

Predation by the Black-clawed Mud Crab, *Panopeus herbstii*, in Mid-Atlantic Salt Marshes: Further Evidence for Top-down Control of Marsh Grass Production

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ABSTRACT: Although top-down control of plant growth has been shown in a variety of marine systems, it is widely thought to be unimportant in salt marshes. Recent caging experiments in Virginia and Georgia have challenged this notion and shown that the dominant marsh grazer (the periwinkle, *Littoraria irrorata*) not only suppresses plant growth, but can denude marsh substrate at high densities. In these same marshes, our field observations suggest that the black-clawed mud crab, *Panopeus herbstii*, is an abundant and potentially important top-down determinant of periwinkle density. No studies have quantitatively examined *Panopeus* distribution or trophic interactions in marsh systems, and its potential impacts on community structure remained unexplored. We investigated distribution and feeding habits of *Panopeus* in eight salt marshes along the Mid-Atlantic seashore (Delaware–North Carolina). We found that mud crabs were abundant in tall (4–82 ind m⁻²), intermediate (0–15 ind m⁻²), and short-form (0–5 ind m⁻²) *Spartina alterniflora* zones in all marshes and that crab densities were negatively correlated with tidal height and positively correlated with bivalve density. Excavation of crab lairs routinely produced shells of plant-grazing snails (up to 36 lair⁻¹) and bivalves. Lab experiments confirmed that mud crabs readily consume these abundant marsh molluscs. To experimentally examine potential community effects of observed predation patterns, we manipulated crab and periwinkle densities in a 1-mo field experiment. Results showed that *Panopeus* can suppress gastropod abundance and that predation rates increase with increasing snail density. In turn, crab suppression of snail density reduces grazing intensity on salt marsh cordgrass, suggesting presence of a trophic cascade. These results indicate that this previously under-appreciated consumer is an important and indirect determinant of community structure and contribute to a growing body of evidence challenging the long-standing notion that consumers play a minor role in regulating marsh plant growth.

Introduction

Predators can have strong effects on the structure of marine communities, both directly by controlling prey abundance through consumption (Menge 1976; Lubchenco 1978) and behavioral-mediation (Trussell et al. 2002) and indirectly through the facilitation of lower trophic levels via trophic cascades (Paine 1966; Estes and Palmisano 1974). Top-down control of community structure has been demonstrated in a variety of benthic systems, including rocky shores (Menge 1976), kelp beds (Estes and Palmisano 1974), coral reefs (Hay 1984), seagrasses (Heck and Valentine 1995), and mud (Posey and Hines 1991) and sand flats (Ambrose 1984). In these habitats, decapod crabs are widely recognized as important predators that can limit distribution and abundance of prey (Knudsen 1960; Menge 1976; Bertness et al. 2003) and, at times, act as keystone predators in trophic cas-

cases, indirectly enhancing plant biomass by suppressing densities of potent grazers (Lubchenco 1978; Silliman and Bertness 2002; Trussell et al. 2002).

In shallow-water habitats, members of the crab family Xanthidae (mud crabs) are important, but often overlooked (because of small size and cryptic behavior), benthic predators. Xanthid crabs are equipped with disproportionately large crushing claws and have voracious appetites for small invertebrates (Williams 1984). Mud crabs typically maintain shallow (~4–10 cm in depth), excavated lairs in soft substrate, under rocks or in shell piles (Williams 1984; Kneib and Weeks 1990). Many studies have suggested that these shell-crushing decapods are important community structuring forces, limiting abundance of gastropods, barnacles and bivalves, in both oyster reef (McDermott 1960; Lee and Kneib 1994; Meyer 1994) and seagrass (Whetstone and Eversole 1981; Zieman 1982; Holmquist et al. 1989) systems; their role in salt marshes has not been explored (but see Seed 1980 for lab experiments). Mud crabs are widely distributed in subtidal habitats and are often locally abundant, at times reaching densities up to 80 ind m⁻² (Kneib and Weeks 1990; Meyer 1994).

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In salt marshes along the Mid-Atlantic coast of the United States, the dominant Xanthid is the black-clawed mud crab, *Panopeus herbstii* (Daiber 1982; Williams 1984). Studies on oyster reefs suggest this crab is primarily carnivorous, consuming molluscs, crustaceans, and annelids (McDermott 1960; Meyer 1994). Its distribution in salt marshes is generally thought to be limited to creek banks in tall-form *Spartina alterniflora* (salt marsh cordgrass) zones and, in creeks specifically, in interstitial spaces of oyster reefs (Teal 1958; Daiber 1982; Lee and Kneib 1994; but see Seed 1980). In Virginia marshes, we observed that *Panopeus* takes up residency (in lairs) throughout the entire extent of the lower marsh, consumes resident invertebrates and fish, and preys on the plant-grazing snail, *Littoraria irrorata* (Silliman and Ziemann 2001; Silliman and Bertness 2002). To quantify these observations, and to test their generality and potential community consequences, we investigated distribution and abundance of *Panopeus* in eight salt marshes along the mid-Atlantic seashore, potential food-web interactions through lair excavation and lab feeding trials, and the effect of crab predation on the intensity of marsh plant-grazer interactions. We hypothesized that contrary to present notions, *Panopeus* is widely distributed and abundant throughout East Coast salt marshes and that by suppressing densities of plant-grazing snails, black-clawed mud crabs indirectly facilitate *Spartina alterniflora* growth.

