Snail behavioral preference for flowering stems does not impact *Spartina alterniflora* reproduction

Robyn A. Zerebecki[1,3,*], A. Randall Hughes[2]

[1]Coastal and Marine Laboratory, Florida State University, St. Teresa, Florida 32358, USA
[2]Marine Science Center, Northeastern University, Nahant, Massachusetts 01908, USA

[3]*Present address:* Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

ABSTRACT: Consumers can be important in controlling the abundance and composition of plants in salt marsh communities. In particular, the marsh periwinkle *Littoraria irrorata* is a common inhabitant of lower latitudinal salt marshes that can cause significant losses of plant (*Spartina alterniflora*) biomass. Research to date has focused on *Littoraria* effects on *Spartina* vegetative biomass, and we have little understanding of whether or how this plant–consumer interaction influences *Spartina* reproductive success. Surveys of natural marshes across the NE Gulf of Mexico highlighted the importance of this knowledge gap, as we observed more *Littoraria* climbing on reproductive *Spartina* compared with vegetative stems. With a series of experiments, we showed that this preference for reproductive stems is based on plant morphology: reproductive stems are taller and more rigid than vegetative stems, and snails preferentially climb on plants with these characteristics. This plant host preference is likely due to refuge value based on stem structure, and not due to variation in food quality. Despite this preference, we found no evidence that this aggregation of snails negatively impacts *Spartina* short-term reproductive success in a field experiment. Instead, we observed a trend towards increased *Spartina* reproductive output in the presence of snails. Thus, *Spartina* may mitigate the negative impact of snail presence on vegetative biomass by increasing allocation to sexual reproduction. Our results highlight the importance of considering each stage of a plant's life history when evaluating the relative importance of plant–consumer interactions.

KEY WORDS: Herbivory · *Littoraria irrorata* · Plant–consumer interactions · Salt marsh · Seed predation · *Spartina alterniflora*

INTRODUCTION

Plant–consumer interactions are complex and can have wide-ranging impacts on community structure and dynamics (Lubchenco & Gaines 1981, Huntly 1991, Maron & Crone 2006, Hakes & Cronin 2012). In most cases, consumers are shown to have strong deleterious effects on plant growth, reproduction, and survival (Crawley 1989, Huntly 1991, Marquis 1992, Karban & Strauss 1993, Maron & Crone 2006, Brys et al. 2011). However, plants can employ a multitude of strategies to defend against and limit susceptibility to herbivores, including morphological defenses, chemical defenses, variation in nutritional content, and phenological escape (Lubchenco & Gaines 1981, Hay & Fenical 1988, Agrawal 2000, Lucas et al. 2000, Hanley et al. 2007). Alternatively, plants can employ a strategy of tolerance to herbivory (Stowe et al. 2000), at times even increasing productivity and re-growth in response to consumption (overcompensation; Vail 1992, Valentine et al. 1997, Strauss & Agrawal 1999, Agrawal 2000, Vergés et al. 2008, Poveda et al. 2012). These mechanisms, alone or in combination, help plant communities persist even in conditions of intense grazing pressure.

Most studies of plant–consumer interactions in marine systems have focused on vegetative tissues (see Heck & Valentine 2006), yet consumers can also have large impacts on plant reproduction. For instance, many vascular plants have differentiated reproductive structures, and herbivores may preferentially consume these specialized tissues (Vergés et al. 2007, Pansch et al. 2008). Herbivore consumption of inflorescences, seeds, or reproductive tissues can reduce plant reproductive success (Holbrook et al. 2000, Orth et al. 2002, Balestri & Cinelli 2003, Lavergne et al. 2005, Thornber et al. 2006, Vergés et al. 2007, Pansch et al. 2008, Planes et al. 2011). As with vegetative tissues, plants can employ a number of strategies to resist or tolerate these losses. For example, higher phenolic content and lower nutritional value have been found in both seagrass and kelp reproductive tissues compared with vegetative tissues, yet this defense does not always lead to reduced consumption (Vergés et al. 2007, Pansch et al. 2008). Plants can also withhold a large portion of their reproductive resources from initial flowers, hedging that the initial investment will be consumed, and then produce secondary inflorescences that have greater reproductive output once herbivory is lessened (Vail 1992, Agrawal 2000). Thus, the impact of consumers on both plants' reproductive output and vegetative biomass is dependent on a combination of consumer foraging preferences and the plants' ability to tolerate, defend, or overcompensate in response to this pressure.

As in other systems, consumers can control the distribution and abundance of ecologically and economically valuable plants in the salt marsh community (Denno et al. 2000, Silliman & Zieman 2001, Silliman et al. 2005, Pennings & Silliman 2005, Bertness & Silliman 2008, Hughes 2012, Kimbro 2012). Consumer intensity is generally stronger in lower latitude marshes (Pennings & Silliman 2005, Pennings et al. 2009), and the dominant marsh grass *Spartina alterniflora* (hereafter referred to as *Spartina*) defends against this consumer pressure with both constitutive (Salgado & Pennings 2005) and inducible (Denno et al. 2000, Long et al. 2011) defenses. Common *Spartina* consumers include a suite of insects such as planthoppers (Denno et al. 2000) and grasshoppers (Pennings & Silliman 2005), along with estuarine invertebrates including crabs (Holdredge et al. 2009) and snails (Silliman et al. 2005). We focus here on the marsh periwinkle *Littoraria irrorata* (hereafter referred to as *Littoraria*), a common inhabitant of marshes along the Gulf of Mexico. These snails remain on the ground during low tide but migrate up standing live and dead *Spartina* stems at high tide to escape both the physical stress and increased predation pressure associated with tidal inundation (Hovel et al. 2001, Lewis & Eby 2002). Traditionally considered solely a detritivore, *Littoraria* also consumes live *Spartina* tissue directly, and thereby promotes and consumes fungal growth on *Spartina* stems (Silliman & Newell 2003). *Littoraria* can cause significant losses of *Spartina* biomass (Silliman & Zieman 2001, Silliman et al. 2005, Gutafson et al. 2006, Kimbro 2012).

To date, studies have focused on the effects of *Littoraria* on *Spartina* vegetative tissues. Yet *Spartina* reproduces by both vegetative rhizome growth and fragmentation, and by flower/seed production on specialized reproductive stems (Daehler & Strong 1994, Proffitt & Young 1999, Proffitt et al. 2003, Proffitt et al. 2005), and thus our understanding of *Littoraria* effects ignores a critical component of the *Spartina* life history. Although conventional wisdom holds that vegetative reproduction dominates in *Spartina* stands, genetic and genotypic diversity can be quite high within its native range (Richards et al. 2004, R. Hughes unpubl. data). Thus, any effects of *Litoraria* on the timing or success of *Spartina* reproduction could have important ramifications for population dynamics. In addition, shifts in the relative success of vegetative vs. sexual reproduction in this species could have cascading effects to the broader salt marsh community by influencing clonal identity and diversity (Proffitt et al. 2005, Hughes et al. 2008, Wang et al. 2012).

In this study we investigated *Littoraria* preferences for vegetative and reproductive *Spartina* stems, and whether snail presence affects the reproductive success of *Spartina*. We used a field survey and a series of experiments to answer the following questions: (1) Does *Littoraria* prefer climbing on reproductive *Spartina* stems compared to vegetative stems? (2) What traits (e.g. plant height, rigidity or nutrient content) influence *Littoraria* climbing preferences? and (3) How does snail presence impact the success of *Spartina* reproduction? Because our previous research demonstrated that snails preferentially climb on a taller and more rigid neighboring plant species (*Juncus roemerianus*; Hughes 2012), we hypothesized that *Littoraria* would prefer to climb on *Spartina* reproductive stems, which are structurally similar to *Juncus*. Alternatively, snails may preferentially climb on reproductive stems to consume inflorescences and seeds (e.g. Vergés et al. 2007). Regardless of the precise mechanism, snail preferences for reproductive stems could adversely impact *Spartina*'s reproductive success and could exacerbate the effect of *Littoraria* on *Spartina* biomass.

