Estuaries and Coasts Vol. 29, No. 4, p. 639–644 August 2006

Relative Effects of *Littoraria irrorata* and *Prokelisia marginata* on *Spartina alterniflora*

DANNY J. GUSTAFSON[1,*], JEFF KILHEFFER[1], and BRIAN R. SILLIMAN[2,†]

[1] *Department of Biology, The Citadel, Charleston, South Carolina 29409*
[2] *Virginia Institute of Marine Sciences, College of William and Mary, Williamsburg, Virginia 23062*

ABSTRACT: *Spartina alterniflora* salt marshes along the southeastern United States are some of the most productive and well studied ecosystems in the world. The role of physicochemical forces in regulating *Spartina* growth is well understood, while the importance of grazers remains less clear. Recent studies have shown that the abundant marsh periwinkle, *Littoraria irrorata*, can exert strong control over *Spartina* through its grazing activities, but relatively little is known about its relative effects in comparison to other marsh plant consumers. To test the relative importance of snail and insect consumers on *Spartina* biomass, we conducted a 7-mo field experiment testing top-down regulation of *Spartina* with all combinations of *L. irrorata* (removed, control, c. 215 periwinkles m^{-2}) and *Spartina* planthopper, *Prokelisia marginata* (removed, control). Snail removal resulted in a 50% increase in *Spartina* biomass while removal of planthoppers had no detectable effect. Planthopper density also increased by 50% when snails were excluded. In this South Carolina marsh, *L. irrorata* exerts a stronger top-down control of *Spartina* than *P. marginata*. These results indicate trophic cascade regulation of *Spartina* salt marsh is more likely to occur through the predator(s)-*Littoraria*-plant interaction than through the predator(s)-*Prokelisia*-plant relationship.

Introduction

Grazers are important in the top-down regulation of primary productivity in seagrasses (Heck et al. 2000), salt marshes (Smith and Odum 1983; Furbish and Albano 1994; Taylor and Grace 1995; Silliman and Zieman 2001; Silliman et al. 2005), arctic ecosystems (Ngia and Jefferies 2004; van der Wal and Brooker 2004), benthic algae (Hillebrand 2005), and rocky intertidal zones (Leonard et al. 1998; Rohde et al. 2004). Because of the difficulty in conducting caging experiments in marine systems, most research has focused on a single consumer and its effects on primary producers. In most of these systems the grazer assemblage is diverse and multiple consumers feed simultaneously on the same plant. Investigations of the effects of multiple grazers on primary producers should include individual species effects as well as any interactive effects between consumers. To more accurately model top-down regulation in marine systems, studies should employ more complex experimental designs that include multiple consumer species within the context of regulating plant growth.

Spartina alterniflora salt marshes of the Atlantic and Gulf coasts of North America are some of the most productive and studied ecosystems (Weinstein and Kreeger 2000). Regulation of *S. alterniflora* productivity has been studied in terms of resource availability (Valiela and Teal 1979; Howes et al. 1986; Bradley and Morris 1990; Mendelssohn and Morris 2000), top-down regulation (Smith and Odum 1983; Furbish and Albano 1994; Taylor and Grace 1995; Daehler and Strong 1997; Pennings et al. 1998), and more recently through the grazing activities of *Littoraria irrorata* (Silliman and Zieman 2001; Silliman and Bertness 2002; Silliman et al. 2004, 2005). This common gastropod's reproductive biology, dispersion ability, vertical migrations, and predator avoidance behavior is well understood (Bingham 1972; Hamilton 1978; Warren 1985; Vaughn and Fisher 1988, 1992); only recently have studies started incorporating the effect of *L. irrorata* activities on marsh primary producers (Silliman and Zieman 2001; Silliman and Bertness 2002). Reduced *L. irrorata* predation and mortality rates are associated with increased animal size (Stanhope et al. 1982; Warren 1985; West and Williams 1986; Tucker et al. 1995; Cotton et al. 2004) and larger animals inflict greater radula damage to *S. alterniflora* (Silliman and Zieman 2001). These snails are fungal farmers and graze on live grass primarily to prepare plant tissue for fungal growth and consume invasive fungi, rather than consume plant tissue directly (Silliman and Newell 2003). Phloem feeding insects, such as *Prokelisia marginata* (*Spartina* planthopper), have also been shown to significantly reduce *S. alterniflora* biomass (Daehler and Strong 1997; Grevstad et al. 2003) and leaves (Moon and Stiling 2002). *P. marginata* has recently been introduced as a biological control of *S. alterniflora* that is invading Pacific salt marsh communities (Grevstad et al.

