GASTROPOD ABUNDANCE AND BIOMASS RELATIONSHIPS WITH SALT MARSH VEGETATION WITHIN OCEAN-DOMINATED SOUTH CAROLINA, USA ESTUARIES

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ABSTRACT   Molluscs, both gastropods and bivalves, appear to disproportionately influence the dynamics of salt marsh habitats. Bivalves typically are facilitators positively affecting the growth and survival of marshes, but gastropods may have unanticipated top-down effects through direct consumption of the predominant marsh vegetation, *Spartina alterniflora*. Natural, elevational differences in *S. alterniflora* density and morphology also may exert an influence on the spatial distributions of marsh snails. We examined the abundance of both plants and snails across an elevation gradient to determine if similarities or differences existed in the observed distribution patterns. Plant, mainly *S. alterniflora*, and snail, *Littoraria irrorata* (Say) and *Melampus bidentatus* Say, densities were measured along tidal creek to forest transects within the intertidal marshes of three marine-dominated South Carolina inlets. Significant differences in *S. alterniflora* density among marsh zones were paralleled by similar *L. irrorata* density differences. A consistent, unimodal pattern with peak *L. irrorata* density in the "short," dense *S. alterniflora* mid marsh occurred within each inlet. In contrast, *M. bidentatus* was restricted almost entirely to the high marsh across all transects and inlets. Densities of *L. irrorata* and *S. alterniflora* were positively correlated in the low marsh consistent with the potential importance of culms as a food source and refuge from predators. *Littoraria irrorata* biomass was significantly different among zones in only one inlet and increased in a shoreward direction in two inlets. Although biomass patterns previously have not been reported for Southeastern US marshes, amounts were consistently greater than expected within the high-marsh zone. In SC, *L. irrorata* appears to be a conspicuous resident across the entire vegetated marsh and our results suggest previous studies focusing on the marsh near tidal creeks could underestimate appreciably the total population and overall significance of *L. irrorata* within coastal marshes.

KEY WORDS: *Littoraria irrorata* (Say), *Melampus bidentatus* Say, *Spartina alterniflora*, marsh zonation, snail biomass

INTRODUCTION

Molluscs, both gastropods and bivalves, appear to influence disproportionately the dynamics of salt marsh habitats. Bivalves often are characterized as facilitators positively affecting the growth and survival of marshes either directly (Bertness 1984) or indirectly (Meyer et al. 1997, Dame et al. 2001). Early evidence suggested resident gastropods had limited to no direct effects on the salt marsh and primarily were involved in the recycling of detritus (Odum & Smalley 1959, Teal 1962, Stiven & Kuenzler 1979). However, recent studies indicate one of the common snail species, *Littoraria irrorata* (Say), has unanticipated top-down effects on the predominant marsh vegetation, *Spartina alterniflora* (Silliman & Zieman 2001, Silliman & Bertness 2002, Silliman et al. 2005).

The extent of potential gastropod effects on salt marsh environments ultimately will depend on the natural abundance and distribution of the various floral and faunal species. In Southeastern US marshes conspicuous plant zonation (see Chapman 1974) results from the interplay between physical tolerance to tidal inundation at lower elevations and interspecific competition at higher elevations (Pennings et al. 2005). Macrofaunal zonation patterns within marshes are less transparent (see however Kneib 1984, Netto & Lana 1997, Richardson et al. 1998, Angradi et al. 2001) with no accepted paradigm to explain observed patterns (Kneib 1984, Levin & Talley 2000). Ecological explanations for gastropod zonation in salt marshes could parallel paradigms established in the rocky intertidal (e.g., Connell 1961a, 1961b, Paine 1969). A result would be an overlap in the peak distribution of a possible keystone species, *L. irrorata*, and the maximum production of its primary food and habitat resource, *S. alterniflora*. To

establish if an overlap exists, we documented the zonation patterns of *S. alterniflora* and the two predominant gastropod species, *L. irrorata* and *Melampus bidentatus* Say, within three South Carolina inlets.

