ELSEVIER

Journal of Experimental Marine Biology and Ecology
195 (1996) 251–265

JOURNAL OF EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

Experimental studies of predation on metazoans inhabiting *Spartina alterniflora* stems

Keith Walters*, Erin Jones, Lisa Etherington

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

Received 13 March 1995; revision received 16 May 1995; accepted 6 June 1995

Abstract

The short-term effects of invertebrate, *Palaemonetes pugio* Holthuis, and vertebrate predators, *Fundulus heteroclitus* Baird and Girard, on *Spartina alterniflora* Loisel resident metazoan assemblages were investigated experimentally in June 1993 and July 1994. Live or standing-dead *S. alterniflora* stems were transplanted into defaunated sand within experimental buckets in which treatment densities of *P. pugio* and *F. heteroclitus* were varied. Harpacticoid copepods were the only stem-associated faunal group affected by both shrimp and fish. The presence of *P. pugio* for one full tidal cycle (24 h) resulted in a significant 62% reduction in the numbers of copepod nauplii on live stems. Varying shrimp densities did not influence appreciably the effect on nauplii numbers. *F. heteroclitus* consumed almost 50% of the juvenile and adult harpacticoid copepods on standing-dead stems over 3 days. Stem architectural and faunal distributional differences between live and standing-dead stems resulted in ≈50% of the fauna on live stems residing on interior surfaces inaccessible to predators. The fauna resident on salt marsh vegetation represents a previously unconsidered resource for macroepibenthic predators foraging in intertidal marshes.

Keywords: *Fundulus heteroclitus*; Harpacticoid copepods; *Palaemonetes pugio*; Predation; Standing-dead stems; *Spartina alterniflora*

1. Introduction

Vegetated habitats typically support greater densities of macroepibenthic predators (e.g. fish, decapod crustaceans) compared to unvegetated habitats (Orth

* Corresponding author. Dept. of Biology, P.O. Box 60, Middle Tennessee State University, Murfreesboro, TN 37132, USA.

SSDI 0022-0981(95)00103-4

et al., 1984; Rozas & Odum, 1987; Heck et al., 1989; Ferrell & Bell, 1991). One of a number of possible explanations for the observed difference in predator abundance is a suspected increased availability of food resources in vegetated habitats. Potential sediment-associated metazoan prey can be more abundant in seagrass (Stoner, 1980; Lewis, 1984; Summerson & Peterson, 1984) and salt marsh habitats (Coull et al., 1979; Feller et al., 1990). Analyses of gut contents and prey abundance also indicate preferential foraging by macroepibenthic predators within vegetated systems (McIvor & Odum, 1988; Rozas & LaSalle, 1990; Webb, 1991). The use of food resources from vegetated habitats actually may confer a selective advantage on predators by increasing growth rates and reproductive outputs (Rozas & Odum, 1988).

The increased abundance and foraging preference of macroepibenthic predators in vegetated habitats should reduce metazoan prey densities if predation rates are not affected by vegetative structure or metazoan abundance is not supplemented by rapid reproduction and immigration. In subtidal seagrass beds densities of both sediment-associated (Summerson & Peterson, 1984; Leber, 1985; Kennelly, 1991) and phytal prey taxa (Russo, 1987; Edgar & Aoki, 1993) are reduced by epibenthic predators. Macroepibenthic predators also can cause significant reductions in sediment-associated metazoan densities within intertidal salt marsh habitats (Bell & Coull, 1978; Van Dolah, 1978; Bell, 1980; Kneib & Stiven, 1982; Kneib, 1988). However, the effects of intertidal predators on the densities of fauna associated with salt marsh vegetation are undocumented.

Marine metazoans are common residents on salt marsh vegetation from low to high intertidal elevations (Healy & Walters, 1994; Walters, unpubl.). Metazoan densities on *Spartina alterniflora* Loisel stems can rival or exceed typical sediment-dwelling faunal abundance (Rutledge & Fleeger, 1993; Healy & Walters, 1994). Phytal assemblages are predominated by nematodes and harpacticoid copepods (Rutledge & Fleeger, 1993). Although the taxonomic composition of phytal- and sediment-associated assemblages is similar, some species are found only on vegetation (Rutledge & Fleeger, 1993; Healy & Walters, 1994). The faunal groups prevalent on intertidal vegetation also are common food items for the early life history stages of fish and crustacea (Coull, 1990).

In this paper we report the results of two experiments designed to test for predation effects on metazoans living on *S. alterniflora* stems. We examined whether two macroepibenthic predators that commonly reside in intertidal salt marshes, the grass shrimp *Palaemonetes pugio* Holthuis and the mummichog *Fundulus heteroclitus* Baird and Girard, are able to cause significant short-term reductions in the densities of stem-dwelling fauna. The possible refuge affect of microhabitat differences in faunal distributions on live stems also was examined.