MATERIALS AND METHODS

Study system

Salt marsh communities are a key feature of the low-energy intertidal sites along the Gulf of Mexico, and many are dominated by the marsh grass *Spartina alterniflora* within the low to mid intertidal zone (Stout 1984, McKee & Patrick 1988, Seliskar et al. 2002). *Spartina* is a foundation species that modifies the surrounding environment to reduce abiotic and biotic stresses, thereby providing habitat for a diverse and ecologically important community (Bruno 2000, Pennings & Bertness 2001, Proffitt et al. 2005). These communities provide many valuable services including storm buffering, erosion control, and nursery habitats for several marine species that make them valuable ecosystems (Barbier et al. 2011); yet there have been extensive die-offs in salt marsh communities in the southeastern United States in the past decade (Bourne 2000, Proffitt 2000, Edwards et al. 2005, Alber et al. 2008, Bertness & Silliman 2008). Therefore, determining the factors that influence salt marsh plant distribution and persistence are important to mitigate the loss of these systems.

Spartina flowering stem production in the northeast Gulf of Mexico occurs annually from July through November, although the specific timing can vary geographically (Fang et al. 2004a,b). Pollination is wind-driven (Davis et al. 2004) and *Spartina* is largely cross-pollinated (Daehler & Strong 1994, Fang et al. 2004b), with seeds produced in late fall. Seeds primarily germinate in the early spring (Biber & Caldwell 2008). Over the course of our research, we noticed that developing reproductive stems move through a number of transitional steps before producing fertile inflorescences, and each of these stages exhibits structural differences from *Spartina* vegetative stems (Fig. 1; R. Zerebecki pers. obs.): The first stage is a vegetative-like stem with a stagger leaf structure along the stem (unlike the normal morphology of vegetative shoots). This stage was followed by pre-flowering stems, characterized by the formation of a single leaf on the top of the stem. Flowering stems were denoted by the presence of inflorescences, and the final seeding stage was classified by the production of seeds on the inflorescence. We catalogued each of these different reproductive stem transitions in our field experiment in order to examine whether snail presence differentially impacted some stages. However, all of our mesocosm experiments were conducted with fully-developed flowering reproductive stems.
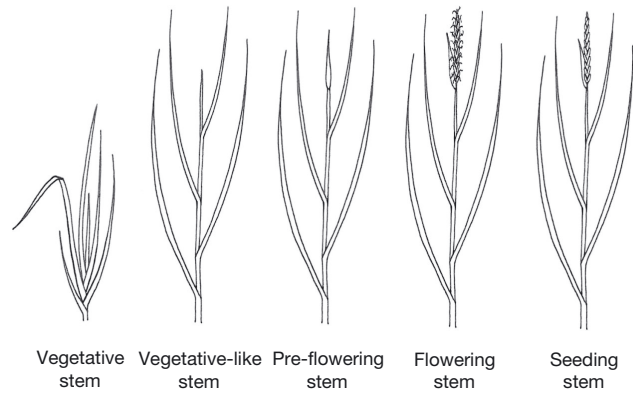

Fig. 1. *Spartina alterniflora.* Sequential stages of reproductive stem development. (Drawing: T. Rogers)

Field surveys

In October 2010 we conducted field surveys at 6 sites along the Florida Panhandle: Fort Walton, St. Andrews Bay, St. Joseph Bay, Turkey Point, Shell Point and Yates Creek (Fig. 2). At each site, we sampled 20 plots randomly located within two 50 × 20 m locations at each site (10 plots in each location, with the exception of St. Andrews which had only 5 plots at one location due to low abundance of *Spartina*; see Kimbro (2012) for additional description of these sites). We recorded the number of vegetative and reproductive *Spartina* stems and the height of 5 haphazardly chosen stems of each type within one 1/16 m² quadrat in each plot. Additionally, we recorded the number of *Littoraria* present on vegetative and reproductive *Spartina* stems within each quadrat to evaluate *Littoraria* climbing preferences. Tissue samples were taken from the
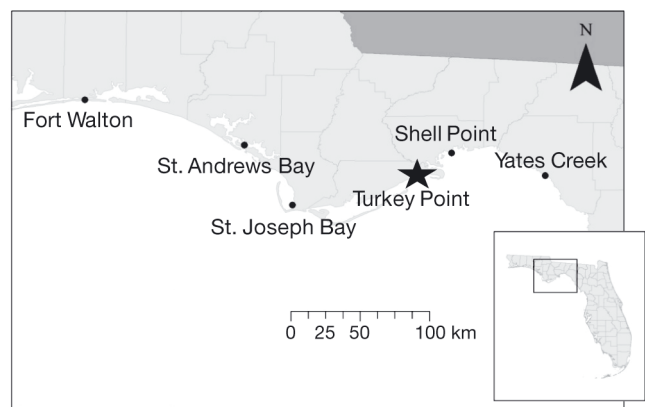

Fig. 2. Field survey sites across the Florida Panhandle. The field experiment site is denoted by a star

innermost leaf of one representative reproductive and vegetative stem within each plot (when present) and frozen for C:N analysis to evaluate potential differences in reproductive and vegetative tissue nutritional quality.

The frozen leaf tissue samples were analyzed for C:N by being dried for at least 24 h at 60°C and then ground into fine powder with a tissue grinder (SPEX Sample Prep 5100 Mixer mill). At the National High Magnetic Field Laboratory in Tallahassee, Florida, 5 to 10 mg of ground sample of known weight was analyzed on a mass spectrometer. Acetamilide (72.1% carbon and 10.4% nitrogen) was used as a standard for comparison with our samples.

Mesocosm experiment

We conducted a factorial mesocosm experiment to examine the independent and interactive effects of *Spartina* stem type (reproductive vs. vegetative), stem height, and tissue nutrient content on the climbing preference of *Littoraria*, as well as whether this preference changes in the presence of a snail predator (crown conch *Melongena corona*, hereafter referred to as *Melongena*).

Reproductive and vegetative stems were collected from St. Joseph Bay, Florida, in October 2010 in 2 height classes (N = 64): tall (mean ± SE reproductive stem height = 73.14 ± 1.1 cm; mean vegetative stem height = 58.44 ± 0.8 cm) or short (mean reproductive stem height = 45.64 ± 0.6 cm; mean vegetative stem height = 36.59 ± 0.8 cm). Plants were potted as a single shoot in 0.65 l flowerpots with a gravel-mulch mix and then housed in the Florida State University Coastal and Marine Laboratory (FSUCML) greenhouse. Half of each stem type × height combination was fertilized with Miracle Gro All Purpose liquid fertilizer (400 ml per flowerpot) 10 d prior to the beginning of the first trial and left to stand in a freshwater-fertilizer mix, whereas the other half only had freshwater. Fertilizer contained NPK at 24:8:16 with trace elements (B, Mo, Cu, Fe, Zn, and Mn) at a concentration of 2.81 g l^{-1}. Plants in the fertilized treatments had fertilizer added weekly.

The experiment was run in 32 outdoor mesocosms (diameter = 42 cm; volume = 75.7 l) during November 2010. All mesocosms received one reproductive and one vegetative *Spartina* stem surrounded by sieved sand collected in the field. Plants were enclosed in cages made with PVC frames and mesh netting to prevent snails from escaping. We tested all possible combinations of the following factors: reproductive stem height (short, tall); vegetative stem height (short, tall); reproductive stem nutrient status (fertilized, not fertilized); vegetative stem nutrient status (fertilized, not fertilized); predator (present, absent). Although reproductive stems were taller on average than vegetative stems, the mean ± SE difference in stem height between the pairs tested in the short-short or tall-tall combinations was 12.17 ± 0.93 cm, compared with 27.5 ± 2.34 cm difference between tall-short combinations. Predator treatments involved either the presence or absence of 2 *Melongena*. The 32 different treatment combinations were randomly assigned to mesocosms. Because of limits on the number of mesocosms available, we replicated through time (N = 4) by conducting four 5 d trials over a 4 wk period. Although there were 32 different treatment combinations, for all analysis we pooled tall–tall and short–short height treatment combinations into a single treatment level (same height; N = 8) and compared it to the other 2 height treatments: tall reproductive (N = 4) and tall vegetative height (N = 4), crossed with levels of both fertilizer and predator treatments. Prior to each trial, tissue samples were taken from each plant on the innermost leaf and were frozen for C:N analysis to confirm the effectiveness of fertilization treatments. Stable isotope analysis was run as previously described in the field survey section.

