

# Competitive displacement of a detritivorous salt marsh snail

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## Abstract

Here we examine the role of competitive interactions in controlling distributions of the most abundant omnivore–detritivore snails in East Coast U.S. salt marshes (*Melampus bidentatus* and *Littoraria irrorata*). Both snails prefer to eat fungi growing on plant material, and the periwinkle *Littoraria*, a much larger snail, destroys marsh canopy when grazing fungal-infected plants, resulting in increased local desiccation stress. To test if *Littoraria* displaces *Melampus* from middle marsh habitats (i.e., short *Spartina alterniflora* zone), we manipulated *Littoraria* density and shading intensity in a two-year field experiment. Both removing snails and increasing shade dramatically increased *Melampus* densities. Addition of periwinkles to high marsh plant zones (*Juncus roemerianus*) where *Melampus* are naturally common induced significant *Melampus* migration. Growth experiments under controlled canopy conditions in the middle marsh showed that periwinkle presence suppresses *Melampus* growth. Experimental results suggest that *Littoraria* may limit the lower distribution of *Melampus* directly (through competition) and indirectly (through habitat modification). Lab experiments show that *Melampus* actively avoid mucus from *Littoraria* and that *Littoraria* may dislodge or consume *Melampus* egg masses. This work identifies several mechanisms of displacement and suggests that periwinkles play an important regulatory role in this detritivore assemblage.

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## 1. Introduction

Decades of field investigation have demonstrated that competition can strongly influence community structure (Connell, 1972; Schoener, 1983; Tilman, 1988) and ecosystem properties (e.g. invasibility, Stachowicz et al., 2002) by regulating abundance and diversity of producers (Chapman, 1945; Dayton, 1975; Tilman, 1977) and

consumers (Hairston, 1980; Pacala and Roughgarden, 1982). Despite recognition that detritus is an important and dynamic resource in aquatic (Teal, 1962; Winemiller, 1990) and terrestrial (Facelli and Pickett, 1991; Polis and Hurd, 1996) communities, the extent to which interspecific competition controls detritivore abundance and distribution is relatively unresolved.

To date, the majority of experimental studies on detritivore assemblages have emphasized the importance of predation and bottom-up controls (Batzer, 1998; Pringle et al., 1999; Rosemond et al., 2001; Levinton and Kelaher, 2004). However, numerous investigations have indicated potential for strong competition among detritivore grazers (Dobson and Hildrew, 1992; Constantini and Rossi, 1998; Halaj and Wise, 2002). Large-scale detrital removal and

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addition experiments have shown that resource availability limits detritivore growth and abundance in a variety of systems (Richardson, 1991; Wallace et al., 1997, 1999; Chen and Wise, 1999). Whether or not competition between detritivores commonly results in growth suppression, distribution shifts and ultimately competitive displacement in detritivore assemblages have not been clearly demonstrated with field experiments. Combined, results from these laboratory and field studies indicate competition and competitive displacement among detritivores may be much more common than currently appreciated, especially in systems that are detrital-based and support high densities of invertebrate grazers.

Salt marsh ecosystems are largely detritus-based, and the overwhelming majority of primary production is processed through detrital pathways (Teal, 1962; Valiela and Teal, 1979). Although microbial decomposers may process the majority of salt marsh detritus, omnivore–detritivores (e.g. snails and amphipods) and filter feeders may also derive significant nutrition from detrital resources (Kemp et al., 1990a). Despite experimental evidence supporting resource limitation between a detritivore–omnivore snail and a filter-feeding bivalve (Stiven and Kuenzler, 1979), few studies have addressed the possibility that competition determines salt marsh detritivore distribution and abundance.

Throughout the southeastern United States, the detritivore–omnivore gastropod *Littoraria irrorata* has the potential to dramatically alter salt marsh habitats by suppressing growth of the foundation marsh grass species, *Spartina alterniflora* (Silliman and Zieman, 2001; Silliman and Bertness, 2002; Silliman et al., 2005). The periwinkle *Littoraria* may also control detrital dynamics by facilitating growth of fungal plant decomposers through its grazing activities (Silliman and Newell, 2003). However, little is known about how periwinkle-induced habitat modifications may affect other salt marsh detritivores. *Littoraria* is in the unique position of being a detritivore–omnivore that creates detritus (by killing *Spartina* leaves without consuming them directly and farming fungus on live grass leaves, Silliman and Zieman, 2001; Silliman and Newell, 2003). In the short term, *Littoraria* may facilitate other detritivores by making a preferred food type (dead, fungus-covered leaves) available via grazing and leaf-shredding (i.e., initiating a detrital processing chain, Paradise and Dunson, 1997). In the long term, *Littoraria* may create a habitat other detritivores find inhospitable by (1) reducing *Spartina* stem density and thereby increasing desiccation stress or (2) decreasing overall detritus availability via heavy fungus consumption.

The detritivorous pulmonate snail, *Melampus bidentatus*, is among the most abundant and widespread macroinvertebrates in salt marshes along the eastern United

States (Price, 1980). The physiological and behavioral adaptations of *Melampus* to life in the marsh have been well established (Price, 1980; McMahon and Russell-Hunter, 1981). Stress tolerance has been considered a primary factor controlling the distribution of this lung-breathing snail (Teal, 1962; Russell-Hunter et al., 1972; Daiber, 1982; Bishop and Hackney, 1987; but see Joyce and Weisberg, 1986) with general consensus that tidal inundation excludes *Melampus* from low-middle marsh habitats. However, field observations suggest that *Littoraria* may affect *Melampus* abundance and distribution where they co-occur. Apparent negative correlations between *Littoraria* and *Melampus* densities in southeastern salt marshes (Kerwin, 1972; Parker, 1976; Subramanyam et al., 1976; Price, 1980; Fell et al., 1982; this study) and strong evidence for dietary overlap (i.e., algae, fungus and dead plant material, Alexander, 1979; Thompson, 1984; Kemp et al. 1990b; Sullivan and Moncreiff, 1990; Currin et al., 1995) suggest competition with *Littoraria* may influence the distribution of *Melampus*. Habitat modification by *Littoraria* also has the potential to effect movement and abundance of *Melampus*. Due to exposed respiratory surfaces in its pallial lungs, this snail is particularly vulnerable to desiccation (Price, 1980) and may be especially sensitive to alterations in vegetative cover. Despite these observations and evidence that interspecific competition determines the distribution of snail species in New England (Brenchley and Carlton, 1983) and northern California marshes (Byers, 2000), *Melampus/Littoraria* interactions have never been experimentally explored.

Here we examine *Littoraria*'s ability to exclude another detritivore–omnivore snail (*M. bidentatus* Say) from middle marsh habitats and evaluate possible mechanisms using a combination of manipulative field experiments, surveys and lab studies.

## 2. Methods

### 2.1. Study site and habitat use

Field research was conducted in marshes on Sapelo Island (31°23'N; 81°17'W) off the southern coast of Georgia, USA. Sapelo Island is part of the Georgia Coastal Ecosystems Long Term Ecological Research project. The principal study sites were Airport and Bourbon Field marshes located on the southwestern and northeastern sides of the island, respectively. These marshes are characterized by three zones, which correspond to tidal elevation. Low elevations along the creek bank are dominated by tall-form salt marsh cordgrass (*S. alterniflora*), mid-elevations by short-form cordgrass, and high elevations along the terrestrial border by black needlerush

(*Juncus roemerianus*). In general, the tall *Spartina* zone spans 3–5 m, the short *Spartina* zone ranges from 30 m to 200 m in width, and the *Juncus* zone is approximately 20–100 m wide. Natural snail distributions were determined both sites to establish habitat use by *Melampus* and *Littoraria*. Twenty-five 0.25 m<sup>2</sup> quadrats were haphazardly tossed within each of the three plant zones and abundances of *Melampus* and *Littoraria* were recorded.

## 2.2. *Littoraria* removal and shading experiment

To determine the relative effects of *Littoraria* presence and insolation stress on the abundance of *Melampus* in the short *Spartina* zone, we conducted a fully factorial *Littoraria* removal and shading experiment in two Sapelo marshes (Bourbon Field and Airport). Factors included *Littoraria* presence (3 levels; *Littoraria* removal cages, control cages with ambient snail densities, and uncaged controls) and shading (2 levels; shaded and unshaded); 6 replicates of every treatment combination were haphazardly established in each marsh. Subsequent loss of a caged plot left unevenly replicated treatments; replicates were randomly excluded from analysis such that  $N=5$  across all treatment combinations. Shaded plots were covered with two layers of black plastic mesh, reducing photosynthetically active radiation by ~55% (determined with a Li-Cor quantum radiation sensor), which mimicked the lower insolation in high plant density marshes (e.g. ungrazed *Spartina*). All cages enclosed 1 m<sup>2</sup> and consisted of 7 mm mesh hardware cloth, which allowed adult *Melampus* to migrate freely into and out of cages but prevented migration by all but the smallest *Littoraria*. Plots were established in late winter of 2000 and monitored bi-weekly to minimize migration of small *Littoraria* into removal plots. In August 2002, we determined the number of individuals within a centered 0.25 m<sup>2</sup> quadrat in each plot.

A 3-factor mixed-model analysis of variance (ANOVA) was conducted to test for effects of site (random factor), *Littoraria* treatment and shading (fixed factors) on *Melampus* densities using JMP software (Version 5, SAS Institute, Cary, NC). In order to meet the assumptions of ANOVA, *Melampus* densities were square root transformed prior to analysis. Planned paired comparisons (caged control vs. uncaged control and caged control vs. removal) were conducted using a protected Tukey–Kramer HSD (honestly significant difference) test.

## 2.3. *Littoraria* additions

We hypothesized that, if *Littoraria* were excluding *Melampus* from mid-marsh habitats through interspecific

interactions, adding periwinkles to high marsh would induce a migration response. To test this hypothesis 18, 1 m<sup>2</sup> plots were established in *Juncus* (where *Melampus* occurs in naturally high densities) at Bourbon Field in July 2001. Treatments were: *Littoraria* addition (cages where *Littoraria* densities were raised from approximately 10 snails m<sup>-2</sup> to 200 snails m<sup>-2</sup>), control (cages with ambient *Littoraria* densities), and uncaged controls ( $n=6$  each treatment). Cages were identical to those used in earlier experiments (see above). In July and August 2001 and August 2002, *Melampus* densities were determined using a centered 0.25 m<sup>2</sup> quadrat. A single factor ANOVA was conducted on final density data (August 2002) to determine the effect of *Littoraria* additions on *Melampus* densities. Graphical comparison between survey dates allowed us to qualitatively describe any temporal trends. Densities were square root transformed and planned comparisons (caged vs. uncaged control and caged control vs. removal) were conducted as described above.

## 2.4. Avoidance trials

To determine whether habitat use by snails was due in part to *Melampus* avoiding chemical cues from periwinkles, we conducted a movement choice experiment in the lab. In each trial, a single adult *Melampus* (9–11 mm shell length) was placed in the center of a Petri dish, one half of which had been covered in either *Melampus* or *Littoraria* mucus. We created this covering by dividing each dish and allowing snails to crawl around on one half. Gaps in the mucus covering were filled by gently pushing snails that were gripping the dish with their foot over the uncovered area. During trials, snails were scored for final choice based on which side (mucus or non-mucus) they first encountered the wall of the Petri dish. One hundred trials were conducted for each mucus type ( $n=100$ ), and the effect of mucus type on snail choice was evaluated using Pearson's chi-squared contingency test.

## 2.5. Growth experiments

To test the hypothesis that *Littoraria* reduce the growth of *Melampus*, we placed *Melampus* in enclosures with and without *Littoraria* in short *Spartina* (treatments= $+Littoraria$  at natural densities,  $-Littoraria$ ;  $n=6$  each treatment). Experimental enclosures were circular cages (area=0.11 m<sup>2</sup>, height=1 m) of 1.5 mm mesh hardware cloth secured with wooden stakes and sunk into the substratum. Into each enclosure we added 15 marked snails from each of two size classes (based on shell length, small=5.5–6.5 mm, medium=7.5–8.5 mm). Two size

classes were added because previous experiments indicated that small *Melampus* are highly vulnerable to predation by small infaunal crabs but also experience the greatest growth rates. Snails were collected 12 weeks later and their shell lengths were measured.

Snails were lost from cages via predation and escape, and as a result, the remaining number of snails differed randomly among cages and treatments. Two cages (one of each treatment) had no remaining snails and in some cages only one size class was represented in final collections. To compensate for different “size structure” (i.e. the distribution of snails among size classes) among cages, we used adjusted growth scores in our final analysis to compare growth between treatments (adapted from adjusted mortality scores in Remington and Schork, 1970). Growth scores were calculated as follows: 1) The mean growth of all snails in the small size class,  $g$ , was computed, as was the mean for all medium snails,  $h$ , 2) An expected mean growth was computed for each cage based on the number of small snails,  $m$ , and medium snails,  $n$ , using the equation  $r = (mg + nh) / (m + n)$ , 3) The scaling factor,  $x$ , that would make the expected mean growth,  $r$ , equal the mean growth of all the snails in the study,  $k$ , was determined for each cage, 4) An adjusted growth score was calculated by multiplying observed growth by the scaling factor,  $x$ . We compared adjusted growth scores between treatments using a single factor ANOVA.

We also raised *Melampus* on *Spartina* and *Juncus* leaves to provide a proxy for habitat-specific growth rates between the *Spartina* and *Juncus* zones, as these are the primary food sources for *Melampus* in each habitat. Five *Melampus* (shell lengths = 6.0–7.0 mm) were placed in each 60 mL jar with four standing dead leaves and ~10 mL seawater ( $n = 7$ , each species of plant). Jars were capped with 2 mm window screening and wetted daily with seawater. Leaves were changed once every two weeks, and after 3 months, snails were collected and their shell lengths measured. Due to uneven loss in jars, a mean change in shell length was determined for the snails from each jar and those data were analyzed for treatment effects with a single factor ANOVA (factor = growth substrate). This approach was chosen over a nested analysis with unbalanced samples in order to minimize the probability of Type I error associated with heterogeneous variances.

### 2.6. Egg mass trials

In order to elucidate possible impacts of *Littoraria* movement and grazing activity on *Melampus* egg masses, in the lab we attached pre-weighed egg masses to *Spartina* stems in containers with and without *Littoraria* ( $n = 10$  each treatment). Twelve hours later, all

stems were sprayed with seawater as a rough approximation of tidal wetting. After 24 h the location of each egg mass within the jar was noted and the egg masses were removed and weighed. The effects of *Littoraria* presence on the location and weight change of egg masses were analyzed using a Pearson's chi-squared contingency test and a Student's  $t$ -test, respectively.

## 3. Results

### 3.1. *Littoraria* manipulations and shading

In short *Spartina*, low *Melampus* densities are correlated with both high densities of potentially competitive periwinkles and low plant cover (Fig. 1). *Melampus* that use this habitat aggregate in shady, moist microhabitats (e.g., beneath dead leaves or wrack, S.C. Lee personal observation). Removing *Littoraria* from the short *Spartina* zone had a dramatic effect on *Melampus* densities, which was independent of site and shading treatment (Table 1). These effects were evident after only 6 months and became stronger the subsequent year. In our final survey, *Melampus* densities were more than 200% greater in plots without *Littoraria* than in plots with ambient *Littoraria* densities (Fig. 2). Comparison of caged (+*Littoraria*, -Predators) and

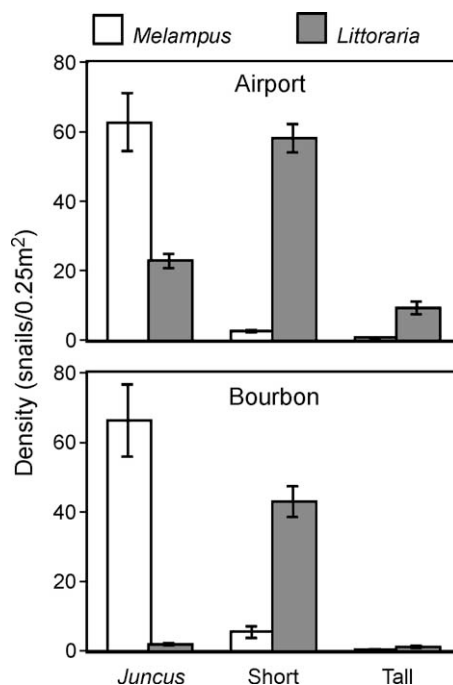


Fig. 1. Natural distribution of *Melampus* and *Littoraria* in two Georgia (USA) salt marshes. Density (means  $\pm$  1 SE) of each species in three vegetational zones (tall *Spartina*, short *Spartina*, and *Juncus*).

Table 1

Results of a mixed model three-factor analysis of variance testing the effects of site, *Littoraria* removal and shading on *Melampus* density in short *Spartina*

Source of variation	SS	F	df	P
Site	32.49	13.44	1	<0.001
Removal	145.3	57.24	2	<0.01
Removal vs. caged control				<0.05
Caged control vs. uncaged control				>0.05
Shading	159.4	324.47	1	<0.05
Site × removal	1.117	0.23	2	0.79
Site × shading	0.0665	0.03	1	0.87
Removal × shading	5.665	0.63	2	0.61
Site × removal × shading	9.009	1.86	2	0.17
Residual	116.0		48	

Paired comparisons based on Tukey's HSD test.

uncaged controls (+*Littoraria*, +Predators) revealed no significant difference in *Melampus* densities. *Melampus*, however, was significantly more abundant in removal cages than in control cages (Table 1). Thus there is no evidence for our treatment effects being due to incidental predator exclusion by our cages.

Shading increased *Melampus* densities by 46% relative to unshaded plots (Fig. 2). These shading effects did not vary significantly with *Littoraria* removal treatments or site (Table 1). It is interesting to note that under natural unshaded conditions, *Melampus* and *Lit-*

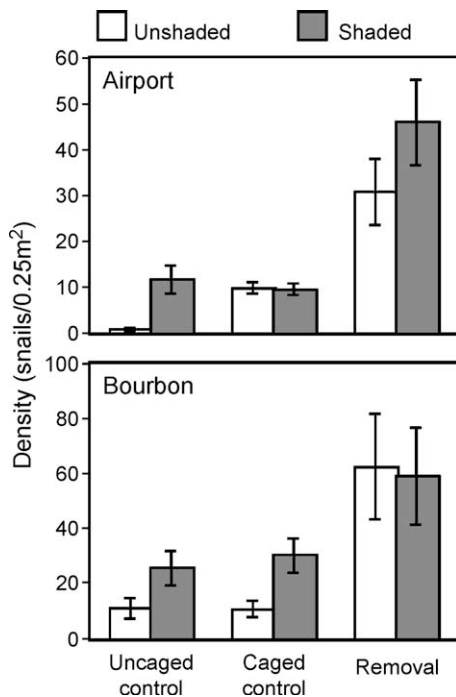


Fig. 2. The effects of removing *Littoraria* and decreasing solar irradiance on *Melampus* density (untransformed means ± 1 SE) at two sites.

*toraria* did not co-occur at significant densities, and often *Melampus* was entirely absent (Figs. 1 and 2). In our shaded plots the two species frequently co-occurred, although these shading effects did not vary by treatment or site (Table 1). In general we found that Bourbon Field had significantly higher densities of *Melampus* than did Airport irrespective of periwinkle removal or shading (Fig. 2). The removal effects measured in August 2002 represent a combination of *Littoraria* presence as well as the integrated effects of preventing grazing for 2 years.

Within three months of establishing the shading and *Littoraria* removal experiment in the short *Spartina* zone, we observed a dramatic increase in *Melampus* densities in removal treatments. In order to determine whether or not *Melampus* would remain in an area after *Littoraria* emigration, we added *Littoraria* to high marsh habitats where *Melampus* are naturally most abundant (Fig. 1). As predicted, addition of *Littoraria* significantly diminished the abundance of *Melampus* in *Juncus* (ANOVA,  $F_{2,15}=10.2$ ,  $P=0.0018$ ), ultimately reducing *Melampus* densities by 78% (Fig. 3). *Melampus* emigration out of plots containing periwinkles occurred quickly and was noticeable 3 weeks after additions. Again there was no significant difference between caged and uncaged controls indicating that possible caging effects did not affect the response of *Melampus* to *Littoraria* additions (Tukey–Kramer HSD,  $P>0.05$ ).

### 3.2. Avoidance trials

The choice made by *Melampus* presented with surfaces with and without mucus was significantly related

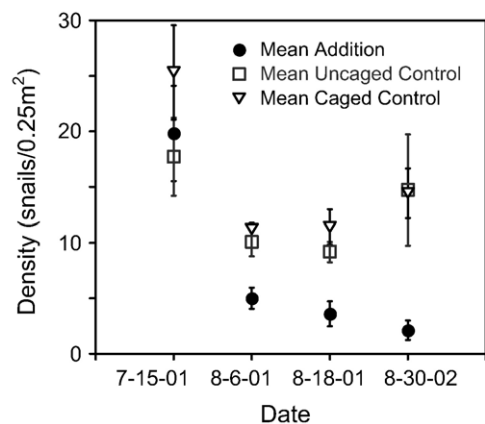


Fig. 3. Change in *Melampus* density in *Juncus* in response to *Littoraria* additions. Densities (untransformed means ± 1 SE) in addition, caged control and uncaged control treatments initially and two weeks, 1.5 months, and 1 year after establishing treatments.

to mucus type (i.e. mucus from a conspecific or *Littoraria*, Pearson's  $\chi^2_{1,1} = 39.3$ ,  $P < 0.0001$ ). Snails showed a weak affinity for mucus-covered surfaces when the mucus was derived from a conspecific (choosing in mucus 66% of the trials) but strongly avoided surfaces covered in *Littoraria* mucus (choosing no mucus 88% of the trials).

### 3.3. Growth experiments

If *Melampus* were being excluded from areas of the marsh via competition with *Littoraria*, then we would expect that co-occurring with *Littoraria* would negatively affect *Melampus*. In a case of exploitative competition for food, suppressed growth rates, indicating food limitation, are a likely result (Wiens, 1989). Periwinkle presence significantly suppressed *Melampus* growth in the field (ANOVA,  $F_{1,9} = 6.558$ ,  $P = 0.0306$ ). On average, medium *Melampus* grew 150% more in *Littoraria* removals than in inclusions (Fig. 4b). Small *Melampus* growth followed a similar and even stronger trend (500% greater growth in periwinkle removals relative to inclusions, Fig. 4a).

Field observations indicated that although *Melampus* was most abundant in *Juncus* (in the high marsh), it became locally more abundant in *Spartina* (in the middle marsh) when *Littoraria* was removed experimentally. This led us to hypothesize that *Melampus* would experience higher growth rates on *Spartina* than on *Juncus*. We found that growth substrate significantly influenced change in *Melampus* shell length (Fig. 4c). Experimentally reared *Melampus* grew 230% more on a diet of *Spartina* than on a *Juncus* diet ( $T_{12} = 11.2$ ,  $P < 0.0001$ ). Mean change in shell length on a *Spartina* diet was  $1.47 \pm 0.16$  mm versus  $0.45 \pm 0.18$  mm (mean  $\pm$  SD) on a *Juncus* diet. Also, the death rate per replicate jar was  $0.57 \pm 0.79$  on *Spartina* versus  $1.14 \pm 1.21$  on *Juncus* (mean  $\pm$  SD).

### 3.4. Egg mass trials

*Melampus* attaches its egg masses (flattened hemispheres 1–3 mm in diameter) on the bases of grass stems and the marsh surface (Russell-Hunter et al., 1972). Periwinkles migrate up stems twice daily with the tide, incessantly probing the stem surface with their feet and rasping with their radulae. We hypothesized that during grazing activity, periwinkles could damage or displace *Melampus* egg masses. *Littoraria* presence had no significant effect on egg mass weight ( $T_{1,18} = 0.921$ ,  $P = 0.3693$ ), however, one egg mass was entirely consumed by *Littoraria* during the 24 h trial, demonstrating that periwinkles are capable of eating *Melampus* egg masses. Although there was no effect on egg mass weight,

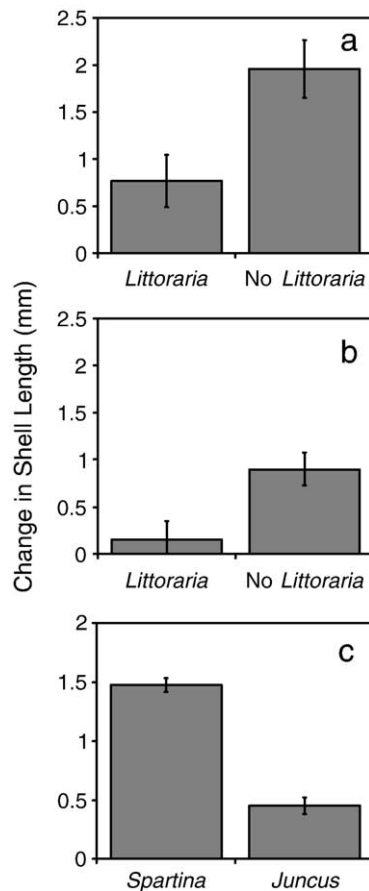


Fig. 4. The effects of *Littoraria* presence and growth substrate on change in shell length of *Melampus* (mean  $\pm$  1 SE). Growth of small (a) and medium (b) *Melampus* in short *Spartina* with and without *Littoraria* present. (c) Growth of *Melampus* raised on standing dead *Spartina* and *Juncus* leaves.

all of the egg masses in jars with *Littoraria* were dislodged from their stems (compared with only one dislodged in the without *Littoraria* treatment, perhaps the result of overzealous spraying). This indicates that the probability of egg mass dislodgement is likely greater in the presence of *Littoraria* (Pearson's  $\chi^2_{1,1} = 16.36$ ,  $P < 0.0001$ ).

## 4. Discussion

Our results demonstrate that interspecific interactions, not simply physiological tolerance, limit the lower distribution of one of the most abundant invertebrates in east coast marshes. Results of *Littoraria* removal and addition experiments reveal that periwinkles suppress *Melampus* abundance in short *Spartina* and effectively limit its lower distribution. In the marshes studied, we

found that displacement occurred between two important salt marsh omnivore–detritivores via direct and indirect mechanisms. Here we discuss possible mechanisms of competitive displacement and the likelihood that competition controls species distributions and abundances in other detritivore assemblages.

#### 4.1. Periwinkles control *Melampus* habitat use

Species density manipulations are a common and powerful way to demonstrate competition and spatial displacement (Hairston, 1989). Through species removal and transplant experiments, researchers have demonstrated the importance of interspecific interactions in determining distribution of plants and sessile invertebrates (Connell, 1972; Bertness, 1991a,b), however it has proven difficult to similarly investigate mechanisms of displacement of mobile organisms. One solution, employed by Brown and colleagues in their study of competition in a desert rodent community (reviewed in Heske et al., 1994), is to create semipermeable enclosures to maintain species removals. We used an analogous design in our addition and removal experiments that explicitly addressed potential problems with removing and adding mobile organisms (Underwood, 1986) by allowing migration of the response species (*Melampus*) but not the treatment species (*Littoraria*) and establishing cage controls.

The immigration of *Melampus* into plots without periwinkles and the corresponding emigration out of plots with periwinkles (Figs. 2 and 3) suggest that *Melampus* actively avoids *Littoraria*. This avoidance behavior could drive the inverse density relationship we observed between the two species of snails in the short *Spartina* and *Juncus* zones (Fig. 1). Where periwinkles were removed, *Melampus* was abundant in middle marsh habitats despite daily tidal inundation (Fig. 2), suggesting that the lower limit of its distribution is not solely defined by physical factors. Although this study addresses these effects on a small spatial scale, snail surveys spanning 3000 km along eastern coast of the U.S. show an inverse density relationship between these two species, possibly indicating that periwinkles may be displacing *Melampus* on a much larger scale (Kerwin, 1972; Parker, 1976; Subrahmanyam et al., 1976; Price, 1980; Fell et al., 1982; this study).

