

# Effects of biogenic structure on prey consumption by the xanthid crabs *Eurytium limosum* and *Panopeus herbstii* in a salt marsh

S. Y. Lee\*, R. T. Kneib

University of Georgia Marine Institute, Sapelo Island, Georgia 31327, USA

**ABSTRACT:** The predatory xanthid crabs *Eurytium limosum* and *Panopeus herbstii* are common components of benthic assemblages in different intertidal habitats within salt marshes around Sapelo Island, Georgia, USA. *E. limosum* feed primarily on other crabs and are found where cordgrass *Spartina alterniflora* stems are the dominant structural elements in the environment. *P. herbstii* feed largely on bivalve molluscs and are abundant in intertidal creeks where oyster *Crassostrea virginica* reefs are the predominant structural elements. We designed laboratory experiments to measure prey consumption rates by these 2 predators under conditions that simulated those experienced by each species in its respective habitat. Biogenic structure within the environment of each species reduced prey consumption rates. The mean ( $\pm$  SD) number of fiddler crabs *Uca pugnax* killed in 24 h by *E. limosum* was less ( $2.0 \pm 0.87$  individuals) in the presence of stems than in their absence ( $2.9 \pm 1.63$  individuals). Fiddler crabs had no refuge in size from predation by *E. limosum*. However, mortality rates of fiddler crabs exposed to predation by *E. limosum* were sex-dependent. Males of *U. pugnax* sometimes escaped the predator's grasp by autotomizing their prominent major chela and consequently when prey were offered in an equal sex ratio significantly (paired *t*-test,  $p = 0.03$ ) fewer males ( $4.3 \pm 2.55$ ) than females ( $5.7 \pm 2.65$ ) were killed by *E. limosum* in 48 h. We believe that predation by mud crabs may contribute to male-biased sex ratios that are commonly observed in natural populations of fiddler crabs. Oyster shell clumps influenced the predator-prey interaction between *P. herbstii* and the ribbed mussel *Geukensia demissa* in a simulated intertidal creek environment. Mussels attached to the exterior (exposed) surfaces of an oyster clump suffered a 3.5 times greater mortality than those attached to the inside (concealed) surface of the clump. Results of previous studies in which prey were offered as isolated individuals suggest that *P. herbstii* should have the greatest impact on small (<20 mm shell length) mussels. However, by simulating natural conditions, we showed that predation by *P. herbstii* inflicted the greatest mortality on mussels of intermediate (20 to 40 mm shell length) size because larger mussels have a refuge in size and small mussels have a spatial refuge within the interstices of oyster clumps. Our findings suggest that xanthid crabs have a greater impact within salt marsh communities than previously recognized and emphasize the importance of using 'context-sensitive' experiments to explore predator-prey interactions.

**KEY WORDS:** Biogenic structure · Mud crabs · Intertidal · Predation

## INTRODUCTION

Brachyuran crabs in the family Xanthidae are common in a variety of intertidal and shallow subtidal habitats ranging from temperate rocky shorelines

(Knudsen 1960) to tropical mangrove forests (Warner 1969) and coral reefs (Chang et al. 1987, Garth 1989). Although the xanthids comprise more genera than any other brachyuran family (Williams 1984), few species have been the focus of ecological studies and little is known about the role of these crabs in many marine benthic communities. Xanthid crabs can be inconspicuous even when abundant because most are relatively

\*Address for correspondence: The Swire Marine Laboratory, The University of Hong Kong, Cape d'Aguilar, Hong Kong

small (usually <50 mm carapace width, CW), slow-moving and secretive (Knudsen 1960, Williams 1984). Some species are herbivorous (Knudsen 1960) and others are believed to be obligate commensals in corals (Chang et al. 1987, Garth 1989), but many are predators, feeding primarily on molluscs and other crabs (Reames & Williams 1983, Sullivan et al. 1983, Brown & Haight 1992).

The broadback mud crab *Eurytium limosum* (Say) and the Atlantic mud crab *Panopeus herbstii* H. Milne Edwards are 2 predatory xanthids whose geographic ranges in the Western Atlantic overlap in the warm temperate and tropical estuaries of the southeastern United States (Williams 1984). In tidal marshes where these mud crabs are sympatric, each species occupies a different habitat. *P. herbstii* is usually associated with oyster reefs in low intertidal or subtidal creek channels (Williams 1983) and *E. limosum* occurs primarily in vegetated habitats at higher intertidal elevations (Teal 1962, Kneib & Weeks 1990). Both species contribute significantly to energy transformations within their respective habitats. *E. limosum* was identified as the most important secondary consumer in salt marshes on Sapelo Island, Georgia, USA, where Teal (1962) estimated that the population assimilated 27.2 kcal m<sup>-2</sup> annually. The estimated annual contribution of a *P. herbstii* population to energy flow in an intertidal oyster reef community at North Inlet, South Carolina, USA, was 273 to 322 kcal m<sup>-2</sup> (Dame & Vernberg 1982).

Feeding studies suggest that each of these mud crab species impacts different components of the salt marsh food web. The effects of predation by *Panopeus herbstii* on bivalve mollusc populations have received considerable attention because of potential economic implications for commercial harvests of American oysters *Crassostrea virginica* Gmelin (Bisker & Castagna 1987) and hard clams *Mercenaria mercenaria* (Linnaeus) (Whetstone & Eversole 1978, 1981). Less is known about the feeding habits of *Eurytium limosum* but its principal prey seems to be other crabs, especially *Uca* spp. (Kneib & Weeks 1990). Previous studies have examined foraging behavior and estimated prey consumption of xanthids under experimental conditions, but often excluded constraints under which the predators must normally function. For example, consumption of the Atlantic ribbed mussel *Geukensia demissa* by *P. herbstii* has been measured by offering mud crabs isolated prey (Seed 1980), even though mussels normally aggregate by attaching their byssus firmly to either conspecifics (Kuenzler 1961) or oysters (Lin 1989a). Mussels living in aggregations are less vulnerable to predators (Bertness & Grosholz 1985, Lin 1991). In reviewing crab foraging studies, Lawton & Zimmer-Faust (1992) highlighted the importance of

using a 'context-sensitive' approach that considers realistic constraints imposed on a predator in its natural habitat.

