DO STONEFLY PREDATORS INFLUENCE BENTHIC DISTRIBUTIONS IN STREAMS?[1]

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Abstract. Experimental manipulations were conducted within the substrate of a Wisconsin stream and a Colorado stream to measure the effect of stonefly predators on the distribution of benthic invertebrates. Screen cages containing free predators, predators restricted from foraging, or no predators, allowed prey migration but no predator migration over 3-d periods. The presence of *Acroneuria lycorias* (Perlidae) in the Wisconsin stream significantly depressed the establishment of prey populations within cage microhabitats. Mechanisms for reduction were consumption of prey by the stonefly, and predator-avoidance by prey using contact and non-contact cues. The presence of *Megarcys signata* (Perlodidae) reduced prey colonization in the Colorado stream by the same mechanisms, but restricted predators produced less consistent effects. This result could be due to colonization of cages by prey that could not detect predators without contact. *Pteronarcella badia* (Pteronarcidae), a large stonefly detritivore that takes occasional prey, did not affect colonization of Colorado stream cages by prey. This differential response by prey to two morphologically similar, but functionally different, stonefly species suggests that predator avoidance was not purely tactile. Chemotactile and non-contact chemical cues are possible mechanisms by which prey differentiated these stoneflies. The presence of *A. lycorias* and *M. signata* in experimental cages significantly increased the attrition of mayfly prey, compared to that from cages with no stonefly or a restricted stonefly in each stream. This result suggests that predation and avoidance by prey of contact with foraging predators were responsible for the higher disappearance of mayflies from cages. Free *P. badia* had a similar effect, probably due to tactile avoidance of this large detritivorous stonefly by some prey in the Colorado stream.

Key words: chemotactile; colonization; Colorado; experimental manipulations; mayfly; non-contact chemical; predation; predator avoidance; stonefly; stream benthos; tactile; Wisconsin.

INTRODUCTION

The importance of biological interactions in determining the distribution and abundance of species in streams has been experimentally documented by Peckarsky (1979*a*), and Peckarsky and Dodson (1980). By manipulating only biological variables, such as densities of predators or competitors within experimental stream habitats, effects upon resultant species distributions can be measured directly. Connell (1975) summarized the evidence from field experiments on the mechanisms controlling community structure in aquatic ecosystems, but no evidence was presented on streams.

Although since 1975 a few investigators have attempted to test the effects of invertebrate predators upon stream distributions, a lack of manipulative studies still exists (Fox 1977, Friberg et al. 1977). Hildrew and Townsend (1976), Siegfried and Knight (1976), and Townsend and Hildrew (1979) presented associations

between invertebrate stream predators and prey distributions, but no direct cause-effect relationship. Peckarsky and Dodson (1980) provided evidence for the role of stonefly predators in determining distributions of other predators in two streams. This paper presents evidence of the effects of stonefly predators on the distribution of prey populations, and provides information regarding the precise nature of the interactions producing the observed effects.

Interstitial stream habitats were manipulated within cages such that physical-chemical parameters were maintained nearly constant. The biological parameter allowed to vary was the presence of a stonefly predator and its access to colonizing prey. The specific objective of the experiments was to determine the community-level effects of a stonefly predator and a stonefly detritivore on the colonization of and attrition from cages by prey.

MATERIALS AND METHODS

Study sites

Experiments were carried out in two second-order streams, Otter Creek, Sauk County, Wisconsin, and

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TABLE 1. Summary of experiments.

