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Amphipod (*Gammarus minus*) responses to predators and predator impact on amphipod density

Abstract Recent theoretical work suggests that predator impact on local prey density will be the result of interactions between prey emigration responses to predators and predator consumption of prey. Whether prey increase or decrease their movement rates in response to predators will greatly influence the impact that predators have on prey density. In stream systems the type of predator, benthic versus water-column, is expected to influence whether prey increase or decrease their movement rates. Experiments were conducted to examine the response of amphipods (*Gammarus minus*) to benthic and water-column predators and to examine the interplay between amphipod response to predators and predator consumption of prey in determining prey density. Amphipods did not respond to nor were they consumed by the benthic predator. Thus, this predator had no impact on amphipod density. In contrast, amphipods did respond to two species of water-column predators (the predatory fish bluegills, *Lepomis macrochirus*, and striped shiners, *Luxilus chrysocephalus*) by decreasing their activity rates. This response led to similar positive effects on amphipod density at night by both species of predatory fish. However, striped shiners did not consume many amphipods, suggesting their impact on the whole amphipod "population" was zero. In contrast, bluegills consumed a significant number of amphipods, and thus had a negative impact on the amphipod "population". These results lend support to theoretical work which suggests that prey behavioral responses to predators can mask the true impact that predators have on prey populations when experiments are conducted at small scales.

Key words *Gammarus minus* · Behavioral responses Predators · Prey density

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Introduction

The impact that predators have on prey behaviour and prey density has received much attention in ecology (reviewed in: Sih et al. 1985; Lima and Dill 1990; Wooster 1994). Recent theoretical work suggests that at the small scales at which ecological experiments are conducted predator impact on prey density is the result of a direct effect, prey consumption by predators, and an indirect effect, prey behavioral responses to predator presence (Sih and Wooster 1994; Englund and Olsson 1996; Wooster et al. 1997). An understanding of the strengths of these two factors in influencing local prey density is important if results at small scales are to be extrapolated to larger, population-level scales.

To examine how predator consumption of prey and prey activity responses to predators interact to produce apparent predator impacts, Sih and Wooster (1994) modeled a system in which prey move between two patches, one that contains predators and one that is predator-free. Prey density in each patch is influenced by immigration into and emigration from the patch, and prey density in the predator patch is reduced by predator consumption of prey. Their model makes two important predictions. First, if prey increase their emigration rates in response to predators, prey density will decline in predator patches even in the absence of any consumption of prey by predators. Second, if prey decrease their emigration rates in response to predators, prey density will tend to increase in patches with predators; however, predator consumption of prey will cause prey density to decline. In this scenario, the impact that predators have on prey density will depend upon the relative strengths of prey emigration responses to predators and predator consumption of prey.

While there has been much work on the behavioral responses of stream prey to predators (Allan 1983; Peckarsky 1984; Williams and Feltmate 1992; Wooster and Sih 1995) and on predator impacts on stream prey density (Wooster 1994), few studies have partitioned

predator impact into prey emigration responses and predator consumption of prey. Such studies have generally found that prey increased their emigration rate in response to predators and that this response was as important as predator consumption of prey in causing a decline in prey density (Feltmate and Williams 1989; Lancaster 1990; Forrester 1994; Kratz 1996). In one case stream prey did not appear to change their movement rates in response to predators and predator impact was a function of predator consumption of prey alone (Sih et al. 1992). None of these studies considered multiple types of predators within the same system.

Here I report the results of experiments designed to examine how stream prey change their activity rates in response to two different types of predators, benthic (e.g., salamanders and stonefly nymphs) and water-column (e.g., many fish), and how these responses in conjunction with predator consumption of prey determine local prey density. I predicted that prey would increase their movement rates in response to benthic predators, resulting in strong negative effects on prey density. In contrast, prey were predicted to decrease their movement rates in response to water column predators, resulting in either weak negative effects or positive effects on prey density. These predictions were made based on the hypothesis that a good way for stream prey to escape benthic predators is to move into the water column and drift or swim downstream; however, this behavior might make prey more susceptible to water-column predators, and prey should decrease activity to avoid predation in response to these predators (Sih and Wooster 1994; Wooster and Sih 1995).