This study examined the potential impacts of 2 predatory xanthid crabs on their principal prey under constraints imposed by the dominant structural elements in the natural habitat of each predator. We compared prey consumption rates of: (1) *Eurytium limosum* offered *Uca pugnax* in the presence and absence of marsh vegetation and (2) *Panopeus herbstii* offered *Geukensia demissa* attached to either the inside or the outside of oyster clumps.

## MATERIALS AND METHODS

The field observations and laboratory experiments were conducted during July and August 1992. Mud crabs and their prey were collected from tidal marshes near the University of Georgia Marine Institute on Sapelo Island, Georgia, USA. Mean tidal range in the area is ca 2.1 m. Daily water temperatures and salinities recorded during the study at a nearby monitoring station ranged from 27.1 to 32.5°C and from 14.9 to 34.1‰ respectively (Marsh Landing monitoring station, UGA Marine Institute). Oyster *Crassostrea virginica* reefs and shell banks were common in the tidal creeks at relatively low intertidal elevations. Smooth cordgrass *Spartina alterniflora* Loisel was the dominant emergent vegetation at intermediate and high intertidal marsh elevations. A detailed description of the marshes in this area can be found in Pomeroy & Wiegert (1981).

**Size measurements.** Carapace width (CW) of crabs and shell length of mussels and oysters were measured with vernier calipers to the nearest 0.1 mm. Dry weights were measured to the nearest mg after 48 h at 60°C.

**Field densities.** Densities of *Eurytium limosum* were not estimated here because data were available from previous studies in marshes on Sapelo Island (Teal 1962, Kneib & Weeks 1990). *Panopeus herbstii* density was estimated by extracting crabs from all oyster clumps and surface sediments in ten 20 × 20 cm samples collected from an oyster reef in South End Creek, Sapelo Island. Crabs were extracted by washing the samples with fresh water on a 0.5 mm mesh sieve while carefully separating the oyster clumps. Small *P. herbstii* were separated and identified from other similar species (e.g. *Eurypanopeus depressus*, *Panopeus obesus* and *Rithropanopeus harrisi*) following the descriptions in Williams (1965, 1984) and Martin & Abele (1986).

Ribbed mussels *Geukensia demissa* and American oysters *Crassostrea virginica* in the samples were

counted and measured to estimate the abundance and population size structure of the principal prey species available to *Panopeus herbstii*. The patchy distribution and relatively low density of mussels required the sampling of additional oyster clumps ( $n > 150$ ) to ensure a reliable measure of the prey population size structure, which ultimately was based on a total of 192 mussels and 300 oysters. Field densities of *Uca pugnax*, the principal prey of *Eurytium limosum*, were not estimated because data were available from previous studies (Wolf et al. 1975) in this area.

**Laboratory experiments.** Experiments were designed to determine whether dominant elements of biotic structure (i.e. *Spartina alterniflora* and *Crassostrea virginica*) in the respective habitats of *Eurytium limosum* and *Panopeus herbstii* influenced the prey consumption rate of each crab species. All experiments were conducted in glass aquaria (25 cm wide  $\times$  38 cm long  $\times$  30 cm high) containing a layer of marsh sediment 7 cm deep and using ambient air temperatures (air: 27 to 35°C; water: 27 to 31°C) and a 12:12 h light:dark photoperiod. In order not to disturb the sediment unduly, the tanks were not aerated. Mud crabs were starved for 24 h prior to their use in each experiment to standardize their hunger levels.

***Eurytium limosum-Uca pugnax* pair:** Each of the 25 replicates in this experiment began with the introduction of a male *E. limosum* (30 to 40 mm CW) to an aquarium in which 10 live fiddler crabs (10.0 to 21.3 mm CW) had been added 24 h earlier. The prey were exposed to the predator for 48 h. A tidal regime similar to that experienced by the crabs in the field was maintained by flooding the aquaria with estuarine water to a depth of 25 cm for 6 h each day. Natural densities of fiddler crabs in western Atlantic coast marshes range from 27 to  $>100$  ind.  $m^{-2}$  (Montague 1980). The relatively high density used here (105 crabs  $m^{-2}$ ) was based on a previous study conducted on Sapelo Island where the estimated field density of *U. pugnax*  $>10$  mm CW was 113 ind.  $m^{-2}$  (Wolf et al. 1975). All crabs (both mud and fiddler) were measured and individually identified by a numbered tag that was attached to the carapace with cyanoacrylate glue. Because fiddler crabs exhibit a strong sexual dimorphism (the major cheliped of males is enlarged) each mud crab was offered an equal number of male and female prey so that we could determine if predation mortality was sex-dependent.

The number of crabs remaining in each aquarium was monitored 4 times  $d^{-1}$ , twice each during simulated low and high tide periods. Individual predation events were confirmed by recovering the numbered carapaces of fiddler crabs from the mud surface after each high tide period. Any evidence of predation overlooked during monitoring was recovered at the end of

the experimental run when the sediments were sieved to remove both living and dead crabs. We assumed that there was no autogenic change (Roa 1992) in the preference of *Eurytium limosum* for any prey type. Because the data were not independent, the nonparametric method of Quade (Conover 1981, p. 294) was used to compare mortality of male and female prey.

