 21% and 32% of the variation in grazing damage to *Spartina* and *Juncus* in a univariate regression, respectively ($P \leq 0.05$ each, Table 3.5, Fig. 3.19). I found no significant model predicting damage to plants in control plots.

I found no regression models that predicted site-to-site variation in feeding preferences of herbivores in the laboratory (results not shown). Similarly, I found no model predicting feeding preferences of one detritivore, *Littoraria* (results not shown). In contrast, feeding preferences of the other detritivore, *Armases*, were correlated with site salinity in a univariate regression (*P*=0.04, Fig. 3.20). At low-salinity sites, fertilized plants were preferred over control plants. At high-salinity sites, control plants were preferred. These results should be interpreted with caution, however, because there was a strong outlier in the dataset, and the regression was not significant when this outlier was removed.

Natural Variation vs. Treatment

Fertilization had a relatively large effect on *Spartina* factors as indicated by CV (site) to CV (treatment) ratios similar to or less than 1, including live and standing dead biomass, live N-content, and grazing damage (Table 3.6). In contrast, *Juncus* factors, including live and standing dead biomass, and live N-content, were less influenced by treatment and more influenced by natural variation across space than *Spartina*, as indicated by ratios less than 2. Intermediate ratio values (2.71-6.74) exhibited by grazing damage to *Juncus*, standing dead *Juncus* N-content, *Paroxya* density, and fungal biomass, showed that treatment had a relatively small effect on their responses. Lastly, natural variation overwhelmed treatment effects on *Littoraria* and *Melampus* densities, as indicated by large ratio values (>20).

Table 3.1. Physical characterization of study sites. Salinity, redox potential, and organic matter are overall means ± SD of monthly means of triplicate subsamples (6 months each for salinity and redox potential; 2 months for organic matter). Silt + clay content and bulk density are means of duplicate subsamples per site. Asterisks indicate sites where leaves were collected for consumer choice experiments and percent nitrogen analysis.

Site	Salinity (psu)	Redox Potential (mV)	Organic Matter (%)	Silt + Clay Content (%)	Bulk Density (g/cm^3)	Sitescore	Island (I) or Mainland (M)
Airport*	43 ± 13	-221 ± 58	21.3 ± 2.5	14.4	0.52	3	I
Apex	45 ± 12	-115 ± 84	6.0 ± 1.4	6.3	0.91	2	I
Belle Bluff Marina*	34 ± 6	-316 ± 17	27.9 ± 1.8	15.9	0.30	5	M
Bourbon Field*	44 ± 11	-222 ± 89	41.2 ± 1.0	16.5	0.28	3	I
Buck Hill Swamp*	31 ± 5	-324 ± 18	20.4 ± 1.0	12.4	0.29	5	M
Chocolate*	33 ± 8	-250 ± 67	12.8 ± 2.3	11.5	0.34	3	I
Dean Creek*	51 ± 8	-217 ± 74	6.7 ± 0.7	1.0	1.06	2	I
Hunt Camp*	30 ± 9	-317 ± 37	7.8 ± 1.6	9.4	0.61	2	I
I-95	33 ± 4	-328 ± 18	27.5 ± 1.9	25.9	0.24	5	M
Lighthouse*	40 ± 7	-346 ± 59	23.0 ± 2.0	20.7	0.35	1	I
Meridian*	40 ± 14	-209 ± 90	4.8 ± 0.6	5.5	1.03	4	M
North Cabretta*	51 ± 16	-210 ± 53	15.7 ± 1.4	12.8	0.87	4	I
Pine Harbor*	39 ± 10	-260 ± 51	5.4 ± 0.3	8.0	1.02	4	M
RV Park*	33 ± 2	-337 ± 26	23.1 ± 1.4	25.6	0.25	2	M
Sapelo Golf	40 ± 10	-253 ± 16	20.2 ± 0.3	14.0	0.50	3	M
South Cabretta*	38 ± 8	-281 ± 35	19.3 ± 0.6	8.2	0.51	5	I
Timber Dock*	33 ± 12	-262 ± 90	6.1 ± 0.8	6.7	0.92	4	I
Valona*	41 ± 15	-236 ± 62	5.7 ± 0.7	3.7	0.95	5	M
Young Man	38 ± 6	-297 ± 43	35.1 ± 0.9	20.2	0.27	2	M

Table 3.2. Cross-site characterization of study area. Overall site means ± SD, lower and upper 95% confidence intervals, and coefficients of variation (CV) are reported for salinity, redox potential, organic matter, silt + clay content, and bulk density (*n*=19 sites).

	Salinity (psu)	**Redox Potential (mV)**	**Organic Matter (%)**	**Silt + Clay Content (%)**	**Bulk Density (g/cm^3)**
Mean ± SD	39 ± 6	-291 ± 59	17.4 ± 10.9	13.0 ± 6.5	0.59 ± 0.31
Lower 95% CI	36	-291	12.1	9.9	0.44
Upper 95% CI	42	-235	22.6	16.2	0.74
CV	16%	22%	63%	50%	53%

Table 3.3. Summary of results of multiple regression models predicting plant growth of live and litter portions of *Spartina* and *Juncus* within control and fertilized plots. Symbols (*, ** and *** indicate $P \leq 0.05$, <0.01, <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. All models had Mallow's $C_p < p$ (the number of parameters), except for percent cover of control *Juncus*, and biomass of fertilized *Spartina*.

Variable Abbreviations: S=soil, R=redox, SAL=salinity, SS=sitescore, ML=island or mainland, SLN=nitrogen content of live *Spartina*, JLN=nitrogen content of live *Juncus*, SDN=nitrogen content of standing dead *Spartina*, JDN=nitrogen content of standing dead *Juncus*, SLB=live *Spartina* biomass, JLB=live *Juncus* biomass, SDB=standing dead biomass of *Spartina*, JDB=standing dead biomass of *Juncus*, GS=grazing damage to *Spartina*, GJ=grazing damage to *Juncus*, O=*Orchelimum* density, P=*Paroxya* density, L=*Littoraria* density, M=*Melampus* density, F=fungal biomass, NS=not significant.

		Control	**Fertilized**
Percent Cover	*Spartina*	-S*, -ML*, -SAL**, -GS** model adjusted R^2=0.72, *P*=0.0004, *n*=17	+O, -SLN** model adjusted R^2=0.59, *P*=0.002, *n*=15
	Juncus	+ML*, +R**, -SS*, -GJ*, +JLN*, +P* model adjusted R^2=0.72, *P*=0.008, *n*=15	NS, *n*=17
Height	*Spartina*	-S***, -ML, -SAL**, +SS*, -GS***, -SLN model adjusted R^2=0.91, *P*=0.0001, *n*=15	-SAL** model adjusted R^2=0.37, *P*=0.003, *n*=19
	Juncus	-S***, -SAL, +SS**, -P model adjusted R^2=0.83, *P*<0.0001, *n*=19	-S**, -SAL**, +SS**, -GJ* model adjusted R^2=0.72, *P*=0.0002, *n*=19
Biomass	*Spartina*	-R**, +SLN* model adjusted R^2=0.61, *P*=0.001, *n*=15	+ML***, +R*, -SAL, -SS**, -GS**, +L***, -SLN*** model adjusted R^2=0.92, *P*=0.0002, *n*=15
	Juncus	-S, -ML, +SS**, +JLN* model adjusted R^2=0.52, *P*=0.02, *n*=15	NS, *n*=19
	Spartina Litter	-R**, -SS* model adjusted R^2=0.40, *P*=0.006, *n*=19	+F** model adjusted R^2=0.37, *P*=0.003, *n*=19
	Juncus Litter	-S**, +SS* model adjusted R^2=0.43, *P*=0.005, *n*=19	NS, *n*=19

Table 3.4. Summary of results of multiple regression models predicting nitrogen-content of live and litter portions of *Spartina* and *Juncus* in control and fertilized treatments. Symbols (*, ** and *** indicate $P \leq 0.05$, <0.01, <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. All models had Mallow's $C_p < p$ (the number of parameters), except for control *Juncus* litter. See Table 3.3. for abbreviations.

	Control	**Fertilized**
Spartina	-S*, +JLB*, -JLN*** model adjusted R^2=0.62, P=0.003, n=15	+ML**, +R**, -SS**, -SLB**, -GS* model adjusted R^2=0.77, P=0.002, n=15
Juncus	-R*, -SLB, +JLB**, -SLN* model adjusted R^2=0.75, P=0.0009, n=15	+SLN* model adjusted R^2=0.25, P=0.03, n=15
Spartina Litter	-ML, -SAL** model adjusted R^2=0.46, P=0.01, n=15	NS, n=15
Juncus Litter	+JLN** model adjusted R^2=0.39, P=0.008, n=15	-S**, +ML, -SAL**, +SS**, -M*, -JLN*, -SLN model adjusted R^2=0.93, P=0.0002, n=15

Table 3.5. Summary of results of multiple regression models predicting consumer density and biomass and grazing damage to *Spartina* and *Juncus* plants within plots of control and fertilized treatments. Symbols (*, ** and *** indicate $P \leq 0.05$, <0.01, <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. All models had Mallow's $C_p < p$ (the number of parameters), except for *Littoraria* density in fertilized plots and *Melampus* density in control plots. See Table 3.3. for abbreviations.

		Control	**Fertilized**
Herbivores	*Orchelimum*	-L***, +SS* model adjusted R^2=0.48, *P*=0.002, *n*=19	-L**, -M* model adjusted R^2=0.32, *P*=0.02, *n*=19
	Paroxya	+JLN**, +L***, +M***, -SS model adjusted R^2=0.79, *P*=0.0004, *n*=15	+L*, +GJ** model adjusted R^2=0.40, *P*=0.006, *n*=19
Decomposers	Fungi (mg/plot)	-R***, -SS* model adjusted R^2=0.53, *P*=0.0009, *n*=19	+S*, -R**, -SS model adjusted R^2=0.38, *P*=0.02, *n*=19
	Fungi (µg/leaf)	NS, *n*=19	-R, +SDB* model adjusted R^2=0.43, *P*=0.005, *n*=19
Detritivores	*Littoraria*	-JLN, -M***, -O*, +GS** model adjusted R^2=0.89, *P*<0.0001, *n*=15	-M***, -O** model adjusted R^2=0.63, *P*=0.001, *n*=19
	Melampus	-JLN**, - L***, +P*** model adjusted R^2=0.90, *P*<0.0001, *n*=15	+JDB**, -SDB*, -L*** model adjusted R^2=0.61, *P*=0.0005, *n*=19
Grazing Damage	*Spartina*	NS, *n*=19	+O* model adjusted R^2=0.16, *P*=0.05, *n*=19
	Juncus	NS, *n*=19	+P* model adjusted R^2=0.28, *P*=0.01, *n*=19

Table 3.6. 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**
Spartina Biomass	46.6	70.3	0.66
Juncus Biomass	38.5	27.3	1.41
Standing Dead *Spartina* Biomass	73.7	65.8	1.12
Standing Dead *Juncus* Biomass	44.5	25.5	1.75
Spartina N-Content	22.3	20.1	1.11
Juncus N-Content	16.2	9.8	1.65
Standing Dead *Spartina* N-Content	26.8	15.4	1.74
Standing Dead *Juncus* N-Content	25.7	6.7	3.84
Orchelimum Density	124.1	68.1	1.82
Paroxya Density	154.2	28.1	5.49
Fungal Biomass (µg/LOM)	41.1	6.1	6.74
Littoraria Density	110.4	5.2	21.23
Melampus Density	228.9	9.5	24.09
Grazing Damage to *Spartina*	68.5	57.5	1.19
Grazing Damage to *Juncus*	88.2	32.6	2.71

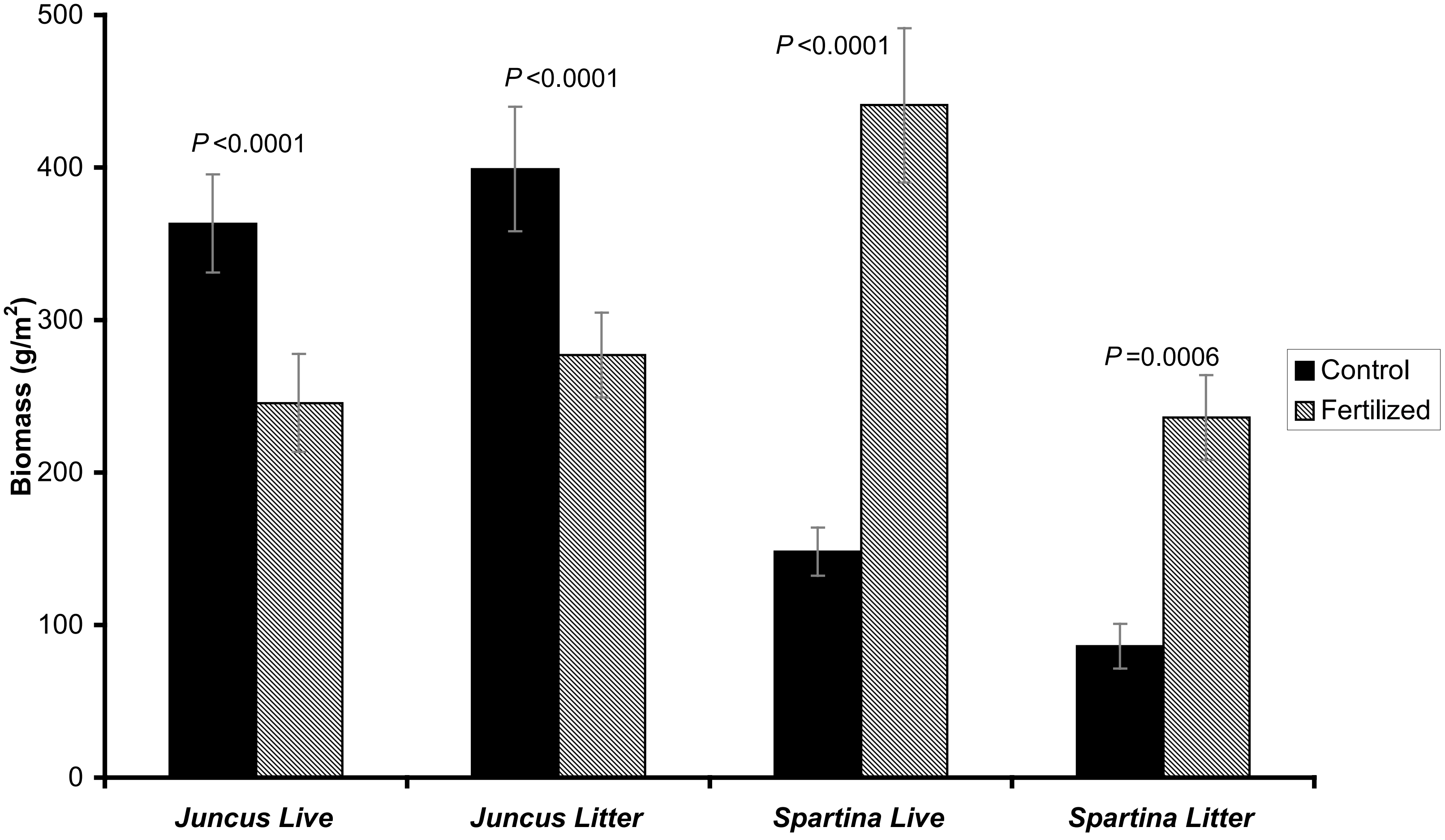

Figure 3.1. Above-ground biomass of live and standing dead *Spartina* and *Juncus* leaves in control and fertilized plots (*n* =19 sites). Data are means ± standard error.