---

[*] Corresponding author; tele: 843/953-7876; fax: 843/953-7264; e-mail: danny.gustafson@citadel.edu

[†] Current Address: Department of Zoology, University of Florida, Gainesville, Florida 32611-8525.

2003). Both *L. irrorata* and *P. marginata* are sympatric and common residents in southeastern salt marshes and have been shown to affect *S. alterniflora* in the field. No studies have investigated the effects of multiple common consumers on top-down regulation of salt marsh productivity.

In this study, we test the relative contributions of two common consumers on a dominant primary producer of southeastern salt marsh. We established a field experiment to test the effect and potential interactions of *L. irrorata* and *P. marginata* on *S. alterniflora*. Differences in life history traits among these consumers may result in differential effects on *S. alterniflora*. Multiple generations during a 12-mo period in southeastern salt marshes and population densities up to 100,000 insects m^{-2} could result in a large *P. marginata* effect on *S. alterniflora* (Moon and Stiling 2002). *L. irrorata* individuals live longer than individual *P. marginata*, can feed year-round in some southeastern marshes, and likely inflict more damage to the plant per individual than the much smaller *P. marginata*. If there is niche separation in consumption strategies between these common animals (we often find *L. irrorata* grazing the bottom surface [adaxil] of the grass blade and *P. marginata* congregating on the upper [abaxil] surface), then understanding the relative effects of these two consumers on *S. alterniflora* is important. Based on previous research and field observations, we hypothesize that both consumers will exert top-down control of *S. alterniflora* and the combination of phloem feeding insects and grazing gastropods will reduce plant growth more than either consumer individually.

Materials and Methods

A field experiment was established in a Charleston Harbor salt marsh (32°49.33′N, 79°53.56′W) to examine the separate and interactive effects of *L. irrorata* and *P. marginata* on growth of the salt marsh cordgrass, *S. alterniflora*. Species will be referred to by genus hereafter. The four experimental treatments were: control, *Littoraria* removal, *Prokelisia* removal, and *Littoraria* + *Prokelisia* removal. Eight replicates of each experimental treatment were randomly established in the marsh on April 20, 2004. The control *Littoraria* density of 215 individuals m^{-2} was selected because that was the maximum density observed in that marsh in April 2004. Each replicate consisted of a 1 m^2 roofless cage constructed of 76 cm high galvanized hardware cloth (12.7 mm mesh) placed 5 cm into the substrate and anchored with wooden stakes (see Silliman and Zieman 2001). Insect removal treatments were established and maintained with weekly applications of 250 ml of a 2% concentration biodegradable insecticide on rainless days during low tide (Garden Safe Insecticidal Soap, Schultz, Spectrum Brands, St. Louis, Missouri). *Littoraria* are typically not active during low tides in the summer (Silliman and Newell 2003) and any excess insecticide was likely washed off during subsequent tides and likely had no effect on *Littoraria* activities. Water was sprayed on noninsect removal treatments in a similar manner as a disturbance control. *Littoraria* treatments were maintained by manually removing or adding snails at weekly intervals.