2. Materials and methods

All studies were conducted on either live or standing-dead *S. alterniflora* stems collected from a low marsh site at Kenan Field, Sapelo Island, GA, USA (81°17′

W, 31°27′ N). Kenan Field is predominated by *S. alterniflora* and is located along the banks of the Duplin River, a tidal river with limited freshwater input from rainwater run-off. For a more complete description of the site see Kneib (1987). Live and standing-dead stems are present in the Kenan Field marsh throughout the year and, unlike Gulf Coast stems (Gleason, 1986; Rutledge & Fleeger, 1993), typically lack a coating of epiphytic algae (Walters, pers. obs.). The first predation experiment was conducted from 20 to 22 June 1993 using live stems and *P. pugio* as the predator. The second predation experiment was conducted from 25 to 28 July 1994 using standing-dead stems and *F. heteroclitus* as the predator. Use of standing-dead stems and *F. heteroclitus* in the second experiment was motivated by a concern that the architectural complexity of live stems (see Section 2.1) and the behavior of grass shrimp complicated our ability to detect a predation effect. Both *P. pugio* and *F. heteroclitus* are predominant macroepibenthic residents within the Georgia salt marsh system and prey on sediment-associated metazoa (e.g. Kneib, 1985, 1986).

2.1. Stem architectural complexity and prey availability

Architectural complexity can have a major effect on predator-prey relationships (Holmlund et al., 1990; Martin-Smith, 1993), and live and standing-dead stems differ in architectural complexity. Stems of live *S. alterniflora* have several layers of leaf sheaths wrapped around a hollow inner stem (see Healy & Walters, 1994). As a culm matures, the stem elongates and leaves senesce and fall off leaving decaying sheaths still attached. The decaying sheaths remain more or less attached to the live stem and provide both an interior and exterior surface that can be occupied by fauna. Standing-dead stems seldom have intact sheaths around the base because of continued sheath decay. The interior surfaces of intact live stem sheaths contain numerous metazoans inaccessible to predators foraging over external stem surfaces (e.g. Healy and Walters, 1994). Inclusion of fauna living between the stem and sheaths in a count of total stem fauna could underestimate predation effects on live stem fauna and confound comparisons of results between live and standing-dead stem predation experiments.

A method was developed before the June 1993 experiment to exclude from consideration organisms that resided on the interiors of live stems and, therefore, were not susceptible to non-stem resident predators. To test the method, 10 live stems were collected from the field site. Five stems were untreated, excised at the sediment surface, cropped 5 cm up, and preserved in a 10% buffered formaldehyde and Rose Bengal solution. The remaining five stems were sampled and preserved after being treated by tying a fine gauge string above and below the points of excision. The string treatment was expected to trap fauna residing on interior stem surfaces at the time of sampling between the sheaths and stem. In the laboratory metazoans were extracted from preserved untreated and treated stems (see Section 2.3), identified to major taxa, and enumerated. The strings on treated stems were then removed and any fauna that remained on the previously tied stem sections extracted a second time and enumerated separately. If tying

stems effectively separated the fauna residing on interior and exterior stem surfaces, than the sum of faunal densities from tied and untied extractions of treated stems should equal faunal densities from untreated stem sections. Metazoan densities from untreated and treated stem sections were compared to evaluate the efficacy of the technique.

2.2. Predation experiments

Shrimp or fish densities were manipulated and the effects on stem faunal densities determined in June 1993 and July 1994 experiments. Experiments followed a similar protocol with noted modifications between dates. The day before experiments began several hundred grass shrimp or mummichogs were either dip-netted from a tidal creek or trapped in trays placed within the high marsh (see Kneib, 1984). Shrimp and fish collected in the field were placed in an aquarium with flow-through, filtered seawater for 24 h. Both shrimp and fish often remain on the marsh surface during low tide and experience protracted periods of restricted food supply. On the first day of each experiment (Day 0), field samples of live ($n = 5$) or standing-dead ($n = 7$) *S. alterniflora* stems were collected from the low marsh site. Prior to sampling, live stems were tied with string above and below the points of excision (see Section 2.1). Stems were excised at the sediment surface, cropped after either 5 cm (live) or 10 cm (standing-dead), and preserved immediately for later determination of ambient field metazoan densities. Although the vertical distribution of metazoans on stems can vary by marsh elevation, a majority of the fauna associated with stems in the low marsh are found on the first 5 cm above the sediment surface (Healy & Walters, 1994). The amount of stem sampled in the July 1994 experiment was increased to preclude any differences in faunal vertical distributions from affecting results. Greater than 99% of all fauna are within the first 10 cm of low marsh standing-dead stems (Walters, unpubl.).

Next a total of 100 live or 50 standing-dead *S. alterniflora* stems of approximately the same age and ranging in height between 30 and 80 cm were collected. Experimental stems were removed from the sediments by cutting around the base with a serrated knife and carefully extracting both the stem and associated rhizome. Excess sediments and fauna were rinsed from the rhizomes with deionized water. Extracted stems ($n = 5$) were placed within 22.7 l capacity experimental buckets (total area = 503 cm^2). The density of stems in buckets, ≈ 100 stems $\cdot m^{-2}$, was within observed low marsh live and standing-dead stem densities at Kenan Field. Stems were positioned haphazardly within each bucket with the rhizome buried in 10 cm of defaunated builder's sand. The builder's sand supported stems during experiments and minimized the likelihood of metazoan migrations between stems and sediment. Experimental buckets were arranged haphazardly within two external flow-through seawater tanks. Mesh-covered (333 μm) holes in the bottom of each bucket allowed seawater to percolate up through the sand to inundate stems and also prevented the introduction of non-stem migrants into buckets. Seawater height was regulated within tanks every 6 h to

simulate natural low, below the sediment surface, and high tides, either ≈5 or 10 cm up stems.