Littoraria irrorata and *M. bidentatus* are both common in western Atlantic salt marshes, but *L. irrorata* typically is reported from monospecific stands of *S. alterniflora* (e.g., Smalley 1959, Crist & Banta 1983). *M. bidentatus* is found in greater densities within the more speciose high marsh (Kerwin 1972, Fell et al. 1991). However, density, size and biomass have not been shown to vary in a consistent manner across the marsh for either species. Factors that may affect snail abundance along a tidal elevation gradient also have been implicated in affecting gastropod size distributions. Vermeij (1972) proposed intertidal gastropods would exhibit one of two possible patterns attributed to either predation or desiccation effects: Type 1 or a shoreward increase in size because larger snails are better able to resist desiccation and Type 2 or a decrease in size over the same gradient, because larger individuals would be less susceptible to aquatic predators. Littorinids in the rocky intertidal primarily exhibit a Type 2 pattern suggesting a response to predation pressure (Vermeij 1972). In saltmarshes, blue crab (*Callinectes sapidus*) predation on *L. irrorata* also decreases with increasing distance away from tidal creeks (Schindler et al. 1994, Lewis & Eby 2002). Although results from Schindler et al. (1994) and Lewis & Eby (2002) suggest *L. irrorata* should exhibit a Type 2 pattern, snail sizes have been shown to exhibit both Type 1 and 2 patterns (Hamilton 1978, Crist & Banta 1983). To indirectly examine the possible effects of desiccation and predation on salt marsh snails we measured all snail shell lengths to test whether saltmarsh snails conformed to either of Vermeij's (1972) hypothesized size distribution patterns.

Differences in snail abundance, size and biomass along a tidal elevation gradient in three ocean-dominated Southeastern marshes

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were examined to test whether physical or biological factors contributed to observed zonation patterns. Specifically, we hypothesized that *L. irrorata* density, biomass and mean length would vary in concert with vegetation zones because of a suspected dependence on *S. alterniflora* for food (Silliman & Bertness 2002, Silliman & Newell 2003) and increased aquatic predation in the low marsh (West & Williams 1986, Schindler et al. 1994, Lewis & Eby 2002). We also expected that *M. bidentatus*, given its small size, thin shell and pulmonate physiology would be more abundant in the mixed vegetation of the high marsh where desiccation and not predation would contribute most to the zonation pattern. Specifically, we set out to: (1) examine if *L. irrorata* and *M. bidentatus* exhibited distinct zonation patterns within southeastern US marshes; (2) evaluate existing size-frequency distributions to gain insights into possible mechanisms influencing salt marsh snail distributions and (3) examine if any relationship existed between the density and biomass of *L. irrorata* and the density of *S. alterniflora* stems.

MATERIALS AND METHODS

Study Site

Salt marshes in three ocean-dominated inlets along the northern South Carolina coast were selected for study: Hog, Murrells and North Inlets. Hog Inlet forms the southern boundary for Waites Island (33°50′43″N, 78°35′12″W), a 0.5 × 4.0-km undeveloped barrier island. Study sites were in the extensive lagoonal marshes that exist along the backside of Waites Island. Murrells and North Inlets have been studied extensively (e.g., Vernberg et al. 1992) but differ in residential development of the local watershed. Murrells Inlet, ca. 62 km south of Hog Inlet, has considerable shoreline and upland development although Huntington Beach State Park protects much of the southern portion of the Inlet. A study site within the mainland marshes just north of the park boundary near public oyster reefs was selected (33°31′17″N, 79°03′53″W). North Inlet is 31 km south of Murrells Inlet, and it is the site of the Baruch Marine Institute. The inlet and marshes are protected as part of the National Estuarine Research Reserve (NERR) system but a few residences and a golf course are located on the northern edge. Mainland study sites within North Inlet marshes were at Oyster Landing (33°31′04″N, 79°11′32″W) and Clambank (33°20′09″N, 79°11′36″W), two extensively studied sites (e.g., Morris & Haskin 1990).