Each mesocosm received 20 snails on the first day of each trial. This density (222 snails m^{-2}) is higher than average densities (56 snails m^{-2}) but within the range of natural densities (0 to 464 snails m^{-2}) in the field (R. Hughes unpubl. data). Snails were allowed to acclimate for one day prior to the predator treatments receiving *Melongena*. We simulated a diurnal tidal regime throughout the experiment, with a high tide of 18 cm depth from 09:30 h to 15:30 h daily, and a low tide of 0 cm depth for the remaining hours, with 1 h for draining and flooding.

On Day 4 only, we quantified the number of *Littoraria* climbing on either reproductive or vegetative *Spartina* stems at low tide (30 min before the water began to rise) and at high tide (30 min before the water began to fall). Because of the short duration of the experiment (5 d), we did not quantify plant responses in this experiment.

Feeding assays

We quantified the palatability of reproductive and vegetative tissues using controlled feeding assays. Fully-developed reproductive and vegetative *Spar-*

tina stems were sampled from field-collected plants that were growing in the FSUCML greenhouse. Feeding assays were set up following the protocol established in Long et al. (2011). Tissue was first dried in kitty litter for 1 month, ground into fine powder using a Wiley Mill, and 0.4 g of this material was combined into 40 ml of 2% agar solution. Approximately 2 ml of this solution was placed in a Petri dish (height × diameter = 4 × 50 mm) to yield 15 replicates. After cooling, reproductive and vegetative dishes were paired within Tupperware containers (N = 15) and 4 *Littoraria* were placed in the middle of the 2 dishes. Assays were stopped when half of one dish was consumed or after 5 d, whichever came first. Consumption was quantified by placing the Petri dish on top of window screen and counting the number of empty window-screen squares. Feeding assays were run in June 2012.

Rigidity tests

To confirm the observed structural differences in vegetative and reproductive stems, we quantified plant rigidity of vegetative and reproductive *Spartina* stems in the greenhouse in February 2012 following the protocol established in Hughes (2012). We used 2 paper clips (1 large, 1 small) as a snail 'mimic': the mass of the clips (1.41 g) approximated the mean mass of an individual *Littoraria* (1.37 g). We attached the clips to the leaf of vegetative (n = 36) and reproductive stems (n = 36) at a height of 30 cm above the sediment surface. Snails regularly climbed to this height in our experimental mesocosms at high tide (R. Zerebecki pers. obs.). We then evaluated rigidity by measuring (1) the angle that each leaf bent from natural position when 3 mimic snails were attached, and (2) the number of snail mimics necessary to bend the leaf beyond 90 degrees. In addition, we quantified the relationship between rigidity and plant height in the field by measuring the height and the angle of leaf bend with 3 mimic snails on 61 vegetative *Spartina* stems in a natural marsh in January 2011.

Reproductive stems were both taller and more rigid than vegetative stems (see 'Results'). To differentiate between height and rigidity as factors in snail climbing preferences, we conducted rigidity-height choice experiments in the greenhouse at FSUCML. We used plastic flexible straws as mimic *Spartina* stems by securing straws in Dixie cups using plaster of Paris. Rigidity was controlled by varying the depth to which the flexible portion of the straw was stabilized

in plaster of Paris: the flexible portion was completely covered by plaster to create 'rigid' stems, whereas the flexible portion was above the plaster for 'flexible' stems. Rigidity tests, performed as described above, illustrated that there were significant differences in rigidity between the flexible and rigid mimics (angle of bend with 3 snail mimics: $t_8 = 2.666$, p = 0.03; number of snails to bend beyond 90 degrees: $t_8 = 9.3867$, p < 0.001). This difference in flexibility is much smaller than the difference observed between reproductive and vegetative stems in nature (see 'Results: Rigidity tests'). To manipulate height, we cut rigid or flexible stems to 25 cm ('tall') or 20 cm ('short'). This height difference (5 cm) was sufficient to elicit a snail behavioral response in a previous mesocosm experiment (Hughes 2012). Each experimental pot (1.70 l) contained 1 mimic stem of each combination of rigidity (rigid, flexible) and height (tall, short), for a total of 4 mimic stems per pot. The plaster portion of the stems was covered with sand. Trials were run in the greenhouse water tables in a depth of 13 cm of seawater and with crown conch *Melongena corona* predators freely roaming throughout the table. One *Littoraria* was placed in the center of the experimental container equidistant from each stem and allowed to roam for 30 min, after which its location was recorded to determine snail preference for different plant morphology. We tested 186 snails throughout March and April 2012.

Field experiment

From July 2011 to January 2012, we conducted a field caging experiment at Turkey Point, Florida, to examine the effects of snail presence on the number, height and seed production of reproductive *Spartina* stems. We installed 32 galvanized hardware cloth cages (30 cm diameter) in a natural marsh just prior to the *Spartina* reproductive season. Cages were paired with less than 1 m between cages within pairs, and greater than 1 m between adjacent pairs: cages within a pair were randomly assigned to snails present (10 snails per cage) or absent. This density (142 snails m^{-2}) is higher than average (56 snails m^{-2}) but within the range (0 to 464 snails m^{-2}) of natural densities in the field (R. Hughes unpubl. data). Snails were censused weekly and added or removed as needed to maintain treatments. Average initial *Spartina* density did not differ (1-way ANOVA, $F_{1,30}$ = 0.12, p = 0.73) between snail (20.0 ± 1.59 stems) and no snail (19.2 ± 1.72 stems) treatments. Each cage had at least 1 reproductive stem at the start of the

experiment (average = 2.44, range = 1–4 stems per cage). Number, height, and stage of reproductive stems (Fig. 1) were quantified weekly. Changes in the number of reproductive stems over the course of the experiment could occur either as previously vegetative stems transition to reproductive stems, or as reproductive stems die (which naturally occurs after seeding). We monitored distinct changes in the morphology of reproductive stems to determine if snail presence could impede this process by examining how many vegetative-like stems actually progressed to seeding. After each reproductive *Spartina* seeded, the seed head was removed and the number of seeds quantified in the lab. At the end of the experiment, we recorded the density and height of vegetative stems. Vegetative stems are produced continually throughout the year so any changes in vegetative stems during our experiment could indicate new stem growth, stem death, or a transition to reproductive stems. We did not quantify plant grazing scars as they were not observed frequently enough to be an informative measure of snail effects.

Data analysis

Field survey

Field survey data were analyzed using paired *t*-tests to compare average height, number of snails climbing per live stem, and C:N ratios between reproductive and vegetative stems. We found that reproductive stems were taller than vegetative stems, so to account for the height difference on snail abundance, we used an ANCOVA to compare the number of snails climbing per live stem between reproductive and vegetative stems (stem type) with plant height as a covariate. All quadrats in the field survey that did not contain both reproductive and vegetative stems were excluded from analyses (N = 32 out of 115 plots). In addition, all plots that had missing C:N values for either reproductive or vegetative stems due to sample loss or not enough tissue (N = 30 out of 115) were excluded from C:N analysis. Analyses with data nested by site yielded similar results; we present the un-nested analyses here.