After placement in seawater tanks, a predetermined number of similar-sized, aquarium-held shrimp (17–34 mm) or fish (8–20 mm) were transferred into experimental buckets. Four *P. pugio* density treatment levels each with five replicates were established: 0X = no shrimp, 1X = 2 shrimp (40 m^{-2}), 3X = 6 shrimp (120 m^{-2}), and 5X = 10 shrimp (200 m^{-2}). Two *F. heteroclitus* density treatment levels were established in five replicates each: 0X = no fish, 15X = 15 fish (300 m^{-2}). Shrimp and fish treatment densities were within the range of natural field densities within tidal pools (Kneib, 1984, 1987). Treatment densities were greater than densities reported from weir samples collected during high tides (Hettler, 1989; Kneib, 1991), but weirs do not produce reliable intertidal density estimates for the shrimp and fish used in our experiments (Kneib, 1991). The ability of shrimp or fish to forage on stems was manipulated by regulating the water level in the seawater tanks to correspond to natural 6 h high tide periods. During low tide periods shrimp or fish were able to retreat into water-filled refuges (either Petri dishes or jars buried flush with the sand within each experimental bucket) that mimicked natural water-filled pits on the marsh surface. A normal 6 h tidal cycle was maintained in seawater tanks for 1 to 3 days. After one full day in June 1993 (Day 1) or three days in July 1994 (Day 3) tanks were drained and shrimp or fish collected, preserved in a 10% buffered formaldehyde solution, and transferred to alcohol for storage. *S. alterniflora* stems were cut at the sediment surface and either 5 or 10 cm segments, live or standing-dead, respectively, placed in 50 ml freestanding centrifuge tubes and preserved in a 10% buffered formaldehyde solution with Rose Bengal. Live stems were again tied above and below the points of excision to prevent the unraveling of leaf sheaths (see Section 2.1). In the July 1994 experiment, the top 2 cm of sand within each bucket also was collected to determine if stem fauna were migrating into the sediments. Fauna (>99%) were removed from sediments by a shake and decant procedure (Wieser, 1960) and preserved.

2.3. Sample processing

In the laboratory stem samples were agitated vigorously in 2 to 3 washings of deionized water within centrifuge tubes and rinsed through a 63 μm sieve to collect metazoans. Live stems from the predation experiment only were processed with the strings attached. Sporadic inspections of stems were carried out to assure >95% of the fauna were extracted from stem surfaces. The length and upper and lower diameter of each stem segment were measured to the nearest 0.5 mm and the lateral surface area calculated based on the formula for a right circular cone. All fauna were enumerated at 25X under a dissecting microscope and identified to lowest possible taxon.

The total length for all shrimp and standard length for all fish used in predation experiments also were determined in the laboratory. Shrimp were measured from the tip of the rostrum to the end of the telson. Fish were measured from the tip of

the snout to the base of the vertebral column. Measurements were taken using a dissecting microscope and ocular micrometer.

2.4. Statistical analyses

Results were analyzed by ANOVA and Ryan's Q multiple comparison tests (Day & Quinn, 1989) on appropriately transformed data. A simple one factor model was used to test for differences between: (1) untreated and treated stems to determine if tying strings on stems was effective at separating fauna living outside or inside sheaths, (2) buckets within predator treatments to assure that the same sized shrimp or fish were used, and (3) field and 0X samples to evaluate whether transplantation or other unknown factors affected the densities of stem metazoans. A nested design in which stems were subsamples and buckets replicates was used to test for differences between shrimp or fish treatment levels. All tests were run on an IBM PS/2 using SAS 6.04 and the GLM statistical routine (Joyner, 1985). Detectable effect sizes for individual tests were calculated based on observed field sample variability using Cohen (1988).

3. Results

Numerous metazoan taxa were found on both live and standing-dead stems in the field (Table 1). Nematodes, harpacticoid copepods, and mites were the predominant taxa found on stems. Major differences between taxonomic groups on live and standing-dead stems were the virtual absence of copepod nauplii and increased presence of ostracods on standing-dead stems (Table 1). A number of

Table 1
The percentage of all metazoan taxa found on 0–5 cm live ($n = 5$) and 0 = 10 cm standing-dead ($n = 7$) sections of *S. alterniflora* stems collected from the low marsh state at Kenan Field, Sapelo Island, GA

Major faunal groups	Percentage on	
	Live stems	Standing-dead stems
Nematoda	40.3	48.4
Copepoda		
juveniles + adults	20.6	31.0
nauplii	22.2	1.5
Halacaroidea	13.6	10.9
Ostracoda	0.0	3.9
Amphipoda	0.5	0.1
Tanadacea	0.5	0.5
Oligochaeta	0.4	0.6
Polychaeta	0.6	0.5
Insect larvae	0.0	0.5
Other (misc. insects, etc.)	1.3	2.1
Total metazoans sampled	1086	1346

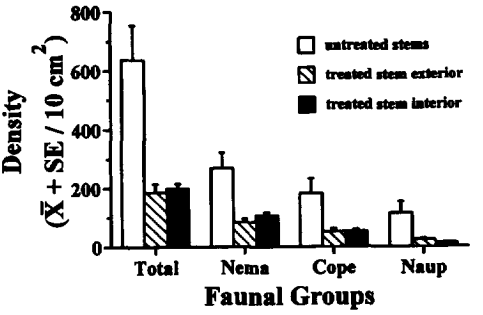

Fig. 1. The density (mean +SE, $n = 5$) of major faunal groups found on 0–5 cm sections of untreated and treated live *S. alterniflora* stems collected from a low marsh site at Kenan Field, Sapelo Island, GA. Faunal densities from untreated stem sections, treated exterior stem surfaces, or treated interior stem surfaces are shown (see Section 2.1). (Total = all fauna, nema = nematodes, cope = harpacticoid copepods, naup = copepod nauplii).

ceratopogonid, dolocopodid, and tabanid insect larvae also were found on standing-dead and not live stems, but were never very abundant.

