Diel variation in predator abundance, predation risk and prey distribution in shallow-water estuarine habitats

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Abstract

Predation by visual predators is often affected by light conditions and may therefore exhibit strong diel variation. The dominant predators on grass shrimp, *Palaemonetes pugio*, are finfish predators that are thought to locate their prey by visual cues. We examined the response of grass shrimp to diel variation in predation risk in the nearshore shallow waters of the Chesapeake Bay. We used diel shoreline seines to assess the relative abundance of predators. We assessed the relative risk of predation with shrimp tethered at refuge (30 cm) and nonrefuge (60 cm) depths. To measure grass shrimp response to predation risk, we used dipnets to monitor habitat use. Four predominantly visual predators dominated the shoreline seine catches, *Fundulus heteroclitus*, *Micropogonias undulatus*, *Morone americana* and *Morone saxatilis*. Total predator abundance had a diel component, with dramatic nighttime decreases in total abundance, whereas guild composition and relative abundance remained unchanged. Relative predation risk for tethered shrimp exhibited significant time by habitat interaction. During the day, depth negatively affected survivorship of tethered shrimp while at night overall survivorship increased and there was no effect of depth. Shrimp habitats use reflected diel predation risks. Abundances in the near shore were highest during the day with decreased abundances at night. Together, the seine and tethering data highlight the importance for a refuge (e.g., shallow water) from predation during the daytime and a relaxation of predation pressure at night.
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Keywords: Chesapeake Bay; Diel effects; *Palaemonetes pugio*; Predation risk; Prey response

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1. Introduction

Over evolutionary time, predation pressure has selected for use of refuge habitat by prey (Dill, 1987). Although refuge habitats allow improved escape from predation, they often provide prey with poor foraging opportunities (Holomuzki and Messier, 1993) and their use can result in lower growth rates (Sogard, 1992). During ecological time, prey must modify refuge habitat use in response to the prevailing levels of predation risk. Prey must 'balance' the cost of refuge use against the risk of predation (Mittlebach, 1981; Werner et al., 1983; Hugie and Dill, 1994). To perform this ecological juggling act, prey need to respond to their level of predation risk. Prey can assess predation risk through interception of cues from the physical presence of the predator. Information from flow regime, chemical signals and visual sightings can all provide prey with estimates of predation risk. However, the physical presence of the predator increases the chance that the predator will detect the prey first. Environmental cues can provide prey with an assessment of predation risk independent of the predator's proximity. By seeking out environmental regimes or conditions that adversely affect the predators' density or efficiency, prey can reduce their level of predation risk.

Light level provides an easily quantifiable assessment of risk from visual predators. Decreases in brightness and contrast can lessen capture rate of visual predators and many visual predators are not active at night (Benfield and Minello, 1996). Prey can respond to diel variation in predation risk by timing activity levels with diel period. These changes may intensify, compensate, or reverse the ecological effect of predator prey interactions observed during daylight hours.

In studies of estuarine systems, submerged aquatic vegetation (SAV) has been identified and emphasized as a refuge for small macrofauna. Small fish and invertebrates attain refuge from predation through an association with submerged aquatic vegetation (Morgan, 1980; Heck and Thoman, 1981; Diehl, 1988; Rozas and Odum, 1988; Ambrose and Irlandi, 1992; Skilleter, 1994). Within SAV, grass shrimp, *Palaemonetes pugio*, are able to respond to the interaction of refuge value and predation risk (Heck and Thoman, 1981).

Though the importance of SAV has been stressed, nonvegetated sediments dominate many estuaries, and historical SAV beds have experienced major declines (Orth and Moore, 1983). Recent work has demonstrated that shallow waters and coarse woody debris (CWD), such as branches and logs, function as critical refuge habitats in the absence of SAV (Everett and Ruiz, 1993; Ruiz et al., 1993). Together, these studies indicate that grass shrimp abundance is greatest in shallow depths (<35 cm) and in association with CWD. Abundance of grass shrimp and other small macrofauna decreases with depth and with distance from logs, and is inversely related to the risk of predation. However, these studies were all done during the day and the predation risk may change at night. If shrimp distribution during the day is constrained by visual predators, imposing a trade-off, these prey may respond to diel changes in predation risk with shifts in habitat utilization.

Grass shrimp are abundant epibenthic predators in US East Coast estuarine systems. They play an important role in regulating the structure of estuarine benthic communities (Kneib, 1988; Posey and Hines, 1991). Grass shrimp have a direct negative effect on the

abundance and diversity of small estuarine macrofauna (Morgan, 1980; Kneib, 1985; Walters et al., 1996) and indirectly affect community structure by preying on benthic predators of other species (Kneib, 1988; Posey and Hines, 1991). Grass shrimp are also an important prey species for estuarine fish and thus provide a trophic link between benthic and nektonic communities (Schmelz, 1964; Welsh, 1975; Kneib, 1984; LaSalle et al., 1991).

We examined the grass shrimp's responses to variation in predation pressure by studying diel components of predator abundance, prey distribution and predation rates in the nearshore shallows of Chesapeake Bay. We tested the hypotheses that (1) predation risk for grass shrimp has a diel component, and (2) grass shrimp respond to diel variation in predation risk with shifts in habitat utilization.