	Experiment 1			Experiment 2		Experiment 3	
Location	Otter Creek			East River		Otter Creek	East River
Cage treatment	(1) One free predator (P) (2) One restricted predator (P*) (3) No Predator (0)			(1) One free predator (P) (2) One restrictred predator (P*) (3) No predator (0) (4) One free detritivore (D) (5) One restricted detritivore (D*)		(1) One free predator + 10 mayfly prey (2) One restricted predator + 10 mayfly prey (3) 10 mayfly prey (4) One free detritivore + 10 mayfly prey	
Season (range of dates)	Spring 1976 (7 May–18 June)	Fall 1976 (10 September–12 November)	Spring 1977 (22 April–9 June)	Summer 1976 Cage treatments (3), (4), (5) (10–28 July)	Summer 1977 Cage treatments (1), (2), (3), (4) (2–29 July)	Spring 1978 (31 March–2 June)	Summer 1978 (9–30 July)
Range of temperatures (°C)	9.5°–22.2°	0.0°–20.0°	7.2°–18.3°	5.6°–18.9°	6.1°–19.4°	0.0°–18.3°	3.3–15.0°
Range of current velocity (cm)	9.3–28.7	3.7–7.0	7.3–28.0	19.7–31.0	10.0–19.0	11.0–37.3	21.7–62.5
Stonefly predator (head capsule width, mm)		*Acroneuria lycorias* (Perlidae) (3.5–5.3)		...	*Megarcys signata* (Perlodidae) (3.5–5.0)	*A. lycorias* (3.5–5.3)	*M. signata* (3.5–5.0)
Stonefly detritivore (head capsule width, mm)		...		*Pteronarcella badia* (Pteronarcidae) (2.8–3.5†)		...	*P. badia* (2.5–3.5†)
Mayfly prey species (head capsule width, mm)					*Baetis phoebus, Ephemerella subvaria, Stenonema fuscum, Heptagenia hebe, Paraleptophlebia* sp. (1–3)		*Baetis bicaudatus, Ephemerella infrequens, Cinygmula* sp., *Epeorus longimanis, Rhithrogena hageni* (1–3)
Number of replicates per cage treatment	9	10	12	6	9	25	12

† Thoracic width is greater than head capsule width in this species. Nymphs with head capsules >2.5 mm were restricted by 3.0-mm mesh baffles.

the East River, Gunnison County, Colorado. Both streams are fully described elsewhere (Peckarsky 1979a). The location of the experimental manipulations provided stony, heterogeneous substrate, and moderate current velocity and depth, except during occasional spring runoff or extreme weather conditions (Table 1).

The experiments

Stainless steel screen cages (0.8-mm mesh) with removable lids and end baffles were filled with natural substrate material ranging in size from 2 to 12 cm in smallest diameter, and from smooth to rough in texture (Peckarsky 1979a). Twenty-eight rocks of similar size and texture classes were included in each cage. The cage habitats offered substrates and interstitial spaces that simulated the adjacent habitat. Twelve to 16 cages were simultaneously introduced into each stream, and covered with 10 cm of substrate within riffles. This cage depth and an experiment duration of 3 d were chosen, after preliminary experimentation, to maximize numbers of replicate trials per season

while allowing adequate time for colonization or attrition of benthos (Peckarsky 1979b). Current velocity was measured at the surface of the substrate of each cage with a Marsh-McBirney model 201 current meter, and stream temperatures were continuously monitored with a maximum-minimum thermometer. The cage end baffle used for all trials and treatments was of 3.0-mm mesh that prevented stonefly predators with larger head capsule widths from migrating to or from the cages, but allowed smaller prey and predators to migrate freely. Cages were oriented with the baffle end downstream to reduce the chance of passive colonization by benthic invertebrates (Peckarsky 1979a). Animals recovered upon cage retrieval were stored in 70% ethanol for counting and identification.