Spartina percent cover was estimated in all experimental units in the middle (June 18, 2004) and at the end (September 14, 2004) of the growing season. *Spartina* biomass, number of leaves, total leaf length, and density at the end of the experiment in September were determined by harvesting aboveground plant material in a 0.0625 m^2 quadrat randomly located within each experimental unit. Samples were washed free of debris in the lab, dried to a constant mass, and weighed. In addition to plant performance, we recorded the number of *Prokelisia*, spiders, and non-*Spartina* planthoppers on five randomly selected plants in each experimental unit in June and September. Because there were less than ten non-*Spartina* planthoppers and spiders observed among the 320 plants surveyed, we restricted our insect analyses to *Prokelisia* density data. In the two experimental treatments that included *Littoraria* (control, *Prokelisia* removal), density and population structure were determined during June and September; each animal assigned to one of five size classes (0–5, > 5–10, > 10–15, > 15–20, and > 20–25 mm) based on shell height. While snails were removed weekly in the *Littoraria* removal treatments, changes in population structure in *Littoraria* control treatments likely reflect the natural recruitment and growth of *Littoraria* in this marsh system over the course of the experiment. *Littoraria* grazing effects on *Spartina* were determined by counting the number of leaves and measuring total leaf and radula scarring length on four randomly selected culms.

End of the growing season plant, snail, and insect data were analyzed using two-way analysis of variance (ANOVA) with snail and insect main effects and all interactions. Repeated measures ANOVAs were used to analyze changes in *Littoraria* density and *Prokelisia* total density between the June and September sampling dates. Throughout this experiment all main effects were considered fixed effects, data were transformed when necessary, and all analyses were preformed using SAS 9.0 (SAS Institute Inc, North Carolina).

Results

There were no *Prokelisia*, or *Prokelisia* by *Littoraria* affects on *Spartina* biomass, density, number of

TABLE 1. Summary ANOVA tables for (A) *Spartina alterniflora* performance and *Prokelisia marginata* density at the end of the growing season. (B) *Littoraria irrorata, P. marginata* density, and *S. alterniflora* percentage cover RMANOVA tables comparing data from June 18, 2004 and September 14, 2004.

A)

Variable	Source	F Statistic	p
Spartina biomass	Snail	$F_{1,28} = 7.0$	0.01
	Insect	$F_{1,28} = 0.4$	0.55
	Snail × insect	$F_{1,28} = 1.3$	0.26
Spartina density	Snail	$F_{1,28} = 561.1$	<0.01
	Insect	$F_{1,28} = 0.6$	0.46
	Snail × insect	$F_{1,28} = 0.4$	0.53
Spartina total leaf length	Snail	$F_{1,124} = 0.1$	0.75
	Insect	$F_{1,124} = 0.03$	0.55
	Snail × insect	$F_{1,124} = 0.4$	0.86
Spartina number of leaves	Snail	$F_{1,124} = 0.04$	0.83
	Insect	$F_{1,124} = 0.9$	0.36
	Snail × insect	$F_{1,124} = 0.03$	0.81
Littoraria damage	Snail	$F_{1,124} = 18.2$	<0.01
	Insect	$F_{1,124} = 2.5$	0.12
	Snail × insect	$F_{1,124} = 1.5$	0.33
Prokelisia density	Snail	$F_{1,28} = 9.4$	<0.01
	Insect	$F_{1,28} = 0.8$	0.39
	Snail × insect	$F_{1,28} = 2.5$	0.12

B)

Variable	Pillai's Trace	p
Littoraria (0–5 mm)	$F_{1,15} = 11.4$	<0.01
Littoraria (5–10 mm)	$F_{1,15} = 23.5$	<0.01
Littoraria (10–15 mm)	$F_{1,15} = 41.9$	<0.01
Littoraria (15–20 mm)	$F_{1,15} = 4.9$	0.04
Littoraria (20–25 mm)	$F_{1,15} = 18.6$	<0.01
Prokelisia density	$F_{1,28} = 61.6$	<0.01
Spartina percentage cover	$F_{1,28} = 129.9$	<0.01

leaves, total leaf length, percentage cover, or *Littoraria* damage in this study (Table 1). Removal of *Littoraria* from the marsh increased *Spartina* biomass and density by approximately 50% (Fig. 1). Grazing damage increased (Table 1) in association with *Littoraria* density and changes in population structure (Fig. 2). The increase in the relative density of *Littoraria* in the largest size class corresponds to increased grazing damage and reduction in *Spartina* biomass and density.

