The effect of macrophytic cover on survival of *Palaemonetes pugio* and *P. vulgaris* (grass shrimp) in the presence of predatory *Fundulus heteroclitus* (killifish)

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Abstract

Effects of three different macrophytic covers and the presence of alternative prey on survival of grass shrimp (*Palaemonetes pugio* and *P. vulgaris*) subjected to predation by killifish (*Fundulus heteroclitus*) were studied in the laboratory. Overall, survival of *P. vulgaris* was significantly greater (82%) than that of *P. pugio* (70%). This difference in survival was attributed to the greater tendency of *P. pugio* to swim outside the covers, making it more vulnerable to predation. Both prey species responded similarly to the different cover conditions. Survival without cover (gravel substrate) was 48%. In cover provided by a plastic plant made to resemble *Ambulia*, 75% of the starting population survived. In cover furnished by field-collected specimens of the flat chlorophyte, *Ulva*, survival was 71%, compared to 98% survival in the branched green alga, *Codium*. Predation pressure on neither species was significantly enhanced or diminished by the presence of a second prey species.

For both grass shrimp species, increased survival in *Codium* in the presence of the predator was attributed to the physically more complex nature of this macrophytic cover.

Contents

Introduction

Vast numbers of grass shrimp (*Palaemonetes* spp.) occur in shallow water of estuaries and bays of the U.S. Atlantic and Gulf coasts (Anderson, 1985), where they congregate on areas of bare mud, sand and shell flats, and on wooden pilings (Knowlton et al., 1994), but they are particularly abundant in dense stands of underwater macrophytes (Orth et al., 1984). The two most common species of *Palaemonetes* associated with tidal marshes and creeks of the mid-Atlantic region are *P. pugio* and *P. vulgaris* (Williams, 1984). Because these two species are especially common in areas with macrophytic cover, the nature of the vegetation may be presumed to have a major influence on their abundance, distribution, and loss to predation. Indeed, distributional differences in relation to structural characteristics of macrophytic algae have been demonstrated in a laboratory setting (Khan et al., 1997).

Predation has been shown to influence the distribution and abundance of species within marine habitats (Kneib, 1988; Primavera, 1997). When predators are present, prey organisms frequently switch microhabitats, choosing a site where they are less vulnerable (Main, 1987; Everett and Ruiz, 1993). Both laboratory and field experiments have indicated that for many species of invertebrates, including *Palaemonetes* spp., macrophytic vegetation can provide protection from predators (Rozas and Odum, 1988; Tayasu et al., 1996). With the decline of submerged aquatic vegetation in deeper waters of Chesapeake Bay, many animals have been

reported to shift from deeper water (>1 meter) to shallower conditions (<35 cm) along the shoreline where important structural features created by woody debris provide refuge from predation (Ruiz et al., 1993).

Interactions between prey species, especially as they influence the use of cover, may alter the impact of a predator upon those prey species. For example, Thorp (1976) felt that oyster shell provides protection from predation and that *P. vulgaris* is more resistant to predation because it displaces *P. pugio* from a shelly substrate.

The killifish *Fundulus heteroclitus* is a permanent marsh resident and is abundant in areas inhabited by *Palaemonetes*. Studies of stomach contents have indicated that grass shrimp are an important component of the killifish diet (Heck and Thomas, 1981; Overstreet and Heard, 1982).

The role of macrophytic covers in predation served as the focus of the present study whose primary purpose was to determine how the presence of *F. heteroclitus* quantitatively affects survival of *P. pugio* and *P. vulgaris* in the various experimental covers. The questions asked were: 1) Is predation pressure the same for both species of grass shrimp? 2) Does macrophytic cover reduce the amount of predatory loss for one or the other prey species of grass shrimp? 3) If macrophytic cover reduces loss to predators, are all kinds of macrophytic cover equally effective in reducing the loss? 4) Does the presence of the second prey species of grass shrimp enhance or lessen the predatory loss of the first prey species?