Table 1 summarizes three experiments that were designed to meet the objective stated in the introduction. All insects introduced into experimental habitats were abundant in the benthos and, where end baffles were not prohibitive, commonly colonized cages. Predators were restrained from foraging within cages of type P* (see Table 1) by placing them in a small
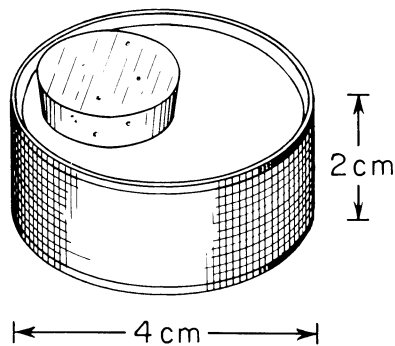
FIG. 1.   Predator cage (mesh 0.3 mm).

predator cage (Fig. 1) with 0.3-mm mesh. Empty pred-
ator cages were included in all other cage treatments
for control purposes. Prey species that were experi-
mentally introduced into cages (experiment 3) were
common in the stomach contents of the predators
tested (Peckarsky 1980). The species composition of
prey was held constant within trials, but varied
through the seasons according to the life histories,
sizes, and abundances of mayflies in the benthos.

For experiment 1, comparison of prey final density
of P vs. 0 cages tested the effect of the presence of a
free stonefly predator on prey colonization. Compar-
ison of P* vs. 0 measured the predator-avoidance by
prey given only non-contact cues. The difference be-
tween colonization of P vs. P* cages showed the por-
tion of the total prey reduction that was due to pre-
dation and predator-avoidance by prey given contact
cues as opposed to the portion due to non-contact
avoidance responses.

The same comparisons could be made for experi-
ment 2. In addition, the response by prey to *Pteron-
arcella badia*, a large stonefly that morphologically
resembles *Megarcys signata*, but is primarily a detri-
tivore that occasionally takes animal prey, could be
compared to the prey response to the predator, *M.
signata* (Fig. 2). In this way, a differential response to
a predator and a large detritivore could be detected.
Comparison of final prey density of cages D vs. 0
showed the effect of the detritivore on prey coloni-
zation; D* vs. 0 measured avoidance of the detritivore
by prey given only non-contact cues (see Table 1).

The addition of 10 mayfly prey to each cage in ex-
periment 3 enabled us to measure the disappearance
of prey from cages. Comparisons of net attrition (cal-
culated as the difference between initial and final den-
sities of stocked species of mayfly prey) between cages
of types P vs. 0 tested the response of prey to a free
predator; P* vs. 0 tested the avoidance of the predator
by prey given only non-contact cues; and P vs. P*
measured the portion of response due to predation and
predator-avoidance by prey given contact cues as op-
posed to the portion of the total prey reduction due to
non-contact avoidance responses. Similarly, differ-
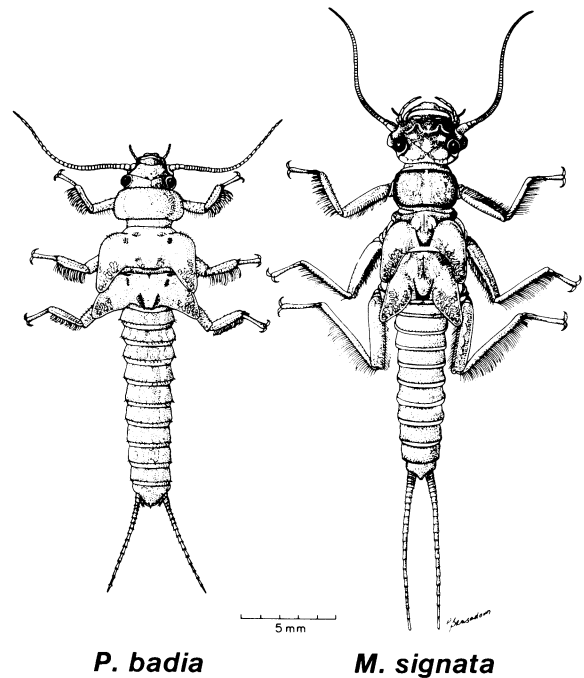

P. badia   M. signata

FIG. 2.   *Pteronarcella badia* and *Megarcys signata*, East
River.

ences between attrition of mayflies from D cages vs.
P cages showed whether the prey responded differ-
entially to the predator and the detritivore. Compari-
sons were also made of net colonization (calculated as
final densities of prey not initially present plus prey of
the introduced mayfly species in excess of 10) among
cages as in experiment 1.