3.1. Live stem prey availability

Tying the sheaths onto live stems before collection and preservation effectively prevented fauna unavailable to surface predators on the interior of sheath surfaces from biasing prey counts. Stem interior surfaces contained almost 50% of all the metazoans found on live *S. alterniflora* shoots (Fig. 1). Compared to densities from untreated stem sections, significantly fewer nematodes, harpacticoid copepods, copepod nauplii, and total fauna were found on exterior stem surfaces (Table 2). When faunal counts from exterior and interior surfaces of treated stems were summed and compared to numbers from untreated stem

Table 2
Results of one-way analyses of variance testing differences in the distribution of fauna on 0–5 cm sections of live stems sampled from the low marsh a Kenan Field, Sapelo Island, GA

Main effects	Faunal groups	*F*-ratio	*p*-value
Untreated stems	Total fauna	14.05	<0.006
vs.	Nematodes	11.14	<0.02
Treated stems (exterior only)	Harpacticoids	6.70	<0.04
	Copopod nauplii	5.35	<0.05
Untreated stems	Total fauna	0.17	ns
vs.	Nematodes	0.19	ns
Treated stems (interior + exterior)	Harpacticoids	0.25	ns
	Copopod nauplii	2.63	ns

Stems were either untreated (no string) or treated (w/string) with the fauna on treated stems divided into individuals found on exterior (w/string tied) or interior surfaces (w/string untied). Degrees of freedom for each test are 1, 8; ns = not significant.

sections there were no significant differences in nematode, copepod, nauplii, and total faunal densities (Table 2).

3.2. Shrimp experiment

The same sized shrimp were utilized for each density treatment level. There was no significant difference between treatments in shrimp sizes ($F = 0.96$; df = 2, 13; $p > 0.05$). The mean length of individuals in each treatment ranged from 23.5 to 25.4 mm.

Densities of the predominant faunal groups were not affected by any uncontrolled factors over the duration of the experiment (Fig. 2). There was no significant difference in the number of nematodes ($F = 0.27$; df = 1, 8; $p > 0.05$), copepods ($F = 1.34$; df = 1, 8; $p > 0.05$), nauplii ($F = 0.72$; df = 1, 8; $p > 0.05$), or total fauna ($F = 0.01$; df = 1, 8; $p > 0.05$) between Day 0 (field) and Day 1 (0X) stems.

Shrimp significantly reduced total faunal densities ($F = 4.39$; df = 3, 16; $p < 0.02$) on live stems in just 12 h of high tide (Fig. 3). The decline in total numbers was the result of a decrease in copepod nauplii ($F = 9.28$; df = 3, 16; $p < 0.001$) and no other faunal group tested (Fig. 3). Significantly fewer nauplii were found on 1X, 3X, and 5X stems compared to 0X stems (Ryan's Q, $p < 0.05$). There was no significant difference in either copepod ($F = 2.38$; df = 3, 16; $p > 0.05$) or nematode densities ($F = 2.55$; df = 3, 16; $p > 0.05$). Copepod and nematode effect sizes based on the variability between field stems ($n = 5$) were large with a 86.0 and 102.3% difference detectable with 80% power at the 0.05 level of significance, respectively.

3.3. Fish experiment

Similar sized fish were utilized in each replicate of the 15X density treatment. There was no significant difference across replicates in mummichog size ($F = 0.28$;

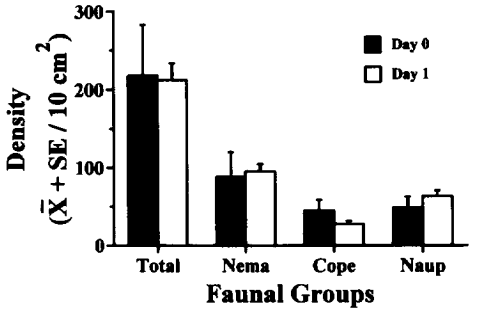

Fig. 2. The density (mean +SE, $n = 5$) of major faunal groups on 0–5 cm sections from Day 0 (field) and Day 1 (0X treatment) live *S. alterniflora* stems initially collected from a low marsh site at Kenan Field, Sapelo Island, GA. Faunal group acronyms are the same as Fig. 1.

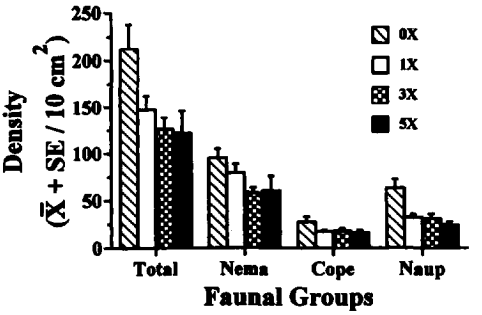

Fig. 3. The density (mean + standard error, $n = 5$) of major faunal groups on 0 to 5 cm sections of live *S. alterniflora* stems initially collected from a low marsh site at Kenan Field, Sapelo Island, GA and exposed to 0X, 1X, 3X, and 5X *P. pugio* treatments (X = 2 shrimp). Faunal group acronyms are the same as Fig. 1.

df = 4, 63; $p > 0.05$). The mean standard length of individuals was 11.9 ± 3.9 mm and indicated fish were either late larval or early juvenile stages (Kneib, 1986).