Mesocosm experiment

Snail climbing preference in the mesocosm experiment was analyzed by comparing the number of snails climbing on the reproductive stems at high and low tide. We used a 4-way ANOVA followed by Tukey's post-hoc tests with height, nutrient status, and predator treatment set as fixed effects and trial as a random effect. C:N analyses of tissue taken at the beginning of each trial revealed no difference between fertilized and unfertilized stems in Trial 1; this trial was then excluded from further analyses. Significant differences in C:N were found between fertilized and unfertilized treatments in both vegetative and reproductive stems for all other trials (1-tailed *t*-test, p < 0.03).

Feeding assays

In the analysis of laboratory feeding assays we used paired *t*-tests to compare the number of empty squares in each Petri dish to establish the consumption of reproductive versus vegetative *Spartina* by *Littoraria.*

Rigidity tests

Paired *t*-tests were also used to analyze the data from the rigidity experiment based on the angle of leaf bending with 3 snail mimics and the number of snail mimics to bend leaf beyond 90 degrees between reproductive and vegetative stems. Linear regression was used to determine the relationship between plant height and rigidity. Finally, the rigidity-height choice experiment used a 2 × 2 contingency analysis of the number of snails that chose each height–rigidity combination compared to an equal frequency or non-preference of each category.

Field experiment

Because we collected multiple, related response variables (number of reproductive stems, average height, total number of seeds produced, number of seeds per stem, number or height of stems at each stage, proportion of vegetative-like stems that proceeded to seeding) in the field experiment, we first conducted a multivariate analysis (MANOVA) on all responses. There was no significant snail effect in this overall analysis, so we did not run ANOVA on individual responses.

All analyses were conducted using R statistical software (version 2.14.1).

RESULTS

Field surveys

Reproductive stems (mean ± SE = 96.56 ± 3.18 cm) were significantly taller than vegetative stems (49.77 ± 1.85 cm; t_{82} =17.02, p < 0.001) in the natural marshes we surveyed. However, there was no difference in tissue C:N content between reproductive (29.54 ± 0.65) and vegetative (28.45 ± 0.82) *Spartina* stems (t_{84} = 1.132, p = 0.26).

In addition to the morphological differences between reproductive and vegetative stems, we found a greater proportion of *Littoraria* on reproductive *Spartina* stems (mean ± SE number of snails per live stem = 0.44 ± 0.11) than vegetative stems (0.16 ± 0.04) in field plots where reproductive stems were present (t_{82} = 3.29, p = 0.001). Even when we corrected for the taller height of reproductive stems, more snails were found on reproductive stems (mean ± SE number of snails per cm of live stem = 0.0046 ± 0.0010) compared with vegetative stems (0.0028 ± 0.00074) in field plots where reproductive stems were present (ANCOVA, stem type: $F_{1,162}$ = 6.10, p = 0.014; stem type × height interaction: $F_{1,162}$ = 0.006, p = 0.94).

Mesocosm experiment

Littoraria climbing behavior was not influenced by either fertilizer treatment (i.e. plant nutritional con-tent) or predator presence (4-way ANOVA, Predator: $F_{1,71}$ = 1.80, p = 0.18, Fertilizer: $F_{3,71}$ = 1.25, p = 0.30), or their interactions ($F \leq 0.97$, $p \geq 0.41$). In contrast, *Littoraria* did respond to plant height in our meso-cosm experiment ($F_{1,71}$ = 11.49, p < 0.001): more snails climbed on reproductive *Spartina* when it was taller than vegetative stems compared to when re-productive stems were the same height as or shorter than vegetative stems (Fig. 3a). This response was consistent across high (Fig. 3a) and low (Fig. 3b) tide.

Feeding assays

Littoraria did not exhibit a feeding preference for either reproductive or vegetative *Spartina* (t_{14} = 0.1257, p = 0.90). Both reproductive tissue (mean ± SE = 30.73 ± 15.84 squares of agar) and vegetative tissue (27.67 ± 16.22 squares of agar) were consumed in comparable amounts.

Rigidity test

Reproductive stems were not only taller on average than vegetative stems, but they were also more rigid when of the same approximate height. We found that reproductive stems bent to a lesser degree (mean ± SE = 56 ± 8.4°) compared with vegetative (126 ± 5.0°) stems when 3 snail mimics were attached to their leaves (t_{35} = −7.36, p < 0.001). Moreover, we observed
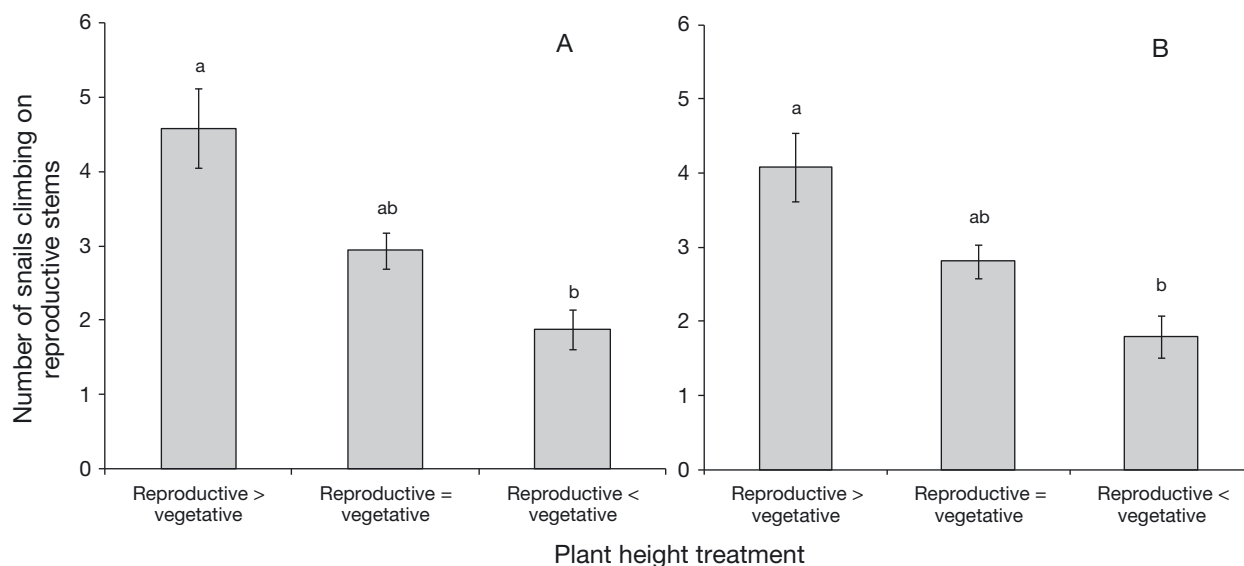

Fig. 3. Mean (±SE) number of *Littoraria irrorata* climbing on reproductive *Spartina alterniflora* in our mesocosm experiment when the reproductive stem was taller than the vegetative stem (Reproductive > Vegetative), both stems were the same height (Reproductive = Vegetative), or the vegetative stem was taller than the reproductive stem (Reproductive < Vegetative) at (A) high tide and (B) low tide. Different letters above the bars indicate statistical differences

that more snail mimics were required on reproductive stems (mean ± SE number of snails = 5.67 ± 0.67) compared with vegetative (mean number of snails = 1.83 ± 0.24) to bend stems to greater than 90° (t_{35} = −3.24, p = 0.002). In the field, we found a weak negative relationship between plant height and flexibility (Angle of Leaf Bend = 180 − 1.07(Height); linear regression, $F_{1,59}$ = 8.713, p = 0.005, R^2 = 0.11), indicating that taller stems are also more rigid.

In greenhouse trials that de-coupled stem height and stem rigidity, *Littoraria* responded to both stem rigidity and height (2 × 2 contingency analysis, χ^2 = 7.91, p = 0.048) largely driven by snail avoidance of short and flexible mimics (12 snails). We found a greater total number of snails chose rigid stems (57) compared with flexible stems (35). More snails also chose taller stems (52) over shorter stems (40).