Statistical analysis

An application of chi-square analysis was used to
test for differences among treatment effects. The fol-
lowing technique was employed to negate the effects
of variation in current velocity, temperature, and prey
species among replicate trials on different dates within
seasons: The within-treatment (between-sampling-
date) marginal totals were not included in the calcu-
lation of the expected values; these were calculated as
the average of the between-treatment marginal totals
for each date. Chi-square values were calculated for
total numbers of colonizing benthos for each date
among all treatments, then partitioned by pairwise
comparisons between specific treatments. Seasonal
chi-square values were obtained by adding the values
for each date within seasons (J. Neess, University of
Wisconsin, *personal communication*).

RESULTS AND DISCUSSION

Response of prey to stonefly predators

If potential prey could detect and avoid stoneflies
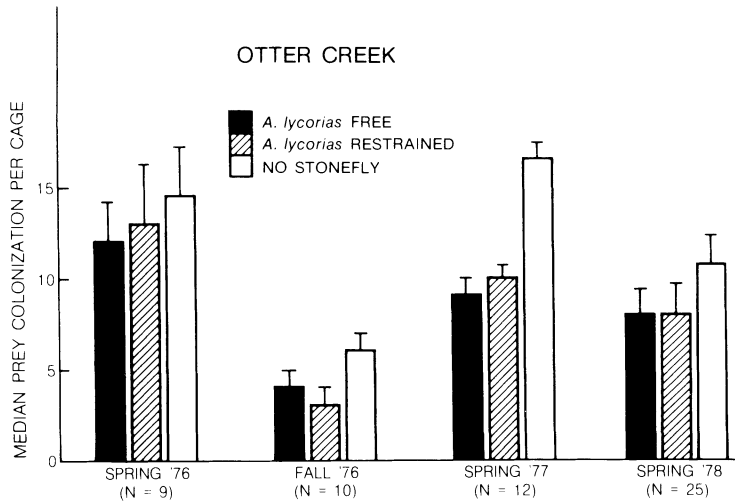given non-contact cues alone, we would expect (a)

FIG. 3.   Median net number of prey colonizing each cage, Otter Creek. N = number of replicates per treatment. Vertical bars indicate 1 SE (Wilcoxon and Wilcox 1964). Note that the magnitude of the differences between medians may not indicate statistical significance, since chi-square tests were applied to total numbers per treatment.

reduced prey colonization of P* cages vs. 0 cages (Table 1). If prey were responding to contact cues or being consumed by predators after entering cages, we would expect (b) colonization of P cages to be further reduced from that of P* cages. The results from each stream are discussed separately.

Prey response to Acroneuria lycorias, Otter Creek

During all trials in Otter Creek, the largest numbers of prey were recovered from cages with no predator. Colonization was reduced in cages with restrained *A. lycorias,* and a smaller number of prey appeared in cages where the stonefly was free to consume colonizers. Fig. 3 represents the median prey colonization per cage. Statistical comparisons between the different treatments were made on total numbers colonizing all cages, and are summarized in Table 2. Percent reductions in colonization of cages P vs. 0, P* vs. 0, and P vs. P* were also calculated from total numbers.

During three of four seasons, differences between treatments P* vs. 0 suggest that prey avoided cages with *A. lycorias* even when the stonefly could not consume colonizers (Table 2A, fall 1976, spring 1977, spring 1978). The effect was qualitatively the same during the spring 1976 season, but not statistically significant. Results of most trials, then, were consistent with expectation (a). Invertebrate prey showed a significant preference for cages without predators over cages in which the only cues available for stonefly detection were non-contact. Stoneflies were not visible within the small-mesh cages due to the opaque quality of the mesh and the interstitial location of the cages themselves. Mechanical disturbance by the restrained stoneflies was probably diluted by the mesh of the predator cages. Auditory or chemical stimuli,

on the other hand, could be transmitted through the mesh.