Materials and methods

Field methods

Animals and natural cover types used in all experiments were collected from Indian River Bay, a small Atlantic estuary in southeast Delaware, U.S.A. This site was chosen because the sympatric grass shrimp species *P. pugio* and *P. vulgaris*, the killifish *Fundulus heteroclitus*, and natural plant covers (the green algae *Codium fragile* and *Ulva lactuca*) were easily found there. A dip net was used to collect both grass shrimp species. Killifish

and submerged macrophytes were collected with a seine drawn over relatively flat areas of tidal creeks. Substrate items were removed from the top 2 cm of marsh surface with a shovel at low tide. At the time of collection, *Ulva* and *Codium* dominated benthic macrophytes within the sampling area, and both were collected by hand. All field collected animals, plants, and substrate materials were transported to the laboratory in separate plastic containers.

Laboratory methods

In the laboratory, macrophytes and substrates were placed in separate 20-l plastic buckets containing aerated seawater. Shrimp were sorted by species and placed into separate 350-l flow-through aquaria equipped with undergravel biological filters. Aeration was provided by air stones that were connected via plastic tubing to a constant air supply. In these stock holding tanks, salinity (35 ppt), temperature (22°C), pH (8.2), dissolved oxygen (18mg/l), and photoperiod (12L:12D) were held constant. Photoperiod was maintained via automatic timers. In an attempt to minimize the influence of possible conditioning during holding, both species of shrimp were held without any cover or vertical structure (including macrophytes) over a level layer of colorless, commercially obtained aquarium gravel composed of quartz fragments. The gravel fragments were not homogeneous in size. The largest particles were 0.95 cm in diameter and were retained on a #5 USA Standard Testing Sieve; the smallest were retained on a #21 sieve. One percent (by weight) of the gravel was retained on the #5 sieve; 72% on a #10 sieve; 18% on a #12 sieve; 9% on the #21 sieve. While awaiting use in experiments, shrimp were fed daily surfeit amounts of commercially obtained fish food (Tetra-Min®, manufactured by TetraWerke, Melle, Germany). Food was not offered during the 12-hour period immediately preceding selection of shrimp for use in the experiments.

In a separate holding aquarium, *Fundulus heteroclitus* (80 ± 5 mm in length) were maintained over bare gravel in the same physico-chemical conditions as the grass shrimp. Killifish were fed a diet of *Palaemonetes* daily except that no prey were pro-

vided for 48 hours prior to their use as predators in experiments.

All experiments took place in four separate aquaria arranged linearly on a bench within the same room and at the same temperature and photoperiod as the holding tanks. Preliminary experiments indicated that there were no position effects associated with the location of the tanks with respect to each other. The experimental aquaria were each 60 × 30 × 35 cm (approx. 63-l) and were half filled with artificial sea water (35 ppt; pH 8.2) prepared by dissolving Instant Ocean® sea salts in deionized water. There was no flow-through system in the experimental aquaria. Air stones connected to the same air supply as the holding tanks provided constant aeration except that in an attempt to remove a possibly confounding source of procedural variation, the stones were removed 12 hours prior to and during the experiments. Earlier experiments (Khan et al., 1995) established species differences in the number of grass shrimp resting on the commonly occurring natural substrates (wood, sand, shell, and mud). Since the use of macrophytic cover in response to the presence of the predator might be influenced by an association with a particular type of natural substrate, the same artificial (and therefore more likely to be neutral) substrate used in the holding tanks (colorless quartz aquarium gravel) was used in the present experiments. Four plastic trays (each 30 × 15 cm) were tightly fitted into the bottom of each aquarium; into each tray a level (2-cm thick) layer of aquarium gravel was placed. In one of the aquaria, all four trays were left without macrophytic cover. In the other three aquaria, individuals of one type of macrophytic cover were randomly selected from the stock tanks and added to all four trays. One of the three aquaria received *Codium*; another, *Ulva*; the third, a synthetic "plant" made of a plastic material (polypropylene) superficially resembling *Ambulia*. Within each aquarium enriched with macrophytes, approximately 90% of the area was covered by individuals of the appropriate macrophyte. Ten gram lead weights held the macrophytes in position. Highly branched *Codium* offered cover that was a more-or-less erect loose tangle of semi-rigid thalli at various levels above the substrate. The individuals of *Codium* were densely covered with periphyton.