Sampling Design

To assess the spatial distribution of snails within the intertidal marshes without having to account for temporal differences, all samples were collected within a relatively short May to June period in 2003. The sampling period likely represents the time of greater snail density just after spring juvenile settlement and before increased summer mortality (KW, pers. obs.). Hog, North and Murrells Inlets were sampled three, two and one times respectively over the 2 mo. Snails were sampled along an approximate transect between tidal creek and forested upland uniquely established at each site on each date. A total of 5–20 samples from 0.25 m² quadrats placed along each transect within each of three vegetated zones was sampled. The low-marsh zone was identified by the presence of a monoculture of "tall" (>1 m) *S. alterniflora*. The short-form, <0.5-m tall, of *S. alterniflora* characterized the mid-
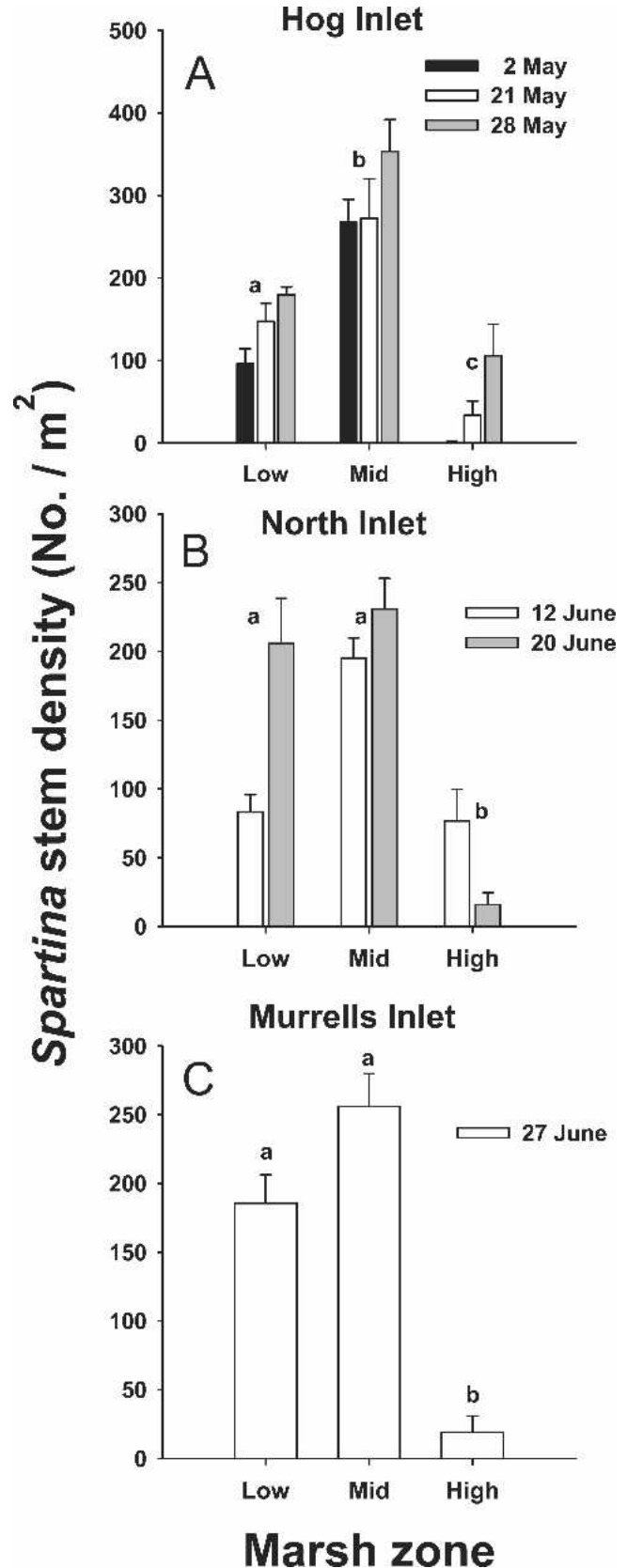

Figure 1. Mean (+1 SE) density of the total number of *Spartina alterniflora* stems in low-, mid and high-marsh zones of salt marshes in Hog Inlet (A), North Inlet (B) and Murrells Inlet (C). Different lowercase letters represent significant differences among zones.

marsh zone. Dense areas of *Spartina patens*, *Distichlis spicata* and *Juncus roemerianus* and the less common *Borrichia frutescens* and *S. alterniflora* identified the high-marsh zone at each site.

