Implications of a fluctuating fish predator guild on behavior, distribution, and abundance of a shared prey species: the grass shrimp *Palaemonetes pugio*

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Abstract

In some systems, the identity of a prey species' dominant predator(s) may not be constant over time. In cases in which a prey species exhibits different responses to various predator species, such changes in predator identity may have population-wide consequences. Our goals were to determine (1) whether mortality of and refuge use by the grass shrimp, *Palaemonetes pugio*, were predator-specific, and (2) how effects of prey size and habitat interacted with predator type. Striped bass (*Morone saxatilis*) exerted twice as much predation pressure as mummichog (*Fundulus heteroclitus*), although not equally as great on large (female) and small (male) shrimp. Mummichog, which fed preferentially on large shrimp, forced a partitioning of habitat between the two shrimp size classes. In contrast, large and small shrimp occupied similar habitats when subjected to striped bass, which fed on both size classes equally. Refuge use of grass shrimp depended on predator type. In the presence of mummichog, which occupied shallower depths in the water column than striped bass, shrimp stayed deep and close to structural habitat. Striped bass, which were deeper, caused shrimp to move high in the water column away from structural habitat. When both predators were present, shrimp distribution was similar to that when only striped bass were present, striped bass predation rate was enhanced, and overall mortality was higher than with either predator alone. Results suggest that at times when mummichogs are the dominant predators, large (female) shrimp experience higher predation than small (male) shrimp and are physically separated from their potential mates. When striped bass are more abundant, male and female shrimp may share a similar, shallow, less structure-oriented distribution and be subjected to higher mortality. When both predators are present, mortality rates may be higher still. This predator-, size-, and habitat-specificity of grass shrimp behavior suggests

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significant population and distribution consequences of fluctuating predator guilds and fluctuating cover of structural habitats in the field.
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1. Introduction

Food webs can be very complicated, with many members, or simple, with only a few clearly definable steps (e.g., Ripa et al., 1998). In some cases, a prey species can have a few main predators that account for the majority of its predation-related mortality. In such a case, changes in a predator population may have a relatively large impact on population dynamics of the prey species.

In naturally variable environments, relative abundances of predator species can fluctuate over time such that, for some prey populations, the identity of the dominant predator can change. For example, abundance of spot and croaker, two fishes of northeastern Atlantic estuaries that share prey species, are often inversely correlated (Hines et al., 1990). When spot are rare, croaker become relatively more important, and vice versa. Similar inverse correlations have been noted between anchovy (*Engraulis* spp.) and sardine (*Sardinops* spp.) in the California Current region and other coastal upwelling zones (Schwartzlose et al., 1999).

In cases in which predator species differ in lifestyle, this fluctuation has potential to influence the evolution of behavior, morphology, and physiology of the prey species. Generally, different prey responses are necessary to defend against predators with different foraging techniques (e.g., Matsuda et al., 1996; Van Buskirk, 2001). If the prey species evolves a set of responses to only one predator species, even one that is usually dominant, the prey may become more vulnerable to another predator (Rahel and Stein, 1988; Crowder et al., 1997; Smith and Jennings, 2000; Relyea, 2001). Predators may also focus on different demographic components of the prey population. For example, one predator might select females; another, males (Johnson and Proctor, 1991; Rodd and Reznick, 1991; Nihoul et al., 1992). One predator might select juveniles; another, adults (Blanckenhorn, 2000; Ghalambor and Martin, 2000). As a result, fluctuations in the predator guild may influence population dynamics as well as behavior of the prey species.

In many estuaries worldwide, grass shrimp of the genus *Palaemonetes* serve important roles in the food chain as prey and as nutrient-recycling detritivores (Holthuis, 1952; Nixon and Oviatt, 1973; Welsh, 1975). In many of these areas, their main predators are fishes (Coen et al., 1981; Schneider and Mann, 1991). Four fishes are responsible for the majority of predation on the one member of this genus, *P. pugio*, present in the upper Chesapeake Bay: striped bass (*Morone saxitilis*), mummichog (*Fundulus heteroclitus*), white perch (*Morone americana*), and Atlantic croaker (*Micropogonias undulatus*) (Clark, 2001). However, all four predators are not always abundant at the same time (Hines et al., 1987, 1990). For example, in 1994, 24% of all fishes in this group were mummichog and 66% were white perch. In 1995, relative abundances were reversed; 82% were mummichog and 13% were white perch (Clark, 2001).

In addition to varying in abundance temporally, all four species have different mouth morphologies, and therefore probably different foraging techniques (Keast and Webb, 1966). Croaker are bottom foragers with ventrally located mouths. Striped bass and white perch have terminal mouths adapted for feeding in mid-water. Mummichog have dorso-terminal mouths, and are therefore more adapted to feed at the water surface. Several of the species also appear to have differences in habitat: mummichog were commonly caught in structural habitats (such as SAV and woody debris) in an upper Chesapeake Bay subestuary, whereas white perch and striped bass were not (Everett and Ruiz, 1993; Davis and Hines, unpublished data).

Perhaps as a result of differences in mouth morphology, feeding strategy, and habitat preferences of these predators, optimal refuge structure of grass shrimp differs among predators. Although structural habitats provided grass shrimp with a significant refuge advantage over bare sediment when faced with both striped bass and mummichog, the relative refuge value provided by different types of structural habitat differed for the two predators (Davis and Hines, unpublished data). For example, woody debris was a relatively better refuge against mummichog predators than striped bass, whereas riprap, a rocky artificial shoreline substrate, was a relatively better refuge against striped bass than mummichog predators.