Prey consumption rate was expressed as g dry wt consumed per g dry wt of predator per unit time. Dry weights were estimated from separate regressions of crab weight on carapace width for each sex and species.

The experiment was conducted in both the presence and absence of *Spartina alterniflora* stems in order to assess the effects of biogenic structure on the predator-prey interaction. Densities of *S. alterniflora* in Sapelo Island marshes vary between 80 and 253 stems  $m^{-2}$  (Odum & Fanning 1973, Haines 1979, Schubauer & Hopkinson 1984). We chose to use an intermediate density of 128 stems  $m^{-2}$  (i.e. 12 stems  $aquarium^{-1}$ ) in this experiment. Fresh *S. alterniflora* stems were collected from the field and cut to 30 cm lengths that were then inserted into the sediment of each aquarium; stem distribution was determined from a random number table. To avoid any biases due to variation in the skill of individual predators, we used the same 25 *Eurytium limosum* in experimental treatments both with and without vegetation. Individual predators were considered replicates and a paired *t*-test was used to compare prey consumption rates in treatments with and without *Spartina* stems.

In a separate experiment we tested the hypothesis that *Uca pugnax* may have a 'size refuge' (Paine 1976) from predation by *Eurytium limosum*. A selection of large (13 to 21 mm CW) male fiddler crabs was offered to mud crabs (30 to 50 mm CW) in 20 cm diameter bowls containing 3 cm of sediment and estuarine water to a depth of 2 cm above the sediment surface. Fiddler crab mortality was monitored daily for 2 d. The largest *U. pugnax* killed by the end of the experiment was considered the maximum prey size for the predator.

***Panopeus herbstii-Geukensia demissa* pair:** Each of the 22 replicates of this experiment began with the introduction of a male *P. herbstii* (29.2 to 47.8 mm CW) to an aquarium containing *G. demissa* (10 to 59 mm shell length) that were attached by their byssus to oyster *Crassostrea virginica* clumps. The size range of mussels used in the experiment reflected the most common sizes encountered in the field and also represents the sizes normally consumed by *P. herbstii* (Seed 1980). Aquaria were flooded daily to a depth of 25 cm with estuarine water for 21 h to simulate the tidal regime experienced by *P. herbstii* in the low intertidal zone.

Table 1. *Eurytium limosum* and *Uca pugnax*. Mean ( $\pm$  SD) daily consumption of *U. pugnax* by *E. limosum* in the presence and absence of *Spartina alterniflora* stems

Response variable	n	Treatment	
		<i>Spartina</i> present	<i>Spartina</i> absent
Prey mortality rate ( <i>Uca</i> predator <sup>-1</sup> d <sup>-1</sup> )	23	2.0 $\pm$ 0.87	2.9 $\pm$ 1.63
Specific rate of consumption (g <i>Uca</i> g <sup>-1</sup> <i>Eurytium</i> d <sup>-1</sup> )	22	0.14 $\pm$ 0.088	0.25 $\pm$ 0.195

Natural oyster clumps were unsuitable as standardized experimental units because they were too variable in shape, size and the number of mussels they contained. In order to provide 'standard' experimental units that reflected the biogenic structure of the natural oyster reef assemblage, we separated live oyster clumps collected from the field into smaller shell groups of a few oysters each and placed them in containers of estuarine water to which we added 5 live *Geukensia demissa* in 1 each of the following size classes: 10–19, 20–29, 30–39, 40–49 and 50–59 mm shell length. The mussels attached themselves firmly to the oysters within 3 to 4 d; attachment was restricted to only one side of an oyster shell group. Oyster clumps were then reconstructed by combining 4 shell groups with 5 mussels attached to each so that of the 20 mussels associated with an oyster clump, 10 were on the exposed exterior and 10 were partially concealed within the interior of the clump. Rubber bands held the shell groups of a clump together in the proper spatial arrangement, which offered the predators 2 groups of mussels having the same size composition but occupying different positions (i.e. exposed or concealed) within the oyster clumps. An oyster clump with attached mussels was placed in an aquarium and exposed to predation by *P. herbstii* for 24 h, after which the number of mussels at each location within the oyster clump was counted. Mussel mortality was confirmed by collecting fractured shells after each experimental period. Consumption of mussels on the exterior and interior of the clump was compared using the nonparametric test of Quade (Conover 1981).

## RESULTS

### Behavioral observations

Both of the xanthid species in this study, especially *Panopeus herbstii*, were inactive and remained in their burrows when not inundated by the tide. Some individuals of *Eurytium limosum* remained motionless near

their burrows with chelipeds fully extended, perhaps attempting to capture prey that wandered into striking range. *E. limosum* consistently exhibited wider meral spreads (distance between the tips of the dactyli when the chelipeds are fully extended laterally) than *P. herbstii*. When submerged by the tide, both species were noticeably more active. We also observed that *P. herbstii* exhibited low burrow fidelity.

### *Eurytium limosum-Uca pugnax* pair

Consumption of *Uca pugnax* by *Eurytium limosum*, whether expressed in terms of numbers or a weight-specific rate, was significantly higher (paired *t*-test,  $p < 0.05$ ) in the absence than in the presence of *Spartina alterniflora* (Table 1). Weight-specific consumption rates were calculated using estimates of prey weights derived from CW (mm) using the following regression equations: *U. pugnax* dry weight (DWT, g dry wt) male DWT = 0.000445 (CW)<sup>2.60</sup> ( $n = 30$ ,  $p < 0.0001$ ) and female DWT = 0.000517 (CW)<sup>2.36</sup> ( $n = 28$ ,  $p < 0.0001$ ).