2. Methods

2.1. Study site

Field studies were conducted at the Smithsonian Environmental Research Center on the Rhode River, a lower mesohaline subestuary of the central Chesapeake Bay (Fig. 1). The Rhode River has a mean depth of 2 m and an average tidal range of 0.5 m. Salinity ranges from a low of about 4 ppt in spring to a high of about 15 ppt in fall. Water temperatures also vary seasonally from 2 to 4 °C in January to a high of 27 to 28 °C in July. All fieldwork was done at Fox Point, a heavily wooded peninsula on the upper end of the Rhode River. Fox Point is within 32 km of Annapolis, the state capital of Maryland. Ambient light conditions (perhaps from the city and surrounding suburbs) at night were often bright enough to permit researchers to move about and work without the aid of artificial illumination. However, researchers wore headlamps and sampling transects were marked with plastic reflectors. Headlamps and electric lanterns were used for measurement and identification of organisms.

2.2. Variation in predator guild composition and abundance

We sampled the predator guild with a seine net at Fox Point between May 10th and June 15th of 1993. Seine dates were haphazardly chosen within the time period. The net had a 0.64-cm mesh net with a 10-m mouth and was pulled onto shore from a depth of 100 cm. Seines were pulled in three of six nonoverlapping sites in nine daytime and eight nighttime hauls. Fish caught in the seine were identified to species and fish total length (a straight line from the tip of the snout to the farthest tip of the caudal fin) was recorded in millimeters. A one-way ANOVA was used to test separately for differences in abundance and size of fish between time periods (day and night).

2.3. Grass shrimp distribution and abundance

We sampled grass shrimp distribution and abundance by pushing long-handled dip nets parallel to shore at multiple depths along the bottom of six 10-m transects. There were
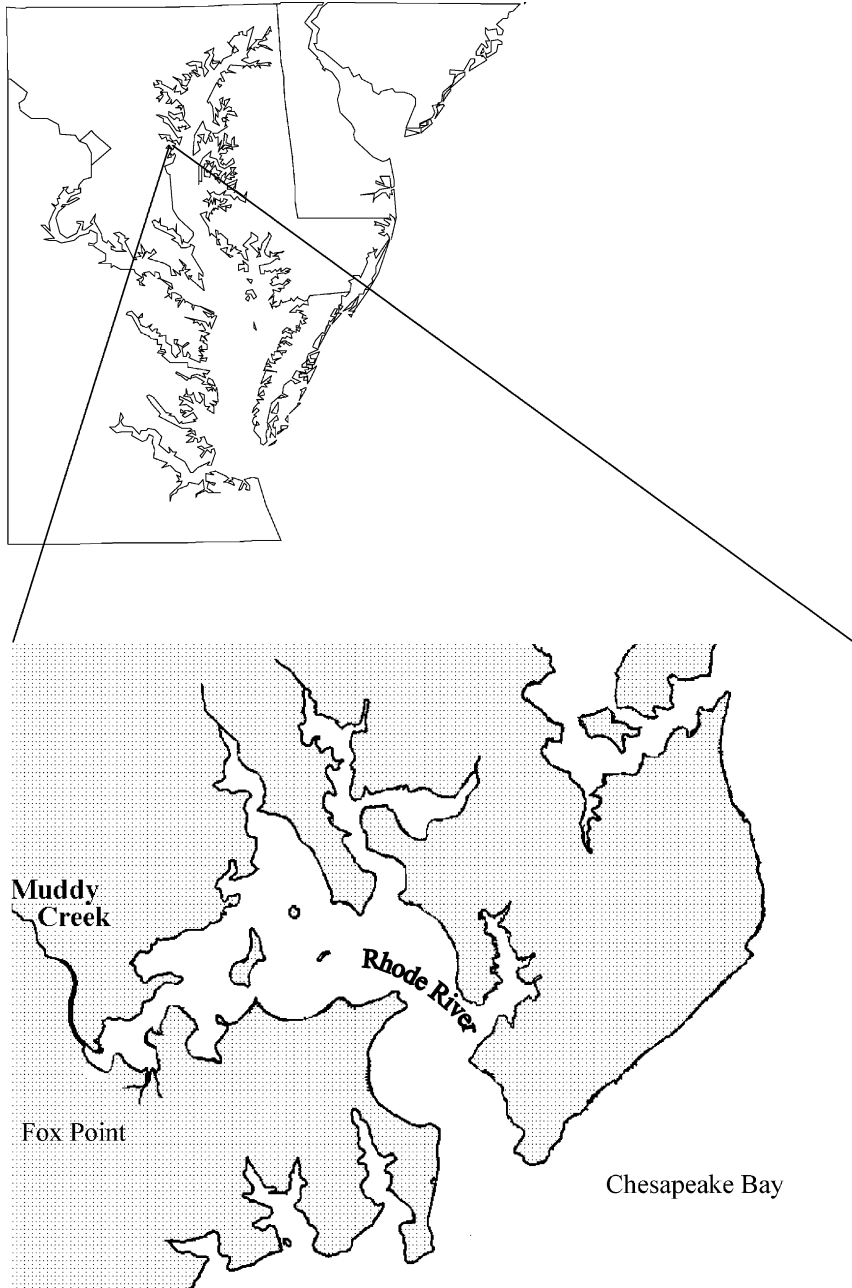
Fig. 1. Map of Rhode River, Maryland. Inset shows location of the Rhode along the western shore of the Chesapeake Bay on the Mid-Atlantic coast of the United States.

three daytime and three nighttime sampling events during May and June 1993. The nets had an opening of 40×25 cm and a 3-mm mesh. Each transect was sampled at four depths, 15, 30, 45 and 60 cm. With increasing depth there is an increase in the amount of energy required for a researcher to push the net through the water. To standardize sampling speed among all depths, all samples were paced by a researcher pushing a net through a transect at 30-cm depth. Captured grass shrimp were counted, measured in millimeters from rostrum tip to tail end, and the presence of eggs noted. Grass shrimp were then returned to the site of collection.