The purpose of our study was to determine the extent to which two different predators, striped bass and mummichog, differed in the way they preyed on grass shrimp (*Palaemonetes pugio*), and how those differences interacted with effects of prey size and refuge habitat. Our specific objectives were: (1) to compare grass shrimp mortality between striped bass and mummichog predators, (2) to compare relative mortality of different grass shrimp size classes to striped bass and mummichog predators, (3) to compare the behavior of grass shrimp when subjected to predation by the two predators, and (4) to compare shrimp behavior and mortality in a multiple-predator-species guild to behavior and mortality when faced with single predator species. Our laboratory experiments allow us to discuss the potential individual- and population-level consequences of these comparisons.

2. Methods

The general hypothesis that shrimp behavioral and population-level responses differed between the two predators was tested with two types of laboratory experiments. Both were conducted at the Smithsonian Environmental Research Center on the shore of the Rhode River, a Maryland subestuary of the upper Chesapeake Bay.

2.1. Comparative mortality experiment

Predation by the two predator species on two size classes of grass shrimp was compared for both structural and non-structural habitats. Trials were conducted in a set of 12 outdoor 1×2 m fiberglass tanks filled with ambient water from the Rhode River (10–12 ppt and 20–25 °C) to a depth of 40 cm. For the 24-h duration of each trial, a tank contained either no structural habitat (bare tank bottom) or 0.5 m² of one of four 30-cm high structural habitats. These habitats were artificial SAV (polypropylene ribbon tied to a mesh frame),

oyster reef (*Crassostrea virginica* shells strung together), woody debris (three 8-cm-diameter branches), and riprap (approximately twenty 10–20-cm-diameter rocks). Habitats were arranged in either unfragmented patches (1.0 m long by 0.5 m wide) or fragmented patches (two 0.5×0.5 m patches separated by 0.5 m of bare tank bottom); however, because no differences in predation between the two configurations existed (Davis and Hines, unpublished data), this factor was ignored in the present study and only habitat type and predator species were considered.

In each trial, defined as one 24-h period for one tank, 60 shrimp and 6 predators were used. Thirty small (30–36 mm) and 30 large (37–45 mm) shrimp were used, producing an initial density of 120 individuals/m^2. This value was within the range of densities measured in structural habitat patches in the field (50–200 individuals/m^2; Davis and Hines, unpublished data). Size classes corresponded to distinct size groups collected in the field (Fig. 1), which in turn were driven by gender. Small shrimp were adult males and large shrimp were adult females (Welsh, 1975; Alon and Stancyk, 1982).

After addition to the tank, shrimp were allowed 20 min to acclimate, then the six monospecific predators were added. Both striped bass and mummichogs used in the experiment ranged from 80 to 110 mm TL, which for striped bass represented the young-of-the-year size class and for mummichogs represented the adult size class. After 22 h, the tank was drained, and fish and remaining shrimp were collected. The number of shrimp of each size class remaining (i.e., not consumed by fish) was counted.

Six to 16 trials were run for each combination of predator and habitat type (total of 98) during a period from June 19 to August 24. Data from six trials were discarded due to faulty drains resulting in lowered water level or because a predator jumped from the tank, despite mesh covers, leaving a total trial number of 92 (65 for mummichog and 27 for striped bass). Generally, 8 to 12 trials of different habitat treatments were run per day. Habitat types were randomly redistributed among tanks on each day. No predators were used in multiple trials. However, due to the large demand for shrimp (almost 6000), shrimp were reused.

To assess the predation risk of small shrimp relative to large shrimp, the ratio of small/total shrimp consumed was calculated. This ratio, expressed as the proportion of all shrimp eaten that were of the small size class, was compared between predator types and among
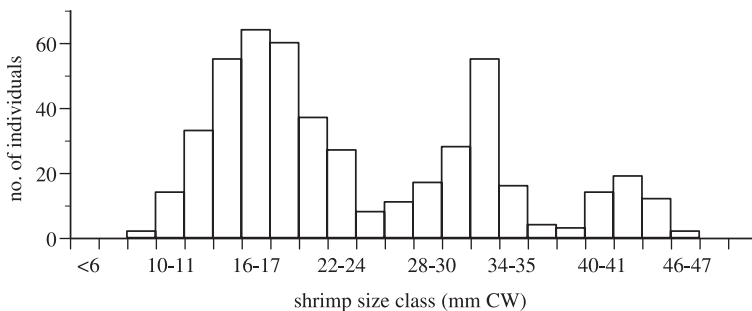

Fig. 1. Size-frequency histogram of shrimp from the Rhode River in July 2001 indicating three distinct size classes: new recruits (~ 17 mm CL); small adults (~ 32 mm), which are mostly males, and large adults (~ 42 mm), which are females. Only the two adult size classes were used in this study.

habitat types. To test for a difference in shrimp mortality (arcsine-square root-transformed; Zar, 1999) between predator species and among habitat types, we used two-way Model I (fixed effects) ANOVAs.