Materials and Methods

DISTRIBUTION AND ABUNDANCE SURVEY

We surveyed mud crab abundance, lair characteristics, and midden (i.e., shell refuse from past predation encounters) composition in eight marshes along the Mid-Atlantic seaboard, from Delaware to North Carolina, in the summer of 1998 (North Carolina: Tarlanding Marsh near Atlantic Beach; Virginia: Cobb Island, Chincoteague Island, Hog Island, Parramore Island, and Raccoon Island; Maryland: Assateague Island; Delaware: Bethany Spit). All sites were exposed to full strength seawater (29–34‰). Within each marsh, we randomly threw ten 1-m² quadrats in each of three *Spartina* height-form zones (tall, intermediate, and short-form), and enumerated density of mud crabs > 5 mm (carapace width) by examining crab species in all visible burrows (using a stick probe inserted behind the burrow to coax crabs to the surface) and number of crabs in mussel and oyster clumps through excavation with shovel. Bivalve clumps were carefully disassembled and rinsed with seawater to dislodge all organisms. Lair attributes included depth, number, and size of

openings, distance between openings, and number, size, and sex of occupants and co-inhabitants. Other mud crabs found included the depressed or flat-backed mud crab, *Europanopeus depressus*, and the oyster mud crab, *Neopanopeus sayi*, but these were in insignificant densities (<0.4 ind marsh⁻¹).

Studies have shown that juvenile and adult *Panopeus* associate with live oysters and oyster shells (Lee and Kneib 1994; Meyer 1994). To test whether distribution of oysters in the tall *Spartina* zone (the zone where oysters are most abundant) affects *Panopeus* abundance, we recorded percent cover of oysters in each 1-m² quadrat in randomly selected subset of sites (Hog Island, Virginia; Cobb Island, Virginia; and Tar Landing, North Carolina, marshes; n = 10 quadrats per tall zone per site). To assess percent cover of oyster shell, we used a quadrat divided into 100 equally-sized parts, and characterized each cell as empty, half full, or full. The hundred cells were summed to provide an estimate of cover for the 1 m² quadrat. In a preliminary study, we compared this method with displacement volume of oysters (Meyer 1994) and found the percent cover and volume method in salt marshes were highly correlated, so we analyzed only percent cover estimates. A linear regression model was used to relate percent cover of oyster shells to density of *Panopeus*.

POTENTIAL FOOD-WEB INTERACTIONS

To identify potential food-web interactions between *Panopeus* and marsh fauna, we counted and identified shells in the middens of lairs. We also estimated density of live epifaunal macro-invertebrates in each survey-quadrat and examined how middens compared to prey availability.

To further examine potential food-web interactions, we starved mud crabs (n = 10 for each run, all ~30–40 mm in carapace width) for 48 hr and then, in the laboratory, presented them with one potential prey item in no-choice predation experiments. Organisms included in trials were the most abundant potential prey in the marsh (see Table 1). Each crab and prey item were housed in a 500 ml square (15 × 15 × 4 cm) plastic container with recirculating seawater to a depth of 3 cm. This level approximated water depth on the marsh surface when crabs are most actively feeding (just after and before flood tide, Teal 1962). Containers were capped with a perforated lid. Both water level and container architecture prevented potential prey items from employing escape responses. Each feeding trial ran for 8 hr and afterwards containers were examined to assess predation. Because we were interested only in identifying potential food-web interactions, we did not use statistics to separate species effects.

TABLE 1. Potential food web interactions of *P. herbstii* in Mid-Atlantic marshes. Crabs (n = 10 for each run) were starved for 48 hr and then presented with one potential prey item in no choice predator experiments. Y signifies that the prey item was consumed by at least one crab and N that no prey were eaten. For Y cases, the number of crabs consuming the prey item is given in parentheses.

Potential Food Items	Consumed
Mud fiddler (<i>Uca pugnax</i>)	Y (6)
Sand fiddler (<i>Uca pugilator</i>)	Y (8)
Purple marsh crab (<i>Sesarma reticulatum</i>)	N
Snapping shrimp (<i>Alpheus heterochaelis</i>)	N
Small (<10 mm) mud crab (<i>P. herbstii</i>)	Y (6)
Mud snail (<i>Illyanassa obsoleta</i>)	Y (10)
Marsh periwinkle (<i>Littoraria irrorata</i>)	Y (10)
Oyster (<i>Crassostrea virginica</i>)	Y (10)
Ribbed mussel (<i>Guekensia demissa</i>)	Y (10)
Killifish (<i>Fundulus heteroclitus</i>)	Y (4)
Naked goby (<i>Gobiosoma boscii</i>)	N