Materials and methods

Study animals

Stream amphipods (*Gammarus minus*) were used as prey. *G. minus* is a common amphipod in small clear streams and springs in the south-central United States (Pennak 1989). Amphipods are important detritivores in streams, consuming both plant and animal detritus (Sutcliffe et al. 1981; Chergui and Pattee 1988; Pennak 1989). Amphipods are a source of food for many stream fish (Newman and Waters 1984), and they respond strongly to the presence of predatory fish by decreasing rates of swimming, crawling and drifting (Williams and Moore 1985; Andersson et al. 1986; Holomuzki and Hoyle 1990; Andersen et al. 1993).

The response of amphipods to three different species of predators was examined. Bluegills (*Lepomis macrochirus*) and striped shiners (*Luxilus chrysocephalus*) are predatory fish that forage from the water column and substrates surface. Visual cues are an important component of the foraging behavior of bluegills (Werner and Hall 1974; O'Brien et al. 1976; Gerking 1994), and many cyprinids are active during the day, presumably using visual cues to detect prey (Tikkanen et al. 1994; Moyle and Cech 1996). Two-lined salamanders (*Eurycea bislineata*) are relatively small benthic predators that prey on a variety of invertebrates, including amphipods (Petranka 1984).

Amphipods, fish, and salamanders were captured in Raven Run Creek located 25 km southeast of the University of Kentucky campus in Lexington, Fayette County, Kentucky, United States. At the time of the experiments (November 1995) bluegills and striped shiners were abundant in downstream pools of Raven Run and two-lined salamanders and *G. minus* were abundant throughout downstream areas. Fish were captured by electrofishing and salamanders and amphipods were captured using dip nets. Captured animals were taken to the University of Kentucky campus where experiments were conducted. Fourteen bluegills (mean standard length ± 1 SE $= 6.5 \pm 0.3$ cm), 15 striped shiners (mean standard length $= 5.7 \pm 0.2$ cm), 28 two-lined salamanders (mean snout-vent length $= 3.8 \pm 0.2$ cm), and approximately 1000 amphipods (mean length of 24 individuals $= 10 \pm 1.2$ mm) were collected from Raven Run.

Experiments were conducted in a controlled-environment chamber at the University of Kentucky campus. The chamber was held at $13 \pm 2°C$ and a natural day:night light cycle (10:14 h). All animals were kept in carbon-filtered tap water. Fish were housed individually in 15-l aquaria and maintained on a diet of commercial fish food, amphipods, and mayflies. Salamanders were housed individually in 1.25-l containers; they were fed commercial brine shrimp, amphipods, and mayflies. Amphipods were held in four 12-l tubs containing leaf litter (a source of food for amphipods) from Raven Run; their diet was supplemented with commercial fish food.

All surviving animals were released back into Raven Run at the end of the trials. Trials were conducted from 11 November to 16 December 1995.

Experimental protocol

Predator consumption of amphipods and predator effects on amphipod emigration, refuge use, and benthic densities were studied in plexiglass laboratory stream channels (1 m long × 20 cm wide). Each channel had a separate recirculating water system. Filtered water flowed from an upstream 24-l reservoir, through the stream channel, and into a lower 30-l reservoir. Water was pumped from the lower reservoir into the upper reservoir by two submersible pumps (Teel 1P805A). Depth of water in the channels was 10 cm and discharge through the channels was approximately 0.43 l/s. All channels had screen lids that prevented fish from jumping out of the channels.

Refuge from fish was provided in each tank by two bricks (19 cm × 9.5 cm × 5.5 cm), a single tile (19 cm × 9.5 cm × 0.5 cm), and three leaf packs. Bricks and tiles were elevated approximately 0.3 cm from the bottom of the tanks so that amphipods and salamanders could use them as refuge. Leafpacks were made by stuffing leaves taken out of Raven Run creek into plastic mesh cylinders (10 cm long × 6 cm diameter and 0.8 cm mesh size; the ends of the cylinders were open). Leafpacks provided food as well as refuge for the amphipods. In each stream channel a single leaf pack was tied to the upstream end of each brick and to the top of the tile. The leaf packs, tiles and bricks provided abundant refuge for the amphipods from the fish predators, but not from the salamanders which were small enough to crawl under the bricks and tiles and were frequently found in the leafpacks.

In natural systems animals move both into and out of patches. To simulate this in the laboratory channels, I introduced amphipods ("immigrants") into the upstream end of the experimental channels during the trials. Funnels were placed at the upstream end of each channel. Plastic tubing (20 cm long × 1.25 cm diameter) was connected to the bottom of the funnels; the end of the tubing was under the water surface in the channel and embedded in the upstream leafpack. Thus, immigrants were added directly into refuge. Immigrants were introduced into the channels every 0.5 h by flushing them through the funnels with water. Emigrants from the channels were collected in drift traps placed at the downstream end of each channel. Mesh (0.8 cm mesh size) covered the downstream end of each channel to prevent fish from swimming out of the channels. Since salamanders were capable of swimming out of the channels, drift traps were checked every hour during experimental trials and any salamanders found in the drift traps were placed back into the upstream end of the channel.

Experimental trials were conducted during the day and at night. For each trial each tank was randomly assigned to one of the following treatments: predator-free control, a single bluegill, a single striped shiner, or three two-lined salamanders. Trials lasted for 5 h. Predators were placed into the experimental channels 24 h before the start of a trial and starved during this time. This allowed the predators to get used to the channels and the water to become conditioned with chemical cues from the predators before the start of a trial. At the start of a trial, the predators were removed and held in small containers next to each channel. The pumps were turned off and 30 amphipods (15 males and 15 females) were placed into each channel. After 15 min the predators were replaced into the stream channels, the pumps were turned on, and the trial began. At the end of each trial, predators were removed from the channels and returned to their original containers. No predator was used twice. All substrate was taken from each channel and sorted to find all remaining amphipods. Water was drained from all channels and reservoirs and replaced with fresh filtered water. All channels, reservoirs, bricks, and tiles were scrubbed between trials to remove chemical cues from the animals and fresh leaves from Raven Run were used in each trial.

For day trials, activity of amphipods was observed during six spot checks of each channel. During each spot check the number of amphipods out of refuge was recorded. The channels were surrounded by black plastic curtains that prevented the animals from being disturbed by my movements. Small slits cut into the curtains were used to make observations. For night trials, three spot checks were made on each stream channel using infra-red lights (40-W tungsten bulbs covered by a filter with peak transmission at 860 nm and no transmission below 750 nm) and an RCA closed-circuit video camera (TC1004/01) fitted with an infra-red sensitive lens (Midwest Telecommunications V17-102AC).

Every 30 min immigrants were added to each stream channel. The number of immigrants added was based on a preliminary experiment designed to determine the emigration rate of amphipods out of the channels in the absence of predators. The channels were set up in the same fashion as in the experimental trials. Male and female amphipods, 15 of each, were placed into each channel with the pumps off. After 20 min the pumps were turned on and the number of amphipods drifting from the channels was determined after 1 h and again 1 h later. This experiment was conducted during the day (i.e., in light) and at night (i.e., in darkness; $n = 4$ for each time period). The number of amphipods emigrating was converted to a per capita rate for each hour by dividing the number of animals found in the drift net by the benthic density at the start of the hour. The results revealed that significantly more amphipods emigrated during the day than at night (47% and 41%, respectively; t-test on arcsine transformed data, $t = 10.46$, $p = 0.002$). These proportions were multiplied by 30, the initial benthic density of amphipods, and the product was divided in half to determine the number of immigrants to be added every 30 min in the main experiment. This resulted in 7 amphipods added every 30 min during the day and 6 amphipods added every 30 min at night. Nine immigrant additions were made in each channel during each trial resulting in a total of 93 amphipods added to each channel (the initial 30 plus all immigrants) during day trials and a total of 84 amphipods added to each channel at night.

Analyses

I measured four amphipod response variables in this experiment: mean numbers observed out of refuge, total numbers emigrating, numbers missing, and final benthic density. Because these variables are correlated I conducted a MANOVA on numbers out of refuge, numbers emigrating, and numbers missing. Final benthic density could not be used in the MANOVA because of collinearity (i.e., final density is a function of the number emigrating and the number missing). Time (day or night) was not used as an effect in the analysis because more amphipods were introduced into the channels during day trials than during night trials; thus, separate analyses were conducted for day and night trials. If the MANOVA was significant, univariate ANOVAs were conducted on each of the three response variables. The results of the univariate ANOVAs were interpreted using a Bonferroni correction to limit the overall experimentwise error rate (Sokal and Rohlf 1995).

I conducted a separate univariate ANOVA on final benthic density to determine if predator effects on prey drift and predator consumption of prey influenced benthic density. The results of this ANOVA should be interpreted cautiously because of the collinearity between final benthic density and numbers emigrating and numbers missing. For all univariate ANOVAs, treatment means were analyzed using a Tukey's test with an experimentwise error rate of 0.05.

Results

The MANOVA analyses revealed that predators had a significant effect on the dependent variables during both the day (Wilk's λ, $F = 6.05$, $P < 0.001$) and at night (Wilk's λ, $F = 6.78$, $P < 0.001$). The Bonferroni adjustment for the univariate analyses set the α value at 0.017.

Numbers exposed

Predators did not have a significant effect on the number of amphipods out of refuge during the day ($F = 3.52$, $P = 0.053$; Fig. 1a). However, at night fewer amphipods were observed out of refuge in the bluegill and shiner treatments than in the salamander and control treatments ($F = 10.80$, $P = 0.001$; Fig. 2a).

Numbers emigrating

Predators had significant effects on the number of amphipods emigrating from the channels. During the day, fewer amphipods emigrated from the channels containing bluegills than from the control channels and those containing salamanders ($F = 6.08$, $P = 0.011$; Fig. 1b). At night, bluegills reduced emigration out of channels to the greatest extent and shiners had an intermediate effect on emigration ($F = 43.49$, $P < 0.001$; Fig. 2b).

Numbers missing

Bluegills had a strong effect on the number of amphipods missing both during the day ($F = 24.63$, $P < 0.001$; Fig. 1c) and at night ($F = 9.66$, $P = 0.002$; Fig. 2c). The presence of the other predators did not result in significantly more amphipods missing than the number missing from the control channels. Because so few amphipods were missing from the control trials, I assumed that those missing from the bluegill trials had been consumed.

Final density

Predators did not influence final benthic densities during the day ($F = 3.33$, $P = 0.060$; Fig. 3). In contrast, at night amphipods were more abundant in the bluegill and shiner treatments than in the salamander and control treatments ($F = 23.40$, $P < 0.001$; Fig. 4).
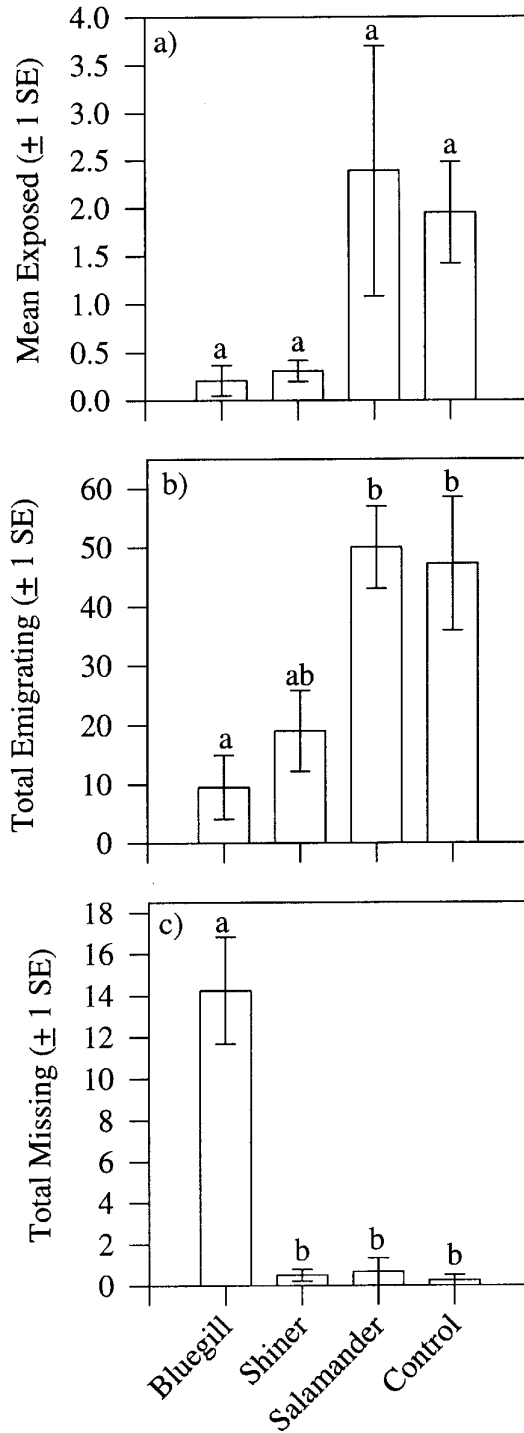

Fig. 1a–c Results of trials conducted during the day. **a** Mean number of amphipods exposed (i.e., out of refuge) in the four predator treatments, **b** mean total number of amphipods emigrating from the stream channels, **c** mean number of amphipods missing from the different treatments. *Error bars* represent standard errors. *Bars* with different *letters* are statistically different (Tukey's test; α = 0.05)
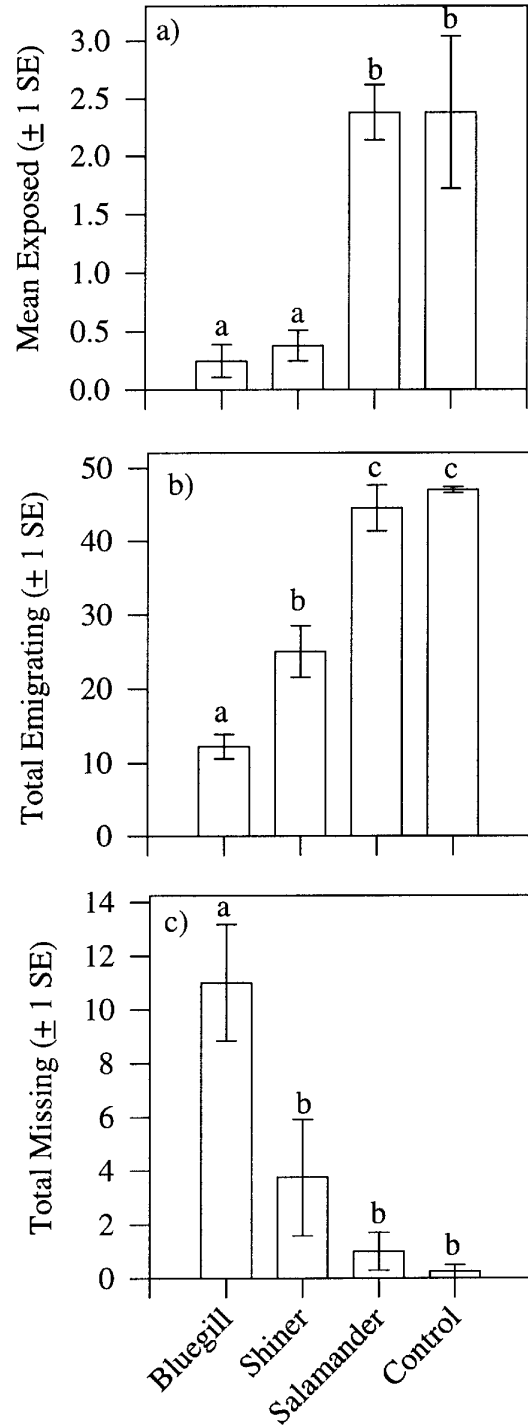