2.2. Behavioral experiment

Because grass shrimp behavior and the use of refugia were observed qualitatively to differ between the two predator treatments and the two prey size classes in the first set of experiments, a second type of experiment was designed in which predator and prey behavior could be filmed and quantified. Our goals were to quantitatively test the hypotheses that (1) shrimp behavior, measured as depth in the water column, distance from a structural habitat refuge, and occupation of structural refuge, differed between predator types; (2) shrimp behavior of the size classes differed; (3) predator behavior was influenced by predator guild composition; and (4) predation rate was influenced by predator guild composition.

A 200-l glass aquarium ($90 \times 30 \times 45$ cm deep) was established with estuarine water (10–12 ppt, 20–22 °C) and a 0.125 m^2 riprap habitat (20 cm high) in the middle. Choice of habitat type was made based on field habitat availability and on data from the first experiment. SAV and oyster reef were eliminated as possibilities because they are not currently available habitats in the upper Chesapeake Bay (Everett and Ruiz, 1993). Woody debris was eliminated because differences in predation pressure between mummichog and striped bass were anomalously high in this habitat (Davis and Hines, unpublished data), thereby inhibiting generalization of comparative behavioral results to other habitat types. Riprap was considered appropriate due to its growing abundance in the Chesapeake and other estuaries (Davis et al., 2002), and due to the similarity in densities of shrimp and other shallow-water organisms occupying riprap and natural structural habitats (Davis and Hines, unpublished data).

All trials involved 14 grass shrimp as prey (7 of the small size class and 7 of the large) and one of 4 predator treatments: (1) no predators, (2) 6 mummichogs, (3) 6 striped bass, and (4) 3 mummichogs and 3 striped bass. This latter treatment kept the total number of predators in the tank constant, though we acknowledge that we cannot attribute differences in this treatment to differences in predator composition rather than number of conspecifics. However, our goal was to test for effects of species composition rather than to test for true effects of varying total number of predators. All predators used were again in the 80–110 mm TL size range. As in the first set of experiments, no predators were used in multiple trials, but shrimp were. Three replicates of each of the four treatments were run, and all were filmed.

Shrimp were allowed 20 min to acclimate in the experimental tank, then one of the four predator treatments was added. After an additional 2 h, the number of shrimp in each size class remaining was determined and mortality calculated. At set intervals on the video-tapes, positions of all predators and all visible shrimp were determined with the aid of a grid affixed to the back of the tank. These intervals were every 7.5 min during the first hour and every 15 min for the second hour. Both depth in the water column and horizontal distance from the habitat structure were recorded to the nearest 2.5 cm. Actual distance from the habitat structure was calculated from depth and horizontal distance values.

Because time of predation events was recorded, the number of shrimp alive but not visible at each time period could be determined. Those shrimp were assumed to be within the structural habitat.

Position values of all shrimp present at each time interval in a trial were averaged. These data were used to test for differences in position among predator treatments and time intervals with a two-way fixed effects ANOVA. Because position (depth and distance) values were limited by the sides of the tank, these values were arcsine-transformed prior to analysis (Zar, 1999, p. 279). The proportion of shrimp using the structural habitat at each time interval was also calculated and similarly compared (arcsine-transformed prior to analysis). In addition, shrimp were divided into size classes to test for effects of predator treatment and shrimp size class on shrimp position using two-way ANOVAs. Such analysis was only possible for the first hour of trials, when enough shrimp of each size class still remained to be measured. For these analyses, positions of each small (or large) shrimp were averaged within a time period, then the means of each time period were averaged to obtain a treatment average. For the two-predator species treatment (three mummichog and three striped bass), the number of shrimp consumed and the number of shrimp "pursued" by each predator species was also determined from the videotapes. A pursuit was defined as an abrupt change in fish swimming velocity in the direction of the prey, regardless of success. Pursuits were never aimed at another fish.

To determine whether mortality in the multiple-predator guild matched predictions based on behavioral and distributional response of shrimp to each predator treatment, we compared the proportion of shrimp that were preyed upon in the multiple-predator treatment to the single-predator treatments.

3. Results

3.1. Interaction of predator and habitat type on mortality of different prey size classes

Predation pressure by striped bass was more than twice as great as that by mummichogs in both structural and non-structure habitats (Fig. 2). However, this increase was not reflected evenly across size classes. Mummichogs consumed almost twice as many large than small shrimp; striped bass consumed equal amounts of both prey sizes (Fig. 3). Therefore, mortality of small shrimp increased relatively more than that of large shrimp upon a switch from mummichog to striped bass predators.

Predation risk for each size class depended on the presence of structure as well as predator species. More large than small shrimp were preyed upon by mummichog only when structural refuge was available. When structure was not available, more small shrimp than large shrimp were preyed upon (Fig. 4). This pattern was the opposite for striped bass; more small shrimp were consumed when structure was present, and more large shrimp were consumed when structure was not present (Fig. 4).