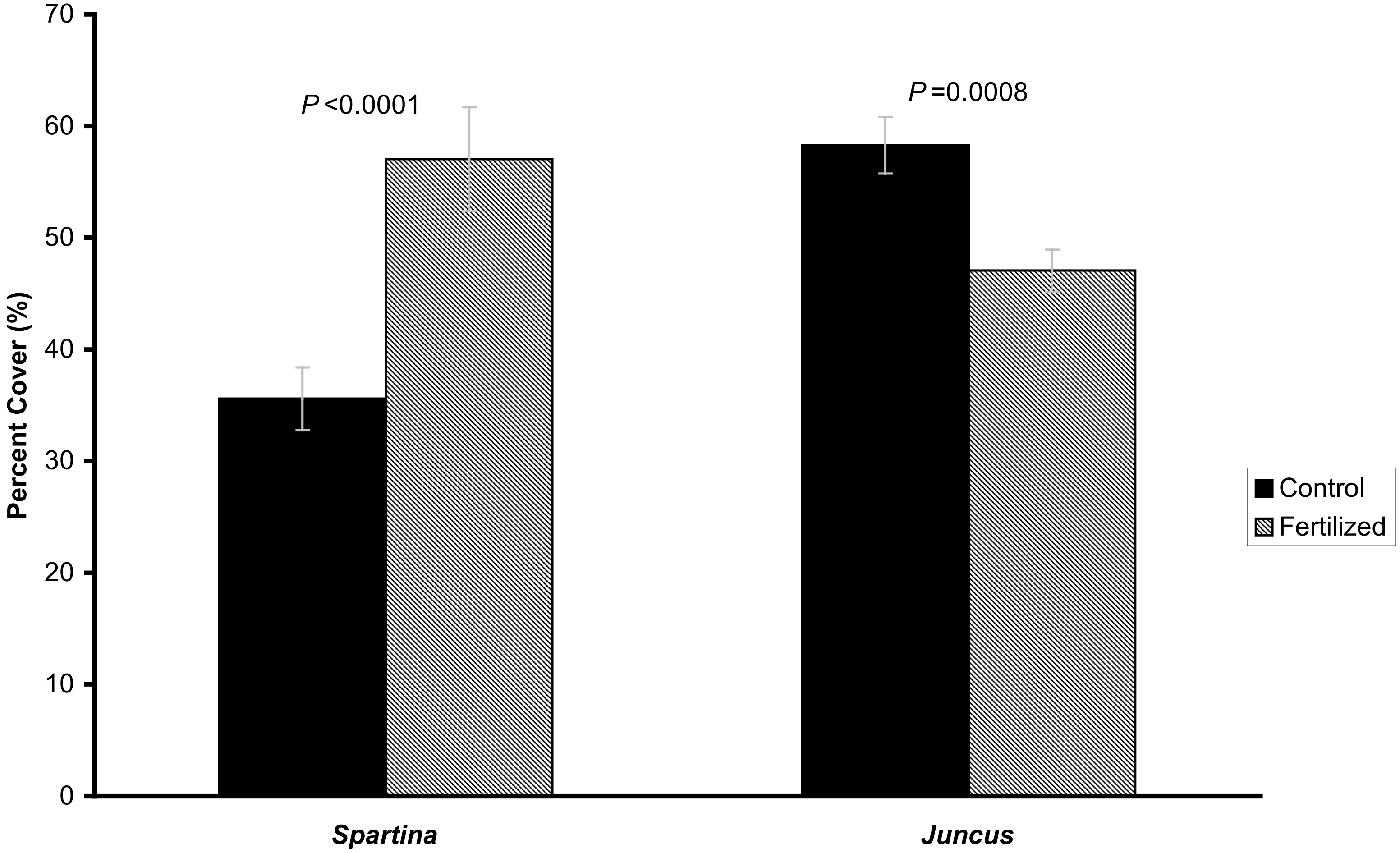

Figure 3.2. Percent cover of live *Spartina* and *Juncus* in control and fertilized plots (*n* =17 sites). Data are means ± standard error.

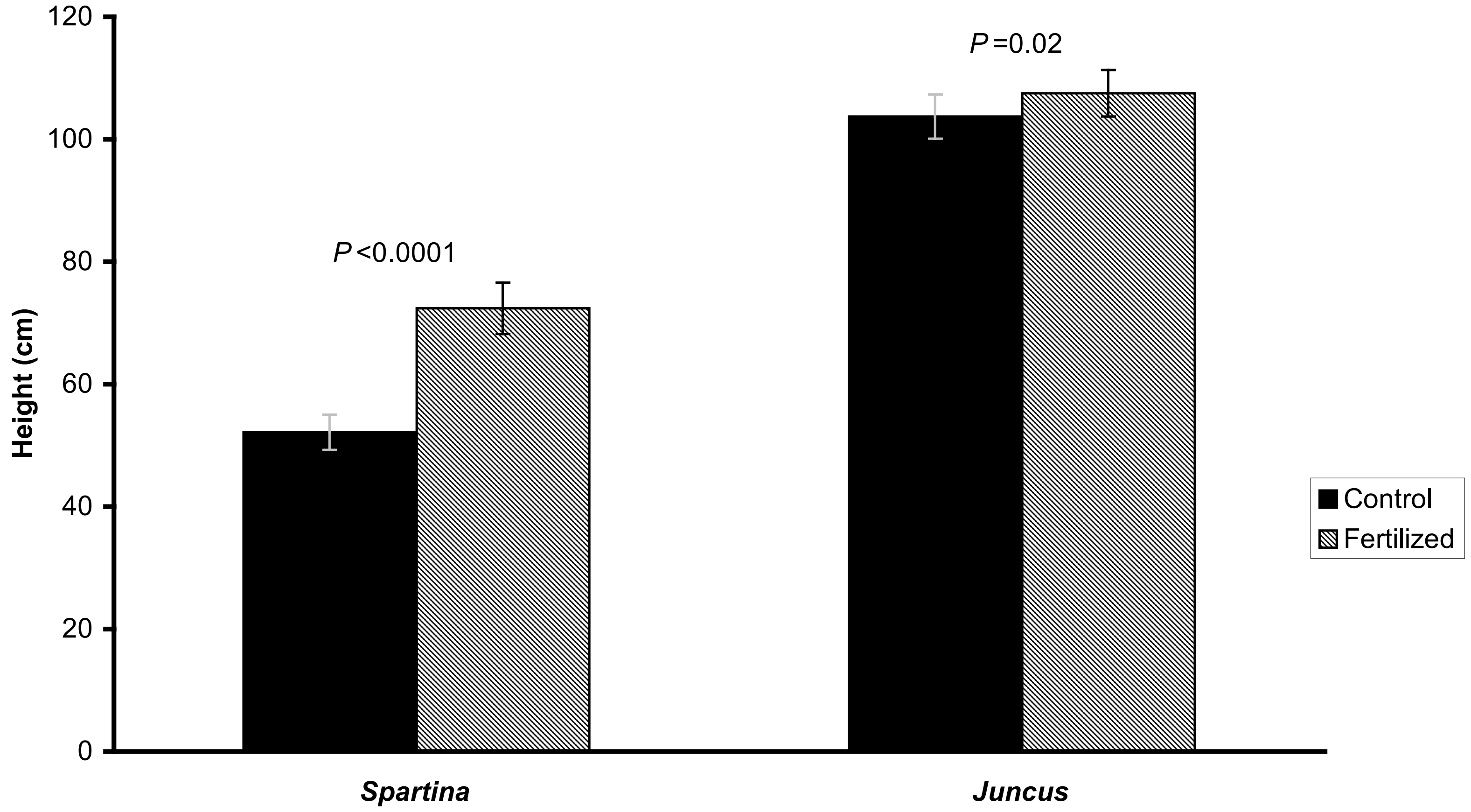

Figure 3.3. Height of live *Spartina* and *Juncus* in control and fertilized plots (n =19 sites). Data are means ± standard error.

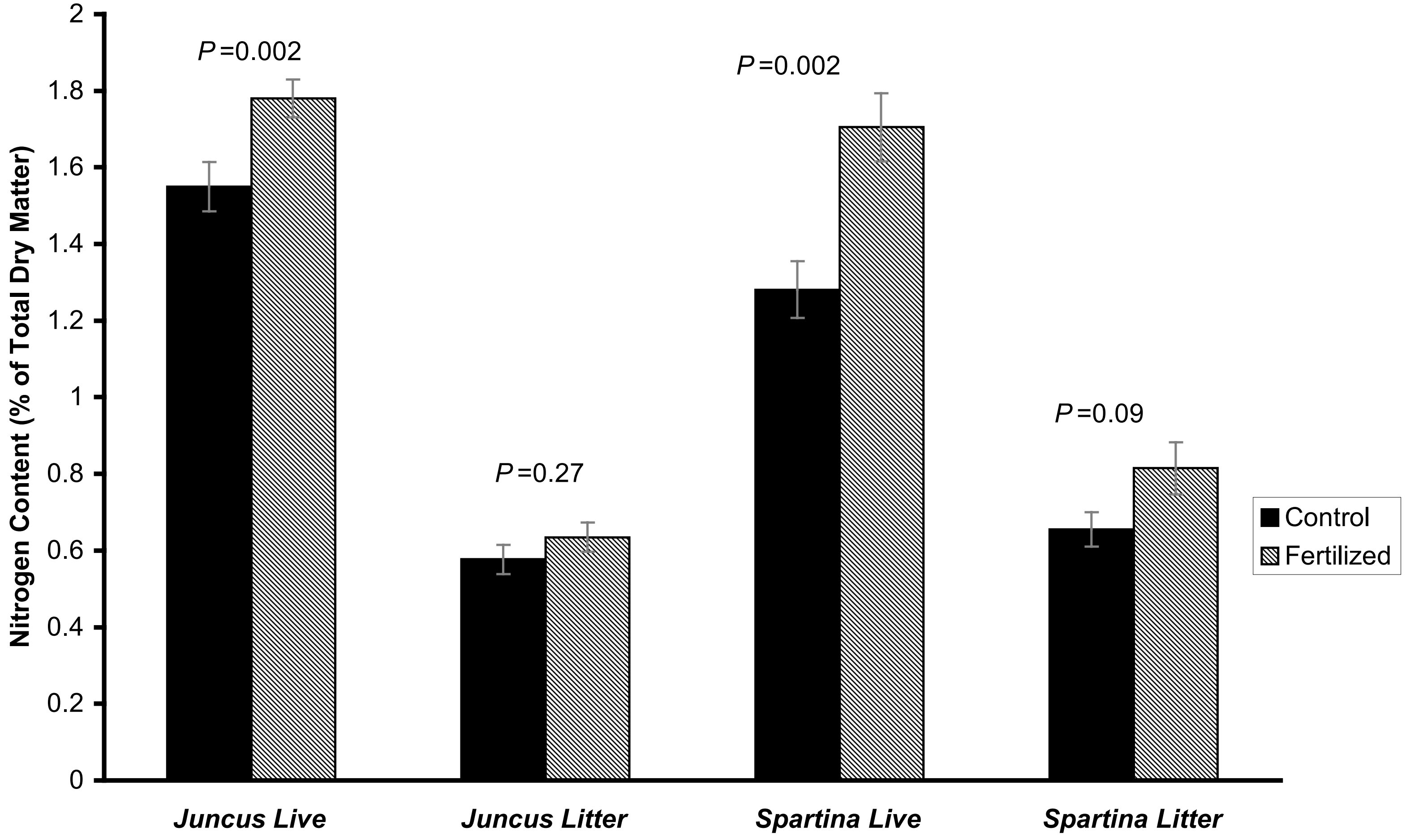

Figure 3.4. Nitrogen content of live and standing dead *Spartina* and *Juncus* leaves in control and fertilized plots (*n* =15 sites). Data are means ± standard error.

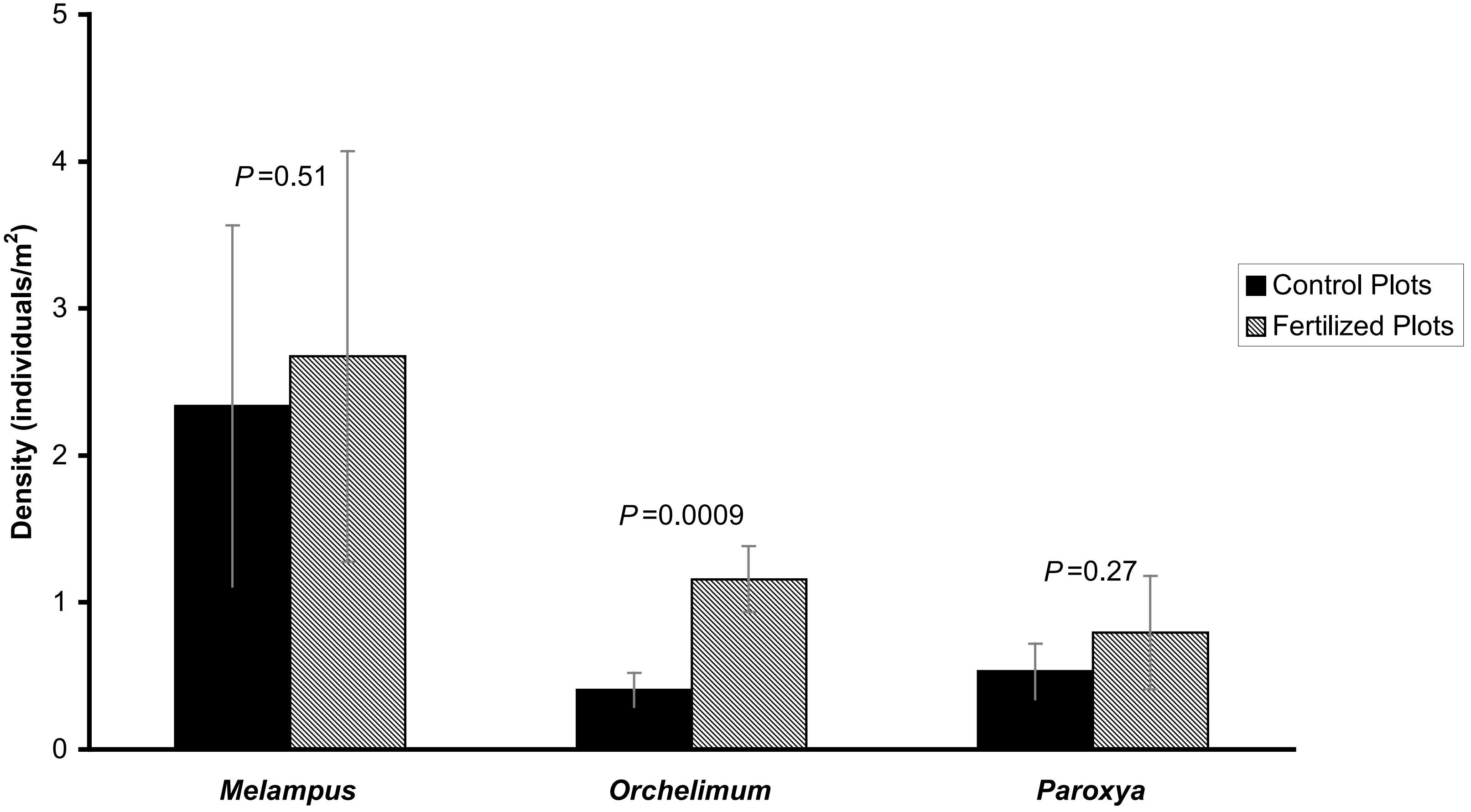

Figure 3.5. Density of *Melampus, Orchelimum,* and *Paroxya* in control and fertilized plots (*n* =19 sites). Data are means ± standard error.

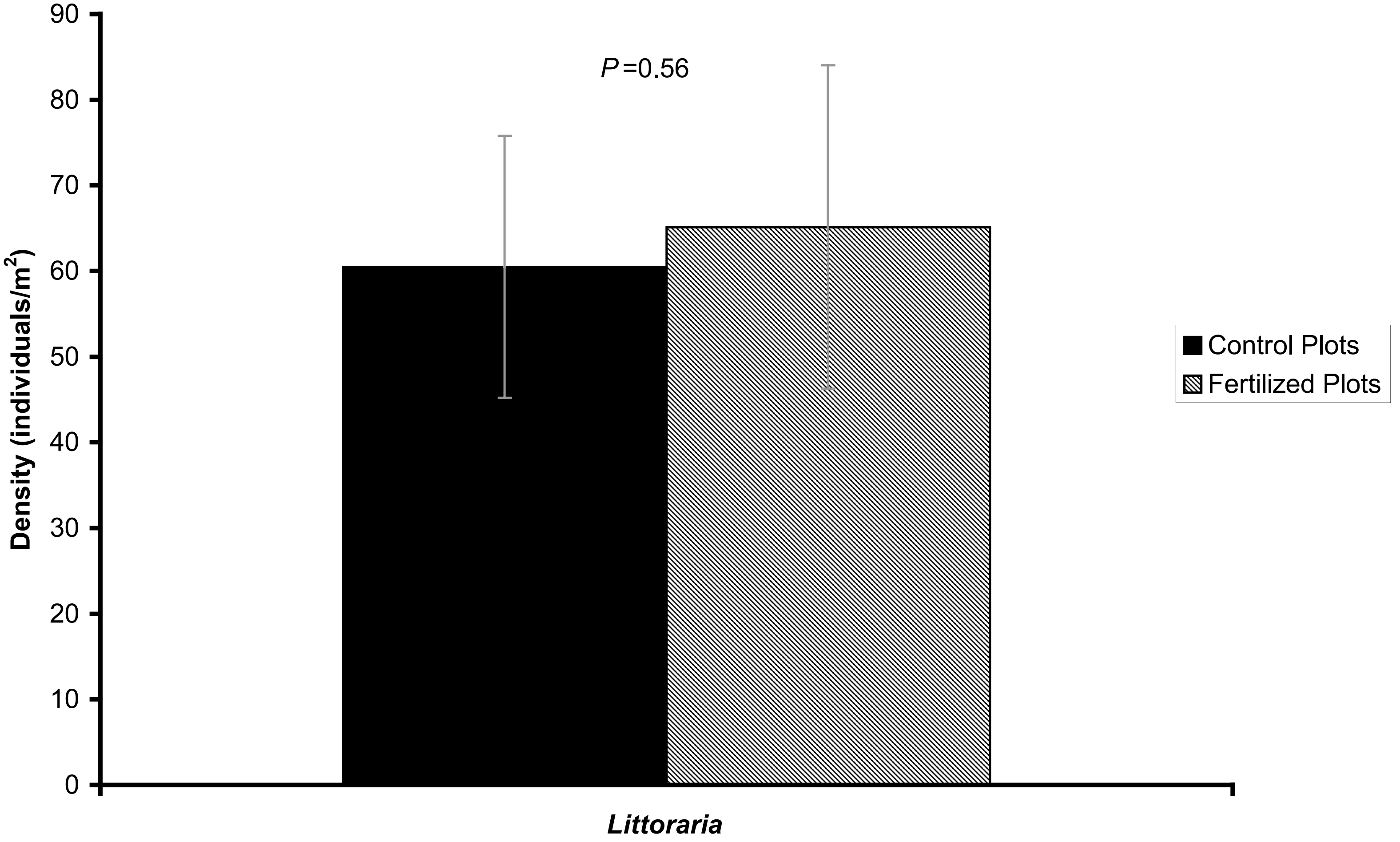

Figure 3.6. Density of *Littoraria* in control and fertilized plots (n =19 sites). Data are means ± standard error.