All snails within each quadrat were collected, returned to the laboratory and frozen at −20°C for later counting, measurement and biomass estimation (see later). On the first sampling date, May2, 2003, snails were counted and not collected; biomass was not estimated. The total number of *S. alterniflora* stems >10 cm tall was also counted from a haphazardly chosen corner (0.25 m × 0.25 m) of each quadrat.

Laboratory Analyses

Snail biomass was estimated by measuring individual shell lengths and applying a length-mass regression for each species. Shell length was measured from the spire apex to aperture tip to the nearest 0.1 mm with digital calipers. To establish species' length-mass regressions shell length and tissue mass (without shell) were measured for a subset of snails collected from Hog Inlet sites ($n = 184$ for *L. irrorata*, $n = 56$ for *M. bidentatus*). Tissue was dissected from individual shells, dried to constant mass at 60°C, and ashed at 500°C for >4 h in a muffle furnace to determine the ash-free dry mass (AFDM). A power curve was fit to the data for each species using nonlinear regressions in Sigma-Plot (Vers. 8.0, SPSS, Inc.).

Statistical Analyses

Statistical differences ($\alpha = 0.05$) among marsh zones and transects within inlets were assessed using analysis of variance (ANOVA) on $\log_{10}(x + 1)$-transformed values. Separate ANOVAs were conducted for each inlet using the General Linear Model procedure in SYSTAT (Vers. 10.0, SPSS, Inc.). Significant main effects were followed by Tukey HSD *post hoc* test to assess differences among levels (i.e., low-, mid and high-marsh zones). Any potential relationship between *L. irrorata* and *S. alterniflora* densities ($\log_{10}(x + 1)$-transformed) were examined with Pearson's Product-Moment correlation. The correlation between *L. irrorata* and *S. alterniflora* densities was calculated separately for each marsh zone using data from all inlets combined to assess overall relationships across inlets. *Melampus bidentatus* and *S. alterniflora* correlations were not considered because the distribution of *M. bidentatus* was restricted to the high marsh where little *S. alterniflora* was present.

The fit of *L. irrorata* to a Type 1 or Type 2 model (*sensu* Vermeij 1972) within each inlet was tested by graphically examining the mean length of *L. irrorata* with respect to marsh zone. Juvenile snails <5 mm were omitted from the analysis because individuals were typically found inside *S. alterniflora* leaf culms and likely were less susceptible to predation (Crist & Banta 1983).

RESULTS

A significant power relationship between shell length and tissue AFDM was identified from the Hog Inlet subsample of both *L. irrorata* (tissue mass $= 0.0080 \times \text{length}^{3.1157}$, $P < 0.0001$, $R^2 = 0.928$) and *M. bidentatus* (tissue mass $= 0.0077 \times \text{length}^{2.4351}$, $P < 0.0001$, $R^2 = 0.930$). Snail biomass differences among zones and transects were estimated using these equations.

Spartina alterniflora stem densities in each inlet marsh exhibited a similar pattern: mid > low > high marsh (Fig. 1). Significant stem density differences existed among zones in each inlet, but they differed only among transects in Hog Inlet (Table 1). Stem density was always significantly lowest in the high marsh (Fig. 1).

Littoraria irrorata density was significantly different among marsh zones in each inlet (Table 1), and showed a similar overall pattern as *Spartina* density in each respective inlet (Fig. 1 and Fig. 2). *Littoraria* density was significantly less in the high marshes of North and Murrells Inlets, and significantly greater in the mid marsh of Hog Inlet (Fig. 2). In contrast, biomass of *Littoraria* was only significantly different among zones in Murrells Inlet (Table 1), where it was significantly less in the low marsh (Fig. 2). Furthermore, biomass tended to increase from low to high marsh in North and Murrells Inlets (Fig. 2). No significant differences in density or biomass of *L. irrorata* were found among transects in any inlet (Table 1).

In each inlet the distribution of *M. bidentatus* primarily was restricted to the high marsh (Fig. 3) and resulted in significantly greater density and biomass in the high marsh zone (Table 1, Fig. 3). Densities were also significantly different among transects at Hog Inlet (Table 1).

Littoraria irrorata density was positively correlated with *S. alterniflora* stem density for low- ($P = 0.008$, $R = 0.423$) but not mid or high-marsh zones ($P > 0.05$).