Within the suite of structural habitat types (excluding the non-structure habitat), however, the relationship between predation on small vs. large shrimp among habitat types was similar between predator species and among habitat types (Fig. 5). The relative risk for a small versus a large shrimp was similar across habitat types (two-way ANOVA, effect of
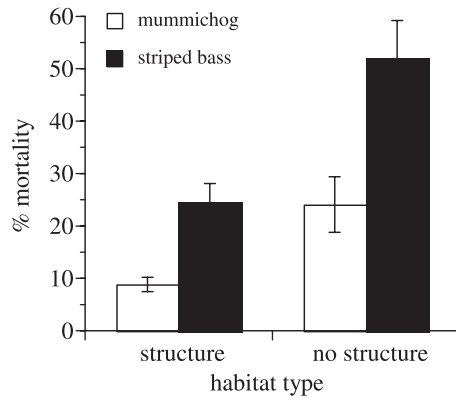
Fig. 2. Shrimp mortality due to mummichog vs. striped bass predators in structure (SAV, oyster reef, woody debris, and riprap combined) and non-structure habitats. Two-way ANOVA, effect of structure: $F_{1,88} = 15.8$, $p < 0.001$, effect of predator: $F_{1,88} = 21.7$. $p < 0.001$, structure × predator interaction: $F_{1,88} = 0.5$, $p = 0.488$. Total trial number = 92. Means and standard errors (SE) are presented.

habitat: $F_{4,78} = 1.4$, $p = 0.26$). Overall, the ratio of small/total shrimp preyed upon was higher for striped bass than mummichog (two-way ANOVA, effect of predator: $F_{1,78} = 12.8$, $p < 0.001$), and this relationship was similar across habitats, as indicated by a lack of significant interaction effect (habitat type × predator: $F_{4,78} = 0.3$, $p = 0.86$). However, several trends were consistent for both species. For both mummichog and striped bass, the ratio of small/total shrimp eaten was lower in oyster reef and woody debris habitats than SAV and riprap. During a predation event, the probability that a large shrimp is eaten rather than a small one may be higher in oyster reef and woody debris habitats than SAV and riprap.
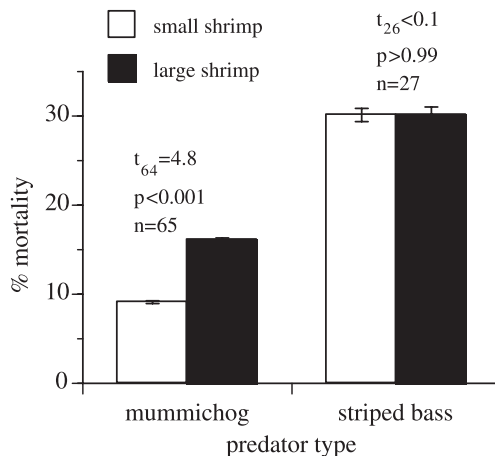

Fig. 3. Mortality of small vs. large shrimp due to mummichog and striped bass predators in all habitats combined. SEs and results of paired *t*-tests are presented.
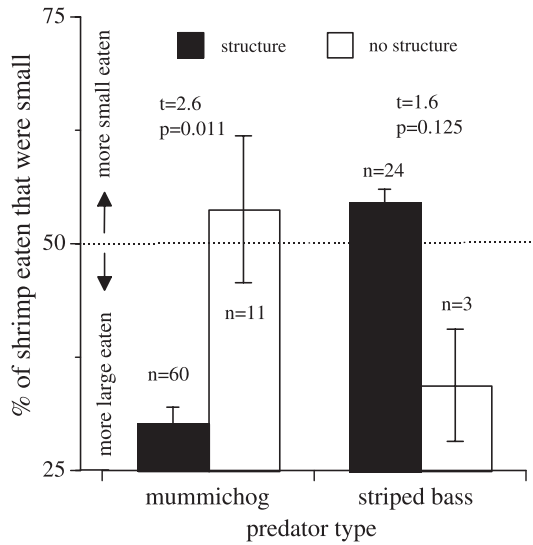
Fig. 4. Relative mortality of small shrimp (percent of all shrimp eaten that were small) in structure (SAV, oyster reef, woody debris, and riprap combined) vs. non-structure habitats for both mummichog and striped bass. SEs and results of *t*-tests comparing this value between structure and non-structure are presented for both species. Trials in which no predation occurred could not be included in the analysis.
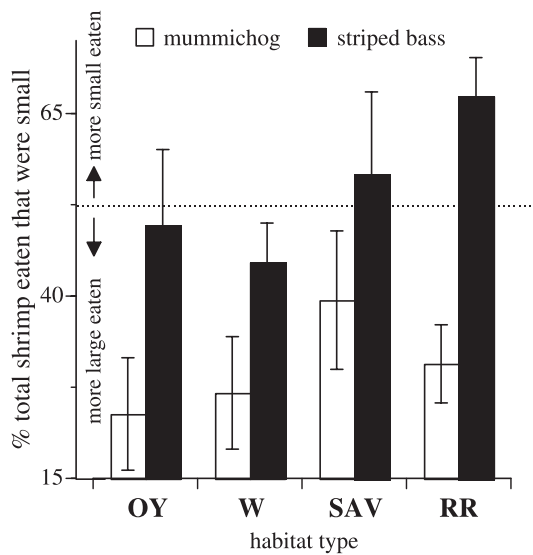

Fig. 5. Relative mortality of small shrimp (percent of all shrimp eaten that were small) compared among structural habitat types for both mummichog and striped bass. No significant differences in this ratio were observed across habitat type (see text for two-way ANOVA results). OY = oyster, W = wood, SAV = submerged aquatic vegetation, RR = riprap. Means and standard errors (SE) are presented.