The broad, flat thalli of *Ulva* "flopped" over, providing a broad sheet of cover appressed at the unanchored edge against the gravel substrate. Periphyton on *Ulva*, if present, was not noticeable. The synthetic "*Ambulia*" provided structure characterized by stiff upright "stems" with regular broader "leaves" at regular vertical intervals. No periphyton was present on the "*Ambulia*."

In all of the experiments reported here, counts of shrimp were made during daylight hours under ambient room lighting. Shrimp tended to be sedentary for sufficiently long times to allow careful counting. When macrophytic covers were provided, their nature and density did not interfere with accurate counting of shrimp. *Codium* was openly branched and the loose tangle of thalli permitted seeing into the cover. Erect portions of *Ulva* provided passages between the thalli that allowed the observer to readily see into the cover, and although *Ulva* tended to flop over on itself, it did so such that shrimp could congregate within the spaces between the bends and folds. Shrimp tended not to push themselves between the appressed edge of the *Ulva* thalli and the substrate, and therefore remained visible to the experimenter. "*Ambulia*" was upright and rigid with many spaces between "stems" and "leaves" that permitted seeing into the cover.

After the experimental aquaria were established, 20 individual *Palaemonetes pugio* (30 ± 5 mm in length) and two *Fundulus heteroclitus* (80 ± 5 mm in length) were selected at random from the stock aquaria and added to each of the experimental aquaria. Numbers of prey and predator individuals used per replicate experiment were based upon pilot studies conducted over bare gravel (as used in the present study) which indicated that one killifish of this size could consume five *Palaemonetes* of either species in 24 hours. If this exploitation rate prevailed in the present study, a starting population of 20 prey individuals would leave 10 live individuals after 24 hours exposure to the predator. The aquaria were left undisturbed for 24 hours after which the *Fundulus* were removed from the aquaria, and the number of surviving prey was counted and recorded. Counts are known to be accurate because at the time of counting, all shrimp were removed, recounted, and discarded. Killifish, live and plastic

plants, and gravel also were removed from the aquaria and discarded. This entire experimental procedure was repeated once using different individuals of the same prey species, different individuals of the predator (*Fundulus*), different individuals of live and plastic macrophytic cover, and different gravel. These procedures were repeated twice more using the second prey species, *Palaemonetes vulgaris* (30 ± 5 mm in length), instead of *P. pugio*.

The experimental protocol was repeated two more times, but in each of these replicates, 15 individuals of each prey species were substituted for the 20 individuals of a single prey species. In these "mixed-species" experiments, distinguishing the two species was made easier by prior staining of one of the species with Alcian blue. It has been established that this procedure affects neither the viability nor the behavior of stained individuals (Coen et al., 1981). In the first of these mixed species replicates, *P. vulgaris* was stained; in the second, *P. pugio*. In the present studies, the similarity in the number of each species consumed by the predator when the prey was stained *vs.* unstained suggests that vulnerability to predation was also not affected by staining.

Analytical and statistical methods

Pilot studies indicated that after an initial acclimation period spent in the holding tanks, and in the absence of a predator, no shrimp died during exposure to the conditions of the experiments. Therefore, the distribution of the mean number of shrimp surviving in each condition of macrophytic cover in the presence of the predator was compared (using a Chi-square test) to the expected distribution based upon the *a priori* assumption that no deaths (thus 100% survival) would occur in each cover condition. A significant Chi-square value was taken to indicate a significant influence of the predator upon the number of survivors in the four macrophytic cover conditions. In the Chi-square analysis, the null hypothesis was that there is no difference between the observed distribution of survivors and the distribution expected by assuming that the predator would consume no prey in any cover condition. The alternative hypothesis was that the

predator would consume enough prey in at least one of the cover conditions to cause the distribution of surviving shrimp among the cover types to be significantly different from that based upon 100 percent survival in all cover conditions.

Since in this study all deaths were assumed to be due to predation, predation pressure was measured by calculating the percentage of the starting population of each prey species that was missing after 24 hours of exposure to the predator.

The number of shrimp surviving in each condition of macrophytic cover in the presence of the predator was converted to percent of the starting population of shrimp of that species. The percent values were normalized using the angular transformation (Sokal and Rohlf, 1995).