Prokelisia density increased over the course of the growing season (Table 1), though this increase did not reduce *Spartina*. Presence of *Littoraria* reduced *Prokelisia* density (Table 1) from 235 to 104 insects m^{-2} (Fig. 3), with *Prokelisia* typically on the abaxil leaf blade and *Littoraria* adaxilly located.

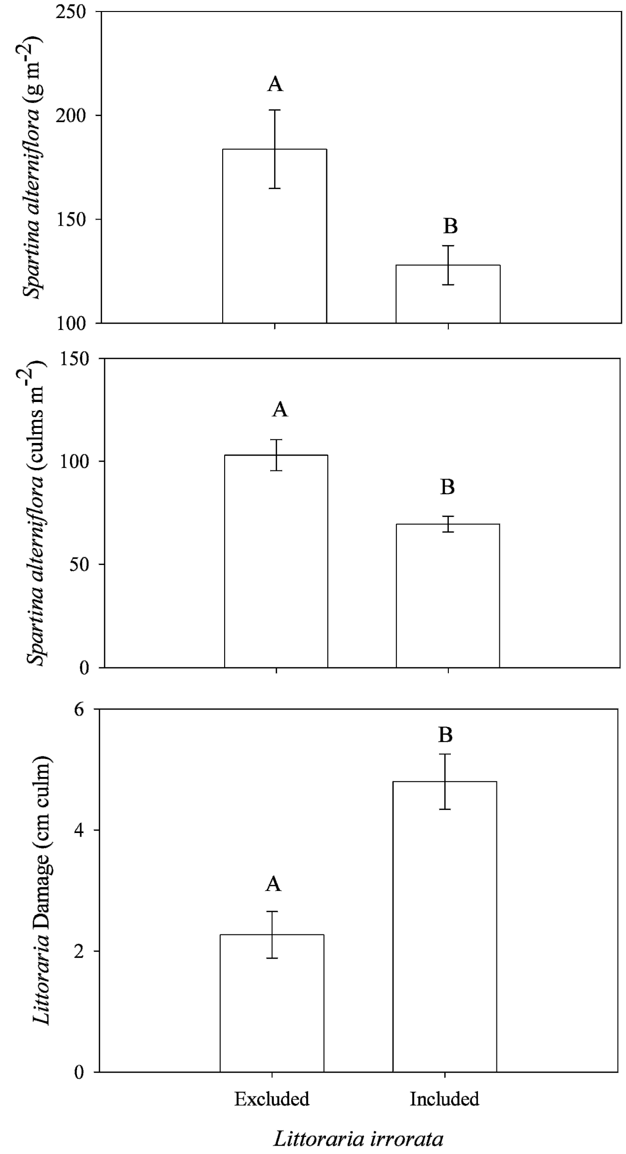

Fig. 1. *Spartina alterniflora* biomass and density and the effect of grazing by *Littoraria irrorata* at the end of the growing season. Significant differences ($p < 0.05$) between *L. irrorata* exclusion (absent) and inclusion (present) treatments are indicated by different letters. Values represent means (± SE).