A. Water depth

B. Structural refuge use

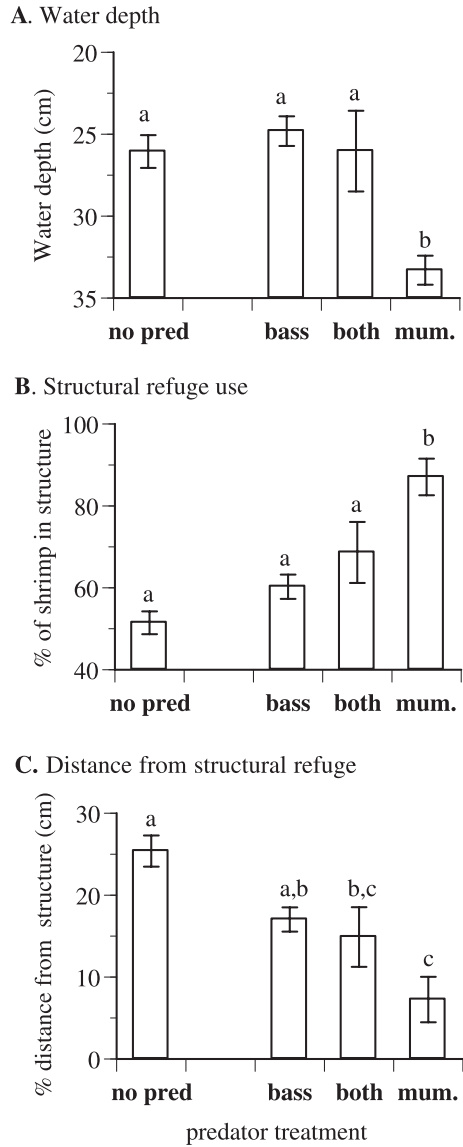**C.** Distance from structural refuge

Fig. 6. Mean positions of shrimp prey in different predator treatments (A) depth, (B) percent of shrimp within the structural habitat, (C) distance of shrimp from the structural habitat. No pred = no predators, bass = striped bass predators alone, both = striped bass and mummichog predators, mum. = mummichog predators alone. Means (± SE) are calculated across all time periods, though time was considered a separate factor in two-way ANOVAs (Table 1). Like letters on the plots indicate multiple comparisons that did not significantly differ (Tukey post-hoc tests).

Table 1
Effects of predator treatment (no predator, mummichog, striped bass, and multiple-predators) and time interval on shrimp depth in the tank, proportion of shrimp within the structural habitat, and distance of shrimp from the structural habitat. Significant effects (based on $\alpha = 0.05$) of the two-way ANOVA are indicated in bold. df = Degrees of freedom, MS = mean square, F = F-statistic, and p = p-values. Data are presented in Figs. 6 and 8

Factor	df	Depth			% in habitat			Distance		
		MS	F	p	MS	F	p	MS	F	p
Predator treatment	3	0.62	9.7	**<0.001**	11.6	8.9	**<0.001**	0.75	12.2	**<0.001**
Time interval	7	0.07	1.1	0.394	1.80	1.5	0.106	0.14	2.2	**0.045**
Pred × time	21	0.08	1.3	0.247	1.67	1.5	0.066	0.10	1.7	0.061
Error	56	0.06			0.08			0.06		

3.2. Prey behavior

The presence of predators had a significant effect on the distribution of shrimp, including depth in the water column, proportion in the structural habitat, and distance from the structure (Fig. 6, Table 1). When shrimp were not subjected to predators, they tended to be high in the water column (Fig. 6A), outside the structural habitat (Fig. 6B), and relatively far away from the structural habitat (Fig. 6C). However, in the presence of all predator combinations (mummichog alone, bass alone, and both predators at once), shrimp moved closer to the structural habitat and a greater proportion actually occupied it (Fig. 6B,C), suggesting that the structure was perceived as a refuge.

Shrimp response to the two predators, striped bass and mummichog, differed in a way that was consistent with a predator-avoidance hypothesis. Mummichogs were significantly more shallow than striped bass, which stayed deeper in the water column (Fig. 7). In the presence of mummichog, shrimp went deep in the water column (Fig. 6A) and moved
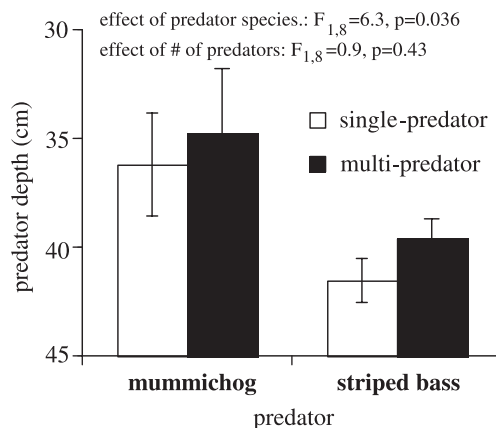