A test for homogeneity of variances between the data for each species was conducted by calculating separately the total variance within the arcsine transformed data for each species (*P. pugio* and *P. vulgaris*). Following Sokal and Rohlf (1995), these variances were compared using an F- test and found to be not significantly different (F = 1.15; df = 15, 15; .10 < P < .25). Therefore, the arcsine transformed survivorship data for both species were combined into a single data set and analyzed using a three-factor analysis of variance (ANOVA). In this analysis, the main effects were "species" (predator's effect on the survivorship of each prey species: *P. pugio* and *P. vulgaris*); "cover" (predator's effect on the prey's survivorship in each type of cover: none, *Ulva*, *Codium*, and "*Ambulia*"); "exposure" (predator's effect on the prey's survivorship when the prey were exposed to the predator alone or in the presence of the second prey species).

In the ANOVA, estimates of the variation contributed by the main effects (the independent sources of variation) and by the interactions between and among them were compared with random (error) variation using F-tests. The working hypothesis was that one or more of the designed sources of variation and/or interactions between and among them contributes more variation than that due to error and thereby is identified as a significant contributor to the differences in observed shrimp survivorship among the different macrophytic covers. When interactions were determined to be significant, further testing of the entangled main effects was

precluded. Multiple-means analyses using Tukey's honestly significant difference (T-method of Sokal and Rohlf, 1995) were performed on sources of variation showing significant F values ($\alpha = .05$).

In each F-test, the null hypothesis was that there is no difference between the variance contributed by the main effect (or by the interaction between or among main effects) and the variance due to chance (error). If the null hypothesis for any source of variation was rejected, then the null hypothesis for the T-method multiple-means comparisons was that all means of all levels for the significant source of variation were not significantly different from each other.

Results

Behavior of prey and predator

Although the focus of the present work was not to describe the behavior of the participants during exposure of the prey to the predator, certain behaviors and features of the predator-prey interaction were repeatedly observed and noted in all of the experiments. These behaviors are reported here because they may provide additional insight into understanding the role of macrophytic cover in the predator-prey interaction between *Fundulus* and *Palaemonetes*.

In the absence of the predator, *Palaemonetes* was found within the cover and on the substrate around the cover. At any given time, a small number of animals (<10%) swam in the water column above the cover.

Outside and within macrophytic cover, individuals of both species of *Palaemonetes* spent the majority of time resting (rest = time spent in no overall body movement; antennae, mouth parts, and appendages may or may not be in motion during rest). Typically *Palaemonetes* moved from one resting place to another by a short burst of swimming activity that was accomplished by typical metachronal waving of the pleopods. This movement of the appendages lifted the individual up (from its resting place), carried it through the water, and settled it at another resting place. An approach or attack by a predator (attack = a short thrust by

the predator toward a prey individual) stimulated the shrimp's caridoid escape reflex (characteristic backward movement of carideans, brought about by sudden flexure of the abdomen) and ended when the predator caught the prey or the prey individual swam rapidly away from the predator (usually towards cover). As reported elsewhere (Khan et al., 1997), both the predator and the prey were observed entering and moving within all three types of macrophytic cover, but *Fundulus*, which tended to rest around the edges of the cover or swim in the water column above the cover, entered the cover rarely and then usually when in pursuit of a prey individual that had entered the cover. In general, predators attacked prey when prey were swimming, and predators would pass by closer, inactive prey to attack more distant moving prey. Chases (chase = a longer episode of *Palaemonetes* swimming while being pursued by an attacking *Fundulus*) were uncommon and occurred when the shrimp was swimming above the cover near the water surface. With and without a predator present, *P. pugio* appeared to be a more active swimmer than *P. vulgaris*, spending consistently more time swimming above or outside the cover. In response, attacks upon and chases of prey more often involved *P. pugio* than *P. vulgaris*. From five to forty attacks (not necessarily directed against the same individual) were required for *Fundulus* to successfully grab an individual shrimp. Capture usually involved *Fundulus* grabbing the head of the shrimp with its mouth. Typically, 5 minutes elapsed from time of capture to complete consumption of a prey individual.