TOP-DOWN CONTROL BY MUD CRABS

To examine potential effects of mud crab predation on the intensity of marsh plant-grazer interactions, we manipulated both periwinkle and crab density in a one-month caging experiment (July 1999). The experiment was completed in low marsh habitat in the intermediate-form *Spartina* zone on Hog Island, Virginia (part of the Virginia Coast Reserve-Long Term Ecological Research Site). A 2 × 2 factorial design was used with two levels of crab (zero and one adult m⁻²) and two levels of snail density (50 and 150 ind m⁻²). We used one adult crab per cage (~35 mm in carapace width) because this density represented natural abundance of large mud crabs (30–40 mm carapace width) in this zone as determined from our large-scale survey (see Figs. 1 and 3; we found ~70 crabs between 30–40 mm in carapace width in 80 quadrats thrown in intermediate *Spartina* zones). Snail densities used in the experiment represented natural (50 ind m⁻²) and high (150 ind m⁻²) periwinkle densities for Hog Island and other Mid-Atlantic salt marshes examined in our broad scale survey (Fig. 4). Subsequent surveys of marshes in North Carolina, South Carolina, Georgia, and Louisiana have shown that *Littoraria* commonly occurs at much higher densities throughout its range (200–800 ind m⁻²; Silliman and Bertness 2002; Silliman and Bortolus 2003), confirming that the

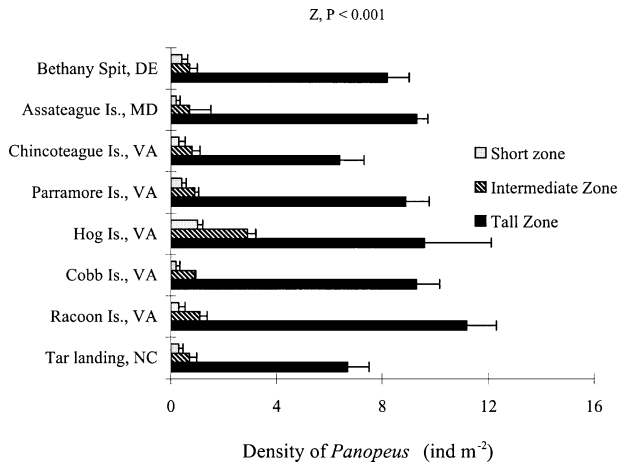


Fig. 1. Density of *Panopeus herbstii* > 5 mm in carapace width in the short, intermediate, and tall *Spartina* zones in eight Mid-Atlantic salt marshes. For analysis of crab density, ANOVA revealed that only zone was significant, with no significant effect of site, or zone × site interaction (for zone: df = 2, F = 275.6, p < 0.001; for site and zone × site, p > 0.18) (±SE).

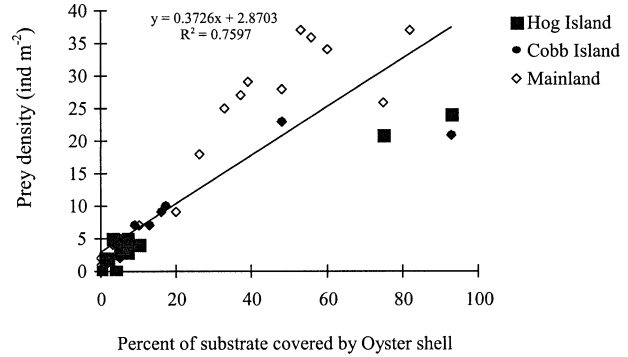


Fig. 2. Least squares linear model of percent oyster cover on the marsh surface and mud crab density in the tall *Spartina* zone in two marshes in Virginia and one in North Carolina (overall n = 30).

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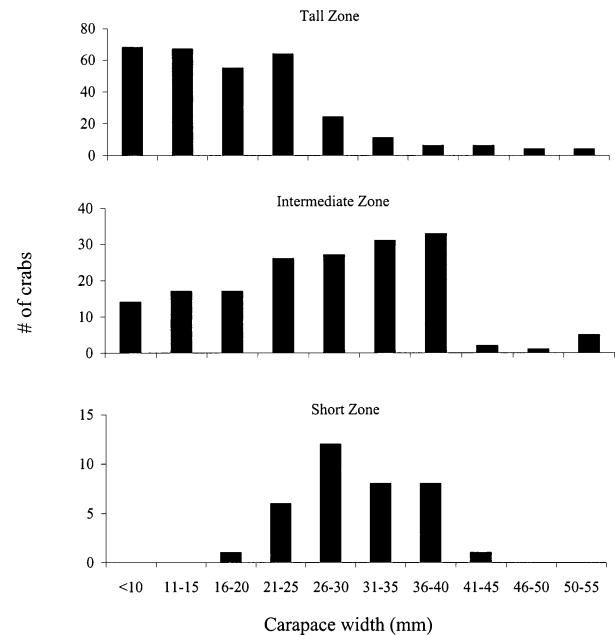


Fig. 3. Size frequency distribution of *Panopeus herbstii* in the *Spartina*-dominated low marsh of eight Mid-Atlantic salt marshes (±SE).