Fig. 7. Mean ($\pm$ SE) depths of mummichog and striped bass predators when alone in single-predator treatments and when together in multiple-predator treatments. Effects of predator species and number of predators (single vs. multiple) in a two-way ANOVA are presented (interaction: $F_{1,8} < 0.1$, $p = 0.90$).
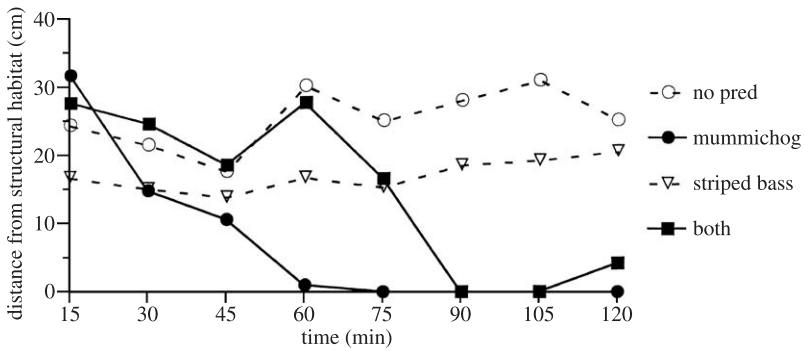
Fig. 8. Interaction between shrimp distance from the structural habitat and time. See Table 1 for statistical results.

closer to the structure (Fig. 6C). In the presence of striped bass, shrimp were high in the water column. Therefore, in single-predator treatments, shrimp used different refuges (structure versus shallow depths) depending on predator type.

Changes in shrimp distribution over time were observed only in the presence of mummichogs. Shrimp became closer to the structural refuge during the 2 h of mummichog and multiple-predator treatments, but not during the striped bass treatment (Fig. 8), accounting for the near-significant effect of time and the interaction between time and predator treatment (Table 1). Decreased distance may have occurred because individuals moved closer to the structure, or because those that were farther away were preyed upon first.

Because shrimp appeared to choose different refuge (shallow depths in striped bass treatments and occupation of structure in mummichog treatments) depending on predator type in single-predator treatments, we expected that shrimp would have an intermediate response when both predators were present. Our hypothesis was that some shrimp would respond to striped bass, going shallow, and some would respond to mummichogs, using the
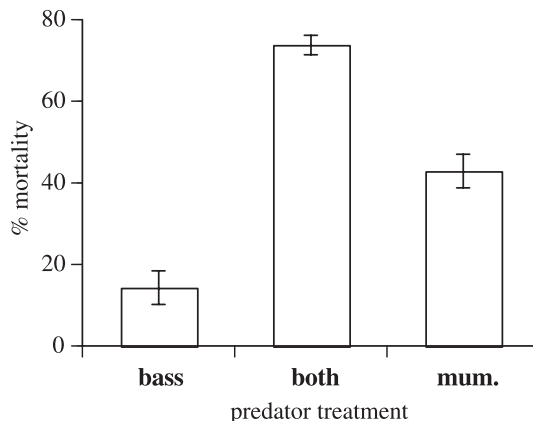

Fig. 9. Shrimp mortality (± SE) in different predator treatments. ANOVA: $F = 67.0$, $p < 0.001$.

structural refuge. As a result, mean positions would be intermediate. This hypothesis was supported only in terms of distance from the structure (Fig. 6C). In terms of water depth and occupation of the refuge, the distribution of shrimp in the presence of both predators resembled more closely their distribution in striped bass treatments, not mummichog treatments (Fig. 6A,B).

3.3. Shrimp mortality

Because shrimp had such opposite behavioral responses to the two predators, our next hypothesis was that, by choosing one response in multiple-predator treatments, shrimp would become more vulnerable to the other predator in the system. Therefore mortality would be highest in multiple-predator treatments. Because shrimp responded behaviorally
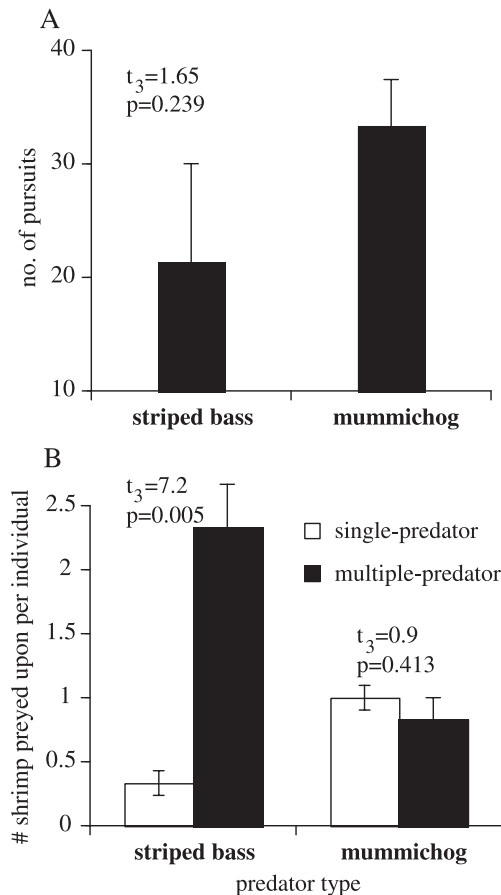

Fig. 10. (A) Mean number of pursuits (± SE) by striped bass and mummichog in multiple-predator treatments. (B) Mean number of shrimp consumed per individual fish in each treatment type for both striped bass and mummichog. Results of *t*-tests are presented.

more to striped bass in multiple-predator treatments (e.g., they were high in the water column, similar to how they responded to striped bass alone), we also hypothesized that they would become more vulnerable to and be consumed by mummichogs, which also occupy shallow depths.