Experiments in which distributions of mayflies were directly observed in the presence of *A. lycorias* suggest the importance of the effect of non-contact chemical cues upon the distribution of some prey species (Peckarsky 1980). The lack of a significant community response during the spring 1976 trials may have been due to colonization by other prey species that did not use chemoreception to detect predators. The feasibility of chemical predator detection by stream invertebrates was discussed by Peckarsky (1980), and was reported to occur in marine invertebrates (Feder 1963, Phillips 1978). Cage results presented here are consistent with the interpretation that some prey detected and avoided stoneflies given only non-contact chemical stimuli.

In all trials at Otter Creek, *A. lycorias,* when free to consume colonizers, significantly reduced the number of prey recovered within the experimental microhabitats (Table 2A, P vs. 0 cages), as in expectation (b). This single comparison did not reveal the mechanism for the reduction, however. Either the stoneflies were consuming significant quantities of prey that entered cages, prey were avoiding the cage habitat due to the presence of the predator, or a combination of both factors was responsible for the observed distribution. Stomach content analysis of the experimental stoneflies offered limited information concerning the relative effects of the two mechanisms. Prey numbers in stomachs of free *A. lycorias* fluctuated widely between seasons. Gut retention time is not known for these insects, which prevents rigorous interpretation of the relationships between numbers of prey recovered in stomachs and numbers eaten within cages during the 3-d period. However, gut contents provided

TABLE 2. A. Possible mechanisms responsible for reduction in prey colonization (Experiments 1 and 2).†

	Mechanisms		
Season	Contact avoidance, non-contact avoidance and predation (P vs. 0)	Contact avoidance and predation (P vs. P*)	Non-contact avoidance (P* vs. 0)
Otter Creek, *A. lycorias*:			
Spring 1976	28.8 (P < .05)	28.0	0.8
Fall 1976	38.7 (P < .05)	1.6	37.1 (P < .05)
Spring 1977	47.5 (P < .001)	14.2 (P < .05)	33.3 (P < .001)
Spring 1978	15.9 (P < .05)	0	15.9 (P < .05)
East River, *M. signata*:			
Summer 1977	38.0 (P < .05)	17.7	20.3
Summer 1978	42.1 (P < .01)	12.9 (P < .05)	29.2 (P < .05)

B. Possible mechanisms responsible for increase in prey attrition across all cages (Experiment 3).†

Otter Creek, *A. lycorias*:			
Spring 1978	20.5 (P < .01)	20.5 (P < .05)	0
East River, *M. signata*:			
Summer 1978	58.3 (P < .01)	52.8 (P < .05)	5.6

† Tabled numbers represent percentages of total reduction for all cages of each treatment. Significance levels are indicated in parentheses (chi square). P, P*, 0 refer to cage treatments (Table 1).

a relative measure of recent feeding intensity, which may be useful in interpreting cage results.

During the 1977 spring sampling period, free *A. lycorias* depressed the number of prey recovered significantly below that in cages with restricted stoneflies (Table 2A, P vs. P*). This suggests that the combination of feeding effects and contact encounters between stoneflies and prey constituted a significant component of the total effect of predators on prey distributions. A lack of difference between P vs. P* treatments for all other trials indicates that one or both of these components were not operating or were operating at a reduced level. Stomachs of the free *A. lycorias* individuals used during spring and fall 1976 trials contained very few prey compared to those found in stoneflies from spring 1977 trials (0.4, 0.5, 7.6 prey per gut). Spring 1978 free stoneflies had intermediate prey numbers per gut (2.1). Intensified feeding of the *A. lycorias* nymphs tested during the spring 1977 trials may have accounted for the further reduction in numbers of prey per cage in P vs. P* cages for that season. Also, a high frequency of avoidance upon contact with intensively foraging predators by prey may have produced the observed response (Peckarsky 1980). In most other trials, non-contact cues alone were as effective as contact cues and feeding in producing reductions of numbers of prey colonizing cages.