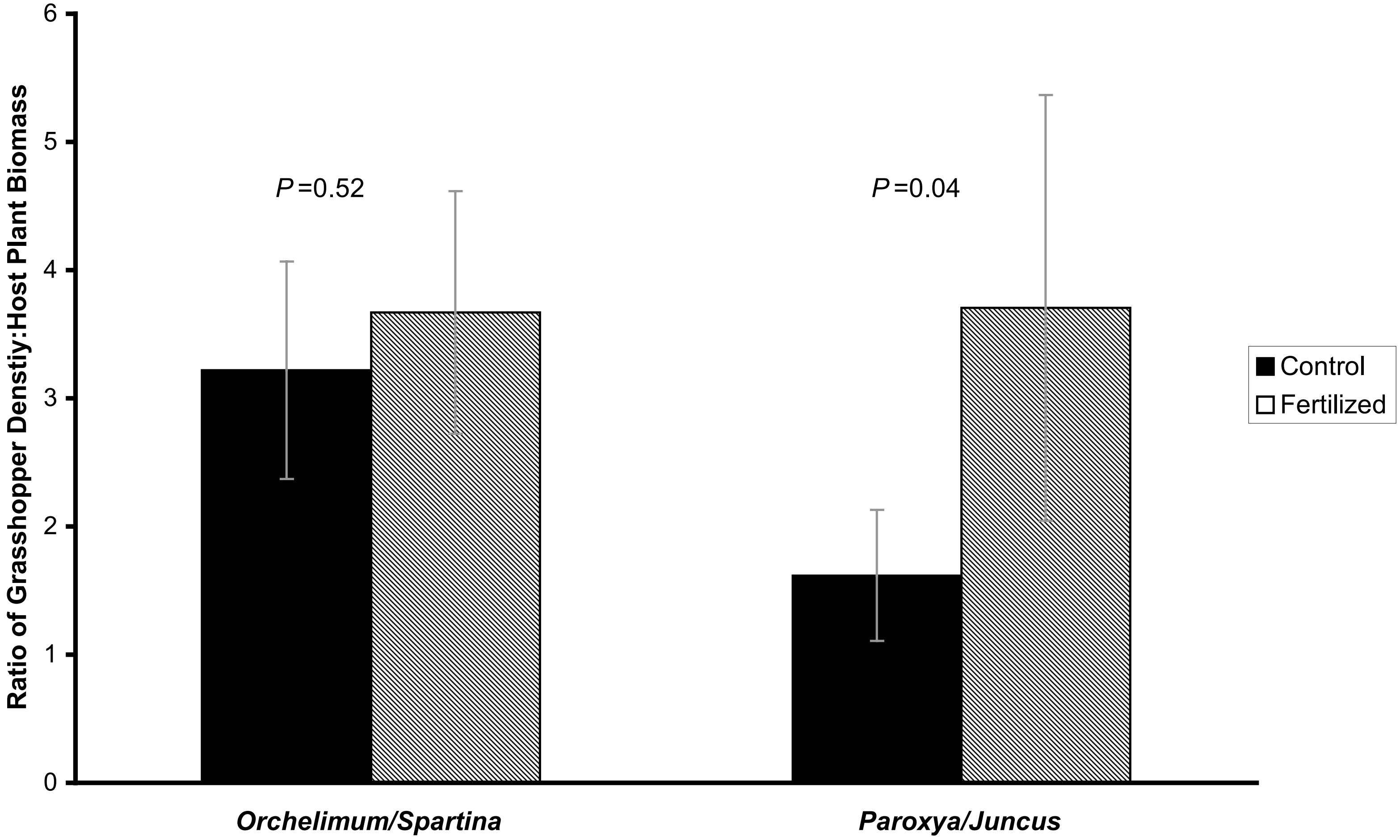

Figure 3.7. Ratio of *Orchelimum* density to *Spartina* biomass and *Paroxya* density to *Juncus* biomass in control and fertilized plots (*n* =19 sites). Data are means ± standard error.

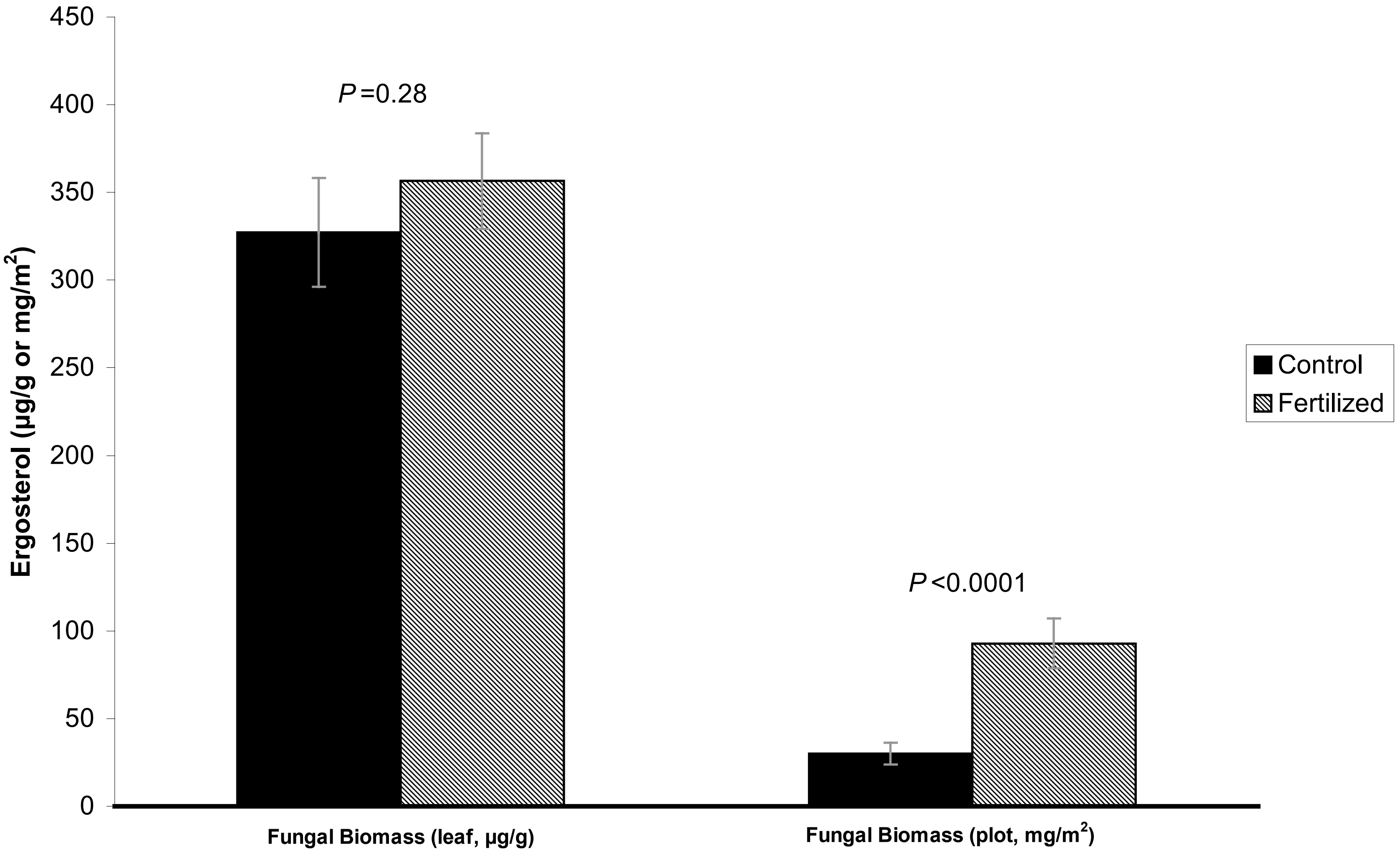

Figure 3.8. Fungal biomass in leaves of standing-dead *Spartina* reported as ergosterol on a per leaf (LOM) and per plot basis (n =19 sites). Data are means ± standard error.

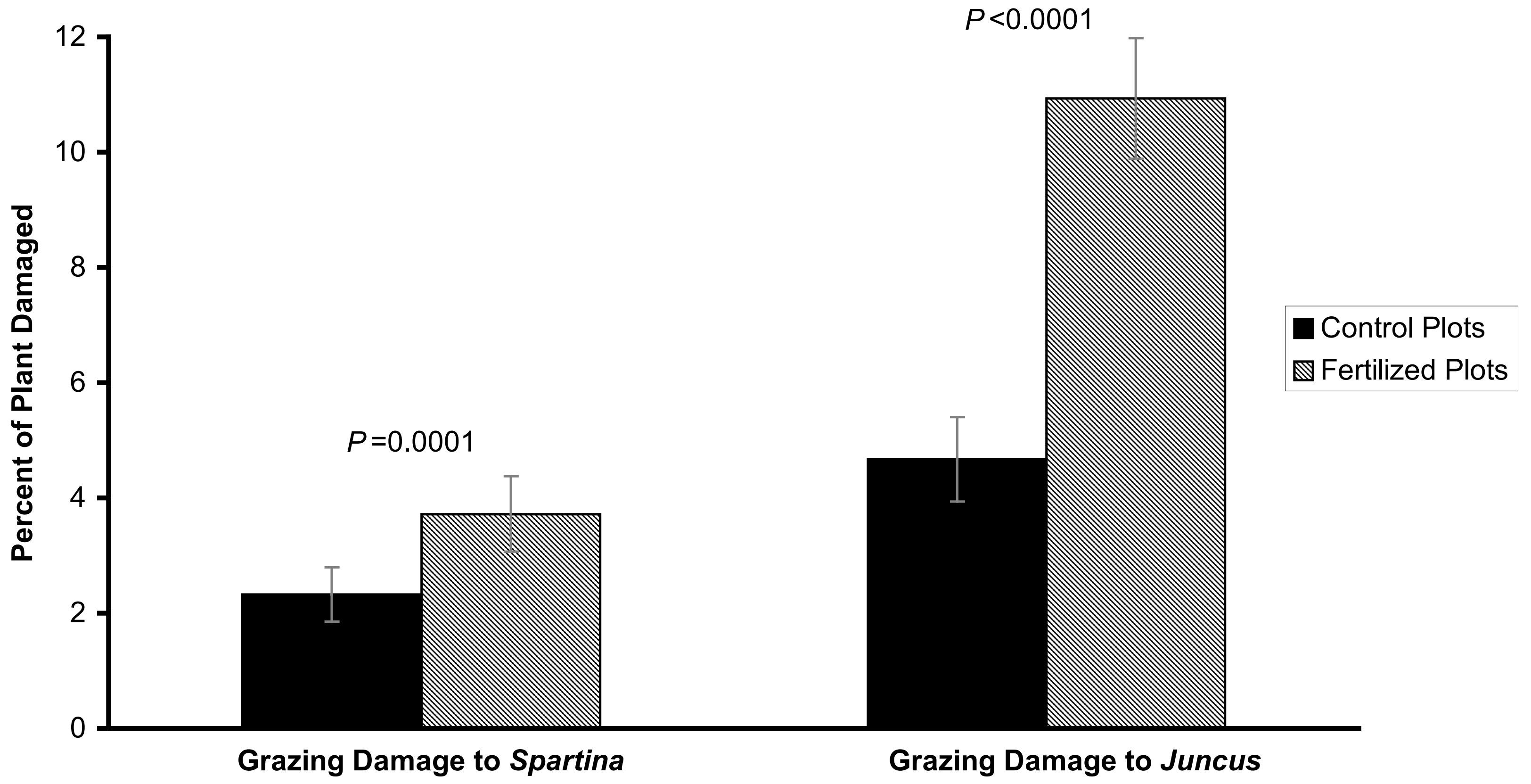

Figure 3.9. Grazing damage by grasshoppers to leaves of live *Spartina* and *Juncus* in control and fertilized plots (n=19 sites). Data are means ± standard error.

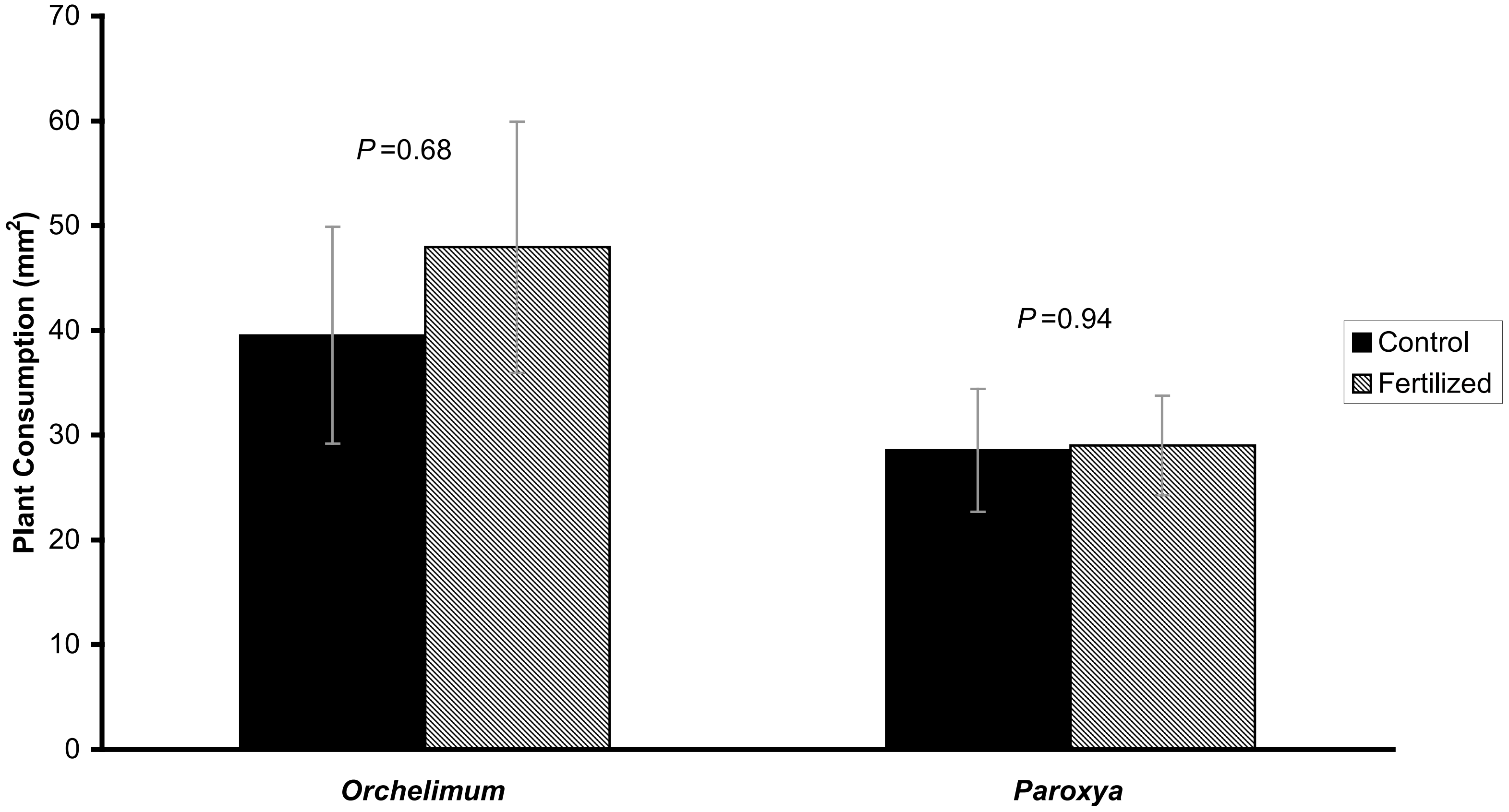

Figure 3.10. Consumption of *Spartina* leaves by *Orchelimum* and *Juncus* leaves by *Paroxya* during two-choice feeding assays (n =15 replicates). Data are means ± standard error.