Macrophytic cover, predation, and survivorship

Mean numbers of prey survivors in two replicates of 24-hr exposure to predators in the experimental cover conditions, and mean numbers of survivors expected on the basis of assuming no loss to the predator are presented in Table I. The pattern of differences between observed and expected distributions is similar for both species. The number of survivors in the condition of no cover is far less than that expected; "*Ambulia*" and *Ulva* are associated with observed numbers of survivors that are

Table I. Comparison of the observed distribution of survivors (mean of two replicates) with that expected by assuming no loss of individuals due to predation. O = observed; E = expected; "*" = significant (α = .05); "ns" = not significant (α = .05).

Each prey species exposed alone to predator:

Palaemonetes pugio

Cover condition	O	E	$(O-E)^2/E$	X^2
No cover	9.5	20.0	5.51	9.84*
"Ambulia"	13.5	20.0	2.11	
Ulva	13.5	20.0	2.11	
Codium	18.5	20.0	0.11	

Palaemonetes vulgaris

Cover condition	O	E	$(O-E)^2/E$	X^2
No cover	12.5	20.0	2.81	4.63ns
"Ambulia"	16.0	20.0	0.80	
Ulva	15.5	20.0	1.01	
Codium	19.5	20.0	0.01	

Both prey species exposed simultaneously to predator:

Palaemonetes pugio

Cover condition	O	E	$(O-E)^2/E$	X^2
No cover	4.5	15.0	7.3	9.86*
"Ambulia"	11.5	15.0	0.82	
Ulva	10.0	15.0	1.67	
Codium	14.5	15.0	0.02	

Palaemonetes vulgaris

Cover condition	O	E	$(O-E)^2/E$	X^2
No cover	8.5	15.0	2.82	4.46ns
"Ambulia"	11.5	15.0	0.82	
Ulva	11.5	15.0	0.82	
Codium	15.0	15.0	0.00	

much closer to the numbers expected; and in *Codium* there is little difference between what is observed and what is expected. This general pattern holds, even when the predator is exposed simultaneously to the two prey species. Chi-square tests comparing the observed and expected distributions (Table I) indicate that for *P. pugio*, whether exposed alone to the predator or simultaneously with *P. vulgaris*, the difference between observed and expected distributions is significant (df = 3; α = .05). For *P. vulgaris*, these differences are not significant.

Predation pressure under the experimental conditions of exposure and cover, as measured by the percentage of the starting prey population missing after 24-hr exposure to the predator, is reported in Table II. Whether exposed alone or together, both prey species are effectively sheltered by *Codium*, where both species lose <10% of the starting population to the predator. However, when exposed alone, the protection afforded *P. vulgaris* by *Codium* is so great that even the small loss of *P. pugio* is 3.5 times that of *P. vulgaris*. Predation pressure in "*Ambulia*" and *Ulva* is similar for both prey species, but for *P. pugio* it is about 1.5 times as much as for *P. vulgaris*. In these moderately protective covers, the presence of the second prey species decreases the predation pressure on *P. pugio* and increases it on *P. vulgaris*. However, neither of the changes associated with the presence of the second prey species is very large. Exposed alone and without cover, predation pressure results in the loss of little more than one-third of the starting population of *P. vulgaris* but removes more than half of the starting population of *P. pugio*. When the two prey species are exposed together without cover to the predator, predatory loss increases for both species (6% for *P. vulgaris* and 18% for *P. pugio*). Whether exposed without cover alone or in combination with *P. vulgaris*, *P. pugio* bears about one and one-half times the predation pressure of *P. vulgaris*.

Results of the ANOVA performed on survivorship values (as arcsine transformed percentage of starting population) in each condition of experimental cover are reported in Table III. The lack of significant variation contributed by any interaction between and among the three independent sources of variation indicates that the prey (*P. pugio* and *P. vulgaris*) responded alike to the designed changes in cover, exposure, and species. The lack of significant variation contributed by exposure reveals that the impact of the predator upon a specific prey species was not reduced or enhanced by the presence of an equal number of individuals of the second prey species. The significant variation contributed by the independent sources, cover and species, shows that these variables influenced importantly the number of prey consumed by the predator.