Field experiment

Reproductive stem density in our field caging experiment peaked in the middle of November (Week 16; Fig. 4), with lower densities at the beginning and end of the experiment. Mean abundance per reproductive stem stage followed similar trends, as pre-flowering, flowering, and seeded stems all had unimodal abundance distributions, and their peaks were sequential in time (data not shown). Additionally, mean reproductive stem height decreased over the course of the experiment (Fig. 4).

Although reproductive stem abundance changed over time, these patterns were consistent regardless
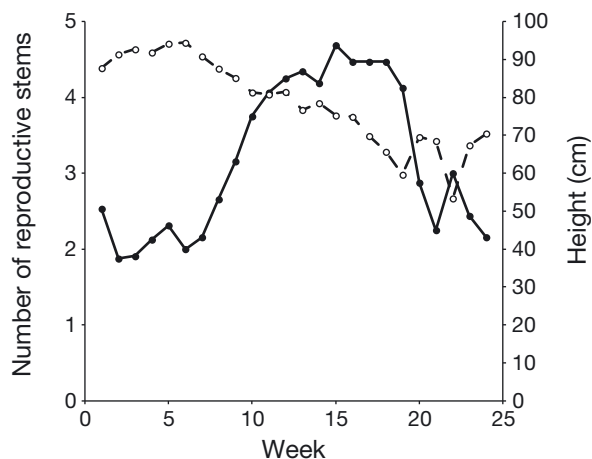

Fig. 4. Mean number (●) and height (○) of reproductive *Spartina alterniflora* stems during the 24 wk field experiment. Stem number and height did not differ depending on the presence or absence of snails

of *Littoraria* presence. In fact, *Littoraria* did not influence any metric of *Spartina* reproductive success that we quantified over the course of the reproductive season: number of reproductive stems, average reproductive stem height, total number of seeds produced, number of seeds per stem, proportion of vegetative-like stems that progressed to seeding, or the number or height of stems in different stages (MANOVA, $F_{1,28}$ = 1.2337, p = 0.35; Fig. 5). There were also no differences in vegetative stem abundance or height between snail and no snail cages at the beginning (1-way ANOVA, abundance: $F_{1,30}$ = 0.005, p = 0.95; average height: $F_{1,30}$ = 0.153, p = 0.70) or at the end of the experiment (1-way ANOVA, abundance: $F_{1,30}$ = 1.456, p = 0.24; average height: $F_{1,30}$ = 0.52, p = 0.48).

DISCUSSION

Our surveys and experiments indicated that *Littoraria* preferentially climb on reproductive *Spartina* stems compared to vegetative stems. In the field, reproductive stems were taller than vegetative stems on average, and a greater proportion of snails climbed on these taller reproductive stems. Our mesocosm experiment revealed that snail preference for reproductive stems is consistent regardless of predator presence or plant nutritional content, as long as reproductive stems are taller than vegetative stems (Fig. 3). Thus, snail preference for reproductive stems seems to be based solely on plant morphology: snails preferentially select taller and more rigid plants. However, this behavior appears to have no impact on *Spartina* short-term reproductive success. The presence of snails during the reproductive season does not have any negative consequences on reproductive stem height (a proxy for biomass; Hughes 2012), number of reproductive stems, or seed set in *Spartina* during a 6 month field experiment compared with plots in which snails were absent (Fig. 5).

Invertebrate grazers commonly select plant hosts that provide both nutritional value and refuge from abiotic and biotic stress (Duffy & Hay 1991, Sotka 2007, Lasley-Rasher et al. 2011). In this study, we found that the grazer *Littoraria* prefers reproductive *Spartina* stems, yet this choice does not appear to be based on feeding preference, as we observed no direct consumption of reproductive stems in our field experiment, nor a preference for reproductive stem tissue in our feeding assays. Instead, reproductive stems may provide greater refuge. *Littoraria* is
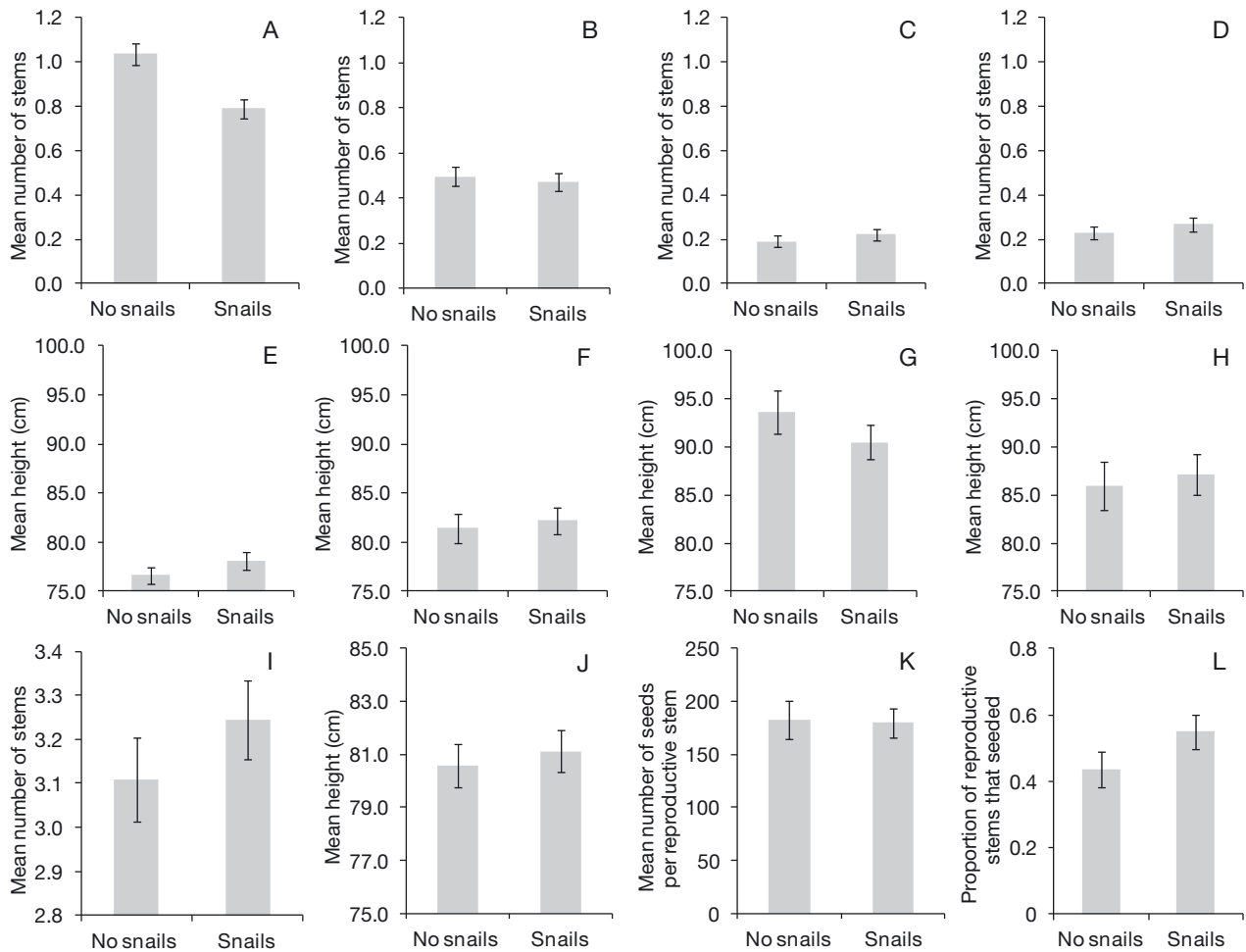
Fig. 5. *Spartina alterniflora.* Mean (±SE) weekly stem abundance (A = vegetative-like, B = pre-flowering, C = flowering, D = seeding, and I = total), height (E = vegetative-like, F = pre-flowering, G = flowering, H = seeding, and J = overall), number of seeds per reproductive stem (K) and the proportion of vegetative-like stems that progressed to seeding compared between snail and no snail treatments in the field experiment (L)

known to climb *Spartina* stems as the tide advances to escape both physical stresses (e.g. temperature, salinity and osmotic) and avoid predators (e.g. blue crab *Callinectes sapidus* and *Melongena*) that forage in the marsh during high tide (Vaughn & Fisher 1988, 1992, Hovel et al. 2001, Lewis & Eby 2002, Moody & Aronson 2007). In tethering experiments, *Littoraria* survival was much higher when above the mean high tide water level than at the base of *Spartina* (Hovel et al. 2001), so the taller and more rigid stature of reproductive *Spartina* may result in a survival advantage by increasing vertical migration potential (see e.g. Hughes 2012). Similar results of host preferences based on refuge value occur in a variety of systems; for example, amphipods tend to inhabit algae that provide superior refuge from predation (Duffy & Hay 1991, Sotka et al. 1999, Lasley-