The first hypothesis was supported. Mortality was significantly higher in the multiple-predator treatment than in either single-predator treatment (Fig. 9). The second hypothesis, however, was not supported. Although mummichogs had a great number of pursuits than striped bass during multiple predator trials (Fig. 10A), the higher shrimp mortality rates in these trials were actually attributable to striped bass (Fig. 10B). By responding more in position to striped bass, shrimp were not becoming more vulnerable to mummichogs, as predicted. The number of shrimp consumed per individual mummichog was the same in the multiple-predator and mummichog-alone treatments, but the number of shrimp consumed per individual striped bass was 600% higher when both predators were present than when
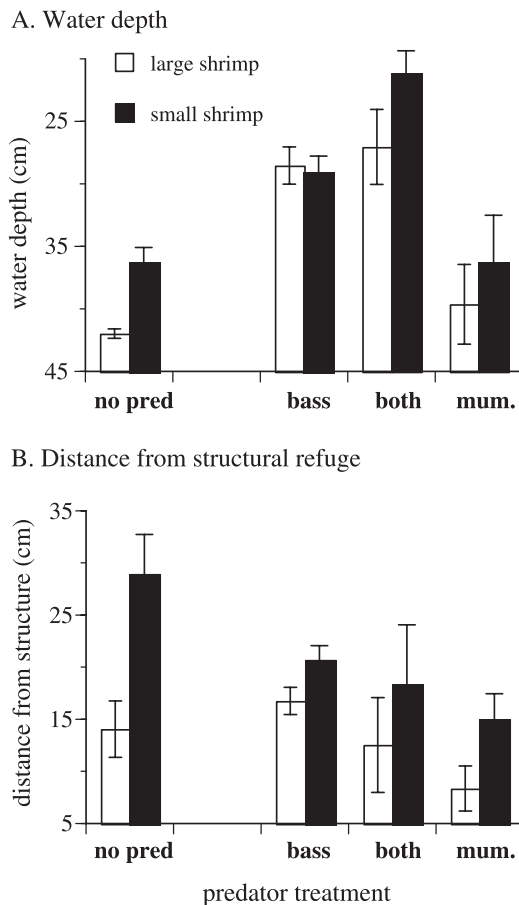

Fig. 11. Mean (± SE) depths (A) and distances (B) of large vs. small shrimp in different predator treatments. Results of two-way ANOVAs are presented in Table 2.

Table 2
Effects of prey size and predator treatment (two-way ANOVA) on shrimp depth and distance from the structural refuge. Position data were averaged over the first hour of each trial. df= Degrees of freedom, MS = mean square, F = F-statistic, and p = p-values. Significant effects are indicated in bold. Data are presented in Fig. 11

Factor	df	Depth			Distance		
		MS	F	p	MS	F	p
Predator treatment	3	0.30	17.0	**<0.001**	0.04	3.6	**0.042**
Prey size	1	0.09	5.0	**0.040**	0.13	11.1	**0.004**
Pred × prey size	3	0.02	0.8	0.502	0.01	0.9	0.463
Error	16	0.02			0.01		

striped bass were present alone (Fig. 10B). It therefore appears that striped bass benefited from the presence of mummichogs.

3.4. Shrimp size

As in the first set of laboratory experiments, mummichogs consumed a greater number of large than small shrimp per trial (t-test, $t_4 = 3.5$, $p = 0.024$), whereas striped bass did not ($t_4 = 2.1$, $p = 0.101$). Because predation risk for the two shrimp size classes differed only for mummichogs, we predicted that position in the tank would differ between large and small shrimp in mummichog but not striped bass treatments. This hypothesis was supported. In the no-predator, two-predator, and mummichog treatments, small shrimp were higher in the water column and farther from the habitat than large shrimp (Fig. 11, Table 2). In striped bass treatments (analyzed separately), positions of large and small shrimp were not significantly different (paired t-test, $t_2 < 0.5$, $p > 0.50$ for both depth and distance).

Because mummichogs consumed a greater ratio of large to small shrimp in the presence, but not the absence, of structural refuge in the first set of laboratory experiments (Fig. 4), we predicted that smaller shrimp must be using the refuge to a greater extent than large shrimp. This hypothesis was not supported. Instead, smaller shrimp were farther from the habitat, closer to the distribution of mummichogs themselves (Fig. 11).

4. Discussion

The grass shrimp *P. pugio*, one of the staple prey species for fishes in the Chesapeake and other North American bays, responded differently to predation pressure by two of its main predator species, both in terms of behavior (and therefore distribution) and mortality. In addition, responses (distribution and relative mortality) of the two shrimp size classes differed between the two predator species. Further, size-specific shrimp responses to predators were habitat-specific. These distinctions suggest several strong behavioral, distributional, and population-level consequences of fluctuating predator frequencies in the system. Based on results of this experimental laboratory study, we considered effects of different predator guild scenarios on prey population dynamics and habitat distribution.

4.1. Ramifications of predator guild composition on absolute mortality

Striped bass were more voracious predators on grass shrimp than mummichogs. This result may be explained by the much larger gape size of a striped bass than mummichog (Keast and Webb, 1966) and by life-history status. Because striped bass in the size range of the study were juveniles, they were likely to have had faster growth rates and therefore higher food requirements than the mummichog adults. These differences suggest that in years or months when striped bass are relatively more abundant, predation pressure on grass shrimp would be higher than in periods when mummichog are the dominant predator.