Mortality of *Uca pugnax* was sex-dependent in this experiment (Quade's test,  $T = 35.21$ ,  $df = 1, 23$ ,  $p < 0.001$ ). The mean ( $\pm$  SD) numbers of male and female fiddler crabs killed per mud crab ( $n = 24$ ) during the entire experiment (including both treatments with and without *Spartina alterniflora* stems) were 4.3  $\pm$  2.54 and 5.7  $\pm$  2.65 respectively. Our direct observations suggest that male fiddler crabs often escaped the grasp of *Eurytium limosum* by autotomizing their major chelipeds. In contrast, almost all females captured were killed by mud crabs.

Large size did not provide *Uca pugnax* a refuge from predation by all *Eurytium limosum*. The size of prey that could be taken by *E. limosum* increased linearly with predator size (Fig. 1). In marshes on Sapelo Island, *U. pugnax* may attain a carapace width of up to 20 mm (Shanholtzer 1973), but this is well within the limit that can be handled by natural populations of *E. limosum* (Fig. 1).

### *Panopeus herbstii-Geukensia demissa* pair

The natural densities of *Panopeus herbstii* and its prey were as follows. Mean ( $\pm$  SD) density of *P. herbstii* in the oyster reef community was 68  $\pm$  46.2 ind. m<sup>-2</sup> and the population was dominated by individuals <25 mm CW (Fig. 2). The *P. herbstii* population contributed a mean ( $\pm$  SD) live (wet wt) biomass of 0.25  $\pm$  0.247 kg m<sup>-2</sup> to the total standing stock of the oyster

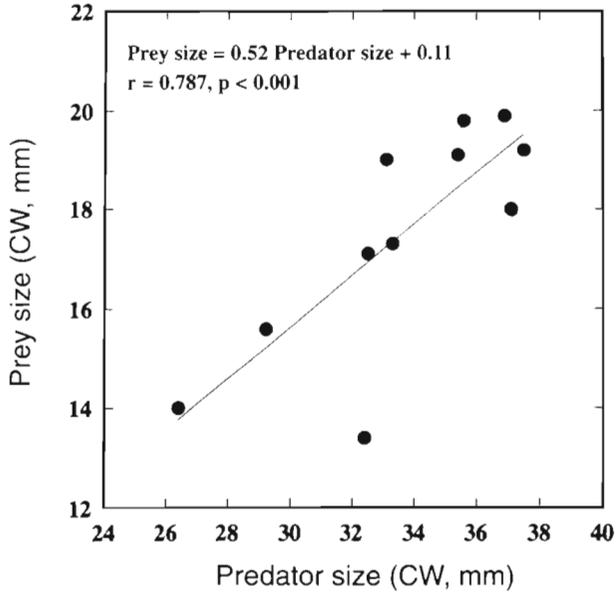


Fig. 1. *Eurytium limosum* and *Uca pugnax*. Relationship between the maximum size of prey (*U. pugnax*) killed and predator (*E. limosum*) size (carapace width, CW). Dotted lines are 95% confidence limits to the regression estimates

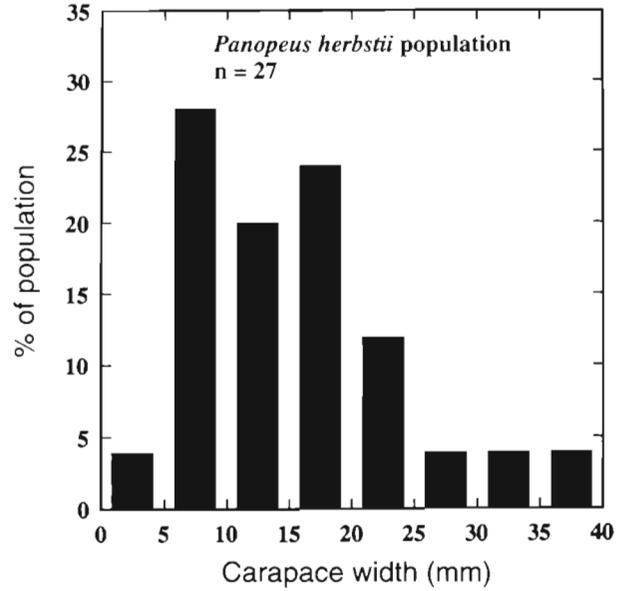


Fig. 2. *Panopeus herbstii*. Size distribution of the population from an oyster reef community in South End Creek, Sapelo Island, Georgia, USA

reef community, which included  $67.2 \pm 14.29 \text{ kg m}^{-2}$  wet biomass of American oysters *Crassostrea virginica*. The oyster population comprised a large proportion of juveniles (<15 mm shell length), which composed 56% of the sample (Fig. 3A). The mussel *Geukensia demissa* exhibited a patchy distribution among the

oyster shells. The mean ( $\pm$  SD) density and live biomass of mussels within the oyster reef were  $212 \pm 168.5 \text{ ind. m}^{-2}$  and  $0.32 \pm 0.401 \text{ kg m}^{-2}$  respectively. Mussels <15 mm shell length represented 69% of the population within the reef (Fig. 3B). Mussels of intermediate size (40 to 55 mm shell length) were under-