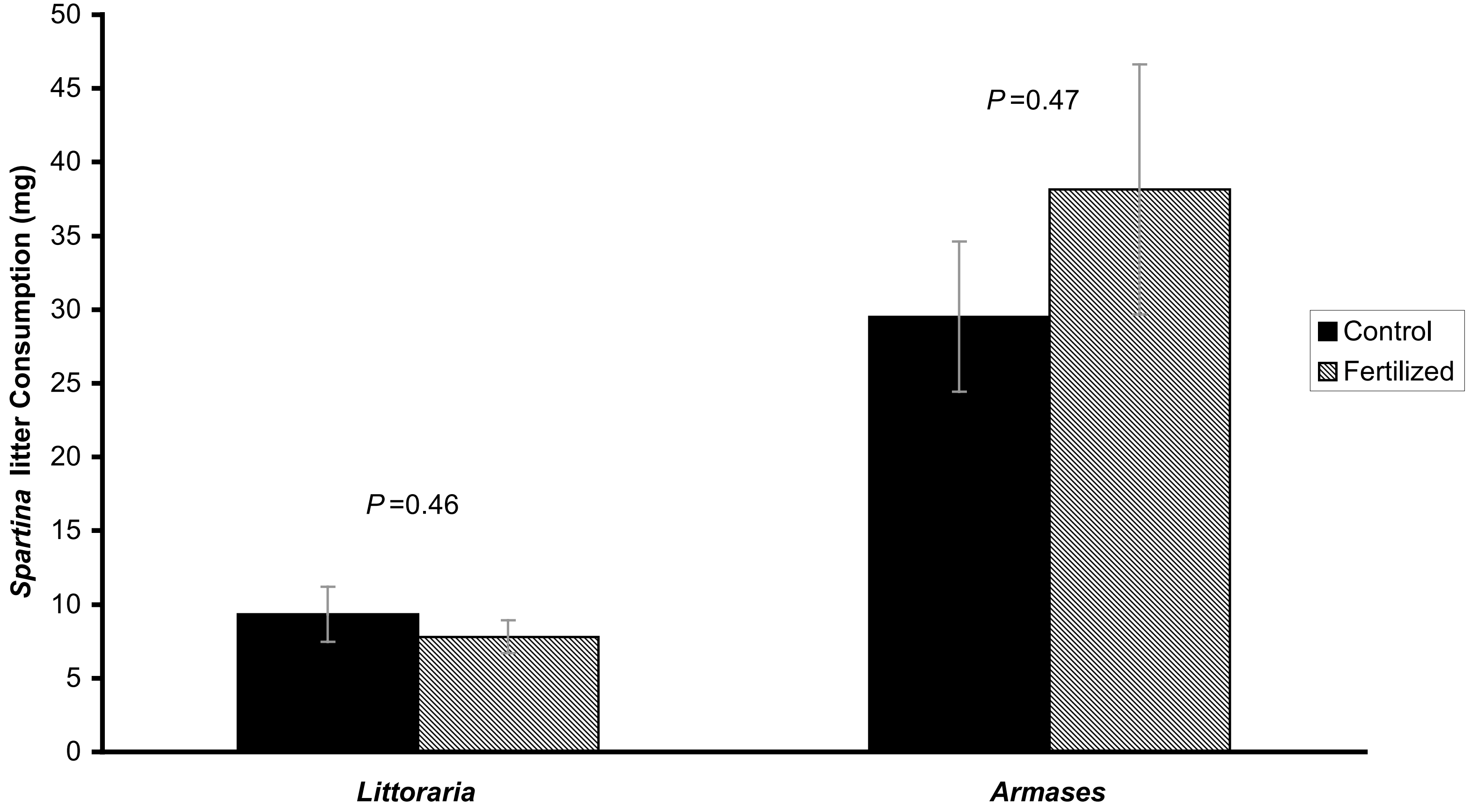

Figure 3.11. Consumption of *Spartina* litter by *Littoraria* and *Armases* during two-choice feeding assays (n =15 replicates). Data are means ± standard error.

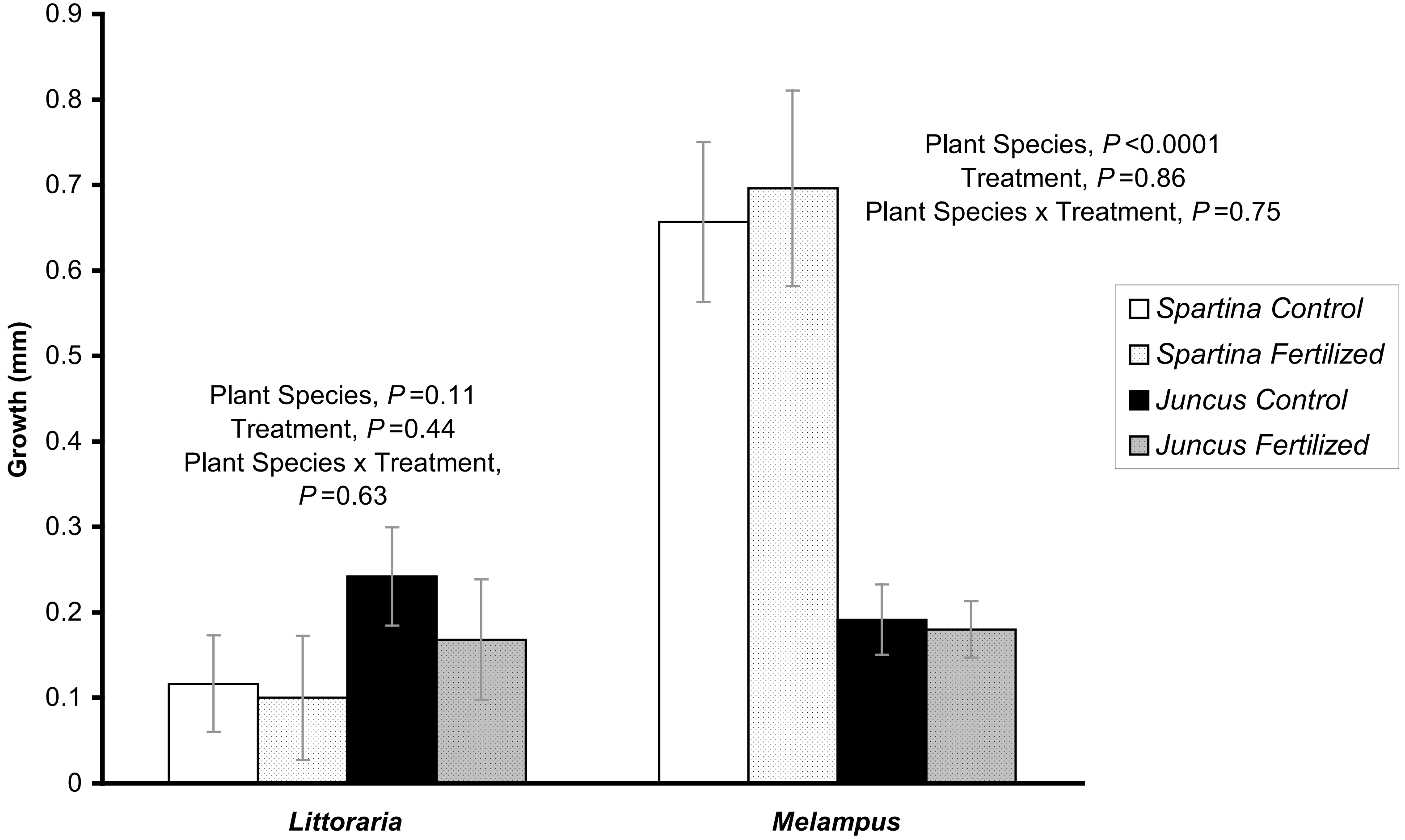

Figure 3.12. Growth of *Littoraria* and *Melampus* fed either a control or fertilized stem of *Spartina* or leaf of *Juncus* litter (*n* =15 replicates, N=240). Data are means ± standard error.

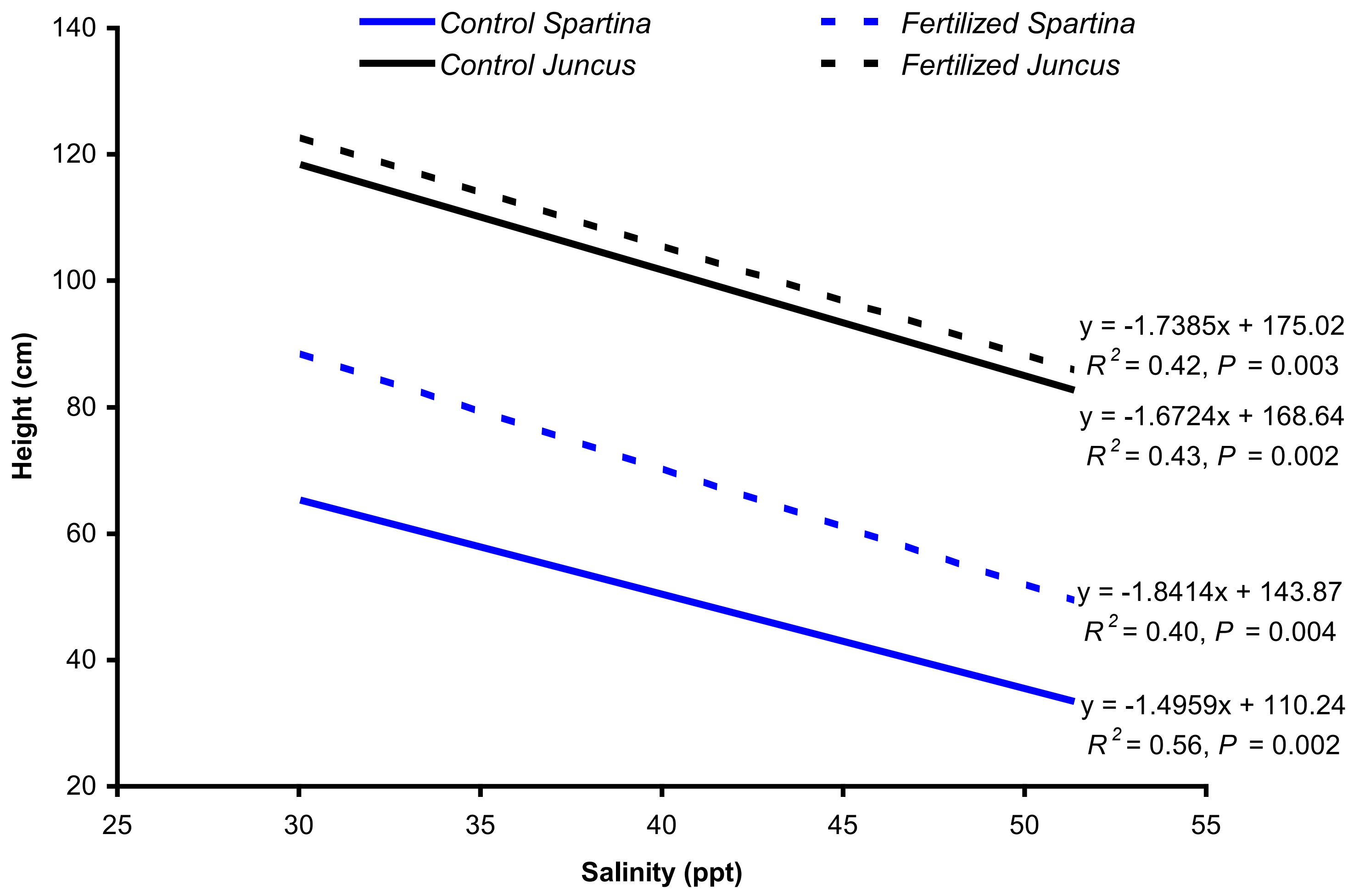

Figure 3.13. Relationship of salinity to height of live *Spartina* and *Juncus* in control and fertilized plots (*n* =19 sites). Data are site means for each species.

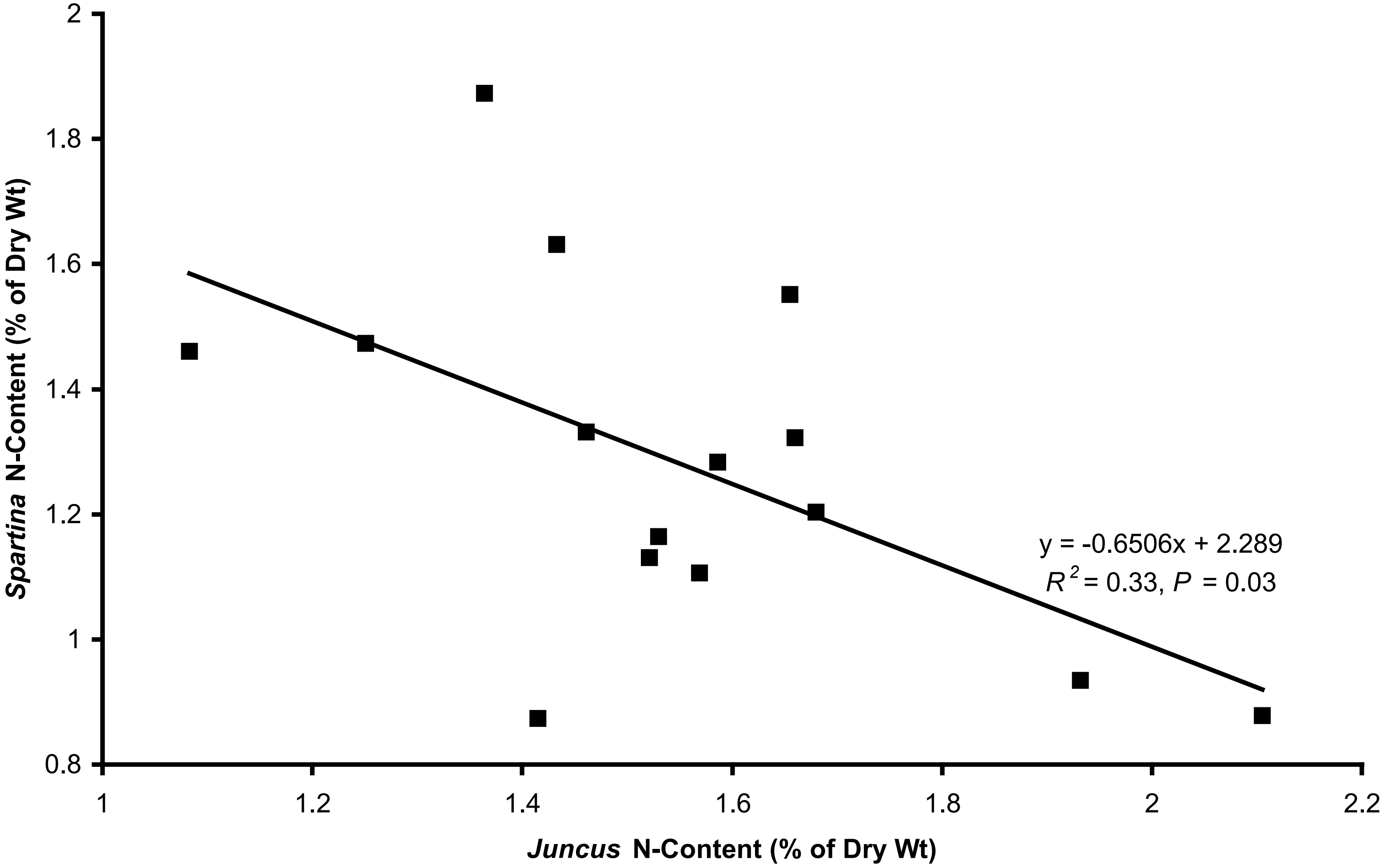

Figure 3.14. Relationship of live *Juncus* N-content to live *Spartina* N-content in control plots (n =19 sites). Data are site means for each species.

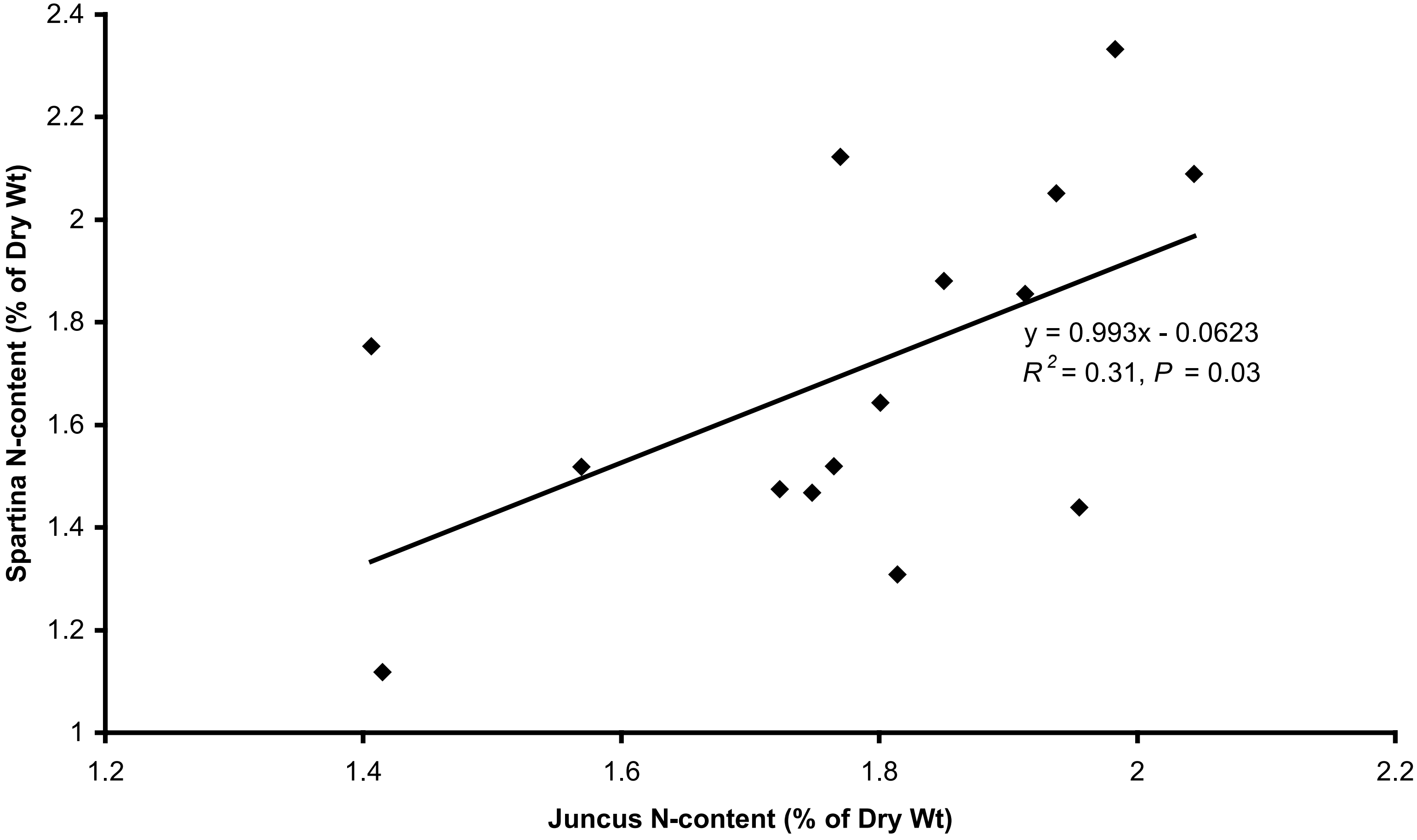

Figure 3.15. Relationship of live *Juncus* N-content to live*Spartina* N-content in fertilized plots (*n* =19 sites). Data are site means for each species.

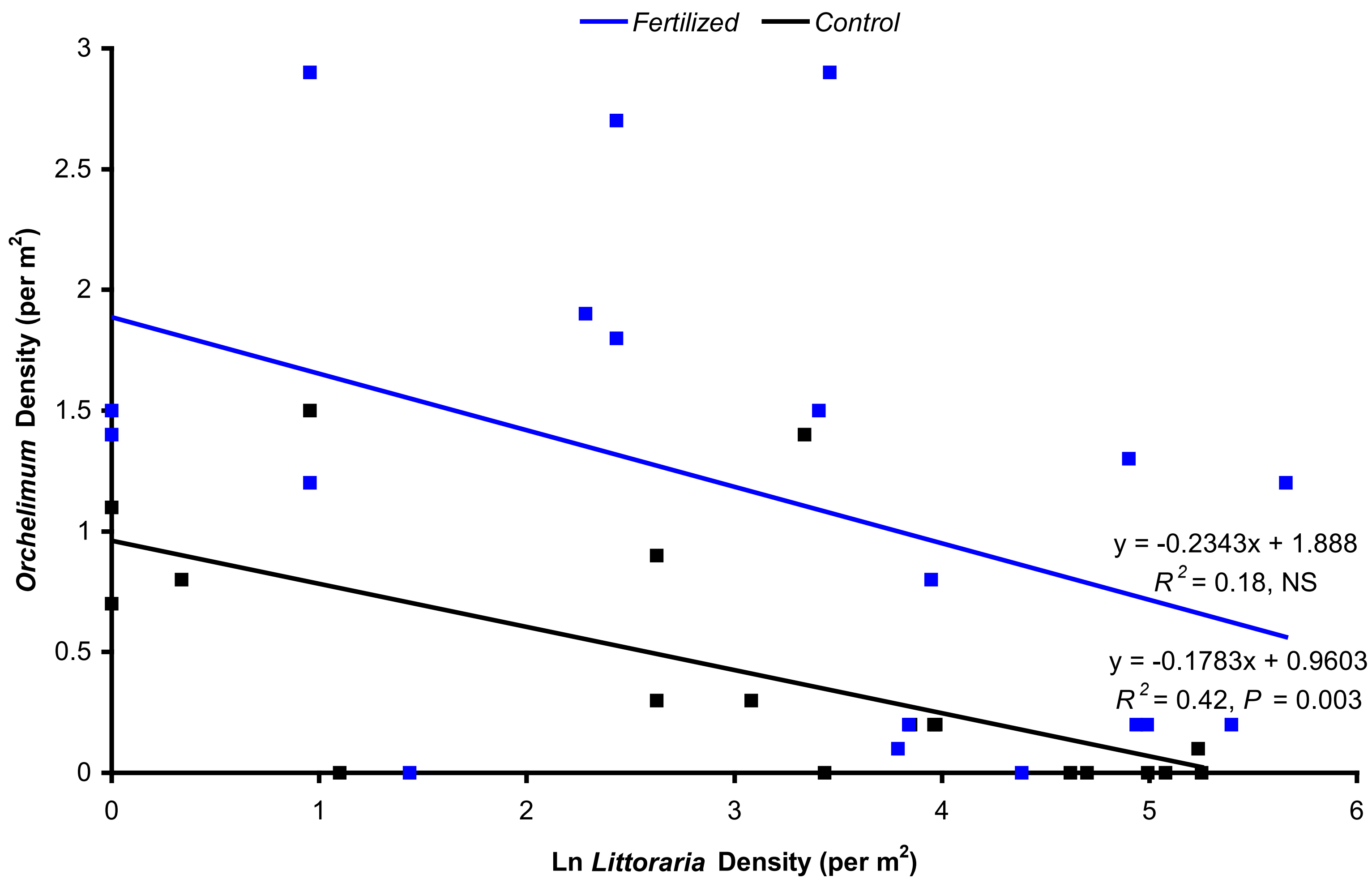

Figure 3.16. Relationship of *Orchelimum* density to the natural log of *Littoraria* density in control and fertilized plots (n =19 sites). Data are site means for each species.

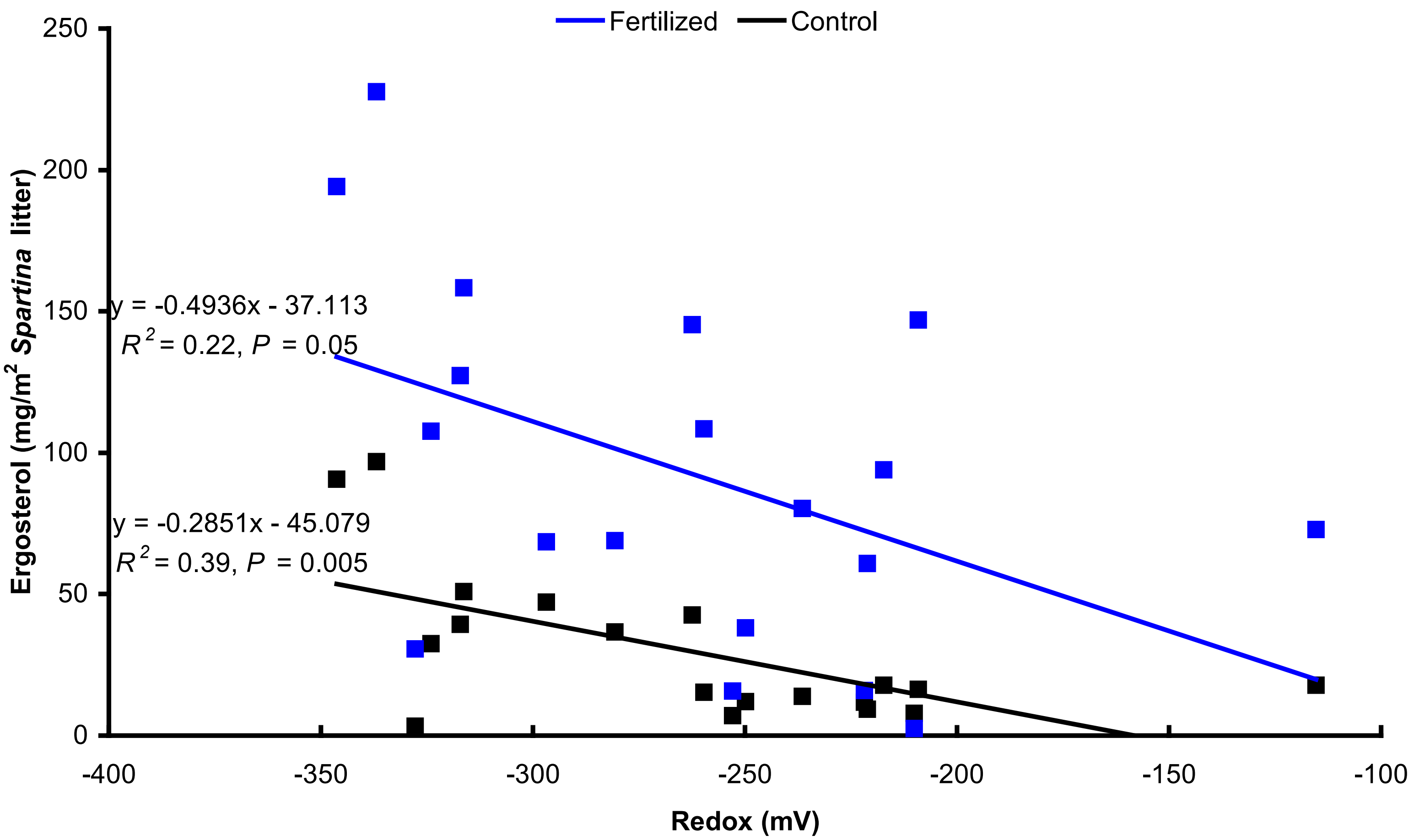

Figure 3.17. Relationship of fungal biomass on a per plot basis to redox in control and fertilized plots (*n* =19 sites). Data are site means .

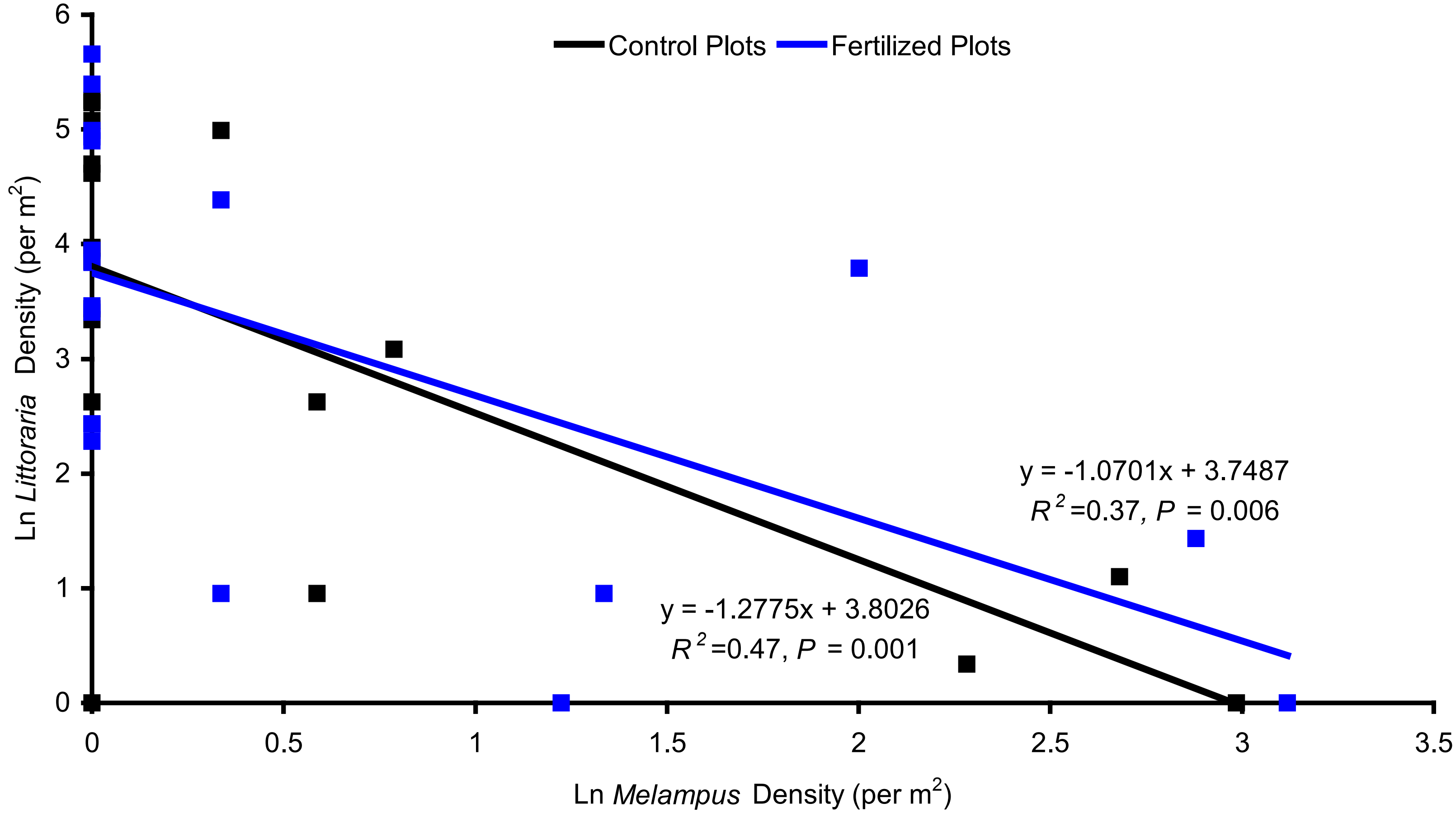

Figure 3.18. Relationship between the natural log of *Littoraria* and *Melampus* densities in control and fertilized plots (n=19 sites). Data are site means for each snail.

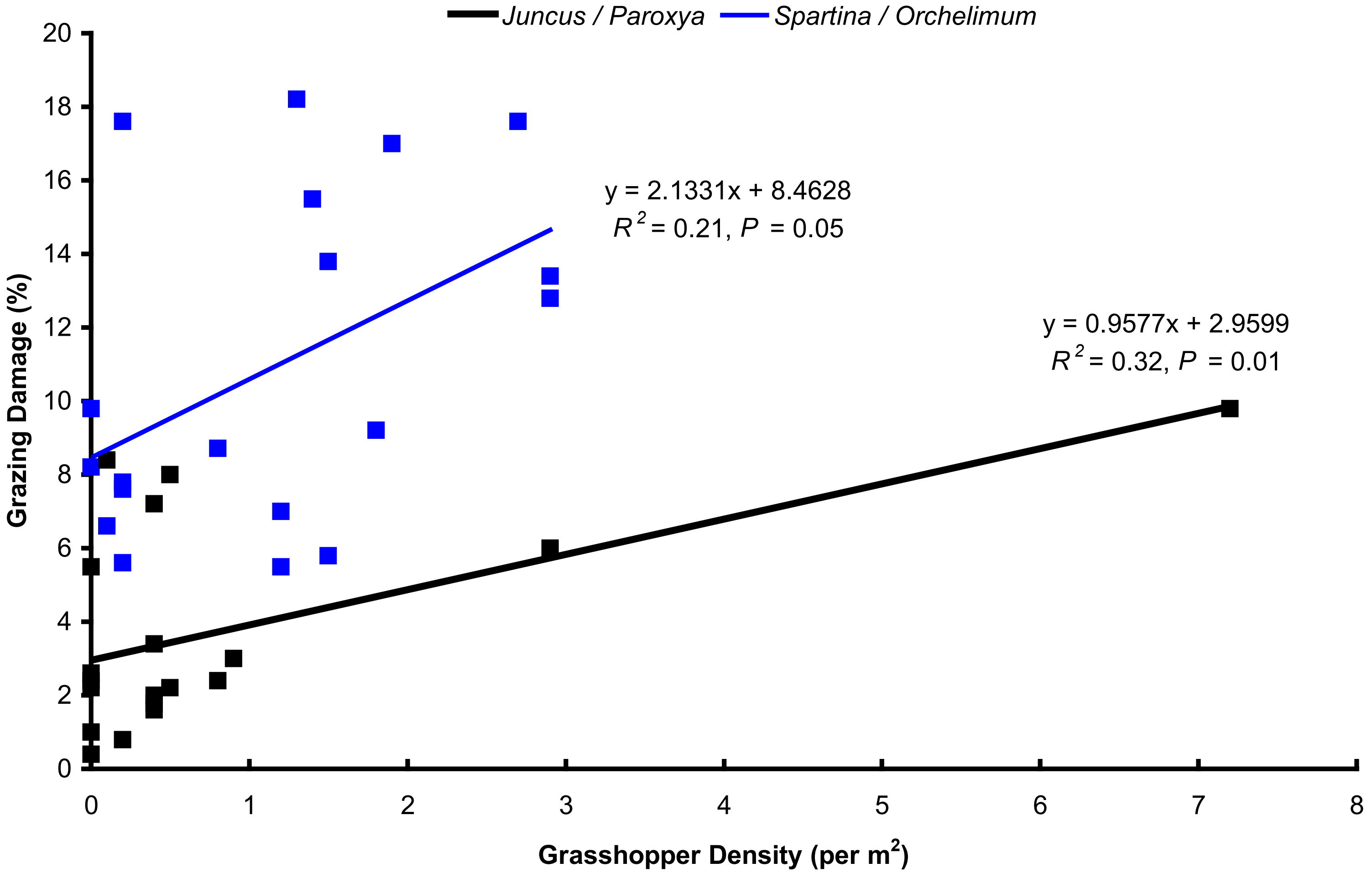

Figure 3.19. Relationship of grazing damage to *Juncus* and *Spartina* to *Paroxya* and *Orchelimum* density in fertilized plots (*n* =19 sites). Data are site means for each species .