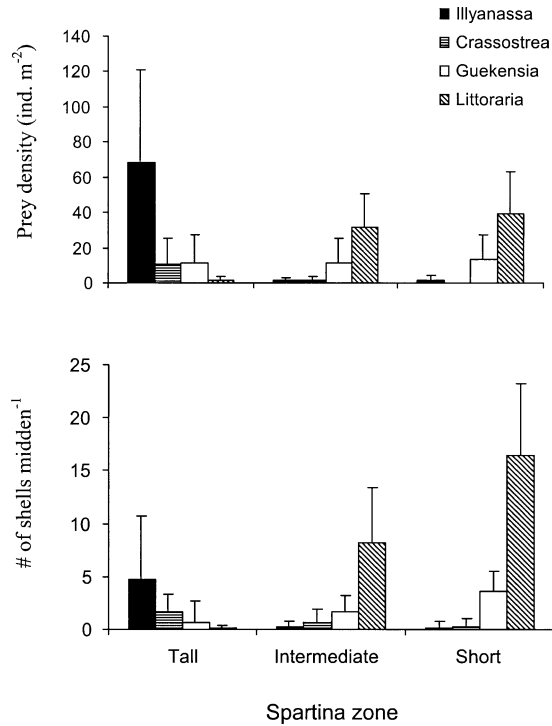


Fig. 4. Density of potential mud crab prey items and density of prey items found in mud crab middens (\pm SE). ANOVA revealed that there was a significant effect of marsh zone on invertebrate density: mussels (df = 2, F = 76.3, $p < 0.01$), periwinkles (df = 2, F = 60.9, $p < 0.01$), mud snails (df = 2, F = 4.64, $p < 0.05$), oysters (df = 2, F = 24.1, $p < 0.03$) and on number of shells in middens: mussels (df = 2, F = 25.62, $p < 0.03$), periwinkles (df = 2, F = 45.15, $p < 0.01$), mud snails (df = 2, F = 11.35, $p < 0.05$), and oysters (df = 2, F = 5.12, $p < 0.05$).

high snail densities used in this study were representative of nature. Experimental units ($n = 4$ treatment⁻¹) consisted of 1 m² roofless cages constructed of galvanized hardware cloth (1.25 cm mesh, 1 m high) and wooden stakes as corner posts. Each cage was sunk to a depth of 10 cm to prevent crab movement under cage sides. Initially, mud crabs and snails were removed from all plots. In the middle of each cage, we constructed artificial lairs designed to mimic a typical mud crab lair, as found in our survey of Mid-Atlantic marshes (Table 2). All enclosures were checked prior to adding crab and no empty shells were found. We then added one adult *Panopeus* (carapace width = 45–50 mm) to each crab treatment. Any crab that did not immediately accept the artificial lair was replaced. During the length of the study no mud crabs abandoned their lairs. We added adult *Littoraria* (shell height = 16–20 mm) to snail density treatments at assigned levels.

The experiment ran for 1 mo and, at completion, we enumerated number of empty *Littoraria*

TABLE 2. Summary of mud crab lair characteristics in Mid-Atlantic salt marshes. Means (\pm SD) and percentages represent pooled data from 1,042 lairs sampled in Delaware, Maryland, Virginia, and North Carolina marshes, Summer 1998.

Lair type and percent occurrence	
Burrow with single opening	
Excavated divot underneath	8%
oyster clump	29%
Stand alone, U-shaped burrow	63%
Lair occupancy rate	
	72%
Number of crabs per occupied lair	1.13 \pm 0.3
Occurrence of lair associates	
Naked goby (<i>Gobiosoma boscii</i>)	9% of abandoned lairs
Morphometrics of u-shaped burrows	
Diameter of openings (cm)	1.65 \pm 0.56
Depth (cm)	7.74 \pm 2.7
Distance between openings (cm)	7.68 \pm 3.5
Roof/joist composition	
Ribbed mussel (<i>Guekensia</i>) shells	0.70 \pm 1.9
Oyster (<i>Crassostrea</i>) shells	6.28 \pm 6.22

shells (in and around the lair), and total length of snail-induced wounds (i.e., radulations) on all live *Spartina* stems in a centered 25 cm² quadrat (Silliman and Zieman 2001). When grazing live *Spartina*, periwinkles make characteristic longitudinal scars on leaves that are typically 2 mm in width and 1–30 cm in length, resembling a cut made by a razorblade. These wounds (radulations) are infected primarily by the common marsh fungi, *Phaeosporia spartinicola*, *Littoraria*'s preferred food. Periwinkles continue to graze these fungal-laden scars until leaves are completely shredded (\sim a 4–5 mo process), resulting in strong suppression of plant growth and, at times, stem death. The total length of radulations per stem is directly proportional to the magnitude of the negative effects of snail grazing on cordgrass production (Silliman and Zieman 2001; Silliman and Bertness 2002). Given these results and the short duration of the experiment, we used snail-grazing intensity as a proxy to suggest indirect effects of crab presence on *Spartina* growth.