Total grass shrimp abundance was estimated by using a chart of the average depth contour to estimate the area associated with each depth. We constructed the chart by taking depth readings at 1-m intervals from mean high water (mhw). To obtain the depth readings, we divided the study area into 10 sites approximately 10 m apart. At each site a transect was run perpendicular to the shore and depth readings were recorded at 1-m intervals along each transect. The depth of intermediate distances was estimated with the formula for the slope of the mean depths at each 1-m interval (Fig. 2). For each of the target depths (15, 30, 45, and 60 cm), we established depth zone described by the depth ± 7.5 cm and used
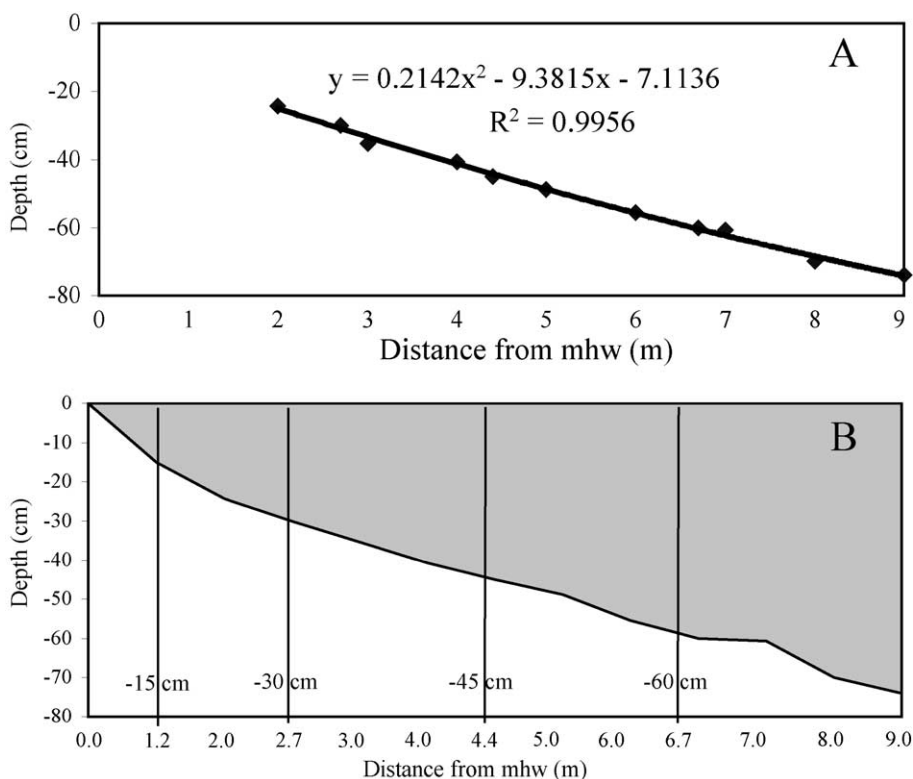

Fig. 2. Depth contour of Fox Point. A slope of the mean depths at 1-m intervals from shore at mean high water (A) was used to calculate the average and intermediate depth contours (B).

the formula for the slope to estimate the length of each slope. Total grass shrimp abundance was calculated with the following formula,

$$\text{shrimp} \times \frac{\text{width of zone}}{\text{net width}}.$$

Shrimp density and length were analyzed separately with a two-factor (depth and time) ANOVA. Differences among means for significant effects were tested using Least Significant Differences (LSD) (Sokal and Rohlf, 1981; Day and Quinn, 1989). Diel variation in the total abundance of shrimp was tested with a Student's t-test.

2.4. Relative risk of predation

Relative risk of predation was assessed with tethered grass shrimp (Everett and Ruiz, 1993). A halter of 0.45-kg test monofilament line was tied around each shrimp and attached to a 1.8-kg test tether line bearing a #20 (2 mm) hook. The diameter and weight of the tether line approximated those of a human hair. The tether line was tied to one end of a 1-m-long steel bar buried in the sediment. To facilitate recovery, the steel bar had a small float attached with monofilament line at the opposite end from the shrimp. All shrimp used in the study were 30 to 35 mm in total length, non-ovigerous and intermolt stage. The shrimp were collected the day of the experiment with long-handled dip nets.

Laboratory checks of tethered shrimp showed that none escaped from tethers during 24 h in the absence of predators. Further, tethered shrimp exhibited the same range of behaviors as untethered shrimp, but tethering may produce greater vulnerability to predators than for untethered shrimp. The potential interaction of diel period and tethering was not tested and may be a confounding artifact (Barshaw and Able, 1990; Peterson and Black, 1994). However, relative mortality is one possible indicator of diel effects and can provide supporting evidence for diel variation in predation risk.

A set of 9 to 12 grass shrimp was tethered at each of two depths (30 and 60 cm) approximately 6 h after sunrise or sunset. Twelve sets, six day and six night, of tethered shrimp were deployed during early summer 1993. Day and night tethering experiments were performed within 24 h of each other. Shrimp survivorship and presence of predators on the hooks were checked at 15-min intervals for the first half hour and then at 30-min intervals for the next 2 h. All predators caught on the tethers were measured, identified to species and released. The data were analyzed with a two-factor (depth and time) ANOVA on arc sine square root transformed percent of shrimp remaining after 30 min.