Results of the multiple means analysis (T-

Table II. Predation pressure under experimental conditions of cover and exposure. Mean number consumed is the difference between the starting number of each prey species (20 in single exposure; 15 in combined exposure) and the mean number (two replicates) surviving after 24 hours exposure to the predator. Predation pressure is the percentage of starting population of prey species consumed.

Each prey species exposed alone to predator

Palaemonetes pugio

Cover condition	Mean number consumed	Predation pressure
No cover	10.5	52
"Ambulia"	6.5	32
Ulva	6.5	32
Codium	1.5	7

Palaemonetes vulgaris

Cover condition	Mean number consumed	Predation pressure
No cover	7.5	37
"Ambulia"	4.0	20
Ulva	4.5	22
Codium	0.5	2

Both prey species exposed simultaneously to predator

Palaemonetes pugio

Cover condition	Mean number consumed	Predation pressure
No cover	10.5	70
"Ambulia"	3.5	23
Ulva	5.0	33
Codium	0.5	3

Palaemonetes vulgaris

Cover condition	Mean number consumed	Predation pressure
No cover	6.5	43
"Ambulia"	3.5	23
Ulva	3.5	23
Codium	0	0

method) of the effect of cover are given in Table IV. Predation by *Fundulus* in the absence of cover caused a loss >50% of the experimental population of *Palaemonetes* prey. This loss of population was reduced significantly by adding cover, allowing

at least 70% of the prey population to survive. The different macrophytic covers, however, were not equally effective in increasing prey survivorship. While *Ulva* and the plastic "*Ambulia*" allowed about 30% loss to the predator, *Codium* permitted the predator to consume an average of only 2% of starting population of prey.

The results of means comparison (T-method) of the effect of species are in Table V in which it is shown that overall mean survivorship by *P. vulgaris* was significantly greater than that of *P. pugio*.

Discussion

1) Is predation pressure the same for both species of grass shrimp?

Because in Table II, the loss of *P. pugio* is about 1.5 times that of *P. vulgaris*, it can be concluded that in the absence of macrophytic cover, predation pressure upon *P. pugio* is greater than that upon *P. vulgaris*. In addition, since the differences between the numbers observed and the numbers expected in Table I are the direct result of predation by *Fundulus heteroclitus*, it is obvious that predatory loss is greater for *P. pugio* than for *P. vulgaris*. The importance of this difference is emphasized by the fact that for *P. pugio*, loss of individuals is sufficient to cause the distribution of survivors among the cover types to be significantly different from what it would have been if there had been no predator. For *P. vulgaris*, the numbers taken by the predator are insufficient to cause the distribution among the cover types to deviate significantly from that expected without predation. The significance of species as an independent source of variation (Table III) and the subsequent means analysis (Table V) reiterate the conclusion that predation on *P. pugio* is greater than that on *P. vulgaris*. Furthermore the failure of the cover-by-species interaction to be significant (Table III) indicates that although altering the cover type does significantly change the number of individuals lost to the predator, it does not change the relationship of predatory loss between the two prey species, *i.e.* more *P. pugio* are eaten regardless of the cover type. The behavioral observations of the present study may pro-

vide some insight as to why losses of *P. pugio* are greater than those of *P. vulgaris*. With and without a predator present, *P. pugio* appeared to be a more active swimmer than *P. vulgaris*, spending consistently more time swimming above the substrate or outside the cover. In response, chases between predator and prey more often involved *P. pugio* than *P. vulgaris*.

2) Does macrophytic cover reduce the amount of predatory loss for one or the other prey species of grass shrimp?

Other investigators (Heck and Thomas, 1981; Rozas and Odum, 1988) have suggested that macrophytic cover provides shelter for *Palaemonetes* in the presence of *Fundulus*. Our results (Table I) support this suggestion in that for both prey species, predator induced losses cause the difference in distribution of survivors among the cover types to be different from that expected on the basis of assuming no loss to predators. For both prey species in both exposure conditions, the differences between the observed and expected numbers are greater for the "no cover" condition. However, the difference between the observed distribution (after predatory loss) and the expected distribution of survivors (assuming no predation) is significant only for *P. pugio*. Thus, our results not only point out increased *Palaemonetes* survivorship associated with macrophytic vegetation, they also indicate that macrophytic cover shelters *P. vulgaris* better than it shelters *P. pugio*.