The shell length of *L. irrorata* increased in a shoreward direction (Type 1 pattern) in both Murrells and North Inlets (Fig. 4). However, there was no obvious pattern in *L. irrorata* shell size at Hog Inlet (Fig. 4).

TABLE 1.

Results (*F*-values) from analysis of variance for comparisons among marsh zones and transects of total *Spartina alterniflora* density, and abundance and biomass of *Littoraria irrorata* and *Melampus bidentatus* in three South Carolina inlets. Asterisks represent level of significance: *$P \le 0.05$, **$P \le 0.01$, ***$P \le 0.001$. Data were $\log_{10}(x + 1)$ transformed.

Parameter	df	*Spartina* Density	*Littoraria* Density	*Littoraria* Biomass	*Melampus* Density	*Melampus* Biomass
Hog Inlet						
Zone	2, 116[1]	66.96***	27.79***	0.73	97.42***	320.93***
Transect	2, 116[1]	17.89***	1.69	0.08	10.09***	0.28
North Inlet						
Zone	2, 32	17.43***	4.46*	1.78	121.74***	457.20***
Transect	1, 32	0.683	1.64	0.02	3.85	0.03
Murrells Inlet						
Zone	2, 12	15.65***	14.23***	24.42***	49.35***	101.68***

[1] Transect df $= 1$ and Error df $= 63$ for biomass of *Littoraria* and *Melampus* at Hog Inlet only.
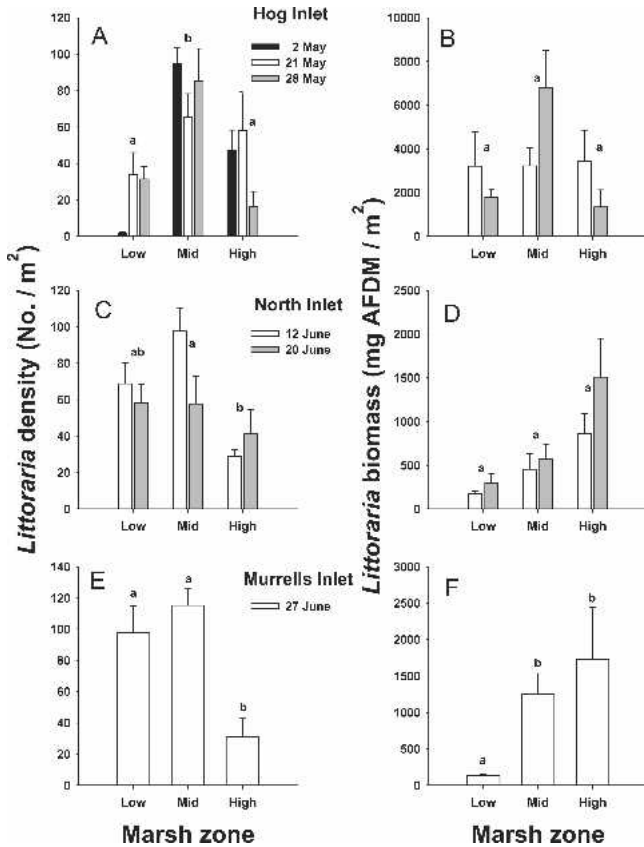
Figure 2. Mean (+1 SE) density of *Littoraria irrorata* in low-, mid and high-marsh zones in Hog Inlet (A), North Inlet (C) and Murrells Inlet (E). Mean (+1 SE) biomass of *Littoraria irrorata* in low-, mid and high-marsh zones of salt marshes in Hog Inlet (B), North Inlet (D) and Murrells Inlet (F). Different lower-case letters represent significant differences among zones.
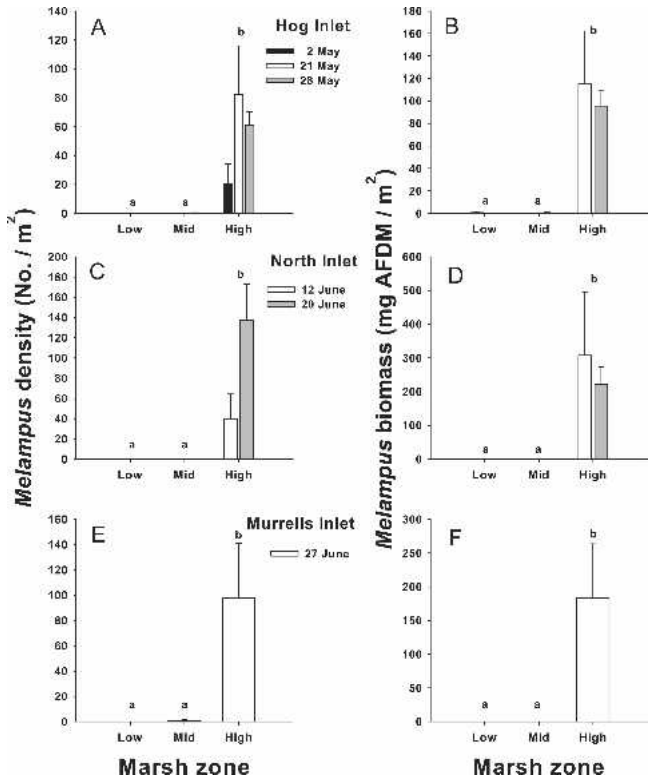