3. Results

3.1. Variation in predator guild composition and abundance

A total of 13 species of fish and one species of crab were caught in nine daytime and eight nighttime seine haul samples (Table 1). Five fish species made up 91.3% of

Table 1
Composition of fish and crabs collected in 17 diel seine hauls at Fox Point on the Rhode River in May and June 1993

Scientific name	Common name	Total caught
Fundulus heteroclitus	mummichog	1060
Fundulus majalis	striped killifish	625
Menidia menidia	Atlantic silverside	623
Micropogonias undulatus	Atlantic croaker	524
Anchoa mitchelli	Bay anchovy	454
Brevoortia tyrannus	Atlantic menhaden	100
Morone americana	white perch	83
Callinectes sapidus	blue crab	58
Cyprinodon variegatus	sheepshead minnow	58
Cyprinus carpio	common carp	9
Gobiosoma bosc	naked goby	5
Leiostomus xanthurus	spot	3
Trinectes maculatus	hogchoker	3
Morone saxatilis	striped bass	2
Lepomis gibbosus	pumpkinseed	1

all individuals caught. Four species were identified as predators of grass shrimp, the mummichog *Fundulus heteroclitus*, Atlantic croaker *Micropogonias undulatus*, white perch *Morone americana* and striped bass *Morone saxatilis* (hereafter, in this chapter as predator guild). These fish all share the same attributes: (1) they readily consumed grass shrimp in aquaria or laboratory experiments, (2) they were caught on the hooks of tethered shrimp, and (3) they had grass shrimp reported in stomach contents where grass shrimp were available (Kneib and Stiven, 1982; Everett and Ruiz, 1993). In the case of striped bass and croaker, when grass shrimp were not available other palae-monids or similar size shrimp (i.e., *Crangon*, penaeid shrimp) have been reported in the predators' stomach contents (Hollis, 1952; Homer and Boynton, 1978; Overstreet and Heard, 1978; Gardinier and Hoff, 1982; Lubbers et al., 1990; Hurley, 1992; Ruder-shausen, 1994). In laboratory experiments, white perch prefer grass shrimp to other prey in the study site region (Hines, Smithsonian Environmental Research Center, MD, unpublished data).

The remaining organisms captured in the seine hauls are not considered to be grass shrimp predators, and thus not members of the predator guild. They can be placed in four categories; the first category consists of striped killifish, *Fundulus majalis*, spot, *Leiostomus xanthurus* and common carp, *Cyprinus carpio*, which grow large enough to prey on adult grass shrimp but apparently do not. The reported diets of these species include small crustaceans, but these were amphipods, tanaids and copepods, not shrimp (Murdy et al., 1997). None of the fish in this category were caught on tether hooks. The second category included the blue crab *Callinectes sapidus*. It is a benthic predator and important bioturbator (Hines et al., 1990). Palaemonoids and other shrimp have been reported as minor constituents in the diets of blue crabs from the Gulf of Mexico (Laughin, 1982; Alexander, 1986; Hsueh et al., 1992; Rosas et al., 1994), the Atlantic coast of Georgia (Fitz and Wiegert, 1991), the Pacific coast of Central Mexico (Stoner

and Buchman, 1990) and Florida (Tagatz, 1968). However, we found no evidence of *Palaemonetes* or other shrimp in crab guts from the Chesapeake Bay or any other evidence that blue crabs feed on grass shrimp in this system (Hines et al., 1990). Further, in our observations of blue crabs and grass shrimp in aquaria, they ignored each other. Members of the third category, sheepshead minnow, *Cyprinodon variegatus*, and naked gobies, *Gobiosoma bosc*, seldom grow to a size to be a threat to adult grass shrimp and organisms significantly smaller than grass shrimp dominated the reports of their diets (Murdy et al., 1997). Fish in the last category, Bay anchovies, Atlantic menhaden and Atlantic silversides, are planktivorous (Murdy et al., 1997).

Mummichogs and Atlantic croaker predominated the shrimp predator guild, accounting for 91.7% of the catch, whereas white perch and striped bass were much less abundant.
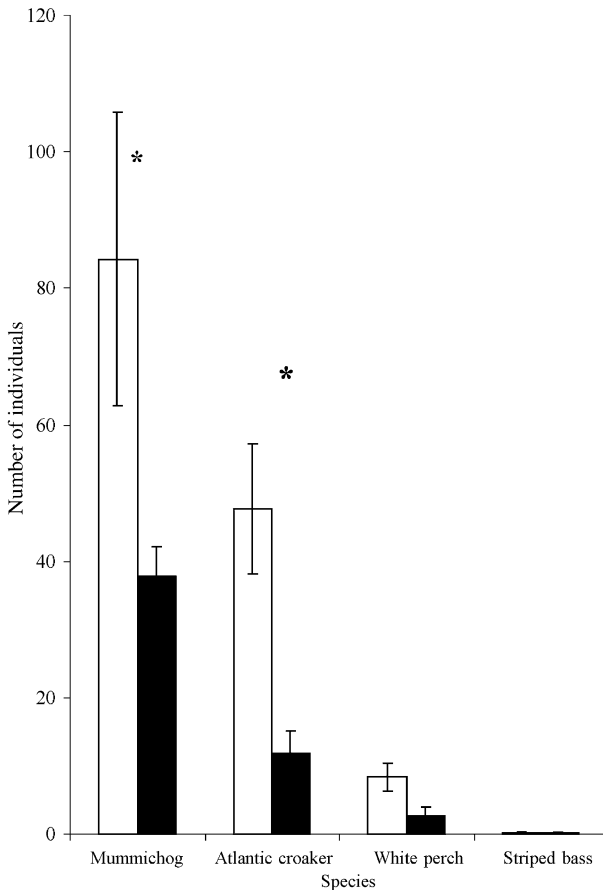

Fig. 3. Diel abundance of grass shrimp predators. Values represent the mean (± standard error) of predators caught in nine day (□) and eight night (■) seine hauls. Seines were pulled onto shore from a depth of 100 cm during mid May to mid June in 1993. Asterisks denote significant differences between treatments (LSD $p < 0.05$).