Discussion

Manipulation of *Littoraria* (marsh periwinkle) and *Prokelisia* (*Spartina* planthoppers) revealed that the grazing activities of *Littoraria* reduced *Spartina* biomass and density by approximately 50% while the phloem feeding *Prokelisia* had no effect, rejecting our hypothesis that both common consumers will effect *Spartina*. Top-down regulation via *Littoraria* has been documented in several studies (Silliman and Zieman 2001; Silliman and Bertness 2002; Silliman and Bortolus 2003; Silliman and Newell 2003; Silliman et al. 2005), but this study is unique because we show the dominance of the grazer activities over a co-occurring phloem feeding insect. *Littoraria* do not regulate *Spartina* through direct consumption, rather they are indirectly effecting the plant through fungal farming (Silliman and Zieman 2001; Silliman and Bertness 2002; Silliman

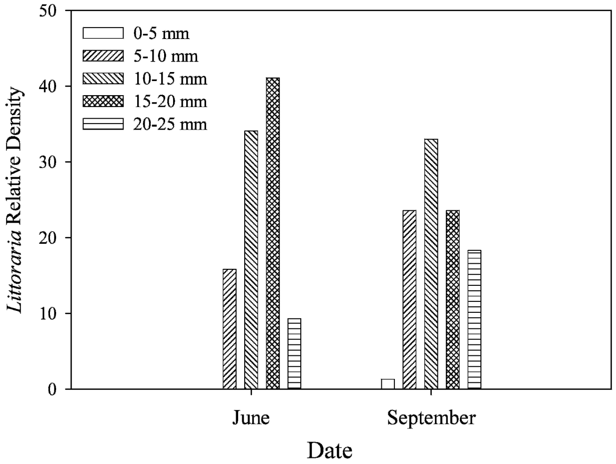

Fig. 2. In the experimental treatments with snails, *Littoraria irrorata* relative density in the largest size class (20–25 mm) doubled between the June and September 2004 sampling dates ($p < 0.05$). Values represent relative density per size class.

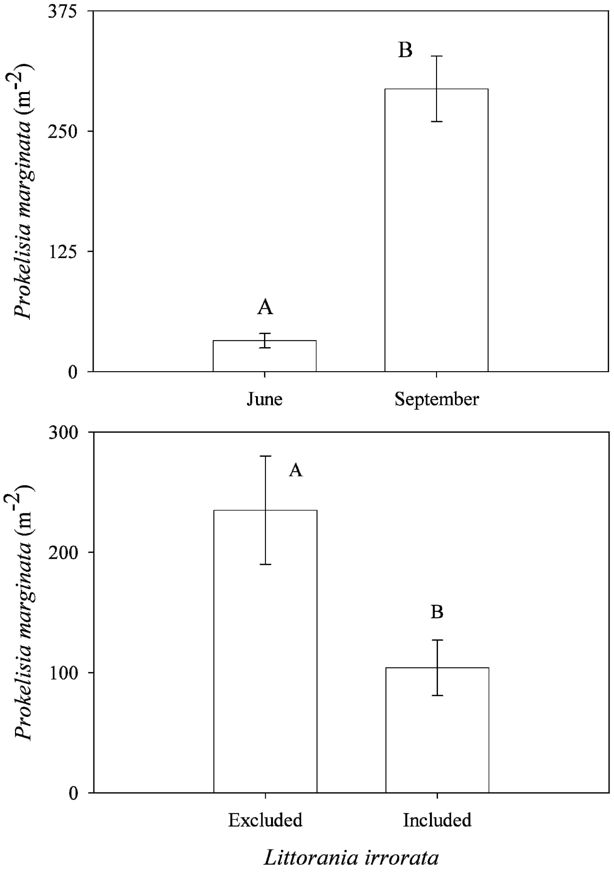

Fig. 3. *Prokelisia marginata* density increased between the June and September 2004 sampling dates. The presence of *Littoraria irrorata* reduced insect abundance by 50% ($p < 0.05$) at the end of the growing season (September). Values represent means (± SE).