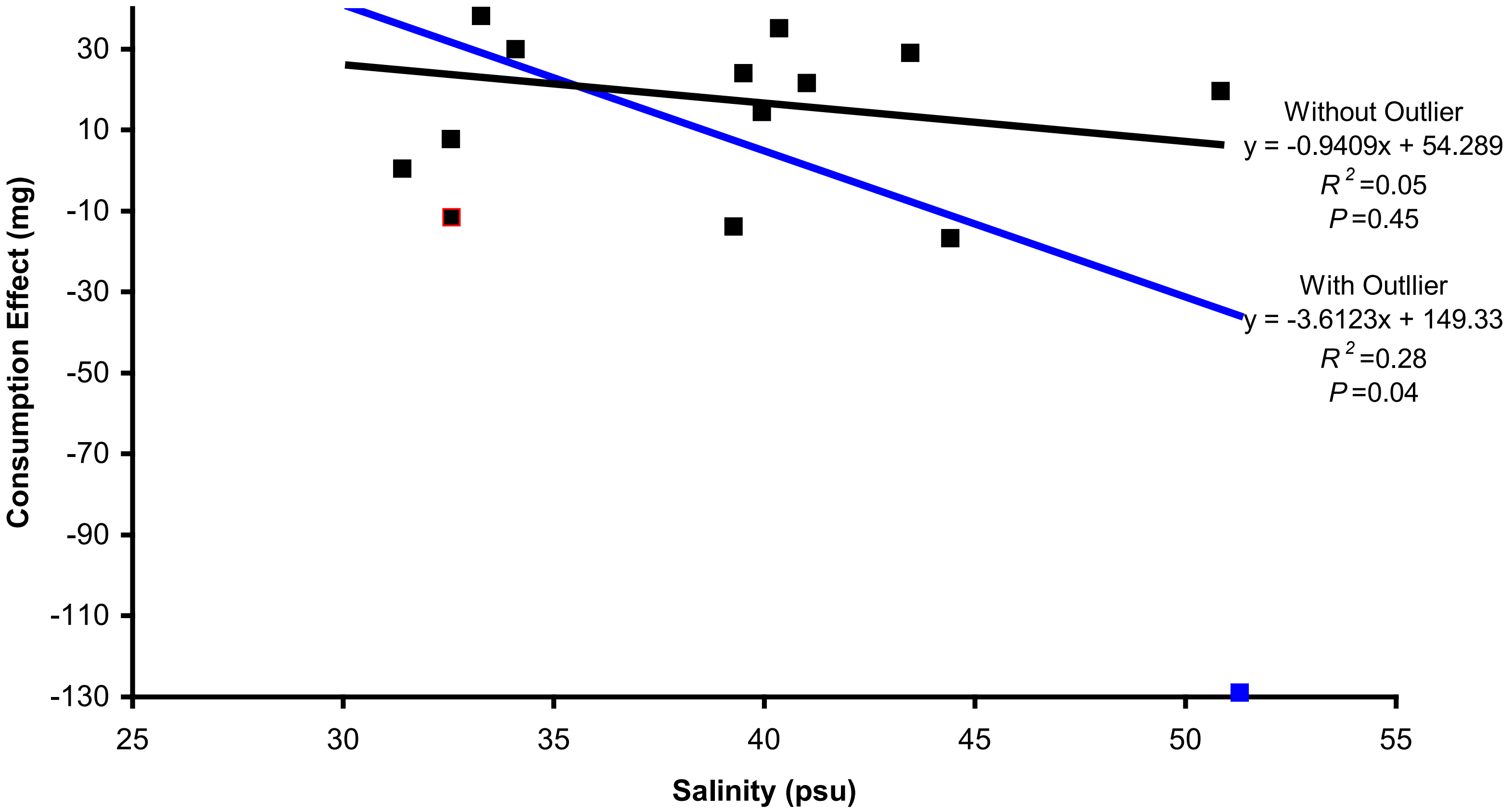

Figure 3.20. Relationship of site salinity to the consumption effect (difference in consumption between control (C)and fertilized (F) litter, F-C) of*Spartina* litter by *Armases* in laboratory paired feeding trials (n=15 sites). Data are site means .

CHAPTER IV

DISCUSSION

The fertilization treatment had broad impacts on the marsh food web. The major findings of this study were: 1) with fertilization, the normally-subordinate plant *Spartina* outcompeted the normally-dominant plant *Juncus* over a broad range of environmental conditions, although abiotic conditions attributed to "sitescore" (upland influence) limited the extent of this effect, because greater upland influence benefited *Juncus* at *Spartina's* expense; 2) the major salt-marsh herbivores were more responsive than the detritivores to fertilization, but were primarily affected by plant quantity rather than quality, 3) populations of marsh detritivores differed strongly among sites, perhaps reflecting differences in larval settlement and post-larval survivorship, but did not differ among treatments (perhaps because litter quality did not change much) and lastly, 4) detritivore growth was not influenced by litter quality, but was influenced by plant species. Below I discuss each of these results, and then compare, for all variables, the overall effect of fertilization versus natural spatial variation.

PLANT GROWTH

Under normal conditions in the high marsh, *Spartina alterniflora* is competitively subordinate to *Juncus roemerianus* (Pennings et al. 2002, 2003). Yet under fertilized conditions, Pennings et al. (2002) found that *Spartina* biomass increased and *Juncus* biomass decreased at a site in Georgia, suggesting that the competitive hierarchy was reversed. In AL and MS, however, where tidal regimes and soil properties differed from those in GA, they found no changes or slight increases in *Juncus* biomass, despite large increases in *Spartina* biomass (Pennings et al. 2002). These results suggest that caution should be taken when extrapolating results across larger environmental gradients. The difference between the New England fertilization studies (Levine et al. 1998, Emery et al. 2002), which consistently found that fertilization led to a decrease in the normally-dominant high-marsh species, and the southeastern study (Pennings et al. 2002), which did not always find decreases of high-marsh species, suggested the hypothesis that the extent of displacement of *Juncus* by *Spartina* is controlled by environmental factors. The current study, which utilized sites that varied widely in environmental conditions, was designed to test this hypothesis.

Consistent with the GA results of the Pennings et al. (2002) study, I found that in fertilized plots, *Spartina* biomass increased strongly, and *Juncus* biomass decreased. *Spartina* is nitrogen limited (Valiela and Teal 1974, Gallagher 1975, Smart and Barko 1980), and all previous fertilization studies have found that biomass increases strongly when nitrogen is experimentally added (Levine et al. 1998, Emery et al. 2002, Pennings et al. 2002). In this study, the increase in *Spartina* biomass was driven by increases in both percent cover and height. In contrast, although *Juncus* decreased in biomass, this was due to a reduction in percent cover; *Juncus* height actually increased slightly in fertilized treatments, suggesting that the fertilizer was not directly toxic. Although this study did not explicitly measure competitive effects, the most reasonable explanation for the decrease in *Juncus* biomass is that it declined in the face of increasing competition from *Spartina*. This explanation is consistent with previous studies in New England, which have suggested that the competitive hierarchy between *Spartina alterniflora* and *Spartina patens* is reversed (to favor *S. alterniflora*) when nitrogen is added (Levine et al. 1998, Emery et al. 2002).

Salinity is one environmental factor that is known to negatively influence marsh plant productivity in monoculture (Smart and Barko 1980, Haines and Dunn 1985, Howes et al. 1986). Salinity also interacts with competition to control many aspects of marsh plant community structure (Bertness and Ellison 1987, Bertness 1991a, Pennings and Callaway 1992, Bertness and Hacker 1994, Greiner La Peyre et al. 2001, Pennings and Moore 2001). Pennings et al. (2002) speculated that the impact of nutrient additions on plant community structure might vary across a gradient of salinity. Although I found that salinity was negatively correlated with

Spartina biomass in fertilized plots, it was not a highly-significant predictor, nor was it included in any of the other 7 biomass models (live and standing-dead). In contrast salinity was the most important predictive variable in models of plant height. The effect of salinity on height, however, did not differ between fertilization treatments (the lines in Fig. 3.13 are nearly parallel), which lead me to reject the hypothesis that salinity would mediate fertilization effects.

The most consistent predictor of plant growth factors (occurring in 8/13 significant models) was not salinity but rather "sitescore", a variable that reflected the nature of the border between the marsh and the upland. *Spartina* biomass decreased and *Juncus* biomass increased at sites that were increasingly surrounded by upland. A similar result was found in a more extensive survey of 55 sites within the same geographic region (Buck and Pennings, *pers. comm.*). The mechanism by which adjacent upland habitats benefit *Juncus* at the expense of *Spartina* was not investigated here, but could be driven by impacts on the water table or delivery of dissolved materials in groundwater. Though high sitescore affected overall biomass differentially between species, both species were taller at sites with high sitescores. Because a high sitescore was not bad for *Spartina* per se (i.e. *Spartina* grew taller), this suggests that *Juncus* outcompeted *Spartina* at sites with greater upland influence. The mechanism of this competition was not investigated here, but likely involves some combination of shading and belowground preemption of the rooting zone (Brewer 2003).

Models predicting plant cover, height, and biomass included a number of additional predictor variables. The nature of some of these relationships is obscure, and all must be interpreted with caution given the potential pitfalls of multiple regression (Graham 2003), but in several cases the relationships accord with our understanding of the ecology and physiology of *Spartina* and *Juncus*. "Soil" and grazing damage were included in at least 50% of the significant multiple regression models predicting live plant growth (percent cover, height, biomass), and made the most sense biologically. The consistent negative relationship to "soil" across growth parameters, treatment, and species indicates a reduction in growth where bulk density was high, and organic matter content and proportion silt + clay content were low. This finding is in accordance with the finding of Pennings et al. (2002) that fertilization responses were weak in plant community mixtures where bulk densities were higher and organic contents lower (i.e. the *Borrichia-Juncus -Batis* mixture). Greater organic matter in the soil likely benefits plants through offering a suite of nutrients including nitrogen and phosphorous, thereby increasing the soil quality to the plant (Padget and Brown 1999, McLaughlin et al. 2000). Morphologic features of salt marsh plants related to growth (i.e. greater height, leaf size, and leaf number) are often associated with higher soil organic content (Richards et al. *in revision*). Similarly, silt and clay hold nutrients better than sand in salt marshes (Eleuterius and Caldwell 1985). On the other hand, a positive relationship between plant growth variables and organic matter and silt + clay content could also be due to greater decomposing plant biomass on the soil surface at sites where inundation is less frequent (Hackney and de la Cruz 1980, Craft et al. 1988). Because the "soil" variable was more important in control models, it suggests that either N-mineralization of plant material was more important when there was a nitrogen deficiency, because fertilization actually inhibits N-mineralization rates of organic matter in some wetland soils due to a subsequent carbon-deficiency of soil microorganisms (McLaughlin et al. 2000), or simply that soil nitrogen does not matter when nitrogen is added in excess.

Grazing damage was negatively correlated with live plant growth variables, suggesting that top-down influences are important determinants in the success of both species (Parson and de la Cruz 1980, Bertness et al. 1987, Gough and Grace 1998, Silliman and Zieman 2001). Conversely, detritivores did not enter into biomass models of dead plants, suggesting that they do not strongly affect standing crops of dead biomass, at least across the range of conditions studied. Instead, dead biomass models had similar environmental variables to models for live biomass, suggesting a reflection (i.e. more live biomass = more litter biomass). My original models for dead biomass did not consider live biomass as a possible predictor variable; however, if live biomass is included, it is usually the most important predictor, and the fit of the models improve sharply (Control *Spartina*: R^2=0.22, P=0.04*;* Control *Juncus*: R^2=0.63, P<0.0001*;* Fertilized *Spartina*: R^2=0.16, P=0.09; Fertilized *Juncus*: R^2=0.51, P=0.0006).

PLANT NITROGEN CONTENT

As expected (Vince et al. 1981, Gratton and Denno 2003), both plant species increased in tissue N-content when fertilized. On the other hand, dead plant material did not differ in N-content between treatments, although there was a trend towards higher nitrogen content in fertilized plots, as found in other studies (Valiela et al. 1984, 1985). In contrast, Valiela et al. (1984) found much greater increases in N-content of fertilized litter than in this study (approx. 3% tissue N-content in their study vs. 1.7% in this study in fertilized plots). This difference was likely due to geographical and methodological differences: First, their study took place in a New England salt marsh, and northern *Spartina* has a higher N-content than southern *Spartina* (Siska et al. 2002). Second, I studied standing dead litter, but Valiela et al. (1984) used litter bags on the soil surface, an approach which does not mimic natural marshgrass decay and thus would differ from standing dead litter due to differential access to soil nutrients, light, wetness, detritivore activity, and microbial flora (Newell 1993). The lack of a treatment effect on nitrogen content of standing 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 into the water during tidal submergence (Valiela et al 1985) or periods of high rainfall (Newell 2001c), and/or were scavenged by ascomycetous decomposers (Valiela et al. 1985 (high marsh results), Newell 1993, Newell et al. 1996b) with subsequent removal of fungal mass by mycophagous invertebrates (Graca et al. 2000). It is also likely that, despite attempts to standardize the collection protocol, the dead plant material was in a range of different decay stages, which would have influenced detrital chemistry and nutrient dynamics (Rice and Tenore 1981, Rice 1982, Valiela et al. 1984, 1985, Newell et al. 1996b).

Comparing across sites, the best predictor of N-content of living plants was the N-content of the opposite species, but the nature of this relationship differed between treatments.

These relationships shed insight into competitive interactions between *Spartina* and *Juncus* that agree with previous fertilization studies that have suggested that there is reduced belowground competition in fertilized plots (Levine et al. 1988, Emery et al. 2001, but see Brewer 2003). In control plots, there was an inverse relationship between the N-contents of *Spartina* and *Juncus*, suggesting belowground competition for nitrogen was taking place, as indicated by several previous studies (Levine et al. 1988, Brewer et al. 1988, Emery et al. 2001). Conversely, in fertilized plots, there was a positive relationship, suggesting a lack of belowground competition when nutrient stress was alleviated (i.e. both plants receive excess nitrogen in fertilized plots), possibly leading to a shift to greater aboveground competition, as suggested by New England studies (Emery et al. 2001, Levine et al. 1998). *Spartina* growth is strongly limited by nitrogen and responds to fertilization with greater aboveground biomass, whereas *Juncus* growth is not nitrogen-limited, likely because it is already at the asymptote of the nitrogen response curve (Gallagher 1975, Gallagher et al. 1980). In New England, *Spartina alterniflora* grew taller under nutrified conditions, shading the usually-dominant plant *Spartina patens*; likewise, in other pairwise mixtures, the usually-subordinate species overtopped usually-dominant species (Levine et al.1998, Emery et al. 2001). In contrast, this study did not suggest that light limitation of the usual-dominant *Juncus* occurred (at least not to the extent that northern studies found) because although *Spartina* did experience a more substantial height increase than *Juncus* in fertilized plots, it was never taller than *Juncus*. Furthermore, the major predictor of plant growth, sitescore, did not have differing effects on the 2 species heights, but did have differing effects on their biomass, indicating that aboveground competition in this study might be more lateral than vertical.

Because *Spartina* did not grow as tall as *Juncus* in this study, I suggest that aboveground competition was mediated by their different growth forms. The relationships of plant biomass to N-content of each species in multiple regression models may derive from morphological differences and fertilization responses of each species. The N-content of

Spartina and *Juncus* in control plots was positively related to live *Juncus* biomass, but the N-content of *Spartina* in fertilized plots was negatively related to its own biomass. In other words, increases in *Spartina* biomass in fertilized plots diluted its N-content, whereas N-content of *Juncus* did not decrease where its biomass was greater (indicated by the positive relationship between live *Juncus* N-content and biomass in the control model). Similarly, other studies have indicated that C:N ratios of *Juncus* remain approximately equal under fertilized conditions despite increases in biomass (Gallagher 1975) and that % tissue N remains relatively constant throughout the growing season despite seasonal spikes in biomass (Gallagher et al. 1980). Conversely, these studies found the opposite for *Spartina* following peaks in aboveground growth, i.e. C:N ratios were higher a year after fertilization, and nitrogen content decreased during the growing season (Gallagher 1975, 1980). These findings may derive from differences in guerilla and turf morphologies, respectively (Harper 1977, Bertness 1999). In particular, *Spartina* expands rapidly along runners when fertilized, with a disproportionately lower investment into underground biomass (Gallagher 1975, Valiela et al. 1976, Smart and Barko 1980), but *Juncus* typically invests more into underground than aboveground biomass (Brewer et al. 1998) Thus, in control plots where *Spartina* biomass was inhibited by competition from *Juncus*, its N-content was high, whereas in fertilized plots the increase in aboveground growth diluted its N-content. The expected concomitant reduction in belowground growth of *Spartina* (Gallagher 1975, Valiela et al. 1976, Smart and Barko 1980) likely contributed to the diluted N-content through reduced nutrient acquisition. On the other hand, *Juncus* N-content was not diluted by its own biomass, evident by the positive association of N-content to biomass in control plots (where *Juncus* biomass was not reduced). Because underground biomass was increased along with aboveground biomass (Brewer et al. 1998), nutrient acquisition was not likely limited when there was greater aboveground growth. Additionally, the lack of abscission in leaves for long periods of time and a nearly constant production:biomass ratio contribute to nutrient conservation by *Juncus* (Kruczynski et al. 1978, Christian et al. 1990).

The best overall predictor of N-content of standing-dead litter was a negative relationship with salinity in a majority of the significant models (control standing-dead *Spartina* litter and fertilized standing-dead *Juncus* litter). Because live plants use nitrogen-based compounds in osmoregulation (Cavalieri and Huang 1981), it may have been that more nitrogen was resorbed from standing-dead litter when salinity was high than when it was low. Salinity, however, was not correlated with live plant nitrogen as one might expect based on the role of nitrogen in osmoregulation. Thus, other factors may be more important than salinity in mediating live plant nitrogen content, at least when comparing among sites.

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 N-content (Vince et al. 1981, Bernays and Barbehenn 1987, Denno et al. 2002, Gratton and Denno 2003). Because herbivores face a general problem of inadequate nitrogen in their food plants (White1978, 1993), plants with higher nitrogen content should, in theory, be better foods. Vince et al. (1981) argued that the C:N ratios of marsh plants were barely sufficient to meet the nutritional needs of herbivores, and thus that food quality could set their growth rate (also see Fox and Maccauley 1977). In many studies, however, impacts of fertilization on plant quantity and quality are confounded. I examined effects on quality separately from quantity, to determine which was most important.