Densities of the predominant stem faunal groups were not affected by transplantation or other uncontrolled factors over the 3 days of the experiment (Fig. 4). There was no significant difference in the number of nematodes ($F = 0.27$; df = 1, 8; $p > 0.05$), copepods ($F = 0.31$; df = 1, 8; $p > 0.05$), nauplii ($F = 0.72$; df = 1, 8; $p > 0.05$), or total fauna ($F = 0.01$; df = 1, 8; $p > 0.05$) between Day 0 (field) and Day 3 (0X) stems.

Fish significantly reduced copepod densities ($F = 8.19$; df = 1, 8; $p < 0.03$) on standing-dead stems (Fig. 5). There was no significant difference in either nematodes ($F = 0.37$; df = 3, 16; $p > 0.05$) or total faunal densities ($F = 0.42$; df = 3, 16; $p > 0.05$) even though a 81.9 and 82.0% difference could be detected with 80% power at the 0.05 level of significance, respectively. Nauplii treatment differences were not tested because densities were very low. Copepod numbers in the sediment also were extremely low; <1 individual 10 cm^{-2}. There was no

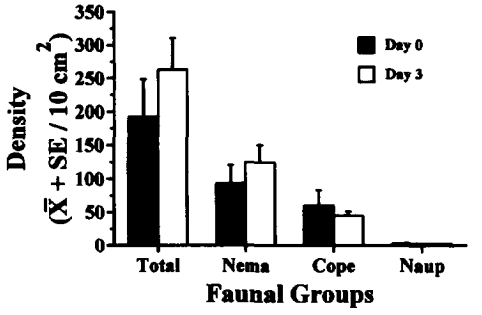

Fig. 4. The density (mean +SE, $n = 5$) of major faunal groups on 0 to 10 cm sections from Day 0 (field) and Day 3 (0X treatment) standing-dead *S. alterniflora* stems initially collected from a low marsh site at Kenan Field, Sapelo Island, GA. Faunal group acronyms are the same as Fig. 1.

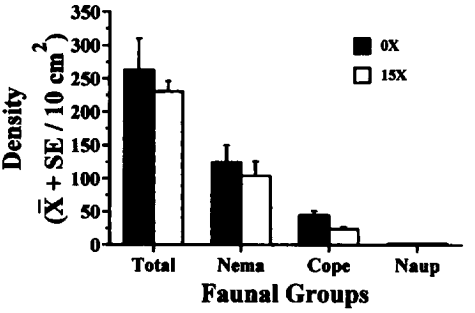

Fig. 5. The density (mean +SE, $n = 5$) of major faunal groups on 0 to 10 cm sections of standing-dead *S. alterniflora* stems initially collected from a low marsh site at Kenan Field, Sapelo Island, GA and exposed to 0X and 15X *F. heteroclitus* treatments (X = 1 fish). Faunal group acronyms are the same as Fig. 1.

significant difference in the numbers of copepods found in the top 2 cm of sediment between treatments ($F = 0.31$; df = 1, 8; $p > 0.05$). The limited numbers and nonsignificant difference in sediment copepod densities indicated that predation and not emigration produced the observed reduction in copepod numbers.

4. Discussion

The densities of metazoan taxa on live and standing-dead *S. alterniflora* stems were affected significantly by two macroepibenthic predators that commonly reside in intertidal habitats. At natural field densities juvenile *P. pugio* produced a 62% reduction in numbers of copepod nauplii on live stems over one tidal cycle (24 h). Direct consumption of nauplii is the most probable explanation for the observed density reduction, but disturbance or a refuge effect might explain results. The nonpredatory activities of adult *P. pugio* may affect densities of a limited number of sediment-associated salt marsh taxa, not including copepod nauplii, through disturbance and increased emigration (Kneib, 1985). Copepod nauplii also may have moved to the interior surfaces of live stems in the presence of grass shrimp. It is unlikely nauplii and no other faunal group would exhibit a disturbance or refuge effect alone, but experimental evidence does not refute either possibility. *Fundulus heteroclitus* unequivocally consumed juvenile and adult harpacticoid copepods on standing-dead stems and caused an ≈50% decline in density over 3 days. The insignificant numbers of copepods in sediments indicated that decreased densities on stems were not the result of a *F. heteroclitus*-induced emigration to the sediments.

The effects by *P. pugio* or *F. heteroclitus* on stem faunal assemblages were selective. Copepod nauplii or juveniles and adults were the only faunal groups effected in either experiment. Selective predation is common on sediment-associated copepods (Nelson & Coull, 1989; McCall & Fleeger, 1993). Individual

copepod species (Gee, 1987; McCall, 1992), sexes (Hicks & Marshall, 1985; McCall, 1992), or ontogenetic stages (Hicks, 1984) are consumed preferentially by a range of vertebrate and invertebrate predators. Selection can result from active predator choice (Coull, 1990; McCall & Fleeger, 1993), predator feeding competency (Hicks, 1984), differential prey distributions (Gee, 1989; Feller et al., 1990), and/or prey behavior (Palmer, 1988; Nelson & Coull, 1989; McCall, 1992). Grass shrimp are considered opportunistic foragers (Morgan, 1980) and the selective predation on nauplii may be related to the unusual numerical abundance of nauplii, >50% of the copepod assemblage, on live stems. The relatively small size and limited dispersal abilities of copepod nauplii also may have contributed to the selection by shrimp. Juvenile grass shrimp may be limited morphologically from preying on larger metazoans or unable to capture taxa that have more active escape responses; e.g. adult copepods. *F. heteroclitus* also is an opportunistic feeder and harpacticoid copepods constitute a major fraction of the material recovered in the gut analyses of juvenile mummichogs (Kneib, 1986). Copepods were the second most numerous prey taxa on standing-dead stems and the preference by *F. heteroclitus* for copepods was expected.