Combined abundance of the four predator species varied with diel period (Fig. 3). The abundance of all four predators was significantly lower at night ($t_{15, \ 0.05} = 12.29$, $p = 0.0009$). Abundance differed significantly among the predator species with mean number per seine ranging from highs of 84.4 *F. heteroclitus* to lows of 2.4 *M. saxatilis*. Diel difference in predator abundance did not affect the relative species composition of the guild ($x^2_{3, \ 0.05} = 573.8$). Mummichogs continued to dominate the guild numerically at night, with three times the mean number of individuals.

There was a significant time by species interaction on mean species length (ANOVA $F_{1, \ 3} = 15.70$, $p = < 0.0001$) (Fig. 4). Compared to day samples, the nighttime mean lengths of white perch decreased from 135 to 100 mm (LSD $p < 0.05$). While the mean size of mummichogs and Atlantic croaker remained unchanged between diel periods. With only
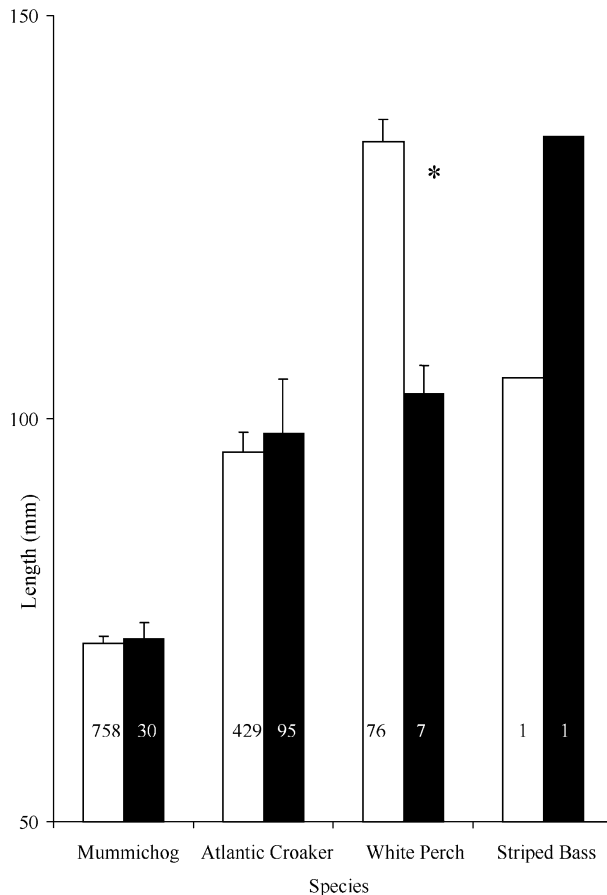

Fig. 4. Lengths (mean ± standard error) of grass shrimp predators caught in nine day (□) and eight night (■) seine hauls. Asterisk indicates significant differences (LSD $p < 0.05$) between day and night mean lengths of fish. Numbers inside of bars indicate number of fish collected.

two (one day and one night) striped bass individuals caught, it is not possible to make statistical inferences. However, the length of the night-caught striped bass (135 mm) was greater than the length (105 mm) of the day-caught fish. Within each time period, there was very little variation in species length. The mean coefficient of variation was 3.9% during the day and 6.9% at night.

3.2. Grass shrimp distribution and abundance

Grass shrimp density varied significantly with the interaction of depth and diel period ($F_{3, 120} = 3.03$, $p < 0.003$) (Fig. 5). Daytime grass shrimp density was highest at mid depths (peak of 171.25 shrimp/m^2), with almost 80% of all shrimp found at 30 cm. At
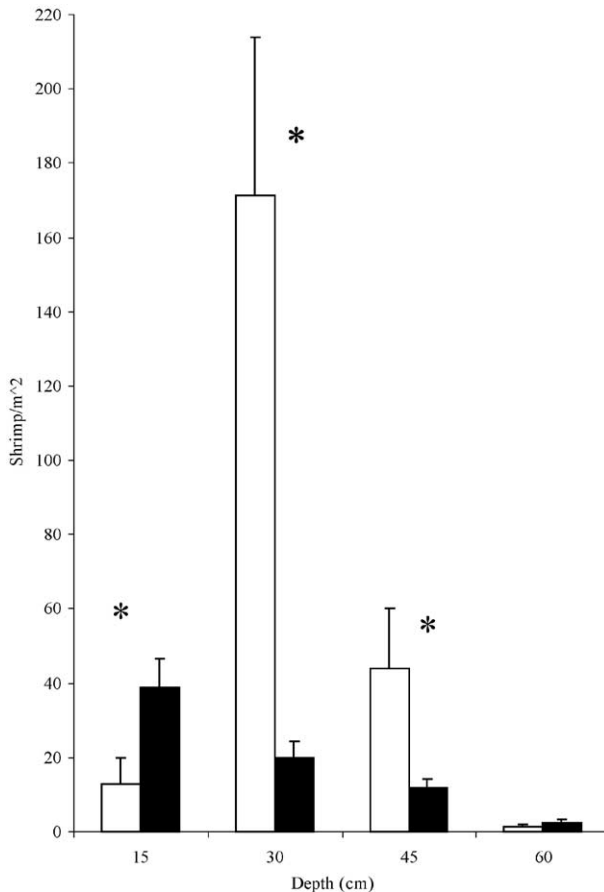

Fig. 5. Mean (± standard error) number of grass shrimp per square meter (day □, night ■). Shrimp were collected with long-handled dipnets pushed along 10-m transects from mid May to mid June 1993. $N = 3$ for each time by depth treatment. Asterisks indicates significant differences between diel periods (LSD $p < 0.05$).