and Bortolus 2003; Silliman and Newell 2003). Radular activity damages the plant's cuticle, promoting fungal growth on green *Spartina* leaves and subsequent leaf senescence (Silliman and Newell 2003). These results, combined with similar experimental evidence in Georgia, Louisiana, and Virginia marshes, demonstrate that *Littoraria* commonly suppresses Spartina production throughout the southeast and that this reduction happens across a wide range of grazer densities (Virginia: 50–150, South Carolina: 215, Georgia: 600–2,200, and Louisiana: 1,200 snails m^{-2}). In order for marsh ecologists to obtain a better understanding of site to site and region to region variation in potential production of *Spartina* dominated marshes, estuarine scientists should incorporate exclusion cages in their assessments of marsh grass growth (see Silliman and Bortolus [2003] for discussion).

Although *Prokelisia* has been shown to reduce *Spartina* biomass and number of leaves (Daehler and Strong 1997; Grevstad et al. 2003), we saw no increase in *Spartina* performance with the removal of these insects or any interaction between the two consumers. These insects require phloem production and translocation, so any insect activities that promote leaf or plant senescence would be disadvantageous. *Littoraria* radula scarring of *Spartina* leaves likely decreases leaf quality and the potential for *Prokelisia* to exert top-down control. Denno and Peterson (2002) showed that *Prokelisia* populations typically consist of flightless (brachypterous wing form) adults at low densities and a significant increase in the proportion of flight-capable (macropterous wing form) adults as population densities increase. In the development of *Prokelisia* as a biological control for *Spartina* invading the Pacific coast, Grevstad et al. (2003) found that *Spartina* from the Pacific coast was controlled by *Prokelisia* while plants from its native range (Atlantic coast) were not affected. Our field research conducted in South Carolina supports the notion that *Prokelisia* is not a strong top-down regulator of *Spartina* within its native species range.

Theoretical and experimental trophic cascade research has focused on interactions among producers (Pauly et al. 1998; Petchey et al. 1999; Duffy 2003), primary consumers or filter-feeders (Mulder et al. 1999; Norberg 2000; Cardinale et al. 2002), and predator diversity (Morin and Lawler 1995; Cardinale et al. 2003; Finke and Denno 2004; Johnson Randall and Foote 2005) effects on maintaining ecosystem function. *Spartina* salt marsh is potentially controlled by trophic cascades through predator-*Littoraria*-plant (Silliman and Zieman 2001; Silliman and Bertness 2002), predator-*Prokelisia*-plant (Denno et al. 2002; Finke and Denno 2004), or some combination. In this study, we experimentally show that top-down control of the *Spartina* salt marsh is through the *Littoraria* pathway and not the *Prokelisia* pathway. If predator diversity dampens enemy effects on herbivores and weakens trophic cascades, then reductions in higher trophic level diversity has the potential to alter ecosystem function (Finke and Denno 2004). Field studies are currently underway to determine if *Littoraria* predator diversity alters herbivore population dynamics in the field and if these changes affect primary productivity.

ACKNOWLEDGMENTS

We gratefully acknowledge Dr. and Mrs. Whitbeck for access to the marsh and S. Goldfinch, W. Pomeroy, and K. Pappas for assistance in the field and three anonymous reviewers for providing helpful comments on the manuscript. This research was supported by grants from South Carolina Department of Natural Resources, South Carolina Sea Grant Consortium, and The Citadel Foundation to D. J. Gustafson.

LITERATURE CITED

BINGHAM, F. O. 1972. Shell growth in the gastropod *Littorina irrorata*. *Nautilus* 85:136–141.

BRADLEY, P. M. AND J. T. MORRIS. 1990. Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora*. *Ecology* 71:282–287.

CARDINALE, B. J., C. T. HARVEY, K. GROSS, AND A. R. IVES. 2003. Biodiversity and biocontrol: Emergent impacts of a multiple-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters* 6:857–865.

CARDINALE, B. J., M. A. PALMER, AND S. J. COLLINS. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426–429.