The ANOVA (Table III), in its indication that cover is a significant source of variation restates \ the conclusion that cover significantly affects survivorship of *P. pugio* and *P. vulgaris*. The means analysis of the effect of cover (Table IV) emphasizes the importance of macrophytes in reducing loss of shrimp to the predatory killifish by showing that without cover, more than half of the starting population of *Palaemonetes* is consumed by *Fundulus*, but in cover provided by the macrophyte, *Codium*, survivorship (percent of starting population) more than doubles. Heck and Thomas (1981) feel that reduction in predatory loss of grass shrimp in dense macrophytes is the direct result of serious restriction of the fish's movement. Although this may be the

Table III. Three Factor Analysis of Variance of arcsine transformed survivorship (expressed as percentage of starting population) of prey species (*P. pugio* and *P. vulgaris*) under different condition of cover and after 24-hour exposure to the predator *Fundulus heteroclitus*. The independent sources of variation were type of "cover" (none, "*Ambulia*", *Ulva, Codium*), "exposure" (prey species exposed to predator alone or with both prey species present) and "species" (*P. pugio* and *P. vulgaris*).

Source	df	MS	F	Decision (α = .05)
Total	31			
Cover	3	2030.70	74.62	significant
Exposure	1	1.37	0.05	not significant
Cover × Exposure	3	79.29	2.91	not significant
Species	1	394.03	14.48	significant
Cover × Species	3	34.83	1.28	not significant
Exposure × Species	1	10.75	0.40	not significant
Cover × Exposure × Species	3	24.23	0.89	not significant
Replicate = Error	16	27.21		

case, observations of behavior in the present study reveal that predators are far more likely to capture prey when they are swimming, and prey typically do not swim but rest or walk slowly among the branches or thalli of the cover. Several investigators have shown that in the presence of predators, movement of invertebrate prey species decreases and prey movement is likely to bring about a predatory attack. Stein and Magnuson (1976) documented such behavior of crayfish in the presence of potentially predatory fish. Heck and Thomas (1981) reported that killifish attacked grass shrimp only when the latter are actively swimming near the water surface. Thus, the behavioral observations of this study and the description associating prey movement with intensity of predation suggest that the protection afforded shrimp by cover is the indirect result of shrimp tending to remain more stationary when in cover.

Khan *et al.* (1997) found that in the absence of predators and when given the opportunity to choose, *P. pugio* and *P. vulgaris* rest least often on bare substrate, most often in *Codium*, and in intermediate numbers in "*Ambulia*" and *Ulva*. The similarity in distribution of individuals seen in this and the present study in the presence and absence of predators suggests that *Palaemonetes* may settle in cover in response to cues that are unrelated to predation

pressure. However, an alternative explanation for the choice of covered resting place in the absence of predators might be that these field-caught but laboratory-tested prey individuals are expressing residual conditioning acquired in the field where predators are common. This alternative explanation is consistent with the reports by Coen et al. (1981), Heck and Thomas (1981), and Primavera (1997) in which it is held that shrimp seek "covered" habitat as refuge from predation. Resolution of this issue awaits further investigation.

3) If macrophytic cover reduces loss to predators, are all kinds of macrophytic cover equally effective in reducing the loss?

The obvious conclusion drawn from Table IV is that different kinds of cover are not alike in the amount of protection they provide. While predatory loss in *Codium* isabout 2% of the starting population, the living macrophyte, *Ulva*, and the plastic plant resembling *Ambulia* are similar in providing significantly less protection (about 22% loss of individuals). The similarity in shrimp survivorship in *Ulva* and in the plastic plant (*"Ambulia"*) strongly suggests that the protective role of cover is simply that of providing increased structural complexity within which the shrimp and their activity is concealed from the predator. Main (1987) concluded that a predator might view macrophytic cover as a complex opaque environment that stands as a visual barrier between predator and prey. *Codium*, a coarsely branched macrophyte, certainly provides a greater physical complexity and heterogeneity than *"Ambulia"* with its regular arrangement of "stems" and "leaves." *Ulva*, with its flopped-over, closely appressed thallus and lower vertical depth may provide even less structural complexity than *"Ambulia,"* however, compared to *"Ambulia"* the effect of this difference on shrimp survivorship is not significant.   "

4) Does the presence of the second prey species of grass shrimp enhance or lessen the predatory loss of the first prey species?

