Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures?

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Experiments in Colorado and New York streams assessed the effects of predaceous stoneflies on benthic invertebrate community establishment in enclosures providing uncolonized habitat. Aspects of prey community structure measured were density, species richness, relative species abundance, and body size. Unexpected inorganic sediment deposition allowed evaluation of direct effects on Colorado stream benthos and indirect effects on predation. Predaceous perlids and perlodids consistently reduced the density and, therefore, rate of prey community establishment in enclosures. Although New York perlids disproportionately reduced densities of some prey species, Colorado stoneflies caused nonsignificant declines in individual prey species densities, the composite effect of which was a significant whole-community response. Predators did not affect prey species richness nor change the taxonomic composition (species additions or deletions) of communities colonizing enclosures. However, the relative abundance of prey taxa differed significantly between cages with and without predators. Most species showed no size differences between individuals colonizing enclosures with predators and those colonizing control enclosures, with a few interesting exceptions. The deposition of silt eliminated the predator effects on prey density, as well as directly causing significant reductions in many Colorado benthic populations. This result demonstrates that abiotic disturbances can periodically override the effects of predation on stream insect communities colonizing enclosures.

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Des expériences dans des ruisseaux du Colorado et du New York ont permis d'évaluer les effets des plécoptères prédateurs sur l'établissement de communautés d'invertébrés benthiques dans des enceintes à coloniser. Les aspects mesurés au sein de la communauté de proies sont les suivants: densité, richesse en espèces, abondance relative des espèces et taille des proies. La sédimentation inorganique, imprévue dans la mise sur pied de ce projet, a donné lieu à une analyse des effets directs sur le benthos du ruisseau du Colorado et à une analyse des effets indirects sur la prédation. Les perlidés et les perlodidés prédateurs ont entraîné une diminution constante de la densité des proies et, par conséquent, de la vitesse de colonisation de la communauté de proies dans les enceintes. Les perlidés du New York ont réduit considérablement la densité de certