Eutrophication and Consumer Control of New England Salt Marsh Primary Productivity

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Abstract: *Although primary productivity in salt marshes is thought to be controlled by physical forces, recent evidence suggests that human disturbances can drive a switch to consumer control in these ecologically valuable ecosystems. We tested the hypothesis that nitrogen enrichment can trigger consumer control in salt marshes in Narragansett Bay, Rhode Island, with (1) a field experiment in which we manipulated nutrient availability (with nutrient additions) and insect herbivory (with insecticide application), (2) a survey of 20 salt marshes that examined the relationship between marsh nutrient status and herbivore pressure, and (3) insect herbivore removal at high and low nutrient input sites to directly test the hypothesis that nutrient enrichment is increasing insect herbivory in these marshes. Experimental nitrogen eutrophication initially increased plant productivity but eventually led to reduced plant biomass due to insect herbivory, and our surveys revealed that marsh nitrogen supply was a good predictor of herbivore damage to plants. Insects had minimal impacts on primary productivity in pristine marshes, but suppressed primary productivity in eutrophic salt marshes by 50–75%. Thus, eutrophication is currently triggering consumer suppression of primary productivity in New England salt marshes and may ultimately jeopardize the ecological and societal services these systems provide.*

Keywords: consumer control, cordgrass, eutrophication, insect herbivory, Narragansett Bay, *Spartina alterniflora*, wetland conservation

Eutrofización y Control de Consumidores de la Productividad Primaria de una Marisma en Nueva Inglaterra

Resumen: *Aunque se piensa que la productividad primaria en las marismas está controlada por factores físicos, la evidencia sugiere que las perturbaciones humanas pueden derivar hacia el control de consumidores en estos ecosistemas ecológicamente valiosos. Probamos la hipótesis que el enriquecimiento de nitrógeno puede disparar el control de consumidores en marismas de la Bahía Narragansett, Rhode Island, con (1) un experimento de campo en el que manipulamos la disponibilidad de nutrientes (mediante la adición de nutrientes) y la herbivoría de insectos (mediante la aplicación de insecticida), (2) el muestreo de 20 marismas para examinar la relación entre el estatus de nutrientes y la presión de herbivoría y (3) la remoción de la herbivoría de insectos en sitios con alta y baja aportación de nutrientes para probar, directamente, la hipótesis que el enriquecimiento de nutrientes está incrementando la herbivoría de insectos en estas marismas. La eutrofización experimental de nitrógeno incrementó la productividad de plantas inicialmente pero eventualmente derivó a la reducción de la biomasa de plantas debido a la herbivoría de insectos, y nuestros muestreos revelaron que la reserva de nitrógeno en la marisma fue un buen pronosticador del daño de herbívoros a las plantas. Los insectos tuvieron impacto mínimo sobre la productividad primaria en las marismas prístinas, pero suprimieron entre 50 y 75% de la productividad primaria en marismas eutróficas. Por lo tanto, la eutrofización está generando la supresión de consumidores de la productividad primaria en marismas de Nueva Inglaterra y en última instancia puede hacer que peligren los servicios ecológicos y sociales que estos sistemas proporcionan.*

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Palabras Clave: Bahía Narragansett, conservación de humedales, control de consumidores, eutrofización, herbivoría de insectos, *Spartina alterniflora*

Introduction

Since the invention of artificial nitrogen fertilizer in the late 19th century, humans have increased dramatically the global supply of fixed nitrogen, altering the global nitrogen cycle and fundamentally changing the structure and dynamics of many natural communities (Vitousek et al. 1997). Estuaries have been affected particularly by nutrient pollution because agricultural fertilizers commonly end up in terrestrial runoff draining into shallow-water coastal habitats and wetlands (Howarth et al. 2000). Estuarine marshes are valued for their ability to mitigate the effects of nutrient runoff into coastal waters; however, nutrient pollution may ultimately degrade the structure of the marsh itself (e.g., Levine et al. 1998; Bertness et al. 2002; Crain 2007). Salt marshes perform other important ecosystem services including serving as nursery grounds for marine species (Boesch & Turner 1984), buffering coastal erosion and storm damage (Frey & Basan 1985), and filtering chemicals from terrestrial runoff (Todd & Todd 1994). They were also heavily affected historically by humans (e.g., Bromberg & Bertness 2005; Lotze et al. 2006), so protecting the integrity of remaining marshes is a conservation priority. Understanding the long-term consequences of nutrient enrichment on salt marsh community structure is critical for managing these important ecosystems.

Salt marsh ecosystems are considered systems under strong bottom–up control, where the physical conditions of the soil and nutrient availability control primary productivity patterns (Teal 1962). The role of consumers in salt marsh systems has been assumed to be trivial. Recent work in a variety of salt marshes, however, challenges this view, and most evidence that consumers can play a leading role in controlling salt marsh productivity comes from systems that have been disturbed by humans (nitrogen fertilization, Jefferies 1997; invasive nutria (*Myocastor coypus*), Gough & Grace 1998; drought and snails (*Littorina irrorata*), Silliman et al. 2005). In New England (U.S.A.) salt marshes, herbivory has long been thought to play an insignificant role in ecosystem dynamics (Teal 1985; Bertness & Ellison 1987), despite the fact that herbivory in these habitats has not received much critical examination. Herbivorous insects (e.g., grasshoppers and beetles) are thought to feed very little on the somatic tissue of the clonal turf plants that dominate New England salt marshes and instead feed almost exclusively on the flowers and seeds (Bertness et al. 1987) and the less-abundant forbs that live inconspicuously hidden in the matrix of unpalatable clonal plants (Rand 1999). Vince et al. (1981, however, found that insect abundance increases dramatically in salt marsh plots enriched with nitrogen fertilizer, which suggests that eutrophication could lead to increasing herbivory on New England salt marsh plants and possibly switch consumption patterns to somatic tissue. Increased nutrient supply and high primary productivity often leads to increased herbivory in other salt marsh systems as well (Stiling et al. 1991; Gough & Grace 1998; Silliman & Zieman 2001).

Although nutrient enrichment increases consumer activity on salt marsh plants, the larger-scale impacts of this interaction are unknown. In a previous study of 30 salt marshes in Narragansett Bay, Rhode Island, we found that shoreline development (operationally defined as the removal of the natural woody vegetation bordering a salt marsh) drives variation in marsh nitrogen supply and community structure (Bertness et al. 2002; Silliman & Bertness 2004). The woody vegetation that borders natural salt marshes processes nutrient-rich runoff entering salt marsh watersheds from terrestrial sources, thereby buffering undisturbed salt marshes from nutrient loading (McClelland & Valiela 1998). If nutrient enrichment triggers consumer control of primary productivity (Vince et al. 1981) and alteration in community structure scales up from experimental plots to landscape scales (Bertness et al. 2002; Silliman & Bertness 2004), then one would expect that marshes of varying nutrient status across Narragansett Bay also vary in the degree of consumer control of primary productivity. Elucidating the indirect effects of nutrient enrichment on marsh food webs and plant community structure is essential for understanding the large-scale and long-term impacts of coastal eutrophication.

We examined the hypothesis that nitrogen eutrophication can trigger consumer control of the primary productivity of New England salt marshes. We specifically addressed whether increased nitrogen supply increases consumer pressure on New England salt marshes where herbivory has been unimportant historically and whether shoreline development triggers increased consumer pressure on salt marsh primary productivity. To examine our hypothesis we determined the interactive effects of nitrogen enrichment and insect herbivory in a manipulative field experiment; quantified insect herbivore damage at 20 Narragansett Bay salt marshes that vary in the extent of shoreline development and nitrogen supply; and experimentally quantified the extent of insect herbivory suppression of plant primary production at pristine and eutrophic salt marshes in Narragansett Bay.

Methods

Nutrient Supply and Consumer Control of Primary Productivity

We experimentally examined whether nitrogen enrichment increases insect herbivory on cordgrass (*Spartina alterniflora*) by manipulating nitrogen supply (with nitrogen fertilizer) and insect herbivory (with a systemic insecticide) in salt marshes at the Narragansett Bay National Estuarine Research Reserve on Prudence Island, Rhode Island. We demarcated 40, 3 × 3 m plots in both tall-form and short-form cordgrass zones in April 2005. In each zone, 10 plots were randomly assigned as unmanipulated controls, insect-removal plots, nitrogen-addition plots, or nitrogen-addition and insect-removal plots. Fertilized plots were treated monthly with topical additions of Scott's Turfbuilder (Scotts, Marysville, Ohio) fertilizer (30% nitrogen, 3% phosphorus, 3% potassium by weight) at a rate of 60 $g{\cdot}m^{-2}{\cdot}month^{-1}$ from May through August 2005 and 2006. We did not intend to mimic any particular level of eutrophication at this level of fertilization; rather, we wanted to examine how these marsh plants would respond if nutrients did not limit their growth. Identical methods of nutrient fertilization in Narragansett Bay salt marshes successfully altered nutrient availability and led to dramatic shifts in competitive dominance among marsh plants (Levine et al. 1999; Emery et al. 2001). No evidence of leaf scorching or other negative impacts of nitrogen enrichment were ever observed during these experiments. Insect-removal plots were treated with a systemic insecticide to reduce insect herbivory. The systemic insecticide used, Discus (Olympic Horticultural Products, Mainland, Pennsylvania; active ingredients 0.7% Cyfluthrin and 2.9% Imidacloprid), which specifically targets arthropods, only needed to be applied twice over the course of the summer, mid-June and early August, did not affect plant growth in greenhouse tests (M.D.B, unpublished), and is nontoxic and safe to use in aquatic systems. The insecticide was applied (at a concentration of 150 mL/550 L) during morning neap low tides to maximize its efficacy and prevent contact with other vegetation and water.

To compare temporal patterns in the effects of insects and nutrients, we quantified plant biomass and insect damage in all plots monthly during the summer of 2005. Plant biomass was quantified by harvesting all cordgrass stems in a randomly placed 100-cm^2 plot in each replicate. This aboveground vegetation was then dried and weighed in the laboratory. In the second year of the experiment, we sampled only plant biomass in the plots at the end of the growing season in September. End-of-season biomass in each year and within each marsh zone was analyzed separately with a two-way, nutrient enrichment × insecticide, analysis of variance (ANOVA).

We quantified herbivore damage in experimental plots by randomly selecting three cordgrass stems per plot and examining each stem for percent mottled leaves, percent yellow leaves, length of shreds (total centimeters), and number of clipped leaf tips. Percent mottled was the percentage of the stem damaged by planthopper (*Prokelesia* sp.) herbivory and included rasped areas of the leaves, which often had a speckled or mottled appearance. Percent yellow was leaf area that was dying from extensive herbivory damage; however, we often could not single out the specific consumer. Length of leaf shredded through the somatic tissue and tips clipped collectively quantified grasshopper damage and accounted for those regions with signature evidence of grasshopper consumption. These two features included tips severed from the plant in a very straight line and distinct grazed regions in which grasshoppers had eaten through the thickness of the leaf. To confirm scarring types, we conducted feeding trials with various consumers on cordgrass stems in the lab and examined the type of damage inflicted. As a measure of cumulative insect damage, we summed the damage scores in each category to calculate a simple herbivory score per plant. Sampled stems were treated as subsamples and averaged for a single measure of herbivore damage per plot. A problem with using leaf damage to infer levels of herbivory is that heavily damaged leaves may not be quantified because most or all of a leaf is eaten. Thus using leaf damage likely underestimates the level of herbivory and these data must be interpreted with caution.

Planthopper and grasshopper damage was by far the most common herbivore damage on cordgrass at our study sites. Planthopper damage to cordgrass becomes apparent in Narragansett Bay marshes in mid June and continues until the plants begin senescing in late September, whereas grasshopper herbivory is not apparent until late July but continues for the remainder of the summer (C.M.C. & M.D.B., unpublished data). Although it was impractical to quantitatively partition the relative importance of planthopper and grasshopper herbivory, planthoppers were responsible for most of the damage we observed to cordgrass. Insect damage to plants at the end of the growing season in 2006 was analyzed with a two-way, nutrient enrichment × insecticide, ANOVA in the short- and tall-form cordgrass zones.

Shoreline Development, Eutrophication, and Insect Herbivory

To examine whether shoreline development and current levels of eutrophication in Narragansett Bay salt marshes is increasing insect herbivory at high-nitrogen-input salt marshes, we examined insect damage to plants in marshes that varied in shoreline development and nitrogen input. Previous work shows that shoreline development, by removing the woody vegetation buffer surrounding marshes, increases the flow of nutrient-rich terrestrial runoff onto marshes, increasing nitrogen supply (Bertness et al. 2002; Silliman & Bertness 2004). To quantify shoreline development, we photographed the upland border of each salt marsh and calculated the percentage of the upland border that was anthropogenically disturbed by roads, farms, golf courses, and housing (Bertness et al. 2002). Marsh nitrogen level was determined previously. Analytical methods and detailed study site locations are in Bertness et al. (2002) and Silliman and Bertness (2004).