Thorp (1976) has suggested that *P. vulgaris* behaviorally dominates *P. pugio*, excluding it from

Table IV. Means analysis of the effect of cover on prey survivorship. Values in the table are mean arcsine transformed survivorship values for prey (*Palaemonetes*) under various conditions of cover after 24-hour exposure to the predator *Fundulus heteroclitus*. Means followed by the same lower case letter are not significantly different (T-method; α = .05). Numbers in parentheses after the tabulated mean are back-transformed mean percent values.

Cover	Mean survivorship
None	44.15 a (48.5)
"Ambulia"	59.77 b (74.6)
Ulva	57.71 b (71.5)
Codium	82.16 c (98.1)

Table V. Means analysis of the effect of species on prey survivorship. Values in the table are mean arcsine transformed survivorship values for prey (*Palaemonetes pugio and Palaemonetes vulgaris*) under various conditions of cover after 24-hour exposure to the predator *Fundulus heteroclitus*. Means followed by the same lower case letter are not significantly different (T-method; α = .05). Numbers in parentheses after the tabulated mean are back-transformed mean percent values.

Species	Mean survivorship
P. pugio	57.00 a (70.3)
P. vulgaris	64.90 b (82.0)

sheltering habitat thereby causing its greater loss to predators. Similarly, the data in Table II suggest that exposure of *P. pugio* to *Fundulus heteroclitus* in the presence of *P. vulgaris* causes greater loss to the predator (especially without cover). If, in the present study, *P. vulgaris* were indeed excluding *P. pugio* from sheltered habitat, then survival of *P. pugio* in the presence of *P. vulgaris* and *F. heteroclitus* should be significantly lower than in the presence of *F. heteroclitus* alone. At the same time, survival of *P. vulgaris* alone should be no different from its survival in the presence of both the predator and the alternative prey, *P. pugio*. However, the ANOVA (Table III) fails to assign a significant amount of variation to the exposure-by-species interaction. This failure indicates that survival of both species was affected similarly by the presence of the other species. Furthermore, variation contributed by exposure as an independent source of variation was not significantly greater than that associated with chance. Thus, the impact of the predator in the presence of a second prey

was not significantly different from the predator's impact with only one prey available. The contradiction between this conclusion of the present work and Thorp's suggestion probably results from Thorp's failure to consider the difference in swimming activity of *P. pugio* and *P. vulgaris*.

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Appendix

Data used in the analysis of survivorship of *Palaemonetes pugio* and *P. vulgaris* in the presence of the predator *Fundulus heteroclitus* under various conditions of macrophytic cover.

Species	Cover type	Exposure condition	Number of survivors	Percent of starting population	Arcsine transformed percent
P. pugio	none	alone	9	45.0	42.13
			10	50.0	45.00
		combined	3	20.0	26.57
			6	40.0	39.23
	"*Ambulia*"	alone	14	70.0	56.79
			13	65.0	53.73
		combined	11	73.3	58.89
			12	80.0	63.43
	Ulva	alone	13	65.0	53.73
			14	70.0	56.79
		combined	9	60.0	50.77
			11	73.3	58.89
	Codium	alone	18	90.0	71.57
			19	95.0	77.08
		combined	14	93.3	75.00
			15	100.0	90.00
P. vulgaris	none	alone	12	60.0	50.77
			13	65.0	53.73
		combined	8	53.3	46.89
			9	60.0	50.77
	"*Ambulia*"	alone	15	75.0	60.00
			17	85.0	67.21
		combined	12	80.0	63.43
			11	73.3	58.89
	Ulva	alone	15	75.0	60.00
			16	80.0	63.43
		combined	11	73.3	58.89
			12	60.0	50.77
	Codium	alone	20	100.0	90.00
			19	95.0	77.08
		combined	15	100.0	90.00
			15	100.0	90.00