A 5-fold increase in *P. pugio* density did not result in a reciprocal increase in predation rates on copepod nauplii or any other stem faunal group. The apparently density-vague (sensu Strong, 1984) response of shrimp predators is not indicative of a species with the ability to regulate prey densities. The relatively short duration of the grass shrimp experiment may contribute to the inability to detect additional effects of increased predator densities. Grass shrimp had less than 12 h during the two high tide periods to forage over stem surfaces. The effects of grass shrimp predation on sediment-associated fauna are far less pronounced in short-term (hours) (Smith & Coull, 1987) compared to long-term (days) experiments (Bell & Coull, 1978). A preference for foraging in other microhabitats, e.g. sediments or standing-dead stems, and a possible refuge effect afforded to fauna living on the exteriors of live stems also may have contributed to an inability to detect density-influenced predation by *P. pugio*.

The difference in architectural complexity between live and standing-dead stems influenced the apparency of predation effects on stem fauna. Approximately half the fauna on live stems reside between the sheaths and stem and are unavailable to macroepibenthic predators moving over the stem surface. In previous studies the consideration of inappropriate prey, either in terms of species or habitats susceptible to predators, resulted in an overestimation of predation effects (Webb, 1991; McCall, 1992). Inclusion of interior stem fauna in current analyses would have underestimated grass shrimp predation effects by 50% and biased comparisons between live and standing-dead stem experiments.

The ability of live stems to provide a refuge from predation will vary both spatially and temporally. Metazoans on *S. alterniflora* in Louisiana typically are associated with epiphytic algae that covers stem exteriors (Rutledge & Fleeger, 1993). Only one copepod species, *Leptocaris brevicornis*, was found to invade interior stem surfaces (Rutledge & Fleeger, 1993). Unlike live stem faunal assemblages in Georgia, a majority of the *S. alterniflora*-associated fauna in

Louisiana would be susceptible to surface-foraging predators. Even the fauna on live stems in Georgia will experience a greater risk from surface-foraging predators as stems continue to decompose and lose sheaths throughout the growing season.

Although shrimp and fish predators were shown to have a major effect on stem-associated fauna in the present study, the general ability of macroepibenthic predators to influence metazoan densities predictably and affect population dynamics significantly remains controversial (see Gee, 1989; Coull, 1990). In intertidal salt marsh habitats predators can have either significant (Bell, 1980; Kneib & Stiven, 1982; Kneib, 1985; Smith & Coull, 1987; Ellis & Coull, 1989) or limited effects (Kneib, 1988; Raffaelli et al., 1989; Service et al., 1992) on sediment-associated assemblages. Habitat complexity (Marinelli & Coull, 1987), tritrophic level interactions (Kneib, 1988; Posey & Hines, 1991), tidal inundation frequency (Fleeger, 1985), reproductive recruitment (Woods & Coull, 1992), and the rapid dispersal and recolonization of predator-impacted areas (Billheimer & Coull, 1988; Kneib, 1994) all can influence the apparency of predation effects on sediment-associated fauna. A failure to consider stem-associated fauna also could affect the apparency of predation effects in intertidal benthic habitats. Macroepibenthic predators actually may prefer foraging on organisms living on stems. The potentially increased visibility of stem-resident fauna and a reduction in handling time, not having to process large amounts of sediment, may contribute to shrimp and fish preferentially foraging on stems. In addition the live stem habitat may act as a refuge or source pool for sediment-associated fauna. During periods of increased exposure to macroepibenthic predators (e.g. spring tides), typical sediment-associated fauna may move onto the interior surfaces of live stems to escape predators. Stem faunal assemblages also may act as a source pool from which the recolonization of predator-impacted benthic areas occurs. Whatever the mechanism, fauna resident on salt marsh vegetation represent a potential resource for intertidal marsh predators and likely will influence the dynamics of sediment-associated metazoan assemblages.

Acknowledgements

We thank L. Townsend and D. Casey for technical assistance and S. Bell, J. Fleeger, and two anonymous reviewers for constructive comments on earlier drafts. This research was supported in part by the University of Georgia Marine Institute's Student Intern Program and is Contribution No. 766 of the University of Georgia Marine Institute.

References

Bell, S.S., 1980. Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecol. Monogr.*, Vol. 50, pp. 487–505.

Bell, S.S. & B.C. Coull, 1978. Field evidence that shrimp predation regulates meiofauna. *Oecologia (Berlin)*, Vol. 35, pp. 141–148.

Billheimer, L.E. & B.C. Coull, 1988. Bioturbation and recolonization of meiobenthos in juvenile spot (Pisces) feeding pits. *Estuarine Coastal Shelf Sci.*, Vol. 27, pp. 335–340.

Cohen, J., 1988. *Statistical power analysis for the behavioral sciences*. Lawrence Erlbaum Associates, Hillsdale, second edition, 567 pp.

Coull, B.C., 1990. Are members of the meiofauna food for higher trophic levels? *Trans. Am. Microsc. Soc.*, Vol. 109, pp. 233–246.