Fig. 2a–c Results of trials conducted at night. **a** Mean number of amphipods exposed (i.e., out of refuge) in the four predator treatments, **b** mean total number of amphipods emigrating from the stream channels, **c** mean number of amphipods missing from the different treatments. *Error bars* represent standard errors. *Bars* with different *letters* are statistically different (Tukey's test; α = 0.05)
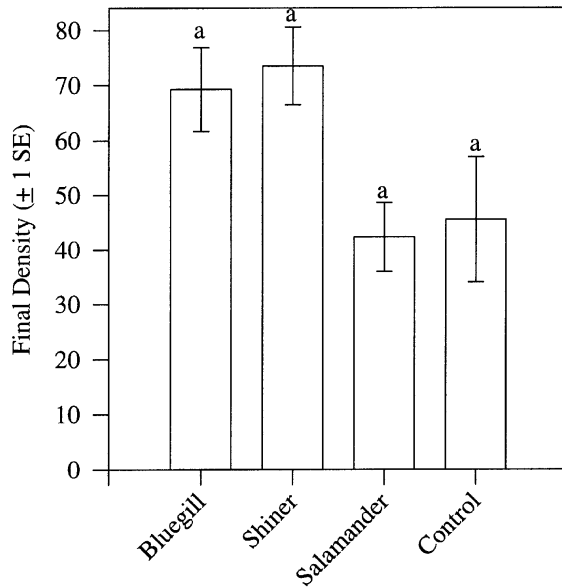
Fig. 3 Final benthic densities of amphipods for day trials for the four predator treatments. *Error bars* represent standard errors. *Bars* with different *letters* are statistically different (Tukey's test; $\alpha = 0.05$)
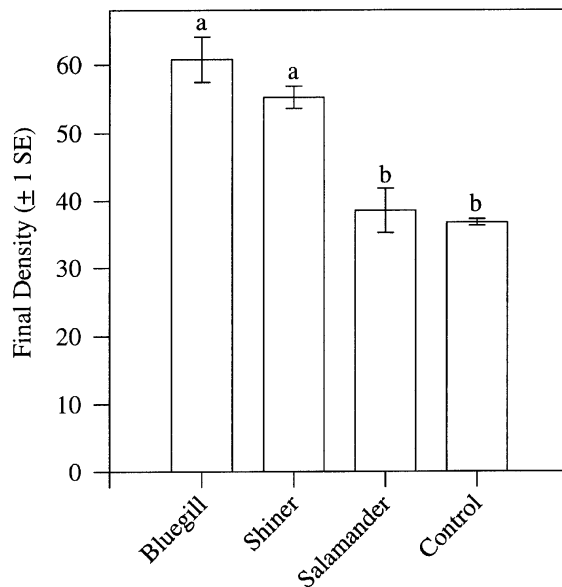

Fig. 4 Final benthic densities of amphipods for night trials for the four predator treatments. *Error bars* represent standard errors. *Bars* with different *letters* are statistically different (Tukey's test; $\alpha = 0.05$)

Discussion

Recent theoretical work suggests that at small scales prey density will be influenced by three factors: immigration, emigration, and predation (Sih and Wooster 1994; Englund and Olsson 1996; Wooster et al. 1997). In addition, this work suggests that prey emigration responses to predators alone, and not predator consumption of prey, might drive the impact that predators have on local prey density (Sih and Wooster 1994). This

impact is quite different from the impact that predators have on the whole prey population, which is the result of consumption only (Englund and Olsson 1996). Field experiments have shown that stonefly and mayfly nymphs increase their drift rates in response to salmonid fish presence and this response accounts for the majority of the negative impact that fish have on prey density (Feltmate and Williams 1989; Forrester 1994). Similar patterns in the field have been found for mayfly nymphs responding to predatory stonefly nymphs (Lancaster 1990; Kratz 1996). In contrast, if situations exist where prey decrease their movement rates in response to predators then prey density will tend to increase in areas with predators and predators will appear to have a positive effect on prey density (Sih and Wooster 1994).