In this study, the univoltine grasshoppers *Orchelimum* and *Paroxya* responded differently to fertilization. *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. Because biomass of *Spartina* increased, but *Juncus* biomass decreased, I examined the ratio of herbivore density: plant biomass (I expected it to increase if herbivores responded to plant quality, stay the same if herbivores responded to biomass, or decrease if they did not respond to either). There was a significant effect of treatment on this ratio for *Paroxya*, suggesting that it responded to plant quality in the field, but there was no significant effect of treatment on the ratio for *Orchelimum* suggesting that its density was roughly proportional to plant biomass regardless of treatment. In other words, *Orchelimum* densities increased in fertilized plots because of changes in plant biomass, not plant quality.

On the other hand, grazing damage was significantly greater to both species of plants in the fertilized versus control plots, suggesting that grasshoppers were feeding on fertilized plants at higher rates than would be expected based on biomass. This likely is incorrect, because laboratory studies indicated that grasshoppers did not preferentially feed on fertilized plants (see below). An alternate explanation for the fact that grasshopper damage to *Spartina* was greater (per unit plant biomass) in fertilized plots than would be expected by the ratio of *Orchelimum* to *Spartina* (which did not change between treatments) would be that I under-counted grasshoppers in the lusher fertilized plots, where it would have been more difficult to see every grasshopper. If this is correct, it would mean that both grasshoppers could have been more abundant than I realized in fertilized plots, which would mean that ratios of grasshoppers to host-plant biomass would have actually been greater in fertilized than control plots for both species. Alternatively, grasshoppers feeding on fertilized plants may have been able to satisfy their nutritional requirements in a shorter time (Valentine and Heck 2001), and thus may have spent more time outside of plots where they would not have been counted.

Although grasshoppers did more damage to fertilized than control plants in the field, feeding choice experiments in the laboratory suggested that they did not select food based on quality. Other studies have had mixed success in predicting food selection solely on nitrogen, and have suggested that choice of food is controlled by multiple factors including the herbivore's current developmental phase, nutritional needs, and a variety of plant physical properties (Chapman and Joern 1990, Pennings et al. 1998, Buck et al. 2003). Neither species of grasshopper significantly preferred to eat the fertilized plant over the control plant when given a leaf of each, in side-by-side comparisons. Moreover, multiple regression analyses suggested that neither salinity nor nitrogen content (two of the factors most likely to influence herbivory in estuarine systems, Vince et al. 1981, Lightfoot and Whitford 1987, Waring and Cobb 1992, Bowdish and Stiling 1998, Pennings et al. 1998, Moon and Stiling 2002) was correlated across sites with grasshopper grazing damage.   Some studies have suggested that leaf-chewing insects, such as the grasshoppers I studied, may not be as responsive as sap-sucking insects are to increased foliar nitrogen (Vince et al. 1981, Lightfoot and Whitford 1987), so it is possible that the grasshoppers responded primarily to plant quantity (or some component of biomass, i.e. percent cover, height), rather than to quality. It is likely that biomass provides a positive visual cue for grasshopper feeding (Chapman and Joern 1990), through color (Bernays and Wrubel 1985) or shape (Mulkern 1967), with a secondarily evolutionary significance, i.e. it invites grasshoppers to feed on healthier, higher quality plants. Arguably, the strong increase in *Spartina* biomass was sufficient to cause an increase in *Orchelimum* densities, whereas the decrease in *Juncus* biomass was too modest to signficantly affect *Paroxya* densities. Alternatively, grasshoppers may have been cued by plant height, rather than biomass per se, but again the modest changes in *Juncus* height may not have been enough to affect *Paroxya* densities. Regardless, grasshopper damage was likely greater to plants in fertilized plots because more grasshoppers were attracted to the plots by high plant biomass, rather than because grasshoppers were attracted to the plots by higher palatability of plants.

Regression models exploring site-to-site variation in grasshopper densities were similar for the two species. Within treatments, neither grasshopper was strongly correlated to N-content or biomass of the species of plant that they consumed. Thus, factors other than plant quantity or quality appear to explain site-to-site variation in grasshopper densities. Densities of both grasshoppers were correlated with *Littoraria* density, but in different ways and likely for different reasons. *Orchelimum* density was negatively correlated with *Littoraria* density, 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 *Orchelimum* and *Littoraria* compete for *Spartina*. In contrast, *Paroxya* density was positively correlated with *Littoraria* density, but the association was not strong and *Littoraria* was not a significant predictor unless *Juncus* N-content and *Melampus* density were also included in the model. Thus, it is likely that some other factor associated with *Littoraria* that was not measured (perhaps some aspect of landscape position) was influencing *Paroxya* density. 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.

DECOMPOSER BIOMASS

Previous work has suggested that, in *Spartina*, fungal biomass per gram of standing-dead leaf material is positively associated with leaf nitrogen content and sufficient water availability (Newell et al.1996b, 1998), but that excessive tidal submergence and persistent wetting is inversely related to fungal biomass (Newell et al. 1996b, Newell 2001c). I found no effect of fertilization on fungal biomass (µg ergosterol/g LOM), likely because the fertilization treatment did not significantly increase the nitrogen content of standing-dead leaves. The trend, however, was toward greater 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 (mg ergosterol/m^2 of *Spartina* litter) was much greater in fertilized plots.

Multiple regression analyses suggested that the variation in fungal biomass per plot between sites was due to a negative relationship with redox and sitescore. These relationships held in both treatments. Because low redox values in the soil would directly affect *Spartina* rather than leaf fungi, it is likely that the increased fungal biomass in plots with highly-reduced soils was driven primarily by the increase in standing-dead biomass in these plots. The relationship between redox and standing-dead biomass, however, was only significant in control plots. Similarly, because standing-dead *Spartina* biomass was greater where sitescore was low (reduced upland influence), increased fungal biomass in plots with low sitescore values is a likely a product of increased standing-dead biomass in these plots, rather than a direct effect of sitescore on fungi.

Although only the fertilized model was significant for fungal biomass per leaf, it reaffirmed the importance of low redox values and more importantly established a direct association between increased fungal biomass per leaf and increased *Spartina* litter biomass (as indirectly indicated in the fungal biomass per plot models), possibly because of greater success of spores reaching new substrate. Spore expulsion rates for salt marsh fungi exhibit extreme spatial patchiness (Newell and Zakel 2000, Newell 2001b), and this may be an adaptation to maximize colonization on newly dead plant material as it becomes available (Newell and Zakel 2000). Therefore, areas with greater standing dead *Spartina* might be expected to allow more successful colonization of spores. Most importantly, consumers examined in this study did not enter any of the fungal biomass models, suggesting that they did not impact fungal accumulation across the range of environmental conditions in this study, though previous findings in the lab have indicated that *Littoraria* can suppress and *Melampus* can enhance fungal growth rates (Graca et al. 2000). It is possible that this laboratory result does not predict patterns in the field (this study, Newell 2001c) where litter biomass: snail ratios are typically higher than those used by Graca et al. (2000) (which could prevent the snails from depressing fungal standing crops), or that I inadvertently chose leaves for fungal samples that were less damaged by snail grazing. Further, snails are not the only grazers on marshgrass fungi; marsh squareback crabs (*Armases sp.*), amphipods, and likely mites, collembolans, and other meiofauna also ingest fungal material (Newell 1996, Newell, *pers. comm.*), and might positively influence microbial production (as amphipods do, Graca et al. 2000), offsetting any negative impacts I might have seen by snail grazers on fungal accumulation.

DETRITIVORE DENSITY, FOOD SELECTION, AND GROWTH RATE

In the absence of predation, *Littoraria* recruitment, growth, and consumption is greater in the nitrogen-rich, tall-form *Spartina* than in the nitrogen-poor, short-form zone (Silliman and Zieman 2001, Silliman and Bertness 2002). Under natural conditions, however, snails are seldom located along tidal creeks where tall-form *Spartina* grows (*pers. obs*., Smalley 1958, Bishop and Hackney 1987, Fierstien and Rollins 1987, Burnham and Fell 1989, Spelke et al. 1995). A number of factors differ between the creekbank and mid-marsh zones, including tidal submergence, predation pressure, plant height, plant nitrogen content and plant phenolic content (Bushsbaum 1984, Howes et al. 1986, Kneib 1997, Bowdish and Stiling 1998, Mendelssohn and Morris 2000, Pennings and Bertness 2001), and no studies have determined whether snail densities are directly affected by plant nitrogen content per se. In contrast, predators (particularly blue crabs and mummichogs) are known to have strong impacts on the abundance and distribution of both *Littoraria* and *Melampus* (Hamilton 1976, Vince et al. 1976, Williams 1984, Joyce and Weisberg 1986, Silliman and Bertness 2002). Predation pressure from crabs and fish tends to be least in higher tidal reaches (Kneib 1984, Kneib 1997). For example, Silliman and Bertness (2002) found that *Littoraria* density was strongly regulated by predation in the low marsh (i.e. 98% loss of snails/day to predators), but not in the high marsh (only 0.4% loss of snails/day). There is also evidence that snail densities are affected by live and standing-dead *Spartina* biomass (Stiven and Kuenzler 1979, Fierstien and Rollins 1987, Silliman and Bertness 2002) and by physiologically-limiting conditions in the marsh such as salinity or tidal inundation (Teal 1962, Russell-Hunter et al. 1972, Bishop and Hackney 1987). Thus, it would have been reasonable to expect that the increase in *Spartina* biomass (both live and standing-dead) that I observed 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 for both species. Thus, it appears that within-site plant biomass alone did not influence snail density. It is possible that I did not see a fertilization response because the snails respond primarily to litter quality, which is likely a function of its N-content and fungal biomass, neither of which differed significantly between treatments.

Laboratory feeding experiments indicated that the fertilization treatment did not change the quality of standing-dead stems enough to influence consumption by *Littoraria* or the omnivorous crab *Armases*. Past studies have shown that detritivores selectively remove fungal-rich portions of *Spartina* litter that have greater nutritive quality and are more palatable due to increased protein, reduced phenolic compounds such as vanillic and coumaric acids, and reduced structural compounds such as lignocellulose (that comprise about 75% of *Spartina*'s organic mass, Hodson et al. 1984), all of which affect leaf toughness and digestibility (Rietsma et al. 1988, Bärlocher et al. 1989a,b, Bergbauer and Newell 1992, Newell and Bärlocher 1993, Kneib et al. 1997, Newell and Porter 1999, Graca et al. 2000). However, Bärlocher and Newell (1994) added 200 mg fungal mycelium per gram of ground leaf dry mass to artificial diets in their study of palatability of *Spartina* litter to *Littoraria*, whereas leaves in this study had approximately ≤2x less fungal mycelium than was used in their study (this study: 108-624 μg ergosterol/g LOM, equivalent to 22-125 mg mycelium/g LOM; Gessner and Newell 2002). Although both studies are within the range of fungal biomass found in previous studies along the east coast (Newell et al. 2000), the Bärlocher and Newell (1994) study represents fungal biomass loads found on the high end of the natural range (≈1000 μg ergosterol/g LOM), rather than average fungal biomass loads. This study more closely coincided with average fungal biomass loads (Newell et al. 2000), and in particular those previously found within high marsh-short *Spartina* zones in Georgia (Newell et al. 1998), where this study took place. Consequently, discrepancies between this study and previous studies on marsh detritivore food selection could be partly due to past studies using greater amounts of fungal biomass (Bärlocher et al. 1989b, Bärlocher and Newell 1994) than were studied here or typically occur in nature (Newell et al. 1998, Newell et al. 2000, Newell 2001a, c).

Another possibility that might have influenced the outcome of my results was that I fed stem and sheath material to the snails, rather than the softer leaf blades that are usually preferred (Graca et al. 2000) and were used as food in previous studies (Newell and Bärlocher 1993, Bärlocher and Newell 1994). Not only do leaves, stems, and sheaths differ in toughness and hence structural palatability to the snails (Graca et al. 2000), but they also differ in dominant fungal inhabitants (Newell and Porter 2000), and hence chemical palatability. At least one past study showed *Littoraria* preferred to eat *Spartina* that was colonized by the fungus *Phaeosphaeria spartinicola*, which is the dominant ascomycete on leaf blades (Bergbauer and Newell 1992, Bärlocher and Newell 1994). In contrast, snails avoided sheath material colonized by *Phaeosphaeria spartinae*, likely due to fungal lipids that are unpalatable to *Littoraria* (Bärlocher and Newell 1994). Thus, it is possible that snails in this study did not choose to eat fertilized *Spartina* litter more than control *Spartina* litter because the chemical palatability was poor for both plant treatments due to the presence of *Phaeosphaeria spartinae* (although the fungal species on litter was not identified in this study).

Laboratory growth studies similarly indicated that fertilization treatments 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 N-content and fungal loads did not differ significantly between treatments. Although fungal biomass in standing-dead leaves of *Juncus* was not analyzed in this study, there is almost as much fungal biomass in *Juncus* litter as there is on *Spartina* litter, although the ascomycetous species differ (Newell 2001a). Although there was no effect of fertilization treatment on growth, I did find a striking difference in the growth of *Melampus* between plant species. *Melampus* grew overwhelmingly better on a diet of *Spartina* than *Juncus*, supporting a previous study that also found >200% better growth on a diet of *Spartina* (Lee and Silliman 2003 *in press*), indicating that *Spartina* should be its preferred food source in nature. One possible reason for better *Melampus* growth on *Spartina* litter could be that it had a higher N-content in both treatments than *Juncus* litter, although previous studies with *Spartina* litter have not shown a positive relationship between *Melampus'* growth rate and N-content of *Spartina* per se (Rietsma et al. 1988, but see Valiela and Rietsma 1984). Further, another study has shown that although *Melampus* prefers dead litter, it is capable of eating a wide variety of graminoids and algae, but higher N-contents do not influence Melampus' preference among them (Rietsma et al. 1982). Many factors other than N-content might influence the value of different types of litter as food to detritivores, and I did not explore other litter traits in detail. It is known, however, that chemical composition can influence digestiblity and palatability to detritivores (Rietsma et al. 1988, Zimmer et al. 2002) and that plant toughness may determine feeding preferences (Rietsma et al. 1982, Pennings et al. 1998, Graca et al. 2000). Though Pennings et al. (1988) only evaluated toughness of live plants in Georgia, *Juncus* was almost 2x as tough as *Spartina*, and Graca et al. (2000) showed that 3 species of detritivores preferred to feed on softer blade tissues versus tougher sheath tissues of *Spartina*. Even though snails were not fed the blade tissues in this study, the *Spartina* litter appeared (sheath and stem only) softer than the *Juncus* litter (*pers. obs.*) and this may have contributed to it being a better food for *Melampus*. I did not see differences in *Littoraria* growth between plant species, perhaps because *Littoraria* has well-developed enzymes capable of digesting structural compounds known to occur in marsh plants (Bärlocher et al. 1989a), and thus may be capable of digesting and growing on a wider range of litter types.

Examining variation in snail densities between sites provided insight into controls on snail distributions in the field, namely why *Melampus* is often observed on *Juncus* despite lush *Spartina* growth in nearby non-physiologically compromising habitats (*pers. obs.*, McMahon and Russell-Hunter et al. 1981). Because only larval recruitment or post-settlement mortality could account for snail density differences between sites, food quality and quantity, or physiological and biological factors could all be possible influences on settlement. According to multiple regression analyses, food quality and quantity may be important in some cases, but salinity was never a significant predictor of snail densities. The dominant predictor in all four snail density models was the inverse relationship exhibited between the 2 snails, supporting previous work indicating that the two snail species compete (Lee and Silliman *in press*). In northeastern states, where *Littoraria* does not occur, *Melampus* is more widely distributed across the marsh, and densities are higher, than in southeastern states (Price 1980, Fell et al. 1982, Burnham and Fell 1989, Spelke et al. 1995). In southeastern states, where *Littoraria* is present, *Melampus* is either confined to the high marsh (*Juncus* zone) or is segregated to sites where *Littoraria* density is low (this study, Lee and Silliman *in press*). Similar negative abundance relationships between the two snails are evident in GCE-LTER monitoring data (2000: n=28 plots, R^2=0.38, P=0.0007; 2001: n=31plots, R^2=0.30, P= 0.001, mid-marsh sites). Experimental studies suggest that *Littoraria* is the competitive dominant, exerting control over *Melampus* density through habitat alteration (increasing solar radiation and/or predation on *Melampus* by reducing vegetation cover), egg removal, and reductions to food availability or quality (Lee and Silliman *in press*).