Only empty shells found in and around lairs were used as data to assess relative predation rates. We used this method so that predation rates were not confounded by snails that happened to migrate out of cages. Over the length of the experiment, <5% of snails escaped from enclosures (number of escapes = initial density – number of live snails present – number of snail shells in middens). Previous studies have shown that snail immigration into these cages is insignificant over a small time scale (usually <2 mo⁻¹; Silliman and Zieman 2001). No empty shells were found in cages without crabs.

STATISTICS

Differences in response variables were assessed using Analysis of Variance (ANOVA) followed by Tukey's post-hoc test. Differences in crab density were determined using a two-way ANOVA (marsh site \times zone); in carapace width, prey density in lairs, and on the marsh surface using one-way ANOVA (marsh zone); and in predation rates and grazing intensity using a two-way ANOVA (snail density \times crab presence). Data exhibited homogeneity of variance and were normally distributed or were transformed using log transformations for analysis.

Results

MUD CRAB LAIR CHARACTERISTICS AND BEHAVIOR IN THE MARSH

When living in salt marshes, black-clawed mud crabs >15 mm in carapace width make and maintain permanent lairs in the marsh substrate (Table 2). Lairs are typically 7–8 cm in depth, u-shaped with two entrances, and have a supporting joist composed of ribbed mussel or oyster shells (Table 2). Empty and broken bivalve and gastropod shells from past predation events are typically found around entrances and inside burrows (Table 2).

The majority of lairs contained one crab. When two crabs were present, it was always one male and a female, but all gravid females were found alone in burrows. This suggests guarding of soft-shelled females by males during mating and separation after copulation, a behavior observed in other crab species (e.g., blue crabs, *Callinectes sapidus*, Williams 1984). Mud crabs were less frequently found in burrows with single openings and excavated divot-like areas underneath clumps of mussels, oysters, or artificial structure (e.g., lumber). Naked gobies, *Gobiosoma boscii*, were found to inhabit abandoned or unoccupied lairs (Table 2).

DISTRIBUTION AND SIZE FREQUENCY

Panopeus crabs and lairs were found in all *Spartina* zones (short, intermediate, and tall) in all eight marshes examined, spanning from Bethany Spit, Delaware, to Tar Landing Marsh, Atlantic Beach, North Carolina. There was a significant effect of marsh zone (Fig. 1) on mean crab density. The mean density of crabs in tall *Spartina* habitats was significantly different than that in both short and intermediate zones (Tukey test, $p < 0.001$, both cases). On average, the mean density of crabs in tall *Spartina* zones (8.69 ± 0.36 ind m^{-2}) was approximately 8 \times greater than that in the intermediate zone (1.1 ± 0.78 ind m^{-2}), and 16 \times greater than that in the short zone (0.47 ± 0.29 ind m^{-2}). Mean crab density in the intermediate zone

was over two-fold higher than densities in the short zone, but this difference was not significant (Tukey test, $p < 0.08$). In the low marsh of two Virginia and one North Carolina sites, the percent cover of live oyster shells on the marsh surface explained nearly 80% of the variation in *Panopeus* density (Fig. 2). There was no significant differences in mean crab density among marsh sites.

There was a significant effect of marsh zone on mean crab size (One-way ANOVA, $df = 1$, $F = 69.15$, $p < 0.03$; see Fig. 3), and all pair-wise contrasts between zones were significantly different (Tukey test, $p < 0.04$). Mean crab size was greatest in the short zone ($29.96 + 1.81$ mm), intermediate in the medium *Spartina* zone ($23.45 + 0.86$ mm) and smallest in the tall-zone ($19.2 + 0.54$ mm). Size frequency distributions showed that smaller mean crab size observed in tall and intermediate *Spartina* habitats was due to high densities of small *Panopeus* (<10 mm) in these areas and their complete absence in short zones. The greatest range in size frequency occurred in the lower reaches of the marsh (10–55 mm).

FOOD-WEB INTERACTIONS

Excavation of 1,042 mud crab burrows in the eight Mid-Atlantic marshes suggests *Panopeus* is a major predator on at least four of the dominant (numerically) members of the marsh epifauna: marsh periwinkle (*L. irrorata*), mud snail (*Illyanassa obsoleta*), ribbed mussel (*Guekensia demissa*), and eastern oyster (*Crassostrea virginica*). Of those four prey items, *Littoraria* was the most abundant in mud crab middens, comprising nearly 66% of all shells collected. On average, twelve *Littoraria* shells were recovered from each midden, for a total of $\sim 12,500$ periwinkle shells (Fig. 4). Southern quahogs (*Mercenaria mercenaria*), various mud snails (*Nassarius* spp.) and oyster drills (*Urosalpinx* spp.) were also found in crab middens, but are not reported graphically because less than ten shells of each species were found.

Panopeus lair location (i.e., *Spartina* zone) had a significant effect on the mean density of prey items found in crab middens. Mean shell density of both mud snails and oysters was greatest in tall *Spartina* zones (Tukey test, $p < 0.03$, all cases). Shells of periwinkles and ribbed mussels were most common in lairs located in short *Spartina* zones (Tukey test, $p < 0.05$, all cases).