night, grass shrimp density was highest at 15 cm and decreased with increasing depth. The nighttime peak of 38.9 shrimp/m^2 was less than one third of the daytime peak. Within the study zone, overall shrimp abundance was lower at night than during day ($t_{4,\ 0.05} = 3.48$, $p < 0.005$).
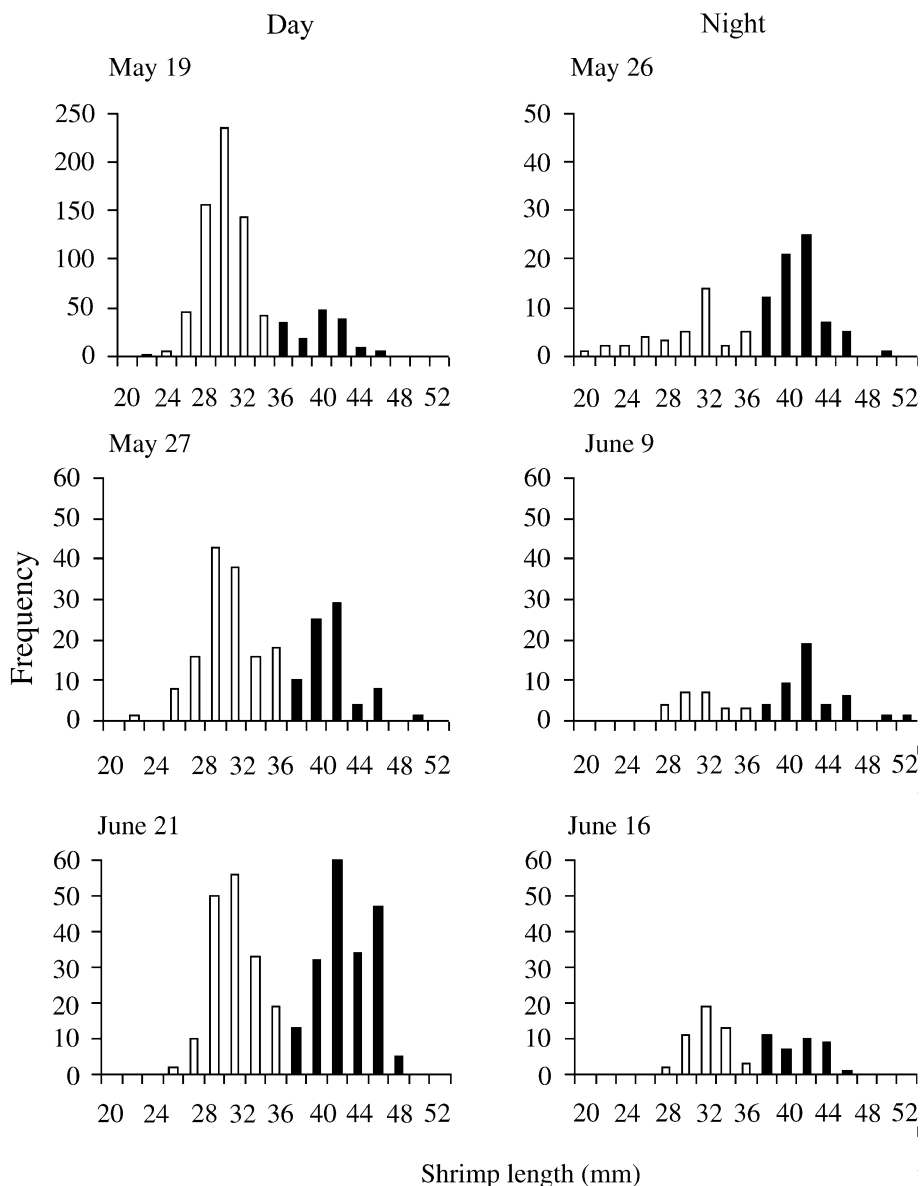

Fig. 6. Diel size distribution of grass shrimp caught across all depths in push net samples in 1993. ■ represents large (>36 mm) shrimp and □ represents small (<36 mm) shrimp.

Although the size distribution of shrimp exhibited the same bimodal distribution for both day and night, there was a much lower proportion ($x^2 = 75.68$, $df = 1$, $p < 0.001$) of smaller shrimp present during the night (Fig. 6). Because of the strong bimodal size distribution, diel differences in size were analyzed as proportion of size class. Grass shrimp were divided into small < 36 mm and large > 35 mm size classes. The data was arc sine-transformed and analyzed in a two-factor ANOVA. There was a significant effect of diel period on mean proportion of small shrimp ($F_{1,\ 88} = 14.03$, $p = 0.0003$) (Fig. 7.). There was no effect of depth ($F_{3,\ 88} = 1.2$, $p = 0.32$) nor was there a depth-by-diel period interaction ($F_{3,\ 68} = 1.7$, $p = 0.17$).