Owing to variation in buffer removal, marshes experience a gradient of nutrient loading around Narragansett Bay (Bertness et al. 2003; Silliman & Bertness 2004). In August 2006 we visited 20 Narragansett Bay marshes where shoreline development and nutrient status had been quantified previously. At each site we examined 15 random stems at the upper border of the cordgrass zone for insect damage as described earlier. We used linear regression to separately examine the relationship between shoreline development and marsh nitrogen level with insect damage to plants in each marsh.

Nitrogen Loading and Suppression of Primary Productivity

To experimentally examine whether current levels of eutrophication in the bay are leading to increased insect-consumer control of salt marsh primary productivity, we conducted a herbivore exclusion experiment in salt marshes with high and low nutrient status around Narragansett Bay. In three marshes with high nutrient input (North Farm, East Greenwich, and East Greenwich Country Club) and three marshes with low nutrient input (Cogshall, Nag East, and Nag West) (as determined by nutrient sampling in Bertness et al. [2002]), we established 10 replicate 3 × 3 m plots in both tall- and short-form stands of cordgrass (see Bertness et al. [2002] and Silliman and Bertness [2004] for information on these sites). Half the plots at each site and in each zone were randomly assigned as insect-removal plots and the remaining plots were assigned as controls. The insect-removal plots were treated with insecticide in 2005 and 2006 as described earlier. Plots for this experiment were established in May 2005 and maintained as described earlier for the nutrient-addition experiment through September 2006. We examined these plots by scoring them for insect damage monthly and determined cordgrass biomass monthly in 2005 and in September 2006, as described earlier for the nutrient-addition experiment. Results from this experiment must be interpreted with caution because the potential disappearance of higher-order consumers from these systems due to anthropogenic stressors, as seen in many systems (Purvis et al. 2000; Dobson et al. 2006), may increase insect herbivory in developed marshes due to increased plant productivity (bottom–up) or decreased predatory consumers (top–down). Our results cannot distinguish between these potential mechanisms. We analyzed plant biomass and damage data from this experiment with an ANOVA, testing for the effects of marsh nutrient status, insecticide treatment, and their interaction on data pooled across high- and low-nutrient marshes.

Results

Nutrient Supply and Consumer Control of Primary Productivity

Nitrogen fertilization strongly increased the impact of insect herbivory on cordgrass in both short-form and tall-form cordgrass zones (Fig. 1; Table 1). In both years and in both forms, the effect of insect herbivory was much greater on fertilized than on control plots (Table 1). Although insect herbivory had no significant effect in control plots in any year or zone, herbivory reduced growth in fertilized plots of short-form cordgrass by 42% and 76% in years 1 and 2, respectively, and in the tall-form cordgrass by 66% and 67% in years 1 and 2, respectively.

In the second year of the experiment, short-form fertilized plots without insecticide had 15% less biomass than control plots. Although this reduction in biomass was not statistically significant (least-squares mean contrast, $F_{1,28} = 1.54, p = 0.22$), the trend indicated that with time fertilization may lead to overconsumption by herbivores,

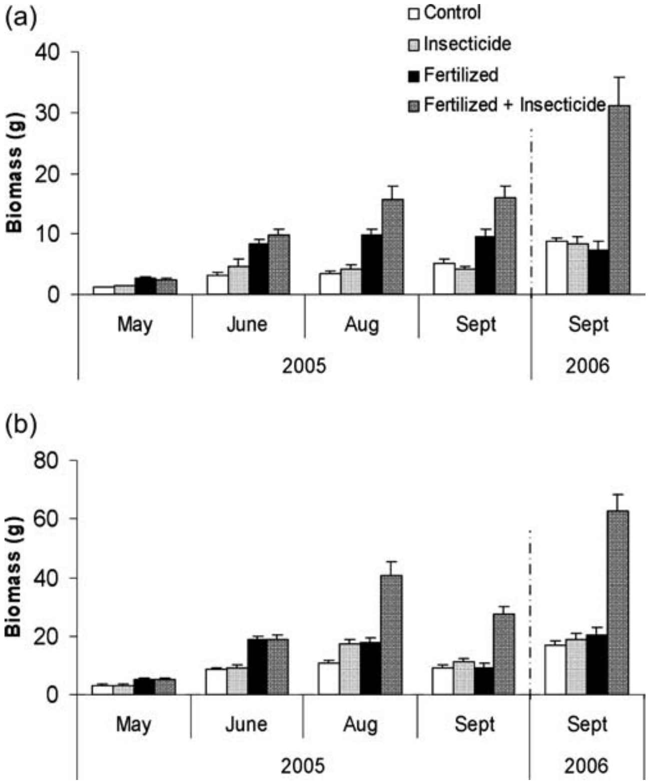

Figure 1. Cordgrass biomass (±SE) results from the nutrient addition × insect herbivore removal experiment on Prudence Island, Rhode Island, on (a) short- and (b) tall-form cordgrass.