Figure 3. Mean (+1 SE) density of *Melampus bidentatus* in low-, mid and high-marsh zones of salt marshes in Hog Inlet (A), North Inlet (C) and Murrells Inlet (E). Mean (+1 SE) biomass of *Melampus bidentatus* in low-, mid and high-marsh zones of salt marshes in Hog Inlet (B), North Inlet (D), and Murrells Inlet (F). Different lower-case letters represent significant differences among zones.

DISCUSSION

Significant differences in *S. alterniflora* density among marsh zones were paralleled by similar *L. irrorata* density differences. The same zonation pattern (mid > low > high marsh) in *S. alterniflora* stem densities occurred in each inlet and is common for western Atlantic salt marshes (e.g., Valiela et al. 1978, West & Williams 1986, Gallagher et al. 1988). Gradients in *S. alterniflora* densities often are attributed to nutrient limitation (Valiela et al. 1978) or soil salinity (Pennings et al. 2005, Silliman et al. 2005), but the actual mechanisms that produce the observed plant density patterns in Southeastern marshes are not understood completely. Variation in *S. alterniflora* stem density typically is counterbalanced by differences in stem height and diameter (low > mid > high) that result in greater cordgrass productivity within the low marsh (Gallagher et al. 1980, Wiegert & Freeman 1990).

The significant differences in *L. irrorata* density among marsh zones in each inlet coincided with the variation in macrophyte density. A significant shoreward increase in *L. irrorata* density from "tall" to "short" *S. alterniflora* zones occurred in this study at Hog Inlet and is reported in previous studies (Crist & Banta 1983, West & Williams 1986, Schindler et al. 1994, Lewis & Eby 2002). Previous *Littoraria* studies typically have not sampled high-marsh areas within close proximity to the terrestrial-marsh boundary. We found that *L. irrorata* density declined from the "short" *S. alterni-*

flora mid marsh to the mixed-species vegetation of the high marsh. However, *L. irrorata* density was not significantly different between high- and low-marsh zones in either Hog or North Inlet. The greater than expected snail densities suggest that the high-marsh zone may be more productive than earlier studies suggest.

Unlike the patterns in snail density, significant variation in *L. irrorata* biomass across marsh zones only occurred in one inlet (Murrells). In two inlets (North and Murrells) a shoreward increase
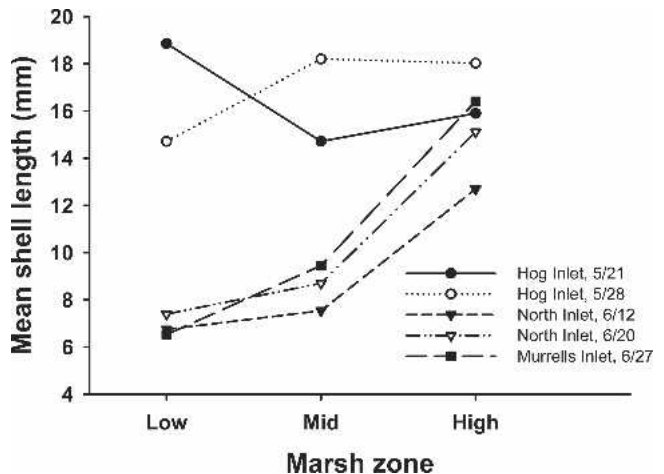

Figure 4. Mean individual length (mm) of *Littoraria irrorata* ≥5 mm in each zone and inlet.