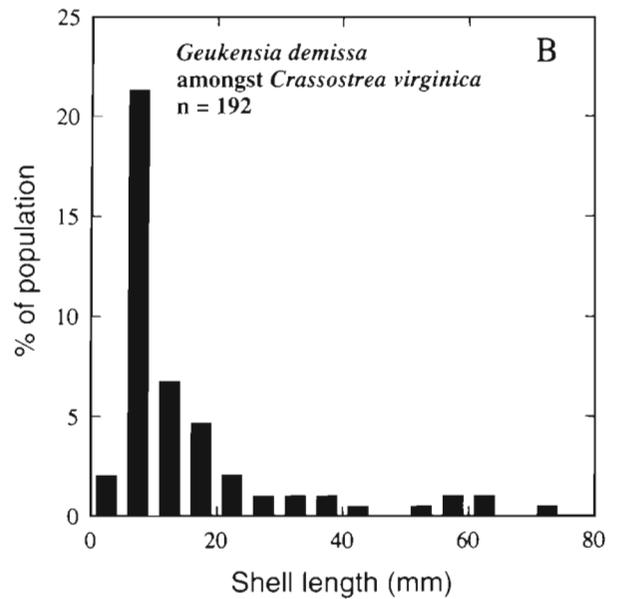
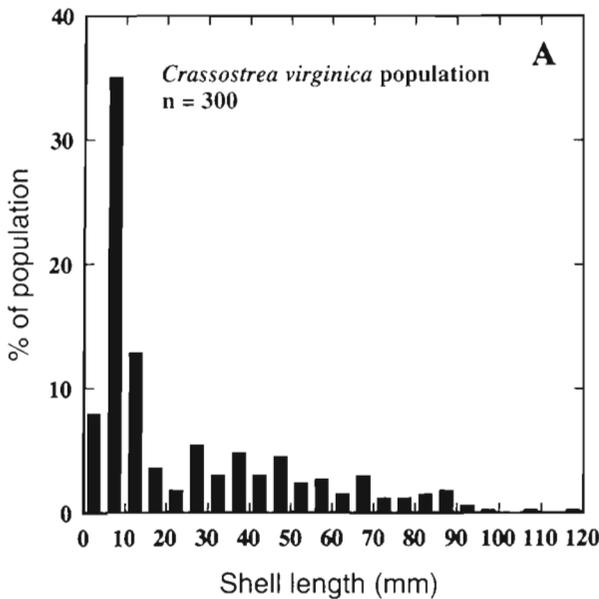


Fig. 3. *Crassostrea virginica* and *Geukensia demissa*. Size distributions of (A) oysters and (B) mussels from an oyster reef community in South End Creek, Sapelo Island, Georgia, USA

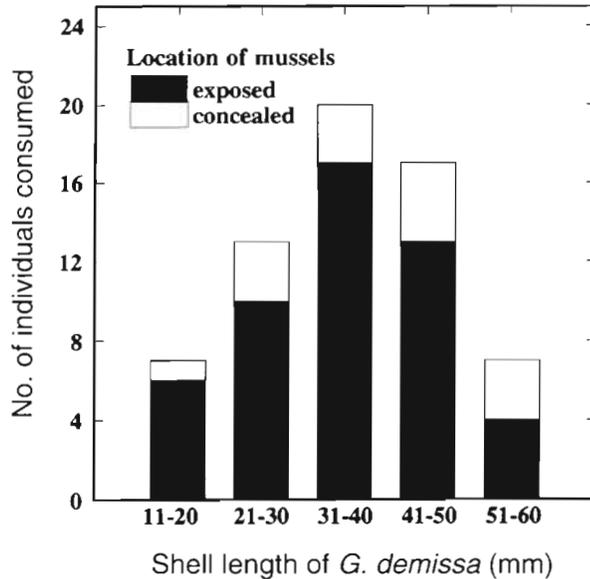


Fig. 4. *Geukensia demissa*. Total number of mussels in each of 5 size classes consumed from both outer (exposed) and inner (concealed) surfaces of experimental oyster clumps by 22 *Panopeus herbstii* in 24 h

represented when compared to oysters within the same size range (Fig. 3A, B).

The consumption of mussels *Geukensia demissa* by *Panopeus herbstii* was influenced by their position within the oyster clumps. The mean ( $\pm 1$  SD) number of mussels consumed from the inner (concealed) surfaces ( $0.6 \pm 0.85$  ind.) was significantly lower (Quade's  $T = 24.48$ ,  $df = 1, 21$ ,  $p < 0.001$ ) than from the outer (exposed) surfaces ( $2.3 \pm 1.67$  ind.) of the oyster clumps. More mussels of intermediate sizes (30 to 50 mm shell length) were consumed than were smaller or larger individuals (Fig. 4). The size selection of mussels by *P. herbstii* was more apparent for exposed than concealed prey.

## DISCUSSION

Predator-prey studies with brachyuran crabs usually offer the predator isolated prey in an artificially simple environment (e.g. Elner 1978, 1980, Seed 1980, Jubb et al. 1983, Bisker & Castagna 1987, Brown & Haight 1992). Although these types of studies contribute to our understanding of certain aspects of crab foraging behavior (e.g. inherent preferences for certain prey sizes or species) they lack the realistic biological constraints that are necessary to explain the impact of crabs on their prey populations in the field (Lawton & Zimmer-Faust 1992). The effects of brachyuran crab predation on *Geukensia demissa* populations are mod-

ified both by degree to which the mussels aggregate into conspecific clumps (Bertness & Grosholz 1985, Lin 1990, 1991) and the mussels' position within an intertidal gradient of predation risk, which decreases with increasing elevation (Bertness & Grosholz 1985, Lin 1989b, Stiven & Gardner 1992).

In marine communities, the interaction between a predator and its prey is also commonly influenced either directly or indirectly by other species (Fairweather 1990, Kneib 1991), particularly when the third species contributes significantly to the structural complexity of the environment. For example, shell debris may provide a refuge for bivalve molluscs by reducing the foraging efficiency of portunid crabs (Arnold 1984, Sponaugle & Lawton 1990). Vegetation can serve a similar function (Blundon & Kennedy 1982), or it may provide an elevated refuge from benthic predators as in the marsh periwinkle *Littoraria irrorata*, which climbs stems of *Spartina alterniflora* during periods of tidal inundation, presumably to avoid predation by crabs (Hamilton 1976, Warren 1985, Vaughn & Fisher 1988), or the bay scallop *Argopecten irradians*, the juveniles of which attach themselves several centimeters above the bottom in the canopy of seagrass beds (Pohle et al. 1991, Ambrose & Irlandi 1992).