Table 1. **Results of analysis of variance (ANOVA) on the effects of fertilization (F), insecticide (I), and their interaction (F × I) on end-of-season biomass of short- and tall-form cordgrass in experimental plots in salt marshes.***

	Short form				*Tall form*			
	September 2005		*September 2006*		*September 2005*		*September 2006*	
Effect tested	F	p	F	p	F	p	F	p
F	57.82	<0.0001	13.20	0.0011	13.75	0.0009	45.49	<0.0001
I	2.32	0.139	24.02	<0.0001	31.60	<0.0001	34.64	<0.0001
F × I	7.35	0.0113	29.03	<0.0001	13.28	0.0011	24.70	<0.0001

**The df for all tests was 1, 28.*

effectively reducing year-end biomass in nutrient-enriched plots.

Plant damage by insects in experimental plots varied due to fertilizer and insecticide treatments (Fig. 2). Data shown for September 2006 were representative of patterns evident throughout the course of the experiment. For the short form, total insect damage to plants increased significantly in fertilized versus unfertilized plots ($F_{1,20} = 11.81, p = 0.003$). Insecticide treatments had significantly less plant damage than control plots in the short-form plots ($F_{1,20} = 9.54, p = 0.006$), and there was no significant fertilization × insecticide interaction. In the tall-form plots only the effect of insecticide significantly reduced plant damage by insects ($F_{1,20} = 7.43, p = 0.013$). Fertilization had no significant effect on plant damage in tall-form plots. The majority of insect damage to plants appeared to come from planthopper herbivory (mottled and yellow plant damage).

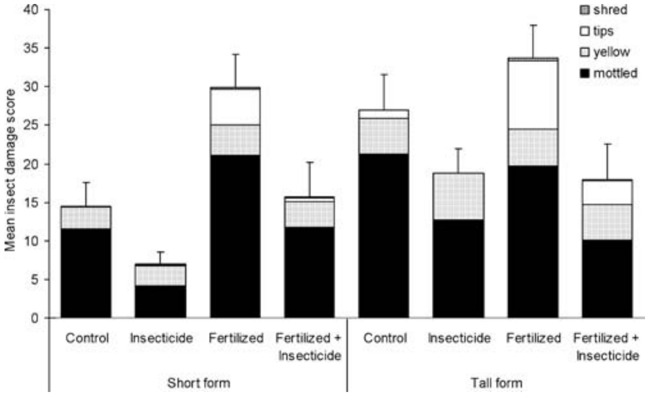

Figure 2. Insect herbivore damage (±SE) to cordgrass (short and tall forms) in the nutrient addition × insect herbivore removal experiment. Data are from September 2006, but are representative of damage patterns seen throughout the 2-year experiment. Insect damage scores for each experimental plot (three random stems were scored per plot) were calculated by summing all the types of insect damage (see key) typically found on damaged plants. Higher damage scores indicate higher insect damage (see text).

Shoreline Development, Eutrophication, and Insect Herbivory

Mean insect herbivore damage to cordgrass, as measured by our cumulative insect damage score, varied considerably among sites, with some sites having <20% damage and others exceeding 80% damage. Among-site variation in nitrogen supply explained 65% of the among-site variation in insect stem damage, with increased nitrogen supply leading to increased insect damage (Fig. 3a). Percentage of developed upland border was correlated with nutrient input to marshes, and explained 60% of the variation in insect damage to plants among sites (Fig. 3b).