For periwinkles, mud snails, and oysters, relative availability (i.e., abundance) of that prey item was almost directly proportional to the density of shells found in mud crab lairs (Fig. 4). For all three species, there was a significant effect of *Spartina* zone on mean abundance. Both mud snails and oysters were most common in tall *Spartina* zones (Tukey

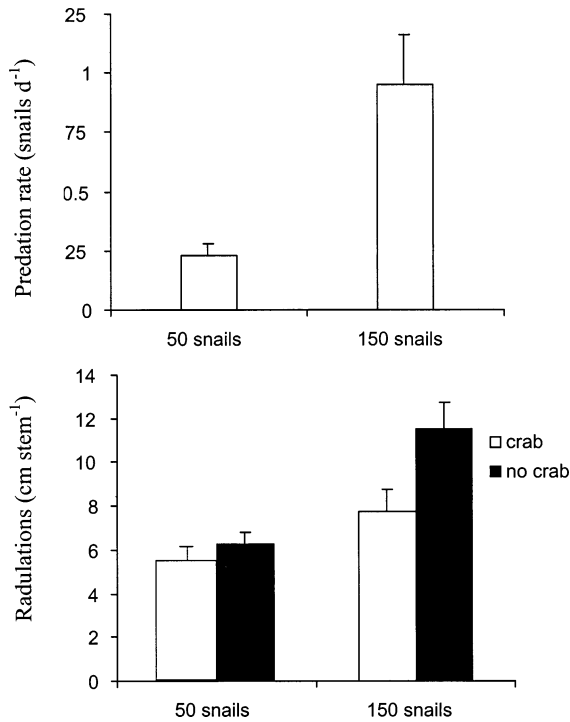


Fig. 5. Effect of snail density on mud crab predation rates (i.e., number of intact shells found in lair). All snail shells recovered from mud crab lairs were intact, although some lips were peeled, as *Panopeus* always pulled large snails out instead of crushing their shells. ANOVA revealed that there was a significant effect of snail density on crab predation rates ($df = 1$, $F = 25.9$, $p < 0.02$). Effects of crab presence and snail density on the intensity of snail grazing (average total length of radulations or stem) on *Spartina*. ANOVA revealed that there was a significant effect of snail density, crab presence, and a snail density \times crab presence interaction on snail grazing intensity: snail density ($df = 1$, $F = 30.9$, $p < 0.02$); crab presence ($df = 1$, $F = 109.6$, $p < 0.01$); snail density \times crab presence ($df = 1$, $F = 12.8$, $p < 0.04$) (\pm SE).

test, $p < 0.01$, all cases), while *Littoraria* was most common in intermediate and short zones (Tukey test, $p < 0.02$, all cases).

TOP-DOWN CONTROL BY MUD CRABS

Field manipulations of mud crab and periwinkle densities showed that *Panopeus* can suppress *Littoraria* abundance and that predation rates increase with increasing snail density. At 50 snails per m², each mud crab consumed approximately six snails (Fig. 5), whereas at high snail densities (150 ind m⁻²: a 2 \times increase in snail density), crab predation rates increased nearly 4 \times , as each *Panopeus* consumed approximately 30 periwinkles (one-way ANOVA, $p < 0.02$). Crab presence reduced grazing intensity on salt marsh cordgrass in high snail density treatments (two-way ANOVA, crab \times snail density, $p < 0.05$), where predation on snails was most intense. Over the 1-mo experiment, crab presence

reduced mean number of radulations or stem by 29% (Tukey-test, $p < 0.02$). In medium density treatments, there was a similar, but non-significant trend for crab presence to reduce mean number of radulations stem⁻¹ (10%, Tukey-test, $p = 0.09$). The magnitude of grazing intensity reduction on *Spartina* in treatments with crabs corresponded closely with suppression of snail densities in the same treatments (for medium snail density treatments, suppression of snail abundance = 12%, reduction in grazing intensity = 10%; for high snail density treatments, suppression of snail abundance = 20%, reduction in grazing intensity = 28%).

Discussion

Our survey of eight salt marshes across four Mid-Atlantic states showed that the black-clawed mud crab, *Panopeus herbstii*, is both widely distributed and locally abundant in low marsh habitat. Excavation of over 1,000 lairs and field experiments suggested *Panopeus* is a major predator on marsh epifauna and may indirectly enhance marsh grass growth by suppressing densities of plant-grazing snails. These results provide further support for consumer regulation of marsh primary production and suggest future marsh food-web models should incorporate the top-down role played by *Panopeus*.