In summary, the presence of *A. lycorias* significantly depressed colonization of cage habitats by prey during all trials with a free stonefly, and during three of four trials when *A. lycorias* was prevented from foraging. The mechanisms causing these reductions

included feeding by free predators, and avoidance of the stoneflies by prey given contact or non-contact cues; their relative importance varied seasonally.

Prey response to Megarcys signata, East River

During summer 1978 trials, restricted and free *M. signata* reduced net prey colonization below that of control cages (P* vs. 0, P vs. 0, Fig. 4, Table 2A). The free predator also showed a greater effect than the restricted predator (P vs. P*). The same trends occurred during 1977 trials. The only statistically significant difference between treatments, however, is the reduction of colonization by prey of cages containing free *M. signata* below that of control cages (P vs. 0).

East River prey, then, significantly avoided cages with *M. signata* given only non-contact cues, as in expectation (a), during trials of one of two seasons. These 1978 results are supported by evidence from direct behavioral observations of mayflies in the presence of *M. signata* (Peckarsky 1980); two of three species, *B. bicaudatus* and *E. infrequens*, showed significant distributional changes in response to non-contact chemical cues from the stonefly predator.

The weaker community response of prey in 1977 trials may be due to cage colonization by prey that did not use chemoreception to detect predators, or it may be related to a peculiarity of that sampling season. During summer 1977, water levels in the East River approached drought conditions (Table 1). Overall colonization of control cages was markedly reduced from 1976, a "normal" summer in terms of water levels. Early emergence of *M. signata* may have confounded
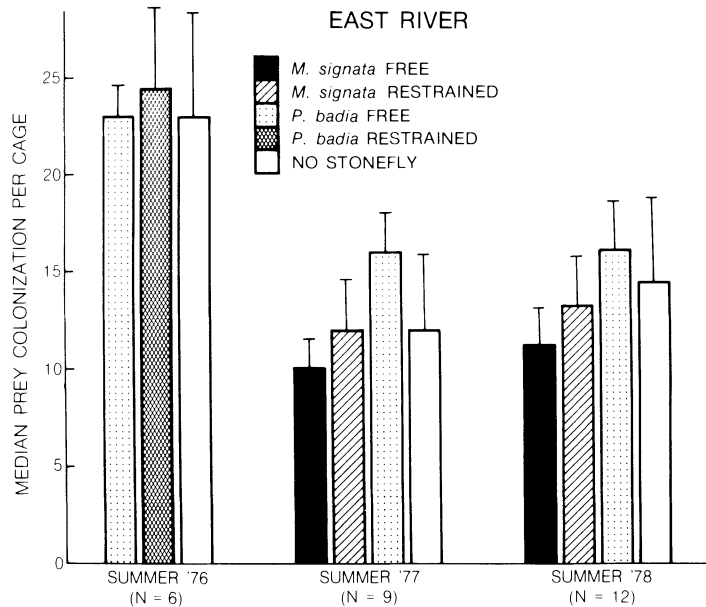
FIG. 4. Median net number of prey colonizing each cage, East River. N = number of replicates per treatment. Vertical bars indicate 1 SE.

results, since these stoneflies do not feed just before emergence (B. L. Peckarsky, *personal observation*). This factor may be responsible for the less pronounced effect of the presence of the predator during 1977 trials. An alternative explanation for the inconsistency between seasons is that some prey may find refuge within the cage habitat out of the stimulus range of the restricted predators. This would reduce the observable effect of non-contact stimuli on prey colonization.