Nitrogen Loading and Suppression of Primary Productivity

Results of the insecticide experiment in marshes with high- and low-nutrient inputs due to shoreline development in Narragansett Bay revealed that herbivory by insects was much greater in developed, eutrophic marshes than in undeveloped, low-nutrient marshes (Fig. 4; Table 2). In short-form cordgrass the marsh nutrient status × insecticide interaction was significant in both years (Table 2). This interaction resulted because at low-nutrient sites insecticide had no effect on primary productivity on short-form cordgrass, but at high-nutrient sites insect herbivory suppressed cordgrass production by 40% and 57% in the first and second year of the experiment, respectively. In post hoc comparisons biomass in high-nutrient control plots was greater than in low-nutrient control plots in 2005 (least-squares contrast, $F_{1,52} = 24.8, p < 0.0001$), but not in 2006 (least-squares contrast, $F_{1,46} = 3.4, p = 0.071$).

In tall-form cordgrass a significant nutrient status × insecticide interaction occurred only in the second year of the experiment (Table 2). In the first year insecticide increased plant biomass in both low- and high-nutrient marshes. In the second year of the study, insecticide had no effect in low-nutrient marshes, but in high-nutrient marshes, insect herbivory reduced biomass by 66%. As in the short-form experiment, post hoc comparisons on tall-form biomass showed that biomass in plots with no insecticide was greater in high-nutrient than low-nutrient marshes in the first (least-squares contrast, $F_{1,40} = 15.4$,

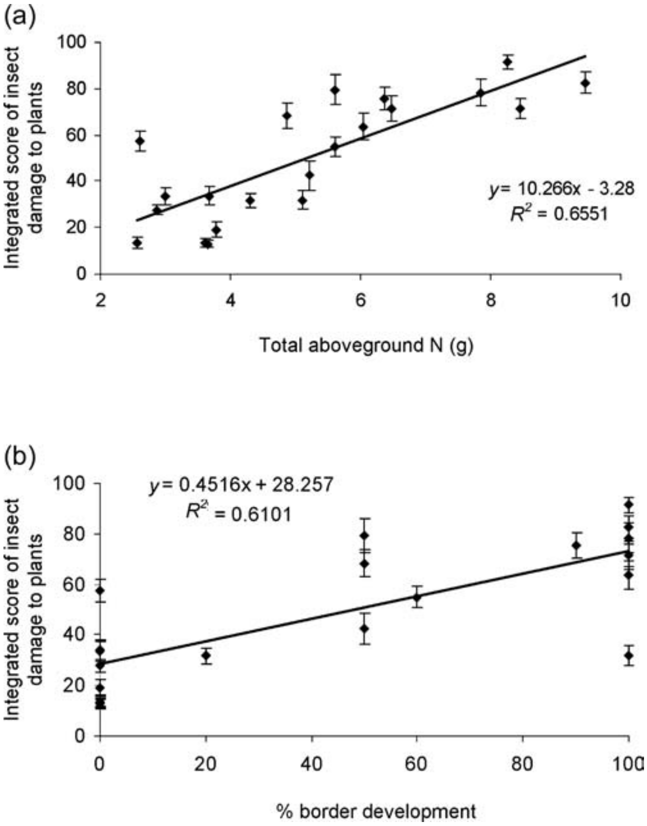

Figure 3. Relationship between insect herbivore damage to cordgrass and (a) total aboveground nitrogen per dried gram of cordgrass tissue and (b) shoreline border development at 20 Narragansett Bay salt marshes with varying levels of human disturbance. For each site plant damage was calculated by scoring 15 random stems at the upper border of the tall-form cordgrass zone for insect damage. Higher damage scores indicate higher insect damage (see text).

$p = 0.0003$), but not second ($F_{1,38} = 0.014$, $p = 0.91$), year of the study. In the second year plant biomass did not respond to eutrophication unless herbivorous insects were removed.

Discussion

Nitrogen enrichment increased insect consumer control of primary productivity in the New England salt marshes we studied. In addition, our results showed that current levels of shoreline development and eutrophication have already led to increased insect herbivory, which suppresses salt marsh primary productivity by 50–75% of what it could be in eutrophic marshes without consumers. Thus, our results suggest that although primary productivity in New England salt marshes was controlled historically by physical forces, shoreline development can increase nitrogen supply and lead to increased consumer control of salt-marsh primary productivity. Because the primary productivity of salt marshes regulates the quality and quantity of most of the ecological services they provide, these results have important conservation and management implications.