TABLE 2.

Studies reporting mean densities (no./m^2) of *Littoraria irrorata* and *Melampus bidentatus* within relatively unimpacted intertidal marsh habitats.

Study	Geographic Location	Marsh Zone	*L. irrorata* Density	*M. bidentatus* Density
This study	Hog Inlet, SC	Low	18	0
		Mid	85	<1
		High	41	51
This study	North Inlet, SC	Low	63	0
		Mid	74	0
		High	36	97
This study	Murrells Inlet, SC	Low	98	0
		Mid	115	1
		High	31	98
Cammen et al. (1980)	Walden Creek, NC	Entire	33	—
Crist & Banta (1983)	Wallops Island, VA	Entire	48	—
Newell & Bärlocher (1993)	Sapelo Island, GA	Mid	460	—
Schindler et al. (1994)	Lighthouse marsh, GA	Low	22	—
		Mid/High	44	—
	Dean Creek, GA	Low	52	—
		Mid/High	66	—
	North End marsh, GA	Entire	52	—
Silliman & Bertness (2002)	Sapelo Island, GA	Low	5	—
		Mid	605	—
Silliman & Bortolus (2003)	Marshes from GA to VA	Low	0–5	—
		Mid	65–458	—
Silliman & Zieman (2001)	Hog Island, VA	Mid	48	—
Silliman et al. (2005)	Marshes from SC to LA	Healthy	1–558	—
		Die-off border[2]	15–2634	—
Stiven & Hunter (1976)	Russell's Creek, VA	Entire	108–135	—
	Ft. Macon, VA	Entire	70–92	—
Stiven & Kuenzler (1979)	Tar Landing marsh, NC	Entire	13	—
	Causeway marsh, NC	Entire	1	—
Warren (1985)	Wakulla Beach, FL	Entire	300	—
West & Williams (1986)	Dauphin Island, AL	Low	65	—
		Mid	145	—
Bishop & Hackney (1987)	St. Louis Bay, MS	Entire	—	6
Fell et al. (1982)	Branford Marsh, CT	Low	—	1–381
		Mid	—	556
		High	—	605–1222
Fell et al. (1991)	Barn Island, CT	Entire	—	392
Joyce & Weisberg (1986)	Canary Creek, DE	Entire	—	449–1234
Kerwin (1972)	Poropotank River, VA[1]	Entire	—	7

[1] Salt marsh sites only.
[2] Border between healthy marsh and *S. alterniflora* die-off zones.

in biomass contrasted with the midmarsh peak in density (Fig. 2). Zonation patterns for *L. irrorata* biomass previously have not been reported, but patterns in mean shell length have been examined (Hamilton 1978, Crist & Banta 1983, Lewis & Eby 2002). Shell length increased in a shoreward direction in one study (Hamilton 1978) and decreased in another (Crist & Banta 1983). Patterns in shell length also can vary within a study, increasing shoreward in a marsh grazed by horses but decreasing in an ungrazed marsh (Lewis & Eby 2002). In both Murrells and North Inlets shell length increased shoreward corresponding to the patterns in snail biomass, but Hog Inlet snail lengths exhibited no clear trend (Fig. 4). Existing data on patterns in *L. irrorata* shell lengths are inconsistent with Vermeij's (1972) gastropod size-gradient framework; snails fit Type I and II patterns depending on the study and site. The extensive geographical range, from Virginia's Eastern Shore (Crist & Banta 1983) to Florida's Gulf Coast (Hamilton 1978), and resultant biotic (e.g., predation pressure) and abiotic differences

(e.g., tidal range) likely complicate interpretation of any shell length patterns.