3.3. Relative risk of predation

Survivorship of tethered shrimp was dependent on diel period exhibited significant interaction between diel period and depth ($F_{1,\ 17} = 11.69$, $p = 0.0033$). At night, shrimp
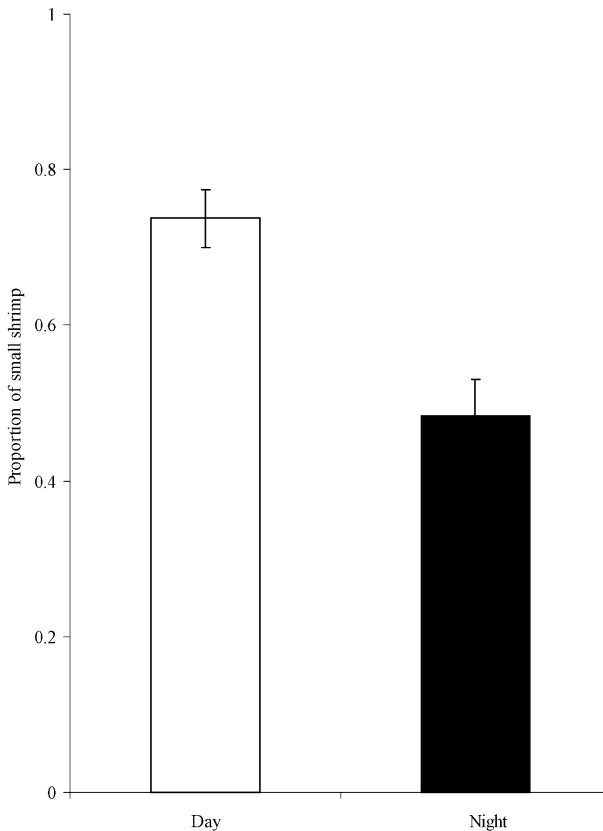

Fig. 7. Mean (± standard error) proportion of small, less than 36 mm, grass shrimp (day □, night ■). Shrimp were collected with long-handled dipnets pushed along 10-m transects from mid May to mid June 1993.
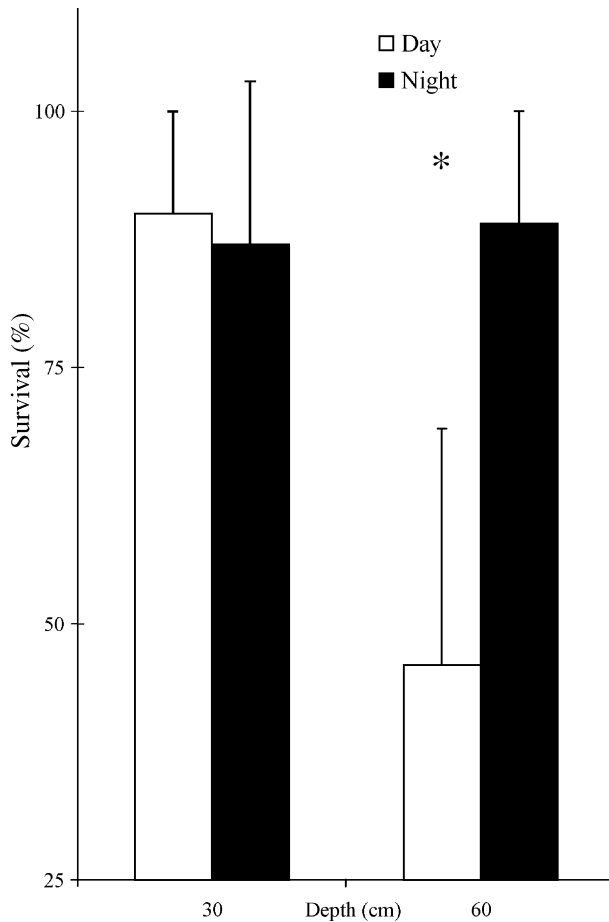
Fig. 8. Diel survivorship of 30–35-mm grass shrimp tethered at refuge and nonrefuge depths (*n* = 12). Tethered shrimp survival varied with diel period and interacted with depth. Asterisk denotes diel treatments with significantly different means (LSD *p* = 0.05).

survivorship was consistently high (>80%) at both 30- and 60-cm water depths (Fig. 8). In contrast, daytime survivorship decreased significantly (LSD *p* = 0.05) with depth from >80% at 30 cm to a low of <40% at 60 cm.

4. Discussion

In the Rhode River, grass shrimp distribution reflected diel variation in predation risk and predator abundance. During the day, shrimp abundance was greater in shallow habitats where survivorship was greatest. These results are consistent with previous work in this system, indicating that shallow waters provide a refuge from predation for small macro-

fauna (Ruiz et al., 1993; Dittel et al., 1995). At night, shrimp exhibited a marked decrease in the use of shallow habitats. The shift is consistent with a decline in predation risk from predominantly visual predators with the decrease in available light.

Two characteristics of the predator guild contribute to diel variation in predation risk for grass shrimp, predator abundance and predation efficiency. Predator guilds can be characterized by relative and absolute abundance. Relative abundance can affect predation risk through the differential predation rates of the component species, while total abundance acts through increased encounter rates. Variation in relative abundance is common in systems characterized by a pattern of nocturnal turnover. Such turnover occurs when nocturnal predators become active or immigrate into the system (Robblee and Zieman, 1984). The Rhode River exhibited no signs of nocturnal turnover. All predators that were present in seine hauls at night were present during the day. These findings agree with Lubbers et al. (1990), who sampled two sites in the mid-Chesapeake Bay in 1979 and 1980. They report a similar diel decrease in large predatory fish with no change in species composition.

Predation efficiency can be affected by both brightness and contrast and may often decline in the dark (Olla and Davis, 1990). Three of the four members of the predator guild, white perch, striped bass and mummichogs, are visual predators (Monteleone and Houde, 1992). Although the fourth predator, Atlantic croaker, may be able to capture prey in low light conditions, predation rates were reported to be highest in clear versus turbid waters (Minello et al., 1987).