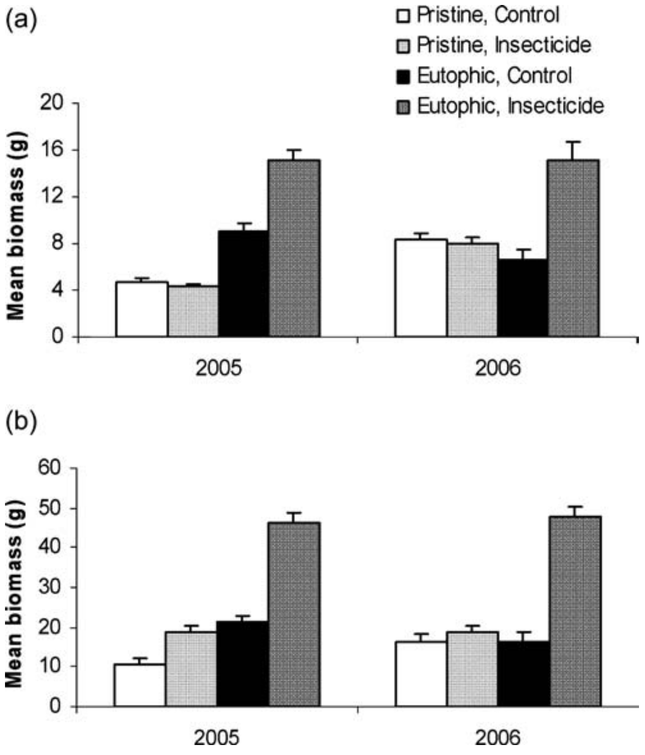

Figure 4. (a) Tall- and (b) short-form cordgrass biomass (±SE) in the insect herbivore removal (insecticide) experiment at Narragansett Bay salt marshes in low (pristine) and high (eutrophic) human-disturbance areas.

Nutrient Supply and Consumer Control of Primary Productivity

Our results support the idea that herbivory does not significantly suppress the primary productivity of undisturbed New England salt marshes. In our experimental study conducted in a low-nutrient-input salt marsh, insecticide had no significant effect on plant biomass in control plots of the short- or tall-form cordgrass in both years of the study (Fig. 1). Similarly, in the baywide herbivore-removal experiment, insecticide did not significantly alter cordgrass biomass in low-nutrient marshes, with one exception. In 2005 tall-form cordgrass in low-nutrient marshes did benefit from insect removals. Tall-form cordgrass has higher nitrogen levels than short-form cordgrass (Mendelssohn et al. 1981), and the increased vulnerability of high-production cordgrass to consumer control is well documented (Stilling et al. 1991; Silliman & Bertness 2003).

Table 2. Results of analysis of variance (ANOVA) on the effects of insecticide (I) at high- and low-nutrient input (N) sites on end-of-season biomass of short- and tall-form cordgrass for 2 years in experimental plots.*

	Short form				*Tall form*			
	September 2005		*September 2006*		*September 2005*		*September 2006*	
Effect tested	F	p	F	p	F	p	F	p
N	120.83	<0.0001	3.42	0.071	43.15	<0.0001	29.63	<0.0001
I	8.96	0.0042	13.09	0.0007	21.67	<0.0001	51.84	<0.0001
N × I	15.6	0.0002	19.91	<0.0001	1.03	0.315	31.48	<0.0001
df	1,52		1,46		1,40		1,38	

**The ANOVA tested for the effects of marsh nutrient status (N), insecticide (I), and their interaction (N × I) on end-season-biomass in each form in September of 2005 and 2006.*

We also found that eutrophication in Narragansett Bay salt marshes is triggering increased consumer activity across landscape spatial scales. Our survey of salt marshes revealed that insect damage varied among marshes by nearly threefold, ranging from <20% to >80% stems damaged (Fig. 3), and was strongly correlated with shoreline development and marsh nutrient status. Salt marshes with developed shorelines, operationally defined as the removal of a natural buffer of woody vegetation (Bertness et al. 2002), had higher insect damage than salt marshes with undisturbed borders, and marshes with higher nitrogen content had higher herbivorous insect damage than marshes with low nitrogen content (Fig. 3). Both percent shoreline development and nitrogen level explained over 61% of the intermarsh variation in insect herbivore damage of cordgrass (Fig. 3).