COTTON, P. A., S. D. RUNDLE, AND K. E. SMITH. 2004. Trait compensation in marine gastropods: Shell shape, avoidance behavior, and susceptibility to predation. *Ecology* 85:1581–1584.

DAEHLER, C. C. AND D. R. STRONG. 1997. Reduced herbivory resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivory-free growth. *Oecologia* 110:99–108.

DENNO, R. F., C. GRATTON, M. A. PETERSON, G. A. LANGELLOTTO, D. L. FINKE, AND A. F. HUBERTY. 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83:1443–1458.

DENNO, R. F. AND M. A. PETERSON. 2002. Caught between the devil and the deep blue sea, mobile planthoppers elude natural enemies and deteriorating host plants. *American Entomologist* 46: 95–109.

DUFFY, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* 6:680–687.

FINKE, D. L. AND R. F. DENNO. 2004. Predator diversity dampens trophic cascades. *Nature* 429:407–410.

FURBISH, C. E. AND M. ALBANO. 1994. Selective herbivory and plant community structure in a mid-Atlantic salt marsh. *Ecology* 75: 1015–1022.

GREVSTAD, F. S., D. R. STRONG, D. GARCIA-ROSSI, R. W. SWITZER, AND M. S. WECKER. 2003. Biological control of *Spartina alterniflora* in Willapa Bay, Washington using the planthopper *Prokelisia marginata*: Agent specificity and early results. *Biological Control* 27:32–42.

HAMILTON, P. V. 1978. Intertidal distribution and long-term movements of *Littorina irrorata* (Mollusca: Gastropoda). *Marine Biology* 46:49–58.

HECK, K. L., J. R. PENNOCK, J. F. VALENTINE, L. D. COEN, AND S. A. SKLENAR. 2000. Effects of nutrient enrichment and small predator density on seagrass ecosystems: An experimental assessment. *Limnology and Oceanography* 45:1041–1057.

HILLEBRAND, H. 2005. Light regime and consumer control of autotrophic biomass. *Journal of Ecology* 93:758–769.

HOWES, B. L., J. W. H. DACEY, AND D. D. GOEHRINGER. 1986. Factors controlling the growth form of *Spartina alterniflora*: Feedbacks between above-ground production, sediment oxidation, nitrogen and salinity. *Journal of Ecology* 74:881–898.

JOHNSON RANDALL, L. A. AND A. L. FOOTE. 2005. Effects of managed impoundments and herbivory on wetland plant production and stand structure. *Wetlands* 25:38–50.

LEONARD, G. H., J. M. LEVIN, P. R. SCHMIDT, AND M. D. BERTNESS. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79:1395–1411.

MENDELSSOHN, I. A. AND J. T. MORRIS. 2000. Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel, p. 59–80. *In* M. P. Weinstein and D. A. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Boston, Massachusetts.

MOON, D. C. AND P. STILING. 2002. The influence of species identity and herbivore feeding mode on top-down and bottom-up effects in a salt marsh system. *Oecologia* 133:243–253.

MORIN, P. J. AND S. P. LAWLER. 1995. Food web architecture and population dynamics: Theory and empirical evidence. *Annual Review of Ecology and Systematics* 26:505–529.

MULDER, C. P. H., J. KORICHEVA, K. HUSS-DANELL, P. HOGBERG, AND J. JOSHI. 1999. Insects affects relationships between plant species richness and ecosystem processes. *Ecology Letters* 2:237–246.

NGIA, J. T. AND R. L. JEFFERIES. 2004. Nutrient limitations of plant growth and forage quality in Arctic coastal marshes. *Journal of Ecology* 92:1001–1010.

NORBERG, J. 2000. Resource-niche complementarity and autotrophic compensation determines ecosystem level responses to increased cladoceran species richness. *Oecology* 122:264–272.