DISTRIBUTION

Although many studies have examined Xanthid crab distribution patterns in subtidal seagrass and oyster reef habitats (e.g., Whetstone and Eversole 1981; McDonald 1982; Holmquist et al. 1989; Meyer 1994), only a small number have done so in salt marshes. Fell et al. (1982) found that in Connecticut salt marshes *P. herbstii* was in low abundances (<5 ind m⁻²) on *Spartina*-dominated creek banks, but absent from higher elevations. In more southern marshes in Georgia, Kneib and Weeks (1990) using coring techniques showed that the white-clawed mud crab, *Eurytium limosum*, was abundant (up to 60 ind m⁻²) in tall-form *Spartina* on the creekbank (1–3 m wide) and throughout the entire lower marsh (both intermediate and short-form *Spartina* zones, hundreds of meters wide). Our results suggest a similar distribution pattern for black-clawed mud crabs—i.e., *P. herbstii* is locally abundant in marshes throughout all *Spartina* height-zones, with greatest densities occurring in tall-*Spartina* habitat along creek banks (Fig. 1). Our extensive surveys show that this distribution pattern is consistent throughout Mid-Atlantic marshes. These findings dispute current notions that black-clawed mud crabs are confined to narrow bands of creekbank *Spartina* (e.g., Daiber 1982) and suggest that predator-prey interactions observed in this study between *Panopeus* crabs and

marsh fauna have the potential to be important on a regional scale.

It is widely recognized *Panopeus* larvae recruit to subtidal and intertidal oyster reef (Welch and Epifanio 1994; Mense et al. 1995) and that juveniles and adults actively seek out oysters for shelter and food (McDermott 1960; Daiber 1982; McDonald 1982; Lee and Kneib 1994; Meyer 1994). Our survey showed that percent cover of oyster shell on the marsh substrate explains nearly 76% of variation in mud crab density, indicating this interspecific relationship extends into intertidal marshlands (Fig. 2). Oyster cover and *Panopeus* density are positively correlated, likely because both habitat complexity (three-dimensional biogenic space provided by oysters) and prey abundance (oyster recruits) increase with increasing oyster abundance (Lee and Kneib 1994; Meyer 1994). The distribution of small mud crabs follows this pattern, with high juvenile crab (10–30 mm in carapace width) densities (Figs. 1 and 3) occurring in tall-zone habitat where oyster cover is greatest (Fig. 4) and lower densities in the upper marsh, as oyster cover decreases.

Density of large mud crabs (>40 mm carapace width), however, remains relatively constant across *Spartina* height-zones. This pattern may be explained partially by our field observations suggesting that large crabs maintain a 40–60 cm territory around their lairs for lie-and-wait prey capture. In this case, low densities of large crabs throughout the low marsh would be explained in part by agnostic, territorial behavior between adult crabs (e.g., pushing, claw locking, and appendage removal, Silliman personal observations). It may reflect independence of adult crabs from oyster shell cover, as large crabs need less protection from predators and desiccation stress and thus can actively seek prey and construct burrows independent of oyster concentrations (large crabs found in the short and intermediate *Spartina* zones commonly used only a few oyster shells when building lair joists; Table 2).

MUD CRAB FORAGING BEHAVIOR IN SALT MARSHES

Our field observations suggest three patterns of crab foraging behavior. *Panopeus* crabs employ a lie-and-wait approach to capture mobile prey. Mud crabs wait outside burrows and grab snails and fiddler crabs. Once captured, crabs take prey inside their burrow for subjugation and consumption (up to 6 hr for snails). *Panopeus* actively search for sessile prey, e.g., bivalves. Because we rarely observed *Panopeus* actively foraging on the marsh surface, this behavior is likely most common with crabs that maintain burrows in large mussel mounds or oyster piles. Mud crabs also concentrate their foraging ac-

tivities just before (~30 min), during, and after flood tides, a pattern also observed by Teal (1962) in Sapelo Island marshes. As Teal (1962) suggested, this activity pattern may take advantage of a time when prey are actively moving across marsh substrate in search of refugia (i.e., climbing *Spartina* stems for periwinkles and burrowing for fiddlers) from predators that come in with the tide (e.g., blue crabs, *C. sapidus*). These three observations are similar to Kneib and Weeks' (1990) and Lee and Kneib's (1994) description of foraging behavior of the white-clawed mud crab, *E. limosum*, in Georgia salt marshes.

MUD CRAB INTERACTIONS IN THE MARSH FOOD-WEB

Although many other studies have shown food-web linkages between black-clawed mud crabs and oysters (McDermott 1960; Lee and Kneib 1994), ribbed mussels (Seed 1980), and clams (Whetstone and Eversole 1981), this is the first study to experimentally demonstrate trophic interactions between *Panopeus* and marsh periwinkles, fiddler crabs, and mud snails.

Density of live prey items (i.e., periwinkles, mud snails, and oysters) found on the marsh surface paralleled species-specific patterns of shell abundance in crab middens (Fig. 4). Ribbed mussels were the notable exception. It is widely recognized that mussel densities in southern marshes are greatest in short and intermediate *Spartina* zones, where mussels form large mounds and are patchily distributed throughout (Daiber 1982). Throwing 1 × 1 m quadrats to assess invertebrate densities (this study) likely resulted in overlooking discrete mussel patches and underestimation of high marsh mussel densities. Our finding that mussels were more common in middens in short and intermediate *Spartina* habitats is likely consistent with our data for periwinkles, mud snails, and oysters, showing that *Panopeus* predation rates are directly proportional to prey availability. This observed pattern of prey consumption in proportion to prey abundance is consistent with optimal foraging theory (Belovsky 1986), which predicts that generalist predators (i.e., *Panopeus*, as suggested by Table 2) take prey in proportion to the relative abundance of those prey items.