In my experiments, the water-column predators striped shiners and bluegills had positive effects on local amphipod density at night. A similar trend occurred during the day; however, because of high variability in amphipod drift rates, final amphipod densities were not significantly different among the treatments. As predicted, the effect on amphipod density was the result of amphipods decreasing overall levels of activity in response to these predatory fish. Amphipods responded in a similar fashion to both species of fish even though bluegills consumed a significant number of amphipods and were thus dangerous predators while shiners consumed very few amphipods making them relatively innocuous predators. Williams and Moore (1985) found that *G. pseudolimnaeus* amphipods from North America decreased activity rates in response to 8 different fish species, including predators and non-predators, as well as an African cichlid with which amphipods do not have any historical contact. Thus, amphipods appear to show a generalized response to fish cues (Williams and Moore 1985). This makes adaptive sense if the costs of being able to discriminate different species of predatory fish are high (e.g., if mistakes are common or lethal or if complex sensory and neural functions are required).

Unlike for shiners, the number of amphipods missing from channels containing bluegills was significantly greater than the number missing from control channels. I assume that this was the result of consumption of amphipods by bluegills. This consumption should drive amphipod density down. However, fewer amphipods emigrated from channels containing bluegills, which should drive amphipod density up. These two conflicting effects on amphipod density produced different predator impacts during the day and at night. During the day, the two effects essentially canceled each other out and final amphipod density in bluegill channels was not different from that in control channels. At night the positive effect on density of amphipod response to bluegills was stronger than the negative effect of bluegill consumption, resulting in bluegills having a positive impact on amphipod density.

Amphipods were predicted to increase emigration rates in response to a benthic predator (*Eurycea* salamanders) resulting in low final densities relative to pre-

dator-free controls. However, amphipods did not appear to respond to salamanders by changing refuge use or emigration rates. The number of amphipods missing from channels containing salamanders did not differ from the number missing from control channels, suggesting that salamanders did not pose a threat to amphipods, which might explain the lack of response by amphipods to salamanders. Since amphipods did not respond to salamanders and salamanders did not consume (or consumed very few) amphipods there was no salamander effect on final density of amphipods. A stream field experiment that manipulated *Eurycea* salamander density also showed a lack of response by the prey community to *Eurycea* presence (Reice and Edwards 1986). Thus, *Eurycea* salamanders do not appear to be important in structuring the macroinvertebrate communities of streams. This might be due to the relatively small size of *E. bislineata*. Other, larger stream salamanders have important effect on stream prey behavior and survival (*Ambystoma:* Huang and Sih 1991; *Gyrinophilus:* Resetarits 1991; Gustafson 1993).

Most studies designed to examine the impact that predators have on prey density do so at small scales and do not examine the mechanisms behind the impact. If such a study were conducted to compare the impact that bluegills and striped shiners have on amphipod density, the conclusion reached would be that they have similar effects which are either zero (during the day) or positive (at night). This conclusion, however, would mask two important features. First, positive predator effects on local prey density might be interpreted as indirect or "keystone predator" effects mediated by the interaction of a third species with the predator and focal prey species. For example, fish predators can reduce the density of predatory invertebrates, resulting in a positive effect on herbivorous invertebrates (Power 1990). The results reported here support the possibility that a much simpler mechanism, decreased activity by prey, can produce positive predator effects (Sih and Wooster 1994). Second, while the impact that bluegills and shiners had on local prey density was the same (zero during the day and positive at night), their impact on the overall amphipod "population" was different. The impact that shiners had on the "population" was essentially zero because they consumed few, if any, amphipods. In contrast, bluegills consumed a moderate proportion of the amphipods (15.3% during the day and 13.1% at night), and thus had a negative effect on the amphipod "population." In conclusion, these results support predictions of Sih and Wooster (1994); prey density can increase in patches with predators when prey respond to predator presence by decreasing emigration rates and increasing refuge use. In addition, this effect can occur even when predators consume a significant number of prey.

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