4.2. Ramifications of predator guild composition on shrimp distribution

Shrimp responded to the two predators differently in terms of distribution and use of structural refuge. Differences were inconsistent with hypotheses based on predators' structural habitat use. Mummichogs commonly use structure in the field, whereas striped bass were less structure-associated (Davis and Hines, unpublished data). As a result, one might have expected grass shrimp to escape striped bass predation by occupying the structural habitat; they did not. Differences in shrimp distribution between predator treatments were, however, consistent with hypotheses based on predators' mouth morphology and depth distribution. When subjected to mummichog predation, a predator with a dorsally positioned mouth and relatively shallow distribution, shrimp stayed deep and relied more on structural habitat refuge. When subjected to striped bass, which were deeper than mummichog and have anterior mouths, shrimp used shallow water as a refuge more than structural habitat. Shrimp similarly used shallower depths when subjected to white perch than when subjected to mummichog predation (Clark, 2001). However, unlike the present study, shrimp use of structural refuge did not differ between the two predators (Clark, 2001).

In addition to exhibiting predator-dependent habitat selection, shrimp exhibited size-dependent distribution, and therefore gender-dependent distribution, because male shrimp are smaller than females (e.g., Welsh, 1975; Alon and Stancyk, 1982; Vernberg and Piyatiratitivorakul, 1998). When no predators were present, small (male) shrimp occurred at shallower depths than large (female) shrimp, perhaps an innate habitat preference derived from the increase in risk for smaller organisms as depth increases (Ruiz et al., 1993). Small shrimp also occurred farther from structural refuge than large shrimp, consistent with observations that small shrimp are more likely to emigrate from structural habitats (Davis and Hines, unpublished data). These size-specific habitat differences persisted in the presence of mummichogs, which had size-specific predation. However, in the presence of striped bass, which fed on both size classes equally, the differences in habitat use between the shrimp size classes disappeared. This shift suggests behavioral plasticity in prey distribution and microhabitat selection.

Differences in shrimp position based on predator type suggest that at times in which mummichogs are the dominant predator, grass shrimp would be found deep and close to structure, with males (small shrimp) and females (large shrimp) occupying different microhabitats. At times when striped bass are more abundant in the field, grass shrimp of all sizes might be found in shallower habitats, relying less on structural habitat as refuge.

At such times, the widespread loss of structural habitats such as SAV and oyster reef in many areas of Chesapeake Bay (e.g. Sinderman, 1968; Brush and Hilgartner, 2000) may become less important. Effects of structural habitat loss in the bay on population sizes are unknown, and some suggest that shallow areas serve at least partially as alternate refuge for shallow-water species like grass shrimp (Ruiz et al., 1993). Results of the present work suggest that the adequacy of shallow non-structural areas as refuge may be a function of predator guild structure at any particular time.

4.3. Ramifications of predator guild composition on shrimp population structure

In addition to driving size-specific habitat partitioning by shrimp, mummichogs consumed more large than small shrimp, especially in the presence of structural habitat. Striped bass consumed members of both shrimp size classes equally. This contrast was unexpected based on comparative gape size. However, mummichogs were observed to feed in groups, which potentially allowed them to take advantage of larger shrimp as much as one-half the length of the fish themselves. Commonly, one fish would strike unsuccessfully at a shrimp, drawing attention and strikes by other mummichog. Often a shrimp would be divided in two, with each piece consumed by a different predator. Striped bass were never observed to "share" prey.

Differences in prey size between mummichogs and striped bass suggest that at times of high mummichog abundance, predation pressure would be higher on females than males. Population structure might therefore change, with fewer females per male. In addition, presence of mummichogs drove differences in habitat use and distribution between large (female) and small (male) shrimp. This separation may result in lower mating success than in years in which striped bass, which do not drive size-specific distribution, are the more dominant predators. The identity of the dominant predator in this system may have a human connection, as the historic striped bass fishery has at least in part driven large fluctuations in abundance of this species (Secor, 2000). In this way, humans may affect grass shrimp distribution and mating success.

4.4. Ramifications of multiple-predator guilds

One of the characteristics of fluctuating predator guilds is that more than one predator may be common at the same time (e.g., Clark, 2001). Because required responses to the predators may be opposite, mortality may be enhanced (Crowder et al., 1997; Rahel and Stein, 1988; Kotler et al., 1992). In the present study, mortality was highest when a fixed number of predators was composed of two species rather than one. Shrimp of both sizes responded in position mainly to striped bass, suggesting that the perceived threat of predation by this species was higher. We predicted that the presence of striped bass would facilitate mummichog predation by pushing shrimp into a more vulnerable position in the water column.

The indirect interaction between the two predators was more complicated, however. Mummichogs were allowed greater access to shrimp; however, their inefficiency in foraging (high number of pursuits but low number of successful strikes, also noted by Heck and Thoman, 1981) simply drew the attention of striped bass predators. Striped bass,

relatively efficient strikers, were often attracted by a shrimp's escape from a failed mummichog attack. As a result, mummichogs did not benefit from the shrimp's primary response to the other predator, as expected. Instead, striped bass benefited from mummichogs' reaction to shrimp's response to striped bass. Similar interactions may occur in the field. Such results provide evidence that at times when more than one predator dominate a system, especially those that elicit different behavioral responses by the prey, mortality can be higher than expected based on absolute predator abundance.

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