Coull, B.C., S.S. Bell, A.M. Savory & B.D. Dudley, 1979. Zonation of meiobenthic copepods in a southeastern United States salt marsh. *Estuarine Coastal Mar. Sci.*, Vol. 9, pp. 181–188.

Day, R.W. & G.P. Quinn, 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.*, Vol. 59, pp. 433–463.

Edgar, G.J. & M. Aoki, 1993. Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese Sargassum. *Oecologia (Berlin)*, Vol. 95, pp. 122–133.

Ellis, M.J. & B.C. Coull, 1989. Fish predation on meiobenthos: field experiments with juvenile spot *Leiostomus xanthurus* Lacepede. *J. Exp. Mar. Biol. Ecol.*, Vol. 130, pp. 19–32.

Feller, R.J., B.C. Coull & B.T. Hentschel, 1990. Meiobenthic copepods: tracers of where juvenile *Leiostomus xanthurus* (Pisces) feed? *Can. J. Fish. Aquat. Sci.*, Vol. 47, pp. 1913–1919.

Ferrell, D.J. & J.D. Bell, 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Mar. Ecol. Prog. Ser.*, Vol. 72, pp. 15–24.

Fleeger, J.W., 1985. Small benthos in estuarine food webs: comparing intertidal and subtidal habitats. In, *Fourth coastal marsh and estuary management symposium*, edited by C.F. Bryan, P.J. Zwank & R.H. Chabreck, Louisiana Cooperative Fishery Research Unit, Baton Rouge, pp. 127–144.

Gee, J.M., 1987. Impact of epibenthic predation on estuarine intertidal harpacticoid copepod populations. *Mar. Biol.*, Vol. 96, pp. 497–510.

Gee, J.M., 1989. An ecological and economic review of meiofauna as food for fish. *Zool. J. Linn. Soc.*, Vol. 96, pp. 243–261.

Gleason, D.F., 1986. Utilization of salt marsh plants by post-larval brown shrimp: carbon assimilation rates and food preferences. *Mar. Ecol. Prog. Ser.*, Vol. 31, pp. 151–158.

Healy, B. & K. Walters, 1994. Oligochaeta in *Spartina* stems: the microdistribution of Enchytraeidae and Tubificidae in a salt marsh, Sapelo Island, USA. *Hydrobiologia*, Vol. 278, pp. 111–123.

Heck, K.L., K.W. Able, M.P. Fahay & C.T. Roman, 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition, seasonal abundance patterns and comparison with unvegetated substrates. *Estuaries*, Vol. 12, pp. 59–65.

Hettler, W.F., 1989. Nekton use of regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA. *Mar. Ecol. Prog. Ser.*, Vol. 56, pp. 111–118.

Hicks, G.R.F., 1984. Spatio-temporal dynamics of a meiobenthic copepod and the impact of predation-disturbance. *J. Exp. Mar. Biol. Ecol.*, Vol. 81, pp. 47–72.

Hicks, G.R.F. & B.A. Marshall, 1985. Sex Selective predation of deep-sea, meiobenthic copepods by pectinacean bivalves and its influence on copepod sex ratios. *N.Z. J. Mar. Freshwater Res.*, Vol. 19, pp. 227–231.

Holmlund, M.A., C.H. Peterson & M.E. Hay, 1990. Does algal morphology affect amphipod susceptability to fish predation? *J. Exp. Mar. Biol. Ecol.*, Vol. 139, pp. 65–83.

Joyner, S.P., 1985. *SAS/STAT guide for personal computers*. SAS Institute Inc., Carey, version 6 edition, 378 pp.

Kennelly, S.J., 1991. Caging experiments to examine the effects of fishes on understorey species in a sublittoral kelp community. *J. Exp. Mar. Biol. Ecol.*, Vol. 147, pp. 207–230.

Kneib, R.T., 1984. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). *J. Exp. Mar. Biol. Ecol.*, Vol. 83, pp. 41–51.

Kneib, R.T., 1985. Predation and disturbance by grass shrimp, *Palaemonetes pugio* Holthuis, in soft-stratum benthic invertebrate assemblages. *J. Exp. Mar. Biol. Ecol.*, Vol. 93, pp. 91–102.

Kneib, R.T., 1986. The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. *Am. Zool.*, Vol. 26, pp. 259–269.

Kneib, R.T., 1987. Seasonal abundance, distribution and growth of postlarval and juvenile grass shrimp (*Palaemonetes pugio*) in a Georgia, USA, salt marsh. *Mar. Biol.*, Vol. 96, pp. 215–223.

Kneib, R.T., 1988. Testing for indirect effects of predation in an intertidal soft-bottom community. *Ecology*, Vol. 69, pp. 1795–1805.

Kneib, R.T., 1991. Flume weir for quantitative collection of nekton from vegetated intertidal habitats. *Mar. Ecol. Prog. Ser.*, Vol. 69, pp. 29–28.

Kneib, R.T., 1994. Spatial pattern, spatial scale, and feeding in fishes. In, *Theory and application in fish feeding ecology*, edited by D.J. Stouder, K.L. Fresh & R.J. Feller, University of South Carolina Press, Columbia, pp. 171–185.

Kneib, R.T. & A.E. Stiven, 1982. Benthic invertebrate responses to size and density manipulations of the common mummichog, *Fundulus heteroclitus*, in an intertidal saltmarsh. *Ecology*, Vol. 63, pp. 1518–1532.