PAULY, D., V. CHRISTENSEN, J. DALSGAARD, R. FROESE, AND F. J. TORRE. 1998. Fishing down marine food webs. *Science* 279:860–863.

PENNINGS, S. C., T. H. CAREFOOT, E. L. SISKA, M. E. CHASE, AND T. A. PAGE. 1998. Feeding preferences of a generalist salt marsh crab: Relative importance of multiple plant traits. *Ecology* 79:1968–1979.

PETCHEY, O. L., P. T. MCPHERSON, T. M. CASEY, AND P. J. MORIN. 1999. Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72.

ROHDE, S., M. MOLIS, AND M. WAHL. 2004. Regulation of anti-herbivore defense by *Fucus vesiculosus* in response to various cues. *Journal of Ecology* 92:1011–1018.

SILLIMAN, B. R. AND M. D. BERTNESS. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences* 99:10500–10505.

SILLIMAN, B. R. AND A. BORTOLUS. 2003. Underestimation of *Spartina* production in western Atlantic salt marshes: Marsh invertebrates eat more than just detritus. *Oikos* 101:549–555.

SILLIMAN, B. R., C. A. LAYMAN, K. GEYER, AND J. C. ZIEMAN. 2004. Predation by the black-clawed mud crab, *Panopeus herbstii*, in mid-Atlantic salt marshes: Further evidence for top-down control of marsh grass production. *Estuaries* 27:188–196.

SILLIMAN, B. R. AND S. Y. NEWELL. 2003. Fungal farming in a snail. *Proceeding of the National Academy of Sciences* 100:15643–15648.

SILLIMAN, B. R., J. VAN DER KOPPEL, M. D. BERTNESS, L. E. STANTON, AND I. A. MENDELSSOHN. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310:1803–1806.

SILLIMAN, B. R. AND J. C. ZIEMAN. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia marsh. *Ecology* 82:2830–2843.

SMITH, T. J. AND W. E. ODUM. 1983. The effects of grazing by snow geese on coastal salt marshes. *Ecology* 62:98–106.

STANHOPE, H. S., W. C. BANTA, AND M. H. TEMKIN. 1982. Size-specific emergence of the marsh snail, *Littorina irrorata*: Effect of predation by blue crabs in a Virginia salt marsh. *Gulf Research Reports* 7:179–182.

Taylor, K. L. and J. B. Grace. 1995. The effects of vertebrate herbivory on plant community structure in the coastal marshes of the Pearl River, Louisiana, USA. *Wetlands* 15:68–73.

Tucker, A. D., N. N. Fitzsimmons, and J. W. Gibbons. 1995. Resource partitioning by the estuarine turtle, *Malaclemys terrapin*: Trophic, spatial and temporal foraging constraints. *Herpetologica* 51:167–181.

Valiela, I. and J. M. Teal. 1979. The nitrogen budget of a salt marsh ecosystem. *Nature* 280:652–656.

van der wal, R. and R. W. Brooker. 2004. Mosses mediate grazer impacts on grass abundance in Arctic ecosystems. *Functional Ecology* 18:77–86.

Vaughn, C. C. and F. M. Fisher. 1992. Dispersion of the salt-marsh periwinkle *Littoraria irrorata*: Effects of water level, size, and season. *Estuaries* 15:246–250.

Vaughn, C. C. and F. M. Fisher. 1988. Vertical migration as a refuge from predation in intertidal marsh snails: A field test. *Journal of Experimental Marine Biology and Ecology* 123:163–176.

Warren, J. H. 1985. Climbing as an avoidance behaviour in the salt marsh periwinkle, *Littorina irrorata* (Say). *Journal of Experimental Marine Biology and Ecology* 89:11–28.

Weinstein, M. P. and D. A. Kreeger. 2000. Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Boston, Massachusetts.

West, D. L. and A. H. Williams. 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology* 100:75–95.

Received, June 1, 2005
Revised, February 28, 2006
Accepted, March 20, 2006