Rasher et al. 2011) or physical stress (e.g. wave action; Sotka 2007) although the plant host is not necessarily a preferred food. Several examples of insect-host preference indicate that generalist herbivorous insects select host plants that provide the highest quality of enemy-free space—yet are of lower nutritional value (Singer & Stireman 2003, Singer et al. 2004). This illustrates an important distinction for consumers when choosing a plant host. Some herbivores are able to choose based solely on the highest food quality, whereas other consumers require plants for structure, thus balancing the tradeoff between food quality and refuge value determines plant preference. In our study system, the role of plant host as a refuge is likely driving the behavioral preference for *Littoraria* to climb on reproductive *Spartina*.

Our observations suggest that *Littoraria* are able to determine refuge value of stems prior to climbing *Spartina*. *Littoraria* are thought to have better vision than most other gastropods, which aids in their ability to locate plants, to escape tidal inundation and predation (Vaughn & Fisher 1992), and to know when the water subsides enough to climb down (Hovel et al. 2001). Thus, it is at least possible that they distinguish the height of plants visually. In addition, they may use stem rigidity as a proxy for height: we found a positive relationship between plant height and rigidity in *Spartina* and our tests of height and rigidity indicate that snail preferences were based on both factors (although the response to rigidity was stronger). The height differences tested in this experiment were slight (5 cm) compared to the differences between vegetative and reproductive stems (~45 cm in field survey), which may have contributed to the relatively weak response of snails to height. Regardless of the particular cues used to assess plant height, both taller and more rigid stems are likely to convey a survival advantage to *Littoraria* by providing escape from predation and physical stress from tidal inundation (Hughes 2012).

Even though *Littoraria* preferentially climb on *Spartina* reproductive stems, we found no effect of snail presence during the reproductive season on the reproductive success of *Spartina*. Previous studies have shown that most consumers reduce plant reproductive success through direct consumption of inflorescences, seeds (Holbrook et al. 2000, Orth et al. 2002, Lavergne et al. 2005, Vergés et al. 2007), and reproductive tissues (Thornber et al. 2006, Pansch et al. 2008), or through foliage consumption that leads plants to reduce the amount of biomass allocated to seed production (Rausher & Feeny 1980, Anderson & Frank 2003, Lavergne et al. 2005, Brys et al. 2011). We did not observe significant direct or indirect (e.g. grazing scars) signs of consumption of reproductive *Spartina* stems by *Littoraria*, perhaps explaining the lack of an effect of snail presence on reproductive success, even though the densities of snails used in our experiment were higher than average densities in the field. In fact, we rarely (if ever) observed *Littoraria* climbing to the very tops of stems where inflorescences and seeds occur with the exception of extreme high tides, and this observation was more common for shorter reproductive stems.

Further, we found no effect of snail presence on vegetative stem density or height, in contrast with previous experiments (Silliman & Zieman 2001, Silliman et al. 2005, Hughes 2012, Kimbro 2012). The apparent discrepancy between our results and our own past work (Hughes 2012) could have resulted despite similar mechanisms. Hughes (2012) found negative effects of snails on *Spartina*, but only in the absence of the structurally taller and more rigid neighboring species, *Juncus roemerianus*, which snails preferentially climbed on as a refuge. In our field experiment, the taller and more rigid reproductive stems were present in every cage; it is at least possible that snails have negative effects on vegetative *Spartina* in their absence. The height difference between reproductive and vegetative stems is similar to the difference between *Spartina* and *Juncus*, suggesting that reproductive stems can provide an associational plant refuge for vegetative stems by acting as a more attractive host due to their height and rigidity, altering the behavior of *Littoraria* and limiting the amount of time snails spend on and consume vegetative stems (Tahvanainen & Root 1972, Atsatt & O'Dowd 1976, Pfister & Hay 1988).

Alternatively, the absence of snail effects on reproductive or vegetative *Spartina* in our field experiment may have resulted from an influx of additional food resources in the form of seagrass detritus ('wrack') at our field site (R. Zerebecki pers. obs.). *Littoraria* consume a variety of organic material including detritus, standing dead plant material, live plants, and fungus on live plants (Graca et al. 2000, Silliman & Newell 2003, R. Hughes unpubl. data). This generalist feeding strategy may contribute to the weaker consumer impacts that we observed (Strong 1992). Alternatively, our results may be a function of tidal regime and its effects on snail behavior: Kimbro (2012) observed lower grazing and higher *Spartina* biomass in mixed tidal regimes, including our study site at Turkey Point. Had we conducted our field experiment at a nearby site within a diurnal tidal regime — one that requires snails to climb on *Spartina* for longer durations between low tides — we may have at least documented an effect of snail presence on vegetative stems. At present, it is unclear whether *Littoraria* may have an impact on *Spartina* reproduction at sites where snail grazing of *Spartina* vegetative stems is high, other than the obvious conclusion that there is a negative effect on reproduction in cases when all vegetation is removed (cf. Silliman et al. 2005).

There also may have been snail effects on *Spartina* reproductive success at levels we did not examine. For instance, we quantified seed production but did not examine the viability of these seeds or resulting seedlings, and previous studies have shown that herbivory can reduce seed viability (Marquis 1992, Mueller et al. 2005). Further, although we estab-

lished our consumer treatments at the onset of the flowering season, the plants at our experimental site may have already determined allocation to reproductive vs. vegetative stems when we started the experiment. If there is a lag time in consumer effects (e.g. Marquis 1992, Karban & Strauss 1993), or if the effects of herbivory on reproductive success require snails to be present for longer periods of time (e.g. Hughes 2012), then we may underestimate consumer effects on reproductive success in this system.

Although the majority of published studies have shown negative impacts of herbivores on plant reproductive success, there are examples of negligible or even positive impacts of consumers that demonstrate the complexity of this relationship (Anderson & Frank 2003, Ginane et al. 2003, Pansch et al. 2008). Herbivory can stimulate flower and seed production, as well as increase the number of reproductive tillers and overall reproductive potential in some plant species (Agrawal 2000, Anderson & Frank 2003). In our field experiment, we found a trend for higher reproductive output in the presence of snails compared with when snails were absent in 7 of the 12 variables measured (Fig. 5). This finding may indicate that *Spartina* shifted their allocation from vegetative (asexual) reproduction to sexual reproduction in the presence of snails. If so, snail presence could contribute to the high genetic diversity observed in *Spartina* populations (Richards et al. 2004) by promoting sexual reproduction.