We have shown how prominent elements of biogenic structure (i.e. *Spartina alterniflora* stems and *Crasostrea virginica* clumps) within the respective habitats of 2 predatory xanthids (*Eurytium limosum* and *Panopeus herbstii*) can reduce the impact of the predators on their prey species (*Uca pugnax* and *Geukensia demissa*). These results contrast with those of previous, less 'context-sensitive' studies of the same predator-prey pairs. For example, Seed (1980) showed that *P. herbstii* preferred small (<30 mm shell length) *G. demissa* when isolated mussels were offered to the predator. We do not claim that our experiments wholly simulated the natural context within which these predator-prey interactions occur, but our findings show how the presence of seemingly 'indifferent' species can modify consumption rates and prey selection behavior of xanthid crabs in 2 salt marsh habitats. Our observation that mussels of intermediate size (30 to 50 mm shell length) were underrepresented in the natural oyster reef community (Fig. 3B) was consistent with our finding that this size class was the most susceptible to predation by *P. herbstii* (Fig. 4) in the presence of oyster clumps and provides additional support for the hypothesis that oysters have a positive indirect effect on the survival of small *G. demissa*, which would not have been predicted from the results of studies that used isolated prey (e.g. Seed 1980).

The results of our experiments have several implications for understanding the role of xanthid crabs in salt marsh communities. Teal (1962) identified fiddler crabs

(*Uca* spp.) as the most conspicuous consumers and *Eurytium limosum* as the most important secondary consumer in salt marshes of Sapelo Island, but did not support the connection between these species with measurements of consumption rates. In fact, few studies (e.g. Kneib & Weeks 1990) have even suggested an important predator-prey relationship between *E. limosum* and *Uca* spp. Teal (1958) indicated that *E. limosum* occurred primarily near the banks of tidal creeks where fiddler crabs were rarely found. In her study of the population dynamics of *U. pugnax*, Shanholtzer (1973) listed 22 predators of fiddler crabs in marshes of Sapelo Island but did not include *E. limosum*, nor did Montague et al. (1981) mention this mud crab in their discussion of important salt marsh macroconsumers. Our findings suggest that *E. limosum* is a major predator of *U. pugnax* on Sapelo Island, and probably on other *Uca* spp. throughout its range. If our findings in the presence of *Spartina alterniflora* stems are any reflection of the potential mortality rates inflicted by this predator on natural prey, each g dry wt of *E. limosum* biomass  $m^{-2}$  could capture the equivalent of  $0.14 \pm 0.088$  (mean  $\pm$  SD) g dry wt of *U. pugnax*  $d^{-1}$ . This value is almost certainly an overestimate of the actual consumption rates because we measured prey mortality inflicted by starved predators, mud crabs rarely consumed all parts of their kills, and alternative prey would be available under natural conditions. However, the value may represent the potential maximum amount of prey biomass (or energy) that can be 'mobilized' by *E. limosum*.

Predation by xanthid crabs also may influence the population structure and intertidal distribution of prey species in some marsh habitats. Collections of *Uca* spp. often have sex ratios that favor males (e.g. Wolf et al. 1975, Montague 1980). The most likely explanations involve sampling bias due to sex-specific differences in behavior or the effects of sex-specific mortality due to predation. Montague (1980) argued that sampling methods relying on the collection of crabs only from the sediment surface would be biased toward males because females spend more time in their burrows. He also suggested that samples taken over much of the marsh surface during the reproductive season would have a similar bias because ovigerous females migrate toward creek bank habitats. However, predatory birds often grasp male fiddler crabs by their major chela, which the crab can autotomize to effect an escape (Wolf et al. 1975, Bildstein et al. 1989), suggesting the other mechanism by which an uneven sex ratio may occur. Our findings provide support for the predation hypothesis. In our laboratory experiments, male *U. pugnax* sometimes escaped the grasp of *Eurytium limosum* by autotomy of the major chela and more female than male fiddler crabs were consumed when

the prey were offered at an initial 1:1 sex ratio. It is unlikely that either sex has an advantage in avoiding an encounter with predators because there is no evidence for a sex-specific difference in running speed of *U. pugnax* (Frix et al. 1991). We believe that a difference in ability to escape the grasp of predators is at least a contributing factor shaping the natural sex ratios of *Uca* spp. populations.

Teal (1958) suggested that the abundance of *Uca pugnax* was low in marsh habitats immediately adjacent to tidal creeks because these fiddler crabs tended to remain outside their burrows during periods of tidal inundation, which made them vulnerable to aquatic predators, including fish, blue crabs *Callinectes sapidus* and mud crabs. *Eurytium limosum* forages primarily during flood tides and its densities are highest in low marsh habitats where *U. pugnax* densities are low (Teal 1958, Kneib & Weeks 1990). Our findings lend support to the hypothesis that mud crabs, at least, could contribute to intertidal distribution patterns observed in salt marsh populations of *U. pugnax*. The presence of *Spartina alterniflora* stems reduced the mortality rate inflicted on the *U. pugnax* by *E. limosum* and may help to explain the higher densities of fiddler crabs in habitats landward of the creek banks, where high stem densities may reduce the efficiency of predatory mud crabs that feed on mobile prey. In comparable estuarine habitats where predators like *E. limosum* are absent, *Uca* spp. are common and abundant. For example, high densities of *Uca arcuata* are found even on unvegetated mud banks low in the intertidal zone of the Mai Po Marshes mangroves, Hong Kong (S. Y. Lee unpubl. data).