Our results indicate that there are at least two mechanisms by which periwinkles can control *Melampus* habitat use. The negative response of *Melampus* to *Littoraria* mucus as well as the rapid response to *Littoraria* manipulations in the field (Fig. 3) suggests that *Melampus* immigrates from habitats with periwinkles based on mucus and potentially other chemical cues. Similar

dispersal responses have been documented in mud snails in response to direct physical contact with a competing species of snail (Brenchley and Carlton, 1983) and reduced resource availability (Byers, 2000). Our results imply that *Melampus* has the chemosensors necessary to distinguish between mucus derived from periwinkles and conspecifics. Molluscs are particularly well known for their ability to distinguish predators using chemosensors (Kohn, 1961) and have been shown to respond to cues present in predator mucus (Dix and Hamilton, 1993). The ability of *Melampus* to distinguish and actively avoid periwinkle mucus cues may indicate *Littoraria*'s strong interaction strength.

Periwinkles may also displace *Melampus* by making the habitat unsuitable. By grazing and farming fungus on habitat-forming *Spartina* (an autogenic ecosystem engineer sensu Jones et al., 1997 or foundation species sensu Dayton, 1975), *Littoraria* significantly decreases *Spartina* stem density and increases the proportion of dead leaves (Silliman and Zieman, 2001; Silliman and Newell, 2003; Silliman et al., 2005). The effects of *Littoraria* grazing on *Spartina* are out of proportion with the amount of *Spartina* it consumes (Silliman and Newell, 2003). Our results suggest that *Littoraria* may act as an allogenic ecosystem engineer (sensu Jones et al., 1997), indirectly controlling *Melampus* grazing and distribution by altering the physical environment. Reduced *Spartina* stem density equates with dramatic reduction in shade canopy as well as a reduction of stems on which to escape from predators (e.g. by crawling out of reach of swimming predators on a high tide) or avoid submergence and could create a hostile environment for *Melampus*. Water loss occurs rapidly in *Melampus* (Price, 1980), and when left exposed without a shade canopy at our study sites, snails die within 24 h (Silliman, unpublished manuscript). Increasing desiccation at the marsh surface may also affect *Melampus* indirectly, if unshaded marsh surfaces have less epiphytic algae for *Melampus* to consume. We found that *Melampus* will co-occur with periwinkles (despite ostensibly present mucus cues) if the shade canopy is increased (shaded controls, Fig. 2). Further, our results likely underestimate the relative importance of shade canopy because the removal effects were due to the elimination of *Littoraria* and grazing pressure on the shade-providing *Spartina*. We conclude that, via mucus cues and alterations in the shade canopy, *Littoraria* effectively displaces another detritivore from short *Spartina*.

*Littoraria* presumably benefits or is unaffected by the exclusion of *Melampus* from short *Spartina*. The consequences for *Melampus* are clearer. Co-occurring with periwinkles in short *Spartina* reduces growth by two orders of magnitude (Fig. 4). Several factors suggest

exploitative competition for detritus and other food resources as a mechanism driving this phenomenon. Gut content analyses of *Littoraria* have shown that its diet, composed mainly of dead plant material, fungal hyphae, and microalgae (Alexander, 1979; Kemp et al., 1990a; Currin et al., 1995), is similar to that of *Melampus* (Thompson, 1984). Manipulations of detritus availability have demonstrated that there is intense intraspecific competition for food in *Littoraria* and resources may become limiting at naturally occurring densities (Stiven and Kuenzler, 1979). These three conditions (habitat overlap, similar resource use, and limited resources) suggest that exploitative competition may occur between *Melampus* and *Littoraria*. Moreover, *Littoraria* grazes almost 10 times more biomass per individual per day than *Melampus* does (Graca et al., 2000), suggesting that in a case of resource competition between individual snails, *Melampus* would be the weaker competitor.

Co-occurring with periwinkles may also increase the probability of egg mass damage. Our results demonstrate that *Littoraria* is capable of consuming *Melampus* egg masses. Furthermore, the dislodgement of egg masses in every replicate of the “with *Littoraria*” treatment is evidence that periwinkles do contact egg masses during migration up stems. Under natural conditions this contact probably would not result in dislodgement, but is nevertheless likely to impact the condition of egg masses as they are probed and scraped by grazing *Littoraria*. There may also be negative consequences for *Melampus* living in an alternate habitat (i.e. *Juncus*). Our growth experiments demonstrate that the quality of available detritus is greater in the middle marsh than in the high marsh (Fig. 4c). Differences in our results and those of Zimmer et al. (2004) may be due to the type of detritus used. Here we raised snails on standing dead leaf blades still attached to live plants (and thus available to snails associated with that type of vegetation) whereas other work used fallen dead leaves and stems exported to high marsh habitats in rafts of wrack (Zimmer et al., 2004). Recent work in Georgia marshes suggests that snails experience higher growth rates in lower marsh habitats, likely as a function of increased food quality and decreased desiccation stress (Silliman and Bertness, 2002). By excluding *Melampus* from middle marsh habitats, periwinkles effectively limit access to high growth substrates (standing dead short *Spartina*) and reduce growth. Based on the results of our shading and removal experiment, it appears that changes in habitat quality are pivotal to *Melampus* habitat choice. When there is an intact (or experimentally added) shade canopy it may be more advantageous to co-exist whereas when shade is absent, using an alternate habitat may be beneficial. However, as

*Littoraria* damages the canopy wherever it grazes (Silliman and Bertness, 2002), interactions between periwinkles and *Melampus* may result in displacement under all natural conditions.