Other variables included in models of snail density were the N-content of live *Juncus,* abundances of grasshoppers *Paroxya* and *Orchelimum*, grazing damage to *Spartina*, and the biomass of standing dead *Juncus* and *Spartina*. It is unclear how live *Juncus* N-content plays a role in controlling snail density, but consistency between models suggests that it is important. On the other hand, the remaining variables fit within what has previously been found and are more readily explained. The negative correlation between *Orchelimum* and *Littoraria* has been previously documented along the east coast (Kunza and Pennings *unpublished data*) and also occurred in *Orchelimum* density models (this study). It is most likely due to *Littoraria* having negative effects on *Orchelimum* rather than the reverse, because *Littoraria* induces senescence and increases fungal biomass (Kemp et al. 1990, Silliman and Zieman 2001, Silliman and Bertness 2002), which would not be advantageous to an herbivore. In contrast, *Orchelimum* grazing, if it had any effect on *Littoraria*, would likely be positive because it would increase the flow of material into the detrital food web (grazing on *Juncus* also increases litter production, Parson and de la Cruz 1980). This relationship is suggested by the positive relationship between *Littoraria* and grasshopper grazing damage to *Spartina*. Further, *Melampus* density was positively associated with *Paroxya* density and vice-versa in the control models, likely because *Melampus* densities were highest in the *Juncus* zone (*pers. obs*., Lee and Silliman in press) where *Paroxya* was primarily located (Davis and Gray 1966, Parson and de la Cruz 1980), as indicated by the positive association between *Melampus* and *Juncus* biomass and the negative association between *Melampus* and *Spartina* biomass in fertilized models.

NATURAL VARIATION VS. TREATMENT VARIATION

To this point, I have focused on statistical significance of results. One way to assess biological significance is to compare variation among treatments to variation among sites. The results of this exercise are in strong support of the previous discussion. For *Spartina*, fertilization had a very large effect on live and standing-dead biomass and live N-content (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 N-contents of either species as it did on live N-contents, standing-dead *Spartina* was more responsive to fertilization than was standing-dead *Juncus*.

The strong effects of fertilization on live *Spartina* quantity and quality were transmitted to the next trophic level (as in Vince et al. 1981, Gratton and Denno 2003), 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 ratios, where *Orchelimum* density was much more influenced by fertilization than was *Paroxya*.

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, again likely because treatment did not alter litter quality. This result is consistent with my previous argument that competition and other biological factors not tested, such as predation and larval recruitment and mortality, are more important determinants of *Littoraria* and *Melampus* densities than is food quality.

CHAPTER V

CONCLUSIONS

OVERALL SIGNIFICANCE OF RESULTS

In summary, I found that, 1) with added fertilizer, *Spartina* outcompeted *Juncus* for space, regardless of site edaphic conditions, although the extent of dominance varied, 2) density responses of grasshoppers *Orchelimum* and *Paroxya* were controlled more by food quantity than quality, 3) decomposers and detritivores did not respond to treatment effects on litter quality, 4) densities of detritivorous snails, *Littoraria* and *Melampus*, are likely mediated by interspecific competition with each other, and may depend more upon predation or larval recruitment than on plant biomass, and 5) compared with natural variation among sites, fertilization strongly affected plant traits of both species (though its impact on *Spartina* was larger than on Juncus), and grazing damage to *Spartina* (grazing damage to *Juncus* was much less influenced by fertilization), likely because *Orchelimum* density was also much more affected by fertilization than *Paroxya* density; fertilization had weak effects on fungal biomass, and fertilization had virtually no effect on detritivorous snail densities. Below, I discuss the significance of each of these results in an ecological context.

ANTHROPOGENIC IMPACTS ON INTERSPECIFIC COMPETITION AMONG PLANTS

Coastal urbanization and development have been explicitly linked to increased nitrogen availability in salt marshes (Bertness et al. 2002), likely through increasing wastewater contributions to marine watersheds (Bowen and Valiela 2001, Valiela and Bowen 2002). Recent studies have indicated that anthropogenic nitrogen can have strong impacts on marsh plant communities, inverting natural competitive hierarchies and changing diversity (Levine et al. 1998, Emery et al 2001, Pennings et al. 2002, Bertness et al. 2002, but see Rogers et al. 1998). For example, with increased nutrient supplies in New England, *Phragmites australis* expanded seaward and *Spartina* expanded landward, outcompeting other plant species, and potentially disrupting the entire marsh food web (Bertness et al. 2002, but see Weis and Weis 2003).

In this study, fertilization allowed *Spartina* to invade the *Juncus* zone, with a subsequent dominance of *Spartina* litter, at a majority of sites, despite variable edaphic conditions across these sites. At most sites, this invasion was paralleled by a concurrent decrease in *Juncus* biomass, but edaphic conditions controlled the extent of dominance by *Spartina*. The results of this study, in combination with previous work in New England (Levine et al. 1998, Emery et al. 2001, Pennings et al. 2002, Bertness and Silliman 2002) indicate that nitrogen should have impacts to marsh community composition along the entire coast if inputs are continually added at their present rate (Vitousek 1994). However, because edaphic conditions do play a role in the dominance by *Spartina*, modifications to marsh composition will likely proceed at different rates at different sites. Several factors were important predictors of *Spartina* and *Juncus* biomass, but salinity and sitescore were the most consistent and important. Salinity had negative effects on both species, as would be expected from a variety of laboratory and field studies (Adams 1963, Phleger 1971, Smart and Barko 1980, Haines and Dunn 1985, Howes et al. 1986, Bradley and Morris 1991). Sitescore had opposite effects on the two species. The extent of *Spartina* dominance was least where upland influence (i.e. sitescore) was greater. Upland influence in this case was not a function of development (this would be represented better by the mainland variable, but in any case few sites had heavy development), rather it reflected the amount of forest surrounding and bordering the marsh. Thus, a high sitescore likely represented a greater input of freshwater, or associated materials in the freshwater, which benefited *Juncus* more than *Spartina*. If this pattern was driven by freshwater input, the freshwater may have entered the marsh as groundwater, below the level of the salinity cores, or may have entered the marsh as runoff during brief periods of high rainfall. Either of these possibilities would explain why this freshwater input was not simply described by the salinity data. Buck and Pennings (*pers. comm.*) found a similar relationship between sitescore and the dominance of *Juncus* and *Spartina* at the landscape level at 54 sites that partially overlapped with mine and were within the same region of the coast. Thus, these results indicate that eutrophication will likely increase *Spartina* dominance, but the magnitude of dominance will vary at different sites depending on upland influence.

HERBIVORE RESPONSES TO ALTERED MARSH COMPOSITION

Collective results of field densities and grazing damage to plants, and lab food selection of grasshoppers *Orchelimum* and *Paroxya*, suggest that these grasshoppers respond to changes in biomass of their host plants, *Spartina* and *Juncus* respectively, through visual attraction to color, vertical shapes or clumps of vegetation (Mulkern 1967, Bernays and Wrubel 1985). *Orchelimum* density likely increased significantly in fertilized plots due to increasing *Spartina* dominance, whereas *Paroxya* did not increase with fertilization due to decreased *Juncus* dominance. Discrepancies between grazing damage data (i.e. each grasshopper grazed significantly more of their host plants in fertilized plots) and food selection in the lab (i.e. fertilized plants were not consumed more than control plants by either grasshopper) suggest that grasshoppers were visually attracted to the taller, greener, lusher biomass in fertilized plots (*pers. obs.*), rather than responding to plant quality within plots. Although the density of each grasshopper was correlated with the densities of one or both snails, the mechanisms driving these associations were likely different. The negative association between *Orchelimum* and *Littoraria* was likely due to *Littoraria* exerting strong top-down control on *Spartina* biomass (Silliman and Zieman 2001, Silliman and Bertness 2002, Silliman and Newell 2003, though snail density in this study was typically much lower than the snail density in their studies). The positive association between *Paroxya* and *Littoraria* is difficult to explain and was not strong, but likely reflects that both were associated with *Juncus*.

Because increasing nitrogen favors *Spartina* over *Juncus*, as discussed above, the *Juncus* zone could eventually be taken over by *Spartina* in eutrophied areas (but see Brewer 2003). The loss of *Juncus* from marsh sites would modify the food webs dependent upon its consumers (detritivores and herbivores). Most likely to be lost would be specialized herbivore species that feed on one host plant. Although grasshoppers tend to be oligophagous, feeding on multiple hosts within a family or genera, they do favor certain species, often obtaining 90% or more of their diet from one species (Joern 1979, Bernays and Barbehenn 1987, Chapman and Joern 1990). In salt marshes, the grasshoppers *Orchelimum* and *Paroxya* primarily eat *Spartina* and *Juncus*, respectively (Smalley 1960, Davis and Gray 1966, Parsons and de la Cruz 1980, Diaber 1982). Thus, losses of *Juncus* biomass would be expected to have strong negative effects on *Paroxya* densities. Therefore with greater anthropogenic nitrogen, *Paroxya* densities will likely decrease, *Orchelimum* densities will likely increase, and these changes may have impacts on their bird consumers, although this has not been tested. Additionally, losses of consumers, such as *Paroxya*, could have extended impacts on other parts of the food web or on marsh function (Parsons and de la Cruz 1980).

DETRITIVORE RESPONSES TO ALTERED MARSH COMPOSITION

Past studies have suggested that feeding choices and growth of salt marsh decomposers are positively influenced by the microbial biomass and quality of detritus (Newell and Bärlocher 1993, Bärlocher and Newell 1994, Bärlocher et al. 1989b, Valiela and Rietsma 1984, but see Rietsma et al. 1988), but this study was the first to examine the impacts of changes in community composition and plant quality on densities of marsh detritivores. Quality of litter did not significantly increase in fertilized plots of this study despite a trend towards greater N-content, although quantity (i.e. biomass) did; however, the lack of response of detritivores to fertilization indicated that neither litter quality nor quantity had a major role in mediating the densities of marsh snails. Although live plants within the same plots did experience substantial increases in N-content, N-content of litter quality rapidly decreases as leaves senesce, due to tidal leaching and nitrogen reallocation to living parts of plants (Christian et al. 1990, Newell 2001c), and thus may not be strongly affected by fertilization. At least one previous study reported increases in fungal densities following fertilization (Newell et al. 1996b), but this effect did not occur here. Although I found no effect of fertilization on snail densities, densities varied strongly among sites regardless of fertilization treatment (Fig. 5.1), suggesting that snail densities are strongly influenced by factors that vary at larger spatial scales, such as larval recruitment, predation, and competition.

COMPETITION AND IMPACTS TO *MELAMPUS*

The major consensus of previous work has been that *Melampus* and *Littoraria* are physiologically separated spatially, between sites (i.e. along the salinity gradient, Henry et al. 1993, Burnham and Fell 1989, Bishop and Hackney 1987) and within sites (i.e. along the tidal gradient, *Melampus* is a pulmonate snail, Russell-Hunter et al. 1972, and *Littoraria* is a prosobranch snail, Meinkoth 1981, Diaber 1982, Ruppert and Fox 1988). However, recent work by Lee and Silliman (2003) and the results of this study indicate that the snails may be structured by competition, specifically in the high marsh, where predation is lower (Kneib 1984, Kneib 1997, Hamilton 1976) and they have a shared food source, *Spartina,* which can become limiting (Stiven and Kuenzler 1979). Because *Melampus* grew substantially better on a diet of *Spartina* than *Juncus* litter (Spelke et al. 1995, Lee and Silliman 2003 *in press*, this study), *Spartina* should be its preferred diet. Therefore, it seems likely that *Melampus* is excluded from the *Spartina* zone by *Littoraria*, and there is experimental evidence to support this hypothesis (Lee and Silliman 2003 *in press*).

If *Spartina* continues to encroach landward, it is likely that competition could become stronger between these two snails because 1) their habitats will overlap further as *Spartina* further invades the *Juncus* zone where *Melampus* is most common (Diaber 1982, *pers. obs.*), 2) *Melampus* cannot move higher into the marsh since they require minimum levels of moisture to keep their gills wet and their reproduction is tidally obligate, i.e. eggs hatch as planktonic veligers during spring tides (Russel-Hunter et al. 1972, Ruppert and Fox 1988) and 3) higher marsh *Spartina* will be optimal habitat for both due to less predation (Hamilton 1976, Kneib 1984). It is likely that the outcome of a shift towards dominance by *Spartina* would be competitive displacement of *Melampus*, as suggested by the competitive dominance of *Littoraria* over *Melampus* in the mid-*Spartina* zone (Lee and Silliman 2003 *in press*). Competitive displacement of one gastropod by another has been observed a number of times (Brenchley and Carlton 1983, Bertness 1984a, Byers 2000, Lee and Silliman 2003 *in press*), and can involve a variety of mechanisms including exploitation competition for food (Stiven and Kuenzler 1979, Cross and Benke 2001, Lee and Silliman 2003 *in press*), habitat modifications (Brenchley and Carlton 1983, Bertness 1984a, Lee and Silliman 2003 *in press*), and greater conversion efficiency of limited resources to growth (Byers 2000).

RELATIVE IMPORTANCE OF ANTHROPOGENIC NUTRIENTS TO THE SALT MARSH FOOD WEB

So far I have discussed the statistical significance of fertilization on various trophic levels of the food web, but how do treatment effects compare to natural variation among sites? I used the ratio of natural variation within a site to mean treatment variation within the study area to determine this for each trophic level in this study. Results varied for different variables, and supported the general conclusion that fertilization had stronger impacts on *Spartina* primary production and quality than on *Juncus*, which subsequently led to greater fertilization impacts on grazing damage by *Orchelimum* than by *Paroxya*. On the other hand, fertilization had weak impacts on the fungal loads on standing-dead *Spartina* litter, which subsequently led to practically no impact of fertilization on the detritivorous snails. These findings support my general conclusions that impacts of fertilization to the live-plant food web can be strong given that quantity and quality of live host plants are altered, but that the detrital food web is not strongly altered by fertilization because the quality of standing-dead litter does not increase significantly. As argued above, however, it is possible that the detrital food web would be indirectly affected by eutrophication through changes in the plant community that would lead to the exclusion of *Melampus* by *Littoraria*. These findings support the idea that snail density is mediated through biological factors such as competition, predation, and larval recruitment or post-larval mortality, rather than eutrophication per se.

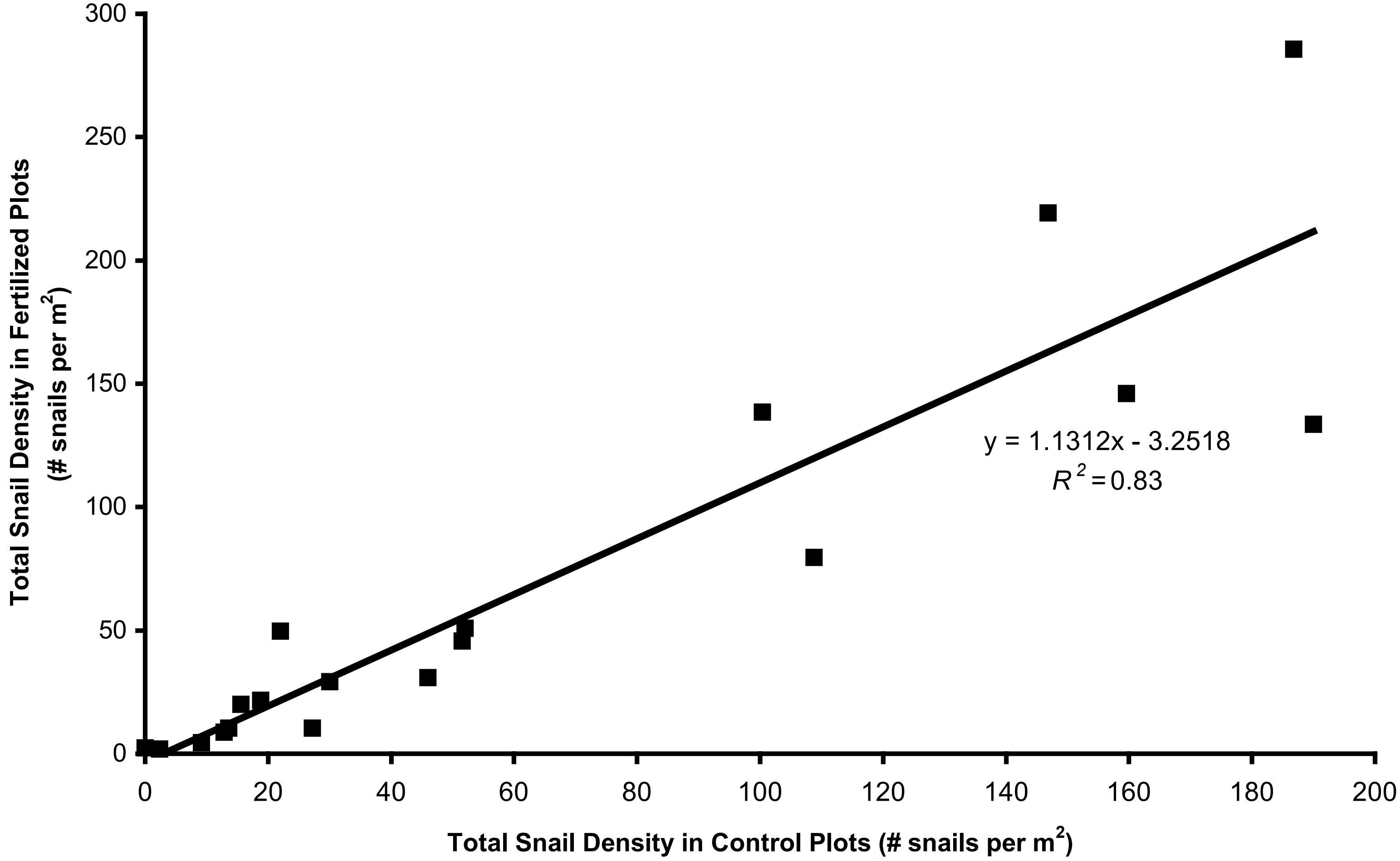

Figure 5.1. Relationship between the total number of snails (*Melampus* + *Littoraria*) at sites within control and fertilized plots (*n* =19 sites). Data are site means.

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