The intertidal distribution of *Geukensia demissa* also may be determined in part by an interaction between the availability of biotic structure and predation pressure along an intertidal elevation gradient. *G. demissa* is abundant in vegetated intertidal marsh habitats (Kuenzler 1961, Bertness & Grosholz 1985, Stiven & Gardner 1992), but is uncommon on unvegetated creek banks low in the intertidal zone (Kuenzler 1961). A correlation between mussel density and *Spartina alterniflora* stem density has been observed in some marshes (West & Williams 1986). However, most studies of *G. demissa* distributions in salt marshes have ignored mussels that occur in association with oyster reefs low in the intertidal zone. Our study and others (e.g. Bahr 1974) have shown that high densities of ribbed mussels can be maintained low in the intertidal zone in the presence of a large population of mud crabs if there are oyster reefs to provide a structural refuge from predators. By using a 'context-sensitive' approach we have shown how predation by xanthid crabs may have a greater role in structuring salt marsh communities than previously recognized.

**Acknowledgements.** This study was conducted while S.Y.L. was a participant in the University of Georgia Marine Institute Visiting Scientist Program, which is supported by the Sapelo Island Research Foundation. The help and hospitality offered by everyone at the UGAMI was much appreciated. In particular, we thank S. Newell, R. Kiene, K. Walters, B. Newell, J. Douglas, T. Lynn, D. Roberson and L. Townsend for their help with a variety of problems. We thank Dr Raymond Seed for his constructive criticism on the paper. This paper is contribution no. 738 of the University of Georgia Marine Institute.

#### LITERATURE CITED

- Ambrose, W. G., Irlandi, E. A. (1992). Height of attachment on seagrass leads to trade-off between growth and survival in the bay scallop *Argopecten irradians*. Mar. Ecol. Prog. Ser. 90: 45–51
- Arnold, W. S. (1984). The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam *Mercenaria mercenaria*. J. exp. mar. Biol. Ecol. 80: 207–212
- Bahr, L. M. Jr (1974). Aspects of the structure and function of the intertidal oyster reef community in Georgia. Ph.D. dissertation, University of Georgia, Athens
- Bertness, M. D., Grosholz, E. (1985). Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. Oecologia 67: 192–204
- Bildstein, K. L., McDowell, S. G., Brisbin, I. L. (1989). Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predations. Anim. Behav. 37: 133–139
- Bisker, R., Castagna, M. (1987). Predation on single spat oysters *Crassostrea virginica* (Gmelin) by blue crabs *Callinectes sapidus* Rathbun and mud crabs *Panopeus herbstii* Milne-Edwards. J. Shellfish Res. 6: 37–40
- Blundon, J. A., Kennedy, V. S. (1982). Refuges for infaunal bivalves from blue crab *Callinectes sapidus* (Rathbun) predation in Chesapeake Bay. J. exp. mar. Biol. Ecol. 65: 67–81
- Brown, K. M., Haight, E. S. (1992). The foraging ecology of the Gulf of Mexico stone crab *Menippe adina* (Williams et Felder). J. exp. mar. Biol. Ecol. 160: 67–80
- Chang, K., Chen, Y., Chen, C. (1987). Xanthid crabs in the corals, *Pocillopora damicornis* and *P. verrucosa* of southern Taiwan. Bull. mar. Sci. 41: 214–220
- Conover, W. J. (1981). Practical nonparametric statistics. John Wiley & Sons, New York
- Dame, R. F., Vernberg, F. J. (1982). Energetics of a population of the mud crab *Panopeus herbstii* (Milne Edwards) in the North Inlet estuary, South Carolina. J. exp. mar. Biol. Ecol. 63: 183–193
- Elnor, R. W. (1978). The mechanics of predation by the shore crab *Carcinus maenas* (L.) on the edible mussel, *Mytilus edulis* L. Oecologia 36: 333–344
- Elnor, R. W. (1980). The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). Mar. Behav. Physiol. 7: 15–24
- Fairweather, P. G. (1990). Is predation capable of interacting with other community processes on rocky reefs? Aust. J. Ecol. 15: 453–464
- Frix, M. S., Hostetler, M. E., Bildstein, K. L. (1991). Intra- and interspecies differences in responses of Atlantic sand (*Uca pugilator*) and marsh (*U. pugnax*) fiddler crabs to simulated avian predators. J. crust. Biol. 11: 523–529
- Garth, J. S. (1989). Xanthidae of Ifaluk Atoll, Caroline Islands, collected in 1953 by D. P. Abbott and F. M. Bayer with special reference to coral commensals. Bull. mar. Sci. 45: 478–486
- Haines, E. B. (1979). Growth dynamics of cordgrass, *Spartina alterniflora* Loisel., on control and sewage sludge fertilised plots in a Georgia salt marsh. Estuaries 2: 50–53
- Hamilton, P. V. (1976). Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). Bull. mar. Sci. 26: 403–409
- Jubb, C. A., Hughes, R. N., ap Rheinallt, T. (1983). Behavioural mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* L. J. exp. mar. Biol. Ecol. 66: 81–87
- Kneib, R. T. (1991). Indirect effects in experimental studies of marine soft-sediment communities. Am. Zool. 31: 874–885
- Kneib, R. T., Weeks, C. A. (1990). Intertidal distribution and feeding habits of the mud crab, *Eurytium limosum*. Estuaries 13: 462–468
- Knudsen, J. W. (1960). Aspects of the ecology of the California pebble crabs (Crustacea: Xanthidae). Ecol. Monogr. 30: 165–185
- Kuenzler, E. J. (1961). Structure and energy flow of a mussel population in a Georgia salt marsh. Limnol. Oceanogr. 6: 191–204
- Lawton, P., Zimmer-Faust, R. K. (1992). Context-sensitivity in crab foraging studies. Am. Zool. 32: 396–404
- Lee, S. Y., Seed, R. (1992). Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Lio-carcinus holsatus*. Mar. Ecol. Prog. Ser. 84: 151–160
- Lin, J. (1989a). Importance of location in the salt marsh and clump size on growth of ribbed mussels. J. exp. mar. Biol. Ecol. 128: 75–86
- Lin, J. (1989b). Influence of location in a salt marsh on survivorship of ribbed mussels. Mar. Ecol. Prog. Ser. 56: 105–110
- Lin, J. (1990). Mud crab predation on ribbed mussels in salt marshes. Mar. Biol. 107: 103–109
- Lin, J. (1991). Predator-prey interactions between blue crabs and ribbed mussels living in clumps. Estuar. coast. Shelf Sci. 32: 61–69
- Martin, J. W., Abele, L. G. (1986). Notes on male pleopod morphology in the brachyuran crab family Panopeidae Ortmann, 1893, sensu Guinot (1978) (Decapoda). Crustaceana 50: 182–198
- Montague, C. L. (1980). A natural history of temperate western Atlantic fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. Contr. mar. Sci. 23: 25–55
- Montague, C. L., Bunker, S. M., Haines, E. B., Pace, M. L., Wetzel, R. L. (1981). Aquatic macroconsumers. In: Pomeroy, L. R., Wiegert, R. G. (eds.) The ecology of a salt marsh. Springer-Verlag, New York, p. 69–85
- Odum, E. P., Fanning, M. E. (1973). Comparison of the productivity of *Spartina alterniflora* and *Spartina cynosuroides* in Georgia coastal marshes. Bull. Ga Acad. Sci. 31: 1–12
- Paine, R. T. (1976). Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57: 858–873
- Pohle, D. G., Bricelj, V. M., García-Esquivel, Z. (1991). The eelgrass canopy: an above-bottom refuge from benthic predators for juvenile bay scallops *Argopecten irradians*. Mar. Ecol. Prog. Ser. 74: 47–59
- Pomeroy, L. R., Wiegert, R. G. (eds.) (1981). Ecological studies, Vol. 38, Ecology of a salt marsh. Springer-Verlag, New York
- Reames, R. C., Williams, A. B. (1983). Mud crabs of the *Panopeus herbstii* H. M. Edw., S. L., complex in Alabama, U.S.A. Fish. Bull. U.S. 81: 885–890