During both summers, free *M. signata* caused consistent significant reduction of cage colonization as in expectation (b). Relative feeding intensity by the stonefly, as indicated by gut analysis, may have been very low during both summers (Dodson and Peckarsky, *personal observation*). The observed depression of prey colonization was probably caused by prey avoidance of predators by contact, as well as some predator feeding.

During summer 1978 trials, the combination of feeding by the stonefly and contact-avoidance by prey had a significantly greater effect on prey colonization than did predator avoidance by non-contact stimuli alone. These results are consistent with observations of the responses of mayfly prey to contact encounters with *M. signata* (Peckarsky 1980). The same trend for 1977 trials is not statistically significant, however, which may reflect the peculiarities of that sampling season mentioned above.

In summary, East River prey cage colonization was consistently depressed by the presence of free *M. signata* due to a combination of predation and predator avoidance by prey given contact cues. Prey avoided cages in which *M. signata* could only be detected by

non-contact cues during one of two seasons. This inconsistency may be due to altered predator behavior related to near-drought conditions during summer 1977 trials, or to cage colonization by prey that could not detect predators without contact.

Prey response to a large stonefly detritivore

If East River benthos could respond to the presence of a large stonefly detritivore upon contact, we would expect (c) reduced prey colonization of cages D vs. 0 (Table 1). If prey could avoid the stonefly given only non-contact cues, a comparison of cage colonization should show (d) fewer colonizers of D* vs. 0 cages.

Trials conducted during the summers of 1976, 1977, and 1978 showed that the presence of *Pteronarcella badia*, a large stonefly that is primarily a detritivore but occasionally consumes small mayflies and chironomids (Peckarsky 1980), did not affect the colonization of cages by East River benthos (Fig. 4). For all trials, there were no significant differences between the numbers of prey colonizing cages with *P. badia* and control cages, regardless of the treatment of the stonefly (D vs. 0, D* vs. 0).

This result, in contrast to the response of prey to free *M. signata*, suggests that prey could differentiate between *M. signata* and *P. badia*. Prey avoided cages containing the larger predatory stonefly, but did not avoid cages containing the morphologically similar stonefly detritivore. The mechanism by which this differentiation occurred could be chemical, tactile, or chemotactile. Or, increased predation by *M. signata* may have lowered successful cage colonization by prey.

Direct observations of East River mayfly species supported differential avoidance of the two stoneflies as the most probable explanation (Peckarsky 1980). None of the observed mayflies avoided *P. badia* given non-contact chemical cues, while two species (*Baetis bicaudatus* and *Ephemerella infrequens*) avoided *M. signata*. Both mayflies also showed reduced responses to contact with *P. badia*, as opposed to contact with *M. signata*. Both stoneflies appeared to forage in the same manner, and neither stomachs of *M. signata* nor *P. badia* revealed excessive feeding within cages during any trials. These observations are consistent with the interpretation that some prey differentiated between predators and nonpredators by a chemotactile mechanism, which may explain the differential cage colonization.

In summary, the presence of a large stonefly detritivore did not affect the cage colonization by East River benthos. The lack of intensive feeding by this stonefly, and lack of significant avoidance by most prey may explain this result.

Effect of stoneflies upon prey attrition from cages

If the presence of a stonefly predator or detritivore had an effect upon the disappearance of prey from cages, we would expect an increase in the attrition of prey from cages containing a stonefly (Table 1, experiment 3). In Otter Creek and in the East River, net prey attrition was significantly higher from cages where *A. lycorias* or *M. signata* were free to forage than from cages with restrained predators or no predators (Fig. 5, Table 2B). Stomach contents of the free stoneflies and behavioral observations of the mayfly species (Peckarsky 1980) indicated that the disappearance of prey was probably caused in part by feeding, and in part by predator avoidance by prey upon contact. The smaller differences between attrition from control cages and cages where the stonefly was prevented from foraging could be due to the presence of spatial refuges for prey out of the range of predator stimulus but still within the cage.