Recent focus on the importance of top-down regulation of *L. irrorata* densities and ultimately salt marsh dynamics in the Southeastern US (Silliman & Zieman 2001, Silliman & Bertness 2002, Silliman et al. 2005) suggest possible mechanisms underlying any across marsh difference in snail density and size. Several studies document the effects of blue crab (*Callinectes sapidus*) predation on *L. irrorata* and the roles of tidal inundation and *S. alterniflora* density on snail predation (Hamilton 1976, Warren 1985, West & Williams 1986, Vaughn & Fisher 1988, Schindler et al. 1994, Hovel et al. 2001, Lewis & Eby 2002). Blue crab predation on snails is more pronounced closer to tidal creeks because of the increased inundation frequency and greater coverage times permitting typically subtidal predators to spend more time foraging and feeding (West & Williams 1986, Schindler et al. 1994, Lewis & Eby 2002). Along with fewer and shorter inundations in the mid

marsh, greater *S. alterniflora* stem densities hinder blue crab foraging (West & Williams 1986, Schindler et al. 1994, Lewis & Eby 2002). *Spartina alterniflora* can also provide an aerial refuge from predators once snails climb the stems (Hamilton 1976, Warren 1985, Vaughn & Fisher 1988, Hovel et al. 2001). The positive correlation between *L. irrorata* and *S. alterniflora* densities in the low-marsh zone of all inlets supports the use of stems as an important vertical refuge from predators. Similarly, West & Williams (1986) document a strong positive relationship between snails and stem density.

In contrast to *L. irrorata*, the distribution of *M. bidentatus* was restricted to the high marsh across all transects and inlets. In more northern marshes *M. bidentatus* also occurs primarily in the high-marsh, but they can also extend into the midmarsh or short-*Spartina* zone (Kerwin 1972, Price 1980, Fell et al. 1982). Our density estimates for *M. bidentatus* were often lower than those in northern Western Atlantic marshes (Table 2). The lack of any appreciable *M. bidentatus* outside of the high marsh in our study may be attributed to differences in soil salinity that result from latitudinal variation in evapotranspiration (Pennings & Bertness 1999). Similar to *L. irrorata*, *M. bidentatus* is also vulnerable to marine predators (e.g., especially *Fundulus heteroclitus*) moving onto the marsh during high tides and having a greater effect in the more frequently inundated low- and mid-marsh zones (Vince et al. 1976, Joyce & Weisberg 1986). Whether physically limited or biologically regulated to living a mostly terrestrial existence in the upper intertidal region, pulmonate *M. bidentatus* must remain in close proximity to areas of the marsh inundated by spring tides to enable development of its planktonic larvae (Russell-Hunter et al. 1972).

Snail densities for *L. irrorata* within Hog, Murrells and North Inlets were very similar to means reported in most other studies, but they were much lower than in some marshes further south, especially at Sapelo Island, GA (Table 2). A preference by *L. irrorata* for regions of higher salinity (as a result of increased evapotranspiration) is a possible explanation, but our study inlets are ocean-dominated and some density estimates from marshes further south are similar to our own. Cross-site comparisons of population-limiting factors (e.g., predator populations, food resources, estuarine conditions experienced by veliger larvae) would be an essential step toward understanding these large differences in density among marshes.

Although variation in *L. irrorata* density has been the focus of several studies (Table 2), biomass of *L. irrorata* has seldom been estimated. In fact, none of the studies listed in Table 2, other than our own, examine variation in biomass within and among marshes. Given that most studies have found *L. irrorata* density peaking in the mid marsh, we expected biomass to show a similar pattern. Instead, the biomass of *L. irrorata* in the high marsh was unexpectedly high compared with the other two zones in North and Murrells Inlets (Fig. 2). The high-marsh prevalence of *L. irrorata* biomass is also not anticipated, given the snail's potentially obligatory association with *S. alterniflora* (e.g., Silliman & Newell 2003) and the plant's sparse occurrence in the high marsh where *S. alterniflora* is typically replaced by other halophytes (e.g., *J. roemerianus*, *S. patens*, *D. spicata*). *Littoraria irrorata* appears to be a conspicuous resident across the entire vegetated salt marsh in SC. Results from previous studies that typically focus only on the marsh near tidal creeks (Table 2) would appreciably underestimate the total population of *L. irrorata* and its overall significance within coastal marshes.

ACKNOWLEDGMENTS

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