- Roa, R. (1992). Design and analysis of multiple-choice feeding-preference experiments. *Oecologia* 89: 509–515
- Schubauer, J. P., Hopkinson, C. S. (1984). Above- and below-ground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnol. Oceanogr* 29: 1052–1065
- Seed, R. (1980). Predator-prey relationships between the mud crab *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia (=Modiolus) demissa*. *Estuar. coast. Shelf Sci.* 11: 445–458
- Shanholtzer, S. F. (1973). Energy flow, food habits and population dynamics of *Uca pugnax* in a salt marsh system. Ph.D. dissertation, University of Georgia, Athens
- Sponaugle, S., Lawton, P. (1990). Portunid crab predation on juvenile hard clams: effects of substrate type and prey density. *Mar. Ecol. Prog. Ser.* 67: 43–53
- Stiven, A. E., Gardner, S. A. (1992). Population processes in the ribbed mussel *Geukensia demissa* (Dillwyn) in a North Carolina salt marsh tidal gradient: spatial pattern, predation, growth and mortality. *J. exp. mar. Biol. Ecol.* 160: 81–102
- Sullivan, B., Miller, K., Singleton, K., Scheer, A., Williams, A. B. (1983). Electrophoretic analyses of hemocyanins from four species of mud crabs, genus *Panopeus*, with observations on the ecology of *P. obesus*. *Fish. Bull. U.S.* 81: 883–885
- Teal, J. M. (1958). Distribution of fiddler crabs in Georgia salt marshes. *Ecology* 39: 185–193
- Teal, J. M. (1962). Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43: 614–624
- Vaughn, C. C., Fisher, F. M. (1988). Vertical migration as a refuge from predation in intertidal marsh snails: a field test. *J. exp. mar. Biol. Ecol.* 123: 163–176
- Warner, G. F. (1969). The occurrence and distribution of crabs in a Jamaican mangrove swamp. *J. Anim. Ecol.* 38: 379–389
- Warren, J. H. (1985). Climbing as an avoidance behaviour in the salt marsh periwinkle, *Littorina irrorata* (Say). *J. exp. mar. Biol. Ecol.* 89: 11–28
- West, D. A., Williams, A. H. (1986). Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *J. exp. mar. Biol. Ecol.* 100: 75–95
- Whetstone, J. M., Eversole, A. G. (1978). Predation on hard clams, *Mercenaria mercenaria*, by mud crabs *Panopeus herbstii*. *Proc. natl Shellfish. Ass.* 68: 42–48
- Whetstone, J. M., Eversole, A. G. (1981). Effects of size and temperature on mud crab, *Panopeus herbstii*, predation on hard clams, *Mercenaria mercenaria*. *Estuaries* 4: 153–156
- Williams, A. B. (1965). Marine decapod crustaceans of the Carolinas. *Fish. Bull. U.S.* 65: 1–298
- Williams, A. B. (1983). The mud crab, *Panopeus herbstii*, S. L. partition into six species (Decapoda: Xanthidae). *Fish. Bull. U.S.* 81: 863–882
- Williams, A. B. (1984). Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC
- Wolf, P. L., Shanholtzer, S. F., Reimold, R. J. (1975). Population estimates for *Uca pugnax* (Smith, 1870) on the Duplin estuary marsh, Georgia, USA (Decapoda, Brachyura, Ocypodidae). *Crustaceana* 29: 79–91

This article was submitted to the editor

Manuscript first received: June 7, 1993

Revised version accepted: October 25, 1993