Finally, the presence of free *P. badia* produced a significantly greater amount of net prey attrition than from control cages (D vs. 0, *P* < .05). These results are in contrast to the colonization results presented in the previous section. Of the five species of mayflies used in cages throughout this season (Table 1), the responses of only three have been directly observed in the presence of *P. badia* (Peckarsky 1980). One of the three, *Cinygmula* sp. did not respond differentially to contact with *M. signata* and *P. badia*. This species accounted for 25–30% of the mayflies introduced into experimental cages during the summer 1978 trials. Its observed avoidance response to *P. badia*, in addition to possibly similar responses of prey not yet observed, may account for the significant difference in attrition of mayflies between D and 0 cages.
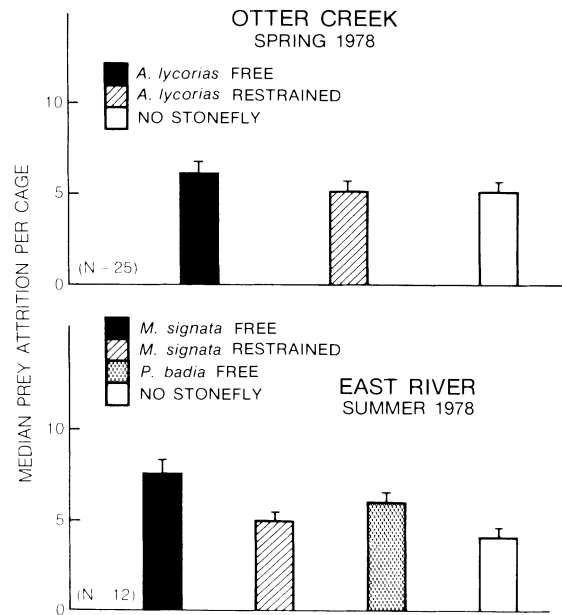

FIG. 5. Median net prey attrition per cage, Otter Creek and East River. *N* = number of replicates per treatment. Vertical bars indicate 1 SE.

In summary, Otter Creek mayflies showed greater attrition from cages where *A. lycorias* was free to forage than from cages with restricted or no *A. lycorias*. East River mayflies showed significantly higher net attrition from cages where *M. signata* and *P. badia* were free than from cages with restricted *M. signata* or no stonefly. These results suggest that feeding and contact-encounters between free stoneflies and the mayflies produced the observed effects.

These experiments represent an attempt to identify the role of stonefly predators in determining prey distributions. The results are a compilation of a total prey-community effect rather than of individual prey species. Direct observations (Peckarsky 1980) showed that different prey species responded differently to the same stonefly predators. Further cage experiments are necessary in order to separate the community effects of predators into effects of individual prey species. Data reported here suggest that stonefly predators have a significant effect on prey distributions in these two streams. Inconsistencies may be due to different responses by prey species, altering the apparent overall community effect. Consistency, however, reflects a strong effect common to a large proportion of the benthic community.

CONCLUSIONS

Given the data from the experiments presented here, the following hypothesis can be generated. The stonefly predators *Acroneuria lycorias* and *Megarcys signata* consistently depressed prey colonization of

and increased prey attrition from experimental cage habitats in Otter Creek and the East River. The mechanisms causing these effects included feeding, predator avoidance by prey upon contact with foraging predators, and predator avoidance by prey given noncontact stimuli from a restricted predator. The relative importance of these mechanisms varied seasonally within and between streams. The presence of *Pteronarcella badia,* a large East River stonefly detritivore that takes occasional prey, did not affect cage colonization by prey. These data suggest that some prey used stimuli other than tactile as a mechanism for differentiation of *P. badia* from *M. signata.* However, an increase in attrition of stocked prey from cages containing *P. badia* may indicate that other prey species avoided both large stoneflies using tactile stimuli.

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