Plants are able to resist herbivory by numerous mechanisms (Lucas et al. 2000, Anderson & Frank 2003, Hanley et al. 2007). For instance, plant structure (toughness and thickness) has been shown to defend reproductive tissue of specific kelps from consumption (Steinberg 1984, Pansch et al. 2008). As illustrated in our rigidity experiments, plant structure also differs between vegetative and reproductive *Spartina*: reproductive stems are more rigid than vegetative stems. This rigidity may translate into toughness, as previous work has shown *Spartina* leaf sheaths are tougher than the blades (Graca et al. 2000), and toughness reduces the palatability or digestibility of plant material (Pennings et al. 1998, Hanley et al. 2007) and therefore inhibits consumption. Reproductive *Spartina* stems also have less leaf biomass compared with vegetative stems, reducing the preferred resource for *Littoraria* to farm fungus (Silliman & Newell 2003). In addition, the timing of *Spartina* reproduction and its co-occurrence with decreased *Littoraria* foraging activity may reduce snail impacts on reproductive success: although *Littoraria* is present within *Spartina* patches all year

long, their activity and foraging decrease in the late fall and winter (Vaughn & Fisher 1992) and it is during this time that *Spartina* flowering peaks (Fig. 4). Thus, both the structure of reproductive stems and the timing of their production may limit snail consumption and thus *Littoraria*'s negative impacts on *Spartina*'s success.

This study highlights the context dependency of consumer effects (Harley 2003, Sanford et al. 2003, Pennings & Silliman 2005, Kimbro 2012) as well as the importance of consumer behavior (Bolnick et al. 2003). Snails can have strong, negative effects on marsh systems (Silliman et al. 2005, Silliman & Zieman 2001), yet recent studies have demonstrated that both the strength and direction of these interactions can vary depending on both the physical and biological context (Hughes 2012, Kimbro 2012). Although variable, these interactions are not necessarily unpredictable: the effects of marsh plant diversity on consumer control are consistent with studies from a broad array of systems showing that prey (in this case, plant) diversity generally dampens consumer control (Edwards et al. 2010). Identifying the factors that influence the strength of consumer control will not only increase our understanding of these interactions, but it will also enhance our ability to conserve these valuable ecosystems.

LITERATURE CITED

Agrawal AA (2000) Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. Trends Plant Sci 5:309–313

Alber M, Swenson EM, Adamowicz SC, Mendelssohn IA (2008) Salt marsh dieback: an overview of recent events in the US. Estuar Coast Shelf Sci 80:1–11

Anderson MT, Frank DA (2003) Defoliation effects on reproductive biomass: importance of scale and timing. J Range Manage 56:501–516

Atsatt PR, O'Dowd DJ (1976) Plant defense guilds. Science 193:24–29

Balestri E, Cinelli F (2003) Sexual reproductive success in *Posidonia oceanica.* Aquat Bot 75:21–32

Barbier E, Hacker S, Koch E, Stier A, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–193

Bertness MD, Silliman BR (2008) Consumer control of salt

marshes driven by human disturbance. Conserv Biol 22: 618–623

Biber PD, Caldwell JD (2008) Seed germination and seedling survival of *Spartina alterniflora* Loisel. Am J Agric Biol Sci 3:633–638

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and importance of individual specialization. Am Nat 161:1–28

Bourne J (2000) Louisiana's vanishing wetlands: going, going ... Science 289:1860–1863

Bruno J (2000) Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora.* Ecology 81:1179–1192

Brys R, Shefferson RP, Jacquemyn H (2011) Impact of herbivory on flowering behaviour and life history trade-offs in a polycarpic herb: a 10-year experiment. Oecologia 166: 293–303

Crawley MJ (1989) Insect herbivores and plant population dynamics. Annu Rev Entomol 34:531–564

Daehler CC, Strong DR (1994) Variable reproductive output among clones of *Spartina alterniflora* (Poaceae) invading San Francisco Bay, California: the influence of herbivory, pollination, and establishment site. Am J Bot 81:307–313

Davis HG, Taylor CM, Lambrinos JG, Strong DR (2004) Pollen limitation causes an allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). Proc Natl Acad Sci USA 101:13804–13807

Denno RF, Peterson MA, Gratton C, Cheng J, Langellotto GA, Huberty AF, Finke DL (2000) Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. Ecology 81: 1814–1827

Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72:1286–1298

Edwards KR, Travis SE, Proffitt CE (2005) Genetic effects of a large-scale *Spartina alterniflora* (Smooth Cordgrass) dieback and recovery in the Northern Gulf of Mexico. Estuaries 28:204–214

Edwards KF, Aquilino KM, Best RJ, Sellheim KL, Stachowicz JJ (2010) Prey diversity is associated with weaker consumer effects in a meta-analysis of benthic marine experiments. Ecol Lett 13:194–201

Fang X, Subudhi PK, Venuto BC, Harrison SA, Ryan AB (2004a) Influence of flowering phenology on seed production in smooth cordgrass (*Spartina alterniflora* Loisel.). Aquat Bot 80:139–151

Fang X, Subudhi PK, Venuto BC, Harrison SA (2004b) Mode of pollination, pollen germination, and seed set in smooth cordgrass (*Spartina alterniflora*, Poaceae). Int J Plant Sci 165:395–401

Ginane C, Petit M, D'Hour P (2003) How do grazing heifers choose between maturing reproductive and tall or short vegetative swards? Appl Anim Behav Sci 83:15–27

Graca MA, Newell SY, Kneib RT (2000) Grazing rates of organic matter and living fungal biomass of decaying *Spartina alterniflora* by three species of salt-marsh invertebrates. Mar Biol 136:281–289

Gutafson DJ, Kilheffer J, Silliman BR (2006) Relative effects of *Littoraria irrorata* and *Prokelisia marginata* on *Spartina alterniflora.* Estuaries 26:639–644

Hakes AS, Cronin JT (2012) Successional changes in plant resistance and tolerance to herbivory. Ecology 93: 1059–1070

Hanley ME, Lamont BB, Fairbanks MM, Rafferty CM (2007) Plant structural traits and their role in anti-herbivore defence. Perspect Plant Ecol 8:157–178

Harley CDG (2003) Species importance and context: spatial and temporal variation in species interactions. In: Kareiva P, Levin SA (eds) The importance of species: perspectives on expendability and triage. Princeton University Press, Princeton, p 44–68

Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. Annu Rev Ecol Syst 19:111–145

Heck KL Jr, Valentine JF (2006) Plant–herbivore interactions in seagrass meadows. J Exp Mar Biol Ecol 330:420–436

Holbrook SJ, Reed DC, Hansen K, Blanchette CA (2000) Spatial and temporal patterns of predation on seeds of the surfgrass *Phyllospadix torreyi.* Mar Biol 136: 739–747

Holdredge C, Bertness MD, Altieri AH (2009) Role of crab herbivory in die-off of New England salt marshes. Conserv Biol 23:672–679

Hovel KA, Bartholomew A, Lipcius RN (2001) Rapidly entrainable tidal vertical migrations in the salt marsh snail *Littoraria irrorata.* Estuaries 24:808–816

Hughes AR (2012) Neighboring plant species creates associational refuge for consumer and host. Ecology 93: 1411–1420

Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M (2008) Ecological consequences of genetic diversity. Ecol Lett 11:609–623

Huntly N (1991) Herbivores and the dynamics of communities and ecosystems. Annu Rev Ecol Syst 22:477–503

Karban R, Strauss SY (1993) Effects of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus.* Ecology 74:39–46

Kimbro DL (2012) Tidal regime dictates the cascading consumptive and nonconsumptive effects of multiple predators on a marsh plant. Ecology 93:334–344

Lasley-Rasher RS, Rasher DB, Marion ZH, Taylor RB, Hay ME (2011) Predation constrains host choice for a marine mesograzer. Mar Ecol Prog Ser 434:91–99

Lavergne S, Debussche M, Thompson JD (2005) Limitations on reproductive success in endemic *Aquilegia viscosa* (Ranunculaceae) relative to its widespread congener *Aquilegia vulgaris*: the interplay of herbivory and pollination. Oecologia 142:212–220

Lewis DB, Eby LA (2002) Spatially heterogeneous refugia and predation risk in intertidal salt marshes. Oikos 96: 119–129

Long JD, Mitchell JL, Sotka EE (2011) Local consumers induce resistance differentially between *Spartina* populations in the field. Ecology 92:180–188

Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. Annu Rev Ecol Syst 12:405–437

Lucas PW, Turner IM, Dominy NJ, Yamashita N (2000) Mechanical defences to herbivory. Ann Bot 86:913–920

Maron JL, Crone E (2006) Herbivory: effects on plant abundance, distribution and population growth. Proc R Soc B 273:2575–2584

Marquis RJ (1992) A bite is a bite is a bite? Constraints on response to folivory in *Piper arieianum* (Piperaceae). Ecology 73:143–152

McKee KL, Patrick WH (1988) The relationship of smooth cordgrass (*Spartina alterniflora*) to tidal datums: a review. Estuaries 11:143–151

Moody RM, Aronson RB (2007) Trophic heterogeneity in salt marshes of the northern Gulf of Mexico. Mar Ecol Prog Ser 331:49–65

Mueller RC, Wade BD, Gehring CA, Whitham TG (2005) Chronic herbivory negatively impacts cone and seed production, seed quality and seedling growth of susceptible pinyon pines. Oecologia 143:558–565

Orth RJ, Heck KL Jr, Tunbridge DJ (2002) Predation on seeds of the seagrass *Posidonia australis* in Western Australia. Mar Ecol Prog Ser 244:81–88

Pansch C, Gómez I, Rothäusler E, Veliz K, Thiel M (2008) Species-specific defense strategies of vegetative versus reproductive blades of the Pacific kelps *Lessonia nigrescens* and *Macrocystis integrifolia.* Mar Biol 155: 51–62

Pennings SC, Bertness MD (2001) Salt marsh communities. In: Bertness MD, Gaines SD, Hay M (eds) Marine community ecology. Sinauer Associates, Sunderland, MA p 289–316

Pennings SC, Silliman BR (2005) Linking biogeography and community ecology: latitudinal variation in plant–herbivore interaction strength. Ecology 86:2310–2319

Pennings SC, Carefoot TH, Siska EL, Chase ME, Page TA (1998) Feeding preferences of a generalist salt-marsh crab: relative importance of multiple plant traits. Ecology 79:1968–1979

Pennings SC, Ho CK, Salgado CS, Wieski K, Davé N, Kunza AE, Wason EL (2009) Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. Ecology 90: 183–195

Pfister CA, Hay ME (1988) Associational plant refuges: Convergent patterns in marine and terrestrial communities result from differing mechanisms. Oecologia 77:118–129

Planes S, Raventos N, Ferrari B, Alcoverro T (2011) Fish herbivory leads to shifts in seagrass *Posidonia oceanica* investments in sexual reproduction. Mar Ecol Prog Ser 431:205–213

Poveda K, Gómez Jiménez MI, Halitschke R, Kessler A (2012) Overcompensating plants: their expression of resistance traits and effects on herbivore preference and performance. Entomol Exp Appl 143:245–253

Proffitt CE (2000) Salt marsh die-back in coastal Louisiana. Coast Estuar Res Fed Newsl 26:7–8

Proffitt CE, Young J (1999) Salt marsh plant colonization, growth, and dominance on large mudflats created using dredged sediments. In: Rozas LP, Nyman JA, Proffitt CE, Rabalais NN, Reed DJ, Turner RE (eds) Recent research in coastal Louisiana: natural system function and response to human influence. Louisiana Sea Grant College Program, Baton Rouge, LA, p 218–228

Proffitt CE, Travis SE, Edwards KR (2003) Genotype and elevation influence *Spartina alterniflora* colonization and growth in a created salt marsh. Ecol Appl 13:180–192

Proffitt CE, Chiasson RL, Owens AB, Edwards KR, Travis SE (2005) *Spartina alterniflora* genotype influences facilitation and suppression of high marsh species colonizing an early successional salt marsh. J Ecol 93:404–416

Rausher MD, Feeny P (1980) Herbivory, plant density, and plant reproductive success: the effect of *Battus philenor* on *Aristolochia reticulata.* Ecology 61:905–917

Richards CL, Hamrick JL, Donovan LA, Mauricio R (2004) Unexpectedly high clonal diversity of two salt marsh perennials across a severe environmental gradient. Ecol Lett 7:1155–1162

Salgado CS, Pennings SC (2005) Latitudinal variation in palatability of salt-marsh plants: Are differences constitutive? Ecology 86:1571–1579

Sanford E, Roth MS, Johns GC, Wares JP, Somero GN (2003) Local selection and latitudinal variation in a marine predator-prey interaction. Science 300:1135–1137

Seliskar DM, Gallagher JL, Burdick DM, Mutz LA (2002) The regulation of ecosystem functions by ecotypic variation in the dominant plant: a *Spartina alterniflora* salt-marsh case study. J Ecol 90:1–11

Silliman BR, Newell SY (2003) Fungal farming in a snail. Proc Natl Acad Sci USA 100:15643–15648

Silliman BR, Zieman JC (2001) Top-down control of *Spartina alterniflora* production by perwinkle grazing in a Virginia Salt Marsh. Ecology 82:2830–2845

Silliman BR, Koppel JVD, Bertness MD, Stanton LE, Mendelssohn IA (2005) Drought, snails and large-scale die-off of southern US salt marshes. Science 310: 1803–1806

Singer MS, Stireman JOI (2003) Does anti-parasitoid defense explain host-plant selection by a polyphagous caterpillar? Oikos 100:554–562

Singer MS, Carrière Y, Theuring C, Hartmann T (2004) Disentangling food quality from resistance against parasitoids: diet choice by a generalist caterpillar. Am Nat 164:423–429

Sotka EE (2007) Restricted host use by the herbivorous amphipod *Peramphithoe tea* is motivated by food quality and abiotic refuge. Mar Biol 151:1831–1838

Sotka EE, Hay ME, Thomas JD (1999) Host-plant specialization by a non-herbivorous amphipod: advantages for the amphipod and costs for the seaweed. Oecologia 118: 471–482

Steinberg PD (1984) Algal chemical defense against herbivores: allocation of phenolic compounds in the kelp *Alaria marginata.* Science 223:405–407

Stout JP (1984) The ecology of irregularly flooded salt marshes of the northeastern Gulf of Mexico: a community profile. US Fish and Wildlife Service Biological Report 85(7.1). US Dept of the Interior, Washington, DC

Stowe KA, Marquis RJ, Hochwender CG, Simms EL (2000) The evolutionary ecology of tolerance to consumer damage. Annu Rev Ecol Syst 31:565–595

Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14: 179–185

Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747–754

Tahvanainen JO, Root RB (1972) The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). Oecologia 10:321–346

Thornber C, Stachowicz JJ, Gaines S (2006) Tissue type matters: selective herbivory on different life history stages of an isomorphic alga. Ecology 87:2255–2263

Vail SG (1992) Selection for overcompensatory plant responses to herbivory: a mechanism for the evolution of plant–herbivore mutualism. Am Nat 139:1–8

Valentine JF, Heck KL Jr, Busby J, Webb D (1997) Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. Oecologia 112:193–200

Vaughn CC, Fisher FM (1988) Vertical migration as a refuge from predation in intertidal marsh snails: a field test. J Exp Mar Biol Ecol 123:163–176

Vaughn CC, Fisher FM (1992) Dispersion of the salt-marsh periwinkle *Littoraria irrorata*: effects of water level, size, and season. Estuaries 15:246–250

Vergés A, Becerro MA, Alcoverro T, Romero J (2007) Variation in multiple traits of vegetative and reproductive seagrass tissues influences plant–herbivore interactions. Oecologia 151:675–686

Vergés A, Pérez M, Alcoverro T, Romero J (2008) Compensation and resistance to herbivory in seagrasses: induced responses to simulated consumption by fish. Oecologia 155:751–760

Wang XY, Shen DW, Jiao J, Xu NN and others (2012) Genotypic diversity enhances invasive ability of *Spartina alterniflora*. Mol Ecol 21:2542–2551