#### 4.2. Trophic interactions among detritivores

Detritus and detritivores play a critical and often underappreciated role in the structure of animal and plant assemblages in many communities (Moore et al., 2004). Detritivores can convert dead plant material to detritivore biomass, creating a food resource for predators (Polis and Strong, 1996; Chen and Wise, 1999), and increasing rates of decomposition and nutrient cycling (Moore et al., 2004). Resource cycling is one of the most important ecosystem functions provided by detritivores, however the rate and type of material processed are species-specific (Pringle et al., 1999; Chong et al., 2000; Ruesink and Srivastava, 2001). Evidence from treehole and stream detritivore assemblages suggests that interspecific facilitation between detritivores can increase the rate of leaf litter breakdown and detritivore growth and abundance (Paradise and Dunson, 1997; Jonsson and Malmqvist, 2003) via detrital processing chains. Species loss from detritivore assemblages has been demonstrated to effect ecosystem characteristics and functioning (Pringle et al., 1999; Moore et al., 2004), although these effects may depend largely on species identity (Ruesink and Srivastava, 2001) and type of detritus (Chong et al., 2000). Detritivore diversity and abundance may indirectly affect diversity at other trophic levels (e.g. primary producers and consumers) by controlling nutrient cycling rates and prey availability. Analyses of detrital processing indicate that *Littoraria* and *Melampus* do not have functionally equivalent effects on detritus; digestion of detritus phenolics, ability to shred litter and promotion of microbial respiration differ between species (Zimmer et al., 2004). Thus by competitively displacing another detritivore from short *Spartina* habitats, *Littoraria* may also alter rates of detrital processing and trophic structure.

Competitive displacement may be uncommon among detritivores because of the transient and heterogeneous nature of many detrital resources (Facelli and Pickett, 1991). For example, in many aquatic systems detrital resource availability varies seasonally (Richardson, 1991) and currents or tidally driven flows can suspend, move, or even remove large quantities of detritus (Reidenbaugh and Banta, 1982). Additionally, competitive displacement between detritivores may be rare in dynamic habitats such as streambeds because of the overwhelming influence of physical disturbance (Resh et al., 1988). Infaunal detritivores may be unlikely to experience

competitive displacement by dominant species because three-dimensional habitats provide additional resource space (Peterson, 1979). Conversely, the importance of competition in spatially structuring detritivore assemblages may often be understudied relative to resource availability and predation (Hearnden and Pearson, 1991; Batzer, 1998; Rosemond et al., 2001). Laboratory and mesocosm experiments suggest that distribution of soil detritivores is determined by interspecific competition (Scheu et al., 1999; Korb and Linsenmair, 2001). There is growing evidence that interspecific competition for resources occurs in detritivore assemblages (Dobson and Hildrew, 1992; Constantini and Rossi, 1998) and can mediate trophic interactions throughout a community (Polis and Hurd, 1996; Halaj and Wise, 2002). Results presented here highlight the need to test experimentally the relative importance of competition, resource availability, and predation in structuring detritivore assemblages.

Detritivores may also be likely to compete via habitat modification. Detritus can both provide shelter and modify the physical environment (Facelli and Pickett, 1991; Moore et al., 2004). Consumption of detrital resources, then, may remove refugia and alter habitat condition. Our evidence suggests that habitat modification is an important mechanism by which *Littoraria* displaces *Melampus*. Although the work reported here gives a species-specific result, habitat changes that accompany *Littoraria* grazing are likely to affect other species and other interspecific interactions because *Spartina* is a critically important member of the community. In addition to generating fundamental marsh structure, *S. alterniflora* and other marsh grasses also substantially affect soil oxygen content (Bertness, 1991b), salinity (Bertness et al., 1992), swimming predator access (Vince et al., 1976), and overall species diversity (Rozas and Zimmerman, 2000) in salt marsh systems. By altering the state of the foundation species (sensu Dayton, 1975) and making habitats more physically severe, *Littoraria* may indirectly impact the distribution of other mobile detritivores (e.g. amphipods fiddler crabs and mud snails) and predators (e.g. mud crabs) that depend on *Spartina* for food and habitat.

The results presented here demonstrate displacement between two abundant salt marsh omnivore–detritivores and suggest resource competition and habitat modification as likely mechanisms. Changes in detritivore species richness or identity can impact the rate and type of detrital processing. Thus far, predation and resource limitation have dominated explanations of detritivore distributions. Considering competitive displacement within detritivore assemblages could reveal underappreciated controls on nutrient cycling and trophic structure in salt marshes and other detritus-based systems.

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