POTENTIAL ROLE IN MARSH TROPHIC CASCADE

Trophic cascades occur when potent grazers, left unchecked by predators, reduce plant standing crop and coverage to bare substrate (Paine 1980; Strong 1992). Over the past 10 yr studies in a variety of habitats (aquatic, McQueen et al. 1989; terrestrial systems, Pace et al. 1999; marine, Duffy and Hay 2002) have shown that top-down control of plant community structure via trophic cascades is

more pervasive than previously thought and that experimental manipulation of consumer densities is critical to test assumptions of bottom-up and top-down forcing in plant-dominated communities.

For nearly 50 yr, the prevailing paradigm in salt marsh ecology has been that edaphic factors and nutrients (i.e., bottom-up forces) regulate primary productivity (Mitsch and Gosselink 2002). Recent research, however, has challenged this theory and shown that one of the most abundant and widespread detritivore in East Coast salt marshes, the marsh periwinkle, *L. irrorata*, actually grazes live *Spartina* grass (i.e., snails farm fungi on the grass surface) and, in the process, strongly suppresses cordgrass growth (Silliman and Zieman 2001; Silliman and Bertness 2002). Further experiments demonstrated that if left unchecked by marine predators, periwinkle numbers increase and high densities of snails (600–1,200 ind m⁻²) graze down 3 m tall *Spartina* in 8–14 mo (Silliman and Bertness 2002). These caging experiments (Silliman and Bertness 2002), however, did not separate the individual effects of marsh consumers on *Littoraria* densities, and thus more information is needed to determine which predators are important regulators of plant-grazing snail populations.

Both excavation of crab middens and field experiments support our hypothesis that mud crabs indirectly facilitate *S. alterniflora* by suppressing densities of potent snail grazers. Throughout the intermediate and short *Spartina* zones in the eight surveyed Mid-Atlantic marshes, Littorine snails were the most abundant prey item found in *Panopeus* lairs. Lab and field experiments along with direct field observations confirmed that black-clawed mud crabs readily consume marsh periwinkles, a predator-prey interaction also observed with other Xanthid crabs (*E. limosum*, Silliman personal observations). Results of our 1 mo caging experiment suggest that mud crabs can consume significant amounts of periwinkle snails (up to one snail day⁻¹, Fig. 5); the *Panopeus-Littoraria* interaction is density-dependent (i.e., as snail densities increase, mud crab predation rates increase) and suppression of moderately high snail densities (i.e., 150 ind m⁻², *Littoraria* densities range from 25–800 ind m⁻² in the southeast and gulf coast marshes; this study; Silliman and Zieman 2001; Silliman and Bertness 2002; Silliman and Bertness 2003) by mud crabs can result in decreased grazing pressure on *Spartina alterniflora* (i.e., decreased radulations stem⁻¹) and, potentially, enhanced primary production (Silliman and Zieman 2001; Silliman and Bertness 2002).

Our observation that predation on *Littoraria* increased with increasing snail density suggests that *Panopeus* predation rates on periwinkles is a func-

tion of encounter rates with snails on the marsh surface (Morin 1999). This observed density-dependent predation rate has important implications for marsh community structure, as it suggests that *Panopeus* may provide top-down compensation if densities of plant-grazing snails increase significantly on a regional or local scale (e.g., due to heavy snail recruitment or declining blue crab densities). *Panopeus* mud crabs thus have the potential to buffer salt marsh communities from runaway grazer effects, which result in denuding of marsh substrate (Silliman and Bertness 2002). Critical to understanding how salt marsh communities are organized and how depletion of estuarine predators will affect marsh structure is experimentally deciphering the degree to which predation by *Panopeus* compensates for abundance declines in other snail predators (e.g., blue crabs declined 40–80% in southeast and Gulf Coast estuaries over the past 10 yr; Lipcius and Stockhausen 2002) and the separate and interactive effects of marsh predators in regulating snail populations. Future studies in marshes should also investigate the degree to which *Panopeus* regulates distribution of critical habitat engineers, i.e., oysters and ribbed mussels, which indirectly enhance marsh health and grass production by depositing nutrient-rich sediments and blocking erosion (Bertness 1984).

ACKNOWLEDGMENTS

We thank J. Spitzer for field and boating assistance and A. Altieri and two anonymous reviewers for helpful comments which improved the quality of this manuscript. Our work was supported by the Virginia Coast Reserve—Long Term Ecological Research project, the Nature Conservancy, and the Odum foundation. We dedicate this work to the memory of Micaiah Weatherly (1975–1999).

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Submitted, February 20, 2003

Revised, June 19, 2003

Accepted, July 17, 2003