Leber, K.M., 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology*, Vol. 66, pp. 1951–1964.

Lewis, F.G., 1984. Distribution of macrobenthic crustaceans associated with *Thalassia, Halodule* and bare sand substrata. *Mar. Ecol. Prog. Ser.*, Vol. 19, pp. 101–113.

Marinelli, R.L. & B.C. Coull, 1987. Structural complexity and juvenile fish predation on meiobenthos: an experimental approach. *J. Exp. Mar. Biol. Ecol.*, Vol. 108, pp. 67–81.

Martin-Smith, K.M., 1993. Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *J. Exp. Mar. Biol. Ecol.*, Vol. 174, pp. 243–260.

McCall, J.N., 1992. Source of harpacticoid copepods in the diet of juvenile starry flounder. *Mar. Ecol. Prog. Ser.*, Vol. 86, pp. 41–50.

McCall, J.N. & J.W. Fleeger, 1993. Recognition and utilization of prey aggregations by juvenile spot (*Leiostomus xanthurus* Lacépède). *J. Exp. Mar. Biol. Ecol.*, Vol. 174, pp. 121–134.

McIvor, C.C. & W.E. Odum, 1988. Food, predation risk and microhabitat selection in a marsh fish assemblage. *Ecology*, Vol. 69, pp. 1341–1351.

Morgan, M.D., 1980. Grazing and predation of the grass shrimp *Palaemonetes pugio. Limnol. Oceanogr.*, Vol. 25, pp. 896–902.

Nelson, A.L. & B.C. Coull, 1989. Selection of meiobenthic prey by juvenile spot (Pisces): and experimental study. *Mar. Ecol. Prog. Ser.*, Vol. 53, pp. 51–57.

Orth, R.J., K.L. Heck & J. van Montfrans, 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries*, Vol. 7, pp. 339–350.

Palmer, M.A., 1988. Epibenthic predators and marine meiofauna: separating predation, disturbance, and hydrodynamic effects. *Ecology*, Vol. 69, pp. 1251–1259.

Posey, M.H. & A.H. Hines, 1991. Complex predator-prey interactions within an estuarine benthic community. *Ecology*, Vol. 72, pp. 2155–2169.

Raffaelli, D., A. Conacher, H. McLachlan & C. Emes, 1989. The role of epibenthic crustacean predators in an estuarine food web. *Estuarine Coastal Shelf Sci.*, Vol. 28, pp. 149–160.

Rozas, L.P. & M.W. LaSalle, 1990. A comparison of the diets of the Gulf killifish, *Fundulus grandis* Baird and Girard, entering and leaving a Mississippi brackish marsh. *Estuaries*, Vol. 13, pp. 332–336.

Rozas, L.P. & W.E. Odum, 1987. Fish and macrocrustacean use of submerged plant beds in tidal freshwater marsh creeks. *Mar. Ecol. Prog. Ser.*, Vol. 38, pp. 101–108.

Rozas, L.P. & W.E. Odum, 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia (Berlin)*, Vol. 77, pp. 101–106.

Russo, A.R., 1987. Role of habitat complexity in mediating predation by the gray damselfish *Abudefduf sordidus* on amphipods. *Mar. Ecol. Prog. Ser.*, Vol. 36, pp. 101–105.

Rutledge, P.A. & J.W. Fleeger, 1993. Abundance and seasonality of meiofauna, including harpacticoid copepod species, associated with stems of the salt-marsh cordgrass, *Spartina alterniflora. Estuaries*, Vol. 16, pp. 760–768.

Service, S.K., R.J. Feller, B.C. Coull & R. Woods, 1992. Predation effect of three fish species and a shrimp on macrobenthos and meiobenthos in microcosms. Estuarine Coastal Shelf Sci., Vol. 34, pp. 277–293.

Smith, L.D. & B.C. Coull, 1987. Juvenile spot (Pices) and grass shrimp predation on meiobenthos in muddy and sandy substrata. *J. Exp. Mar. Biol. Ecol.*, Vol. 105, pp. 123–136.

Stoner, A.W., 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull. Mar. Sci.*, Vol. 30, pp. 537–551.

Strong, D.R., 1984. Density-vague population dynamics. In, *A new ecology: novel approaches to interactive systems*, edited by P.W. Price, C.N. Slobodchikoff & W.S. Gaud, Wiley-Interscience, New York, pp. 313–327.

Summerson, H.C. & C.H. Peterson, 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. *Mar. Ecol. Prog. Ser.*, Vol. 15, pp. 63–77.

Van Dolah, R.F., 1978. Factors regulating the distribution and population dynamics of the amphipod Gammarus palustris in an intertidal salt marsh community. *Ecol. Monogr.*, Vol. 48, pp. 191–217.

Webb, D.G., 1991. Effect of predation by juvenile Pacific salmon on marine harpacticoid copepods. I. Comparisons of patterns of copepod mortality with patterns of salmon consumption. *Mar. Ecol. Prog. Ser.*, Vol. 72, pp. 25–36.

Wieser, W., 1960. Benthic studies in Buzzards Bay. II. The meiofauna. *Limnol. Oceanogr.*, Vol. 5, pp. 121–137.

Woods R.E. & B.C. Coull, 1992. Life history responses of *Amphiascus tenuiremis* (Copepoda, Harpacticoida) to mimicked predation. *Mar. Ecol. Prog. Ser.*, Vol. 79, pp. 225–234.