Shenker and Dean (1979) reported nocturnal behavior for *P. pugio*. Their ebb tide samples of a tidal marsh creek contained grass shrimp at night, and "...emergence started in the late afternoon and the shrimp moved throughout the water till early morning." Sogard and Able (1994) found grass shrimp moved between vegetated habitats at night at a higher rate than during the day and colonization rates of artificial SAV was highest at night compared to daytime. Baur (1985) suggested that caridean shrimp responded to reduced predation risk from visual hunters by moving into the water column above seagrass beds. Vance (1992) proposed a similar explanation for diel patterns of activity in penaeid shrimp.

In the Rhode River there are two pieces of direct evidence that predation risk for grass shrimp changed on a diel basis, mortality of tethered shrimp and predator guild variability. Mortality of tethered shrimp varied diurnally and interacted with depth. During the day mortality for tethered shrimp was depth-dependent and shrimp survival was lowest in deeper water; at night the risk of predation was low and did not differ by depth. This diel collapse of depth-structured mortality indicates that there is a decreased risk of predation at night.

Grass shrimp exhibited a shift in habitat utilization that corresponded to diel fluctuations in predation risk. Grass shrimp densities were higher in refuge habitats during the day when both predator abundance and mortality were highest. At night when there was a decrease in predator abundance and shrimp mortality, there was a breakdown in the pattern of refuge habitat use.

Grass shrimp increased proportional use of shallow waters at night. If grass shrimp move into shallow waters to avoid predation from aquatic predators, then one might predict that their densities would be highest in the shallowest depths. However, their

daytime density was greater in medium depths relative to shallow depths. Grass shrimp's daytime use of medium depths may be the result of conflicting pressures from terrestrial and aquatic predators. During the study period wading birds were seen in and around the study area. These predators may provide a significant predation risk to shrimp in shallow waters that shrimp may respond to by moving offshore. Such offshore movement would then be constrained by pressure from aquatic predators. Prey response to terrestrial and aquatic predators by moving into intermediate depths has been reported in the literature. Water striders (*Aquarius remigis*) who move toward shallow waters or the shore in the presence of green sunfish (*Lepomis cyanellus*) and offshore in the presence of fishing spiders (*Dolomedes vittatus*), move to an intermediate distance from shore when both predators are present (Krupa and Sih, 1998). Similarly, juvenile spot (*L. xanthurus*) in enclosures made greater use of shallow waters in the presence of fish than in the presence of wading birds, and had an intermediate distribution in the presence of both (Crowder et al., 1997).

Within the study area, the abundance of grass shrimp was lower at night than during the day. It is clear that the shrimp did not simply disperse from the narrow 30-cm zone into wider 60-cm zone; as there was no increase in density in the deeper zone at night relative to the day. Therefore, grass shrimp left the 30-cm zone at night and returned to it during the day. The nocturnal migration may be a result of exploitation of foraging habitats that are unavailable during periods of relatively high predation risks. They may, for instance, move into deeper waters than sampled in this experiment. Another possibility is that grass shrimp migrate into the water column where the sweep nets would not sample them. While feeding reports of grass shrimp consistently include benthic or non-nektonic flora and fauna (Welsh, 1975; Sikora, 1977; Kneib, 1985; Walters et al., 1996), these studies were conducted on shrimp collected during daytime. The passage time of the foregut of *P. pugio* has been estimated at within 0.5–4.0 h (Hoyt et al., 2000). Therefore, stomach contents of daytime shrimp may not contain information on nocturnal prey. In aquaria, *Palaemonetes* sp. feed on free-swimming larvae of the fiddler crab *Uca mina* and mud crab, *Rhithropanopeus harrisii* (Morgan, 1992) as well as mosquito larvae (Roberts, 1995). During the day, feeding in the water column may make shrimp vulnerable to the various finfish predators. However, as the risk of predation from visual predators decreases, grass shrimp may be able to exploit the nektonic environment.

4.1. Size-dependent response

The shift in shrimp abundance in the shallow habitat during the day was primarily caused by a decrease in the number of smaller shrimp. At night, with the decrease in predation risk, greater proportions of smaller shrimp left the shallows for under-exploited habitats. Sogard and Able (1994) reported a similar pattern of smaller shrimp exhibiting stronger response than larger shrimp in *P. vulgaris* and *Hippolyte pleuracanthus*, in which smaller shrimp were more likely to cross unstructured sand at night to colonize artificial seagrass.

Ruiz et al. (1993) showed that, for nearshore estuarine residents, there is a relationship between prey size, depth and risk of predation. Small macrofauna were distributed in the nearshore zone by size and depth, with proportions of smaller organisms decreasing with

depth. This pattern was attributed to depth-dependent predation risk. As depth increases, smaller organisms are at a greater risk of predation than larger organisms of the same species.

At shallow depths, smaller shrimp may not be able to obtain adequate resources due to interference competition from larger shrimp. Small shrimp may be outcompeted for foraging resources by larger shrimp. Competition for habitats has been demonstrated in palaemonid shrimp (Coen et al., 1981). *Palaemon floridanus* outcompeted *P. vulgaris* for refuge habitat, resulting in increased mortality for *P. vulgaris* (Thorp, 1976). *P. vulgaris* was able to exclude *P. pugio* from an oyster shell refuge. Chambers (1981) reported that *P. vulgaris* consistently displaced *P. pugio*. He reported the displacement to be related to the use of antennae and relatively larger chelae. In aquarium experiments, large shrimp (using their chelae) excluded smaller shrimp from preferred habitats, the underside of logs (Ruiz, Smithsonian Environmental Research Center, MD, personal communication) The interaction resulted in a halo of smaller shrimp surrounding the log with large shrimp in the safer underside. Small grass shrimp are restricted by predation to a relatively small area shared with a competitive dominant. This combination of factors results in a greater response to reduced predation pressure at night.

Acknowledgements

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