Results of previous work show that shoreline development can increase nitrogen supply (McClelland & Valiela 1998) and shift the dominant plant cover on developed salt marshes (Bertness et al. 2002; Silliman & Bertness 2004). Our results revealed that shoreline development and local eutrophication can also trigger increased insect herbivory in eutrophic marshes and that, in Narragansett Bay salt marshes, insect consumers are suppressing the primary production of cordgrass on high-nutrient content salt marshes by 50–70% (Fig. 4). Insect densities as estimated by sweep nets and manual counts were greater in high-nutrient marshes than pristine marshes (C.M.C. & M.D.B., unpublished data). Whether these greater insect densities are driven by bottom-up factors (eutrophication) or other factors correlated with upland development (e.g., loss of top–down control by predators) is unknown and in need of further investigation. Nonetheless, similar mechanisms appear to be driving increased herbivory and decreased plant productivity in artificially fertilized experimental plots and across large-scale eutrophication gradients. Results of recent studies in other shallow-water marine systems quantifying top–down and bottom–up forces on benthic primary producers show that increasing eutrophication weakens top–down control on plant production (e.g., Burkepile & Hay 2006; Worm & Lotze 2006). This disparity between the response of salt marsh and other shallow-water marine systems to eutrophication has important conceptual and conservation implications and deserves further attention.

Our results add to a growing list of examples of human disturbances triggering consumer control in salt marsh systems, which implies that although natural marsh systems are dominated by bottom–up forcing, human disturbances may commonly trigger consumer control in these systems. Jefferies (1997) found that increases in Snow Goose (*Chen caerulescens*) populations, fueled by nitrogen fertilizer subsidies in North America, are leading to the Snow Geese entirely denuding expansive areas of subarctic marshes in Hudson Bay, which could lead to ecosystem collapse. Marsh die-off is also occurring in salt marshes along the southeastern and Gulf coasts of the United States and has become an urgent conservation and management issue.

Although most work with this die-off has focused on harsh edaphic conditions leading to marsh plant death, recent experimental work has revealed that the marsh snail, *Littoraria irrorata*, can exert powerful top–down control in these marshes (Silliman & Bertness 2002; Silliman & Newell 2003). Most recently, Silliman et al. 2005 found that snail-driven runaway-consumer effects in these marshes are amplified by salt stress and that the recent extensive die-off of these marshes is being driven synergistically by drought stress and snail consumer pressure. Introduced herbivores can also lead to consumer control in salt marsh systems. In Gulf Coast salt marshes the introduced herbivorous mammal, nutria, can control marsh plant growth and species diversity (Gough & Grace 1998). On the barrier islands off the coast of Maryland and Virginia, introduced feral horses can similarly control marsh primary productivity (Furbish & Albano 1994; Levin et al. 2002).

Together, this collection of examples of increased consumer pressure from salt marsh systems ranging from subarctic to semitropical latitudes, suggests that human disturbances including eutrophication (Jefferies 1997; this study), overharvesting of top consumers (Silliman & Bertness 2002), and invasive species (Furbish & Albano 1994; Gough & Grace 1998; Levin et al. 2002) are leading to increased consumer control of salt marsh primary productivity. Thus, North American salt marshes that were once largely controlled by bottom-up forces are now vulnerable to significant consumer control.

The unanticipated, indirect, and higher-order interactions of nutrient enrichment on plant communities has been seen in many ecosystems (reviewed in Throop & Lerdau 2004). In temperate forests nutrients initially increase primary productivity, but eventually lead to foliar decline due to increased herbivory, ultimately depressing carbon sequestration capacity in these systems (Throop & Lerdau 2004; Throop et al. 2004). Our results suggest that this series of events under eutrophic conditions may be common across ecosystems and initial increases in productivity due to eutrophication may be ultimately unsustainable due to indirect increases in herbivore populations and consumption rates. Our results also indicate that the long-term impacts of eutrophication on community structure and ecosystem functions in coastal marshes are more complex than originally thought. Understanding the indirect effects of coastal eutrophication is critical for managing the structure of these ecosystems.

Our findings have critical implications for the conservation and management of Atlantic coast salt marshes. Because salt marsh ecosystems are still widely understood to be under the control of physical processes, management and conservation efforts focus entirely on marsh hydrology and factors that affect the physical nature of marshes. Nevertheless, our study adds to a growing body of research that suggests that herbivory and top-down control of salt marshes may be highly correlated with human disturbance and eutrophication and therefore should be incorporated into marsh management strategies. The long-term effects of human-altered physical conditions in salt marshes, such as sea-level rise, may be of less consequence than human disturbances that trigger shifts in the structure of the food web, which immediately degrade marsh functions. Because salt marshes provide important ecological and societal services to coastal systems that are closely tied to marsh primary productivity, understanding the determinants of salt marsh primary productivity is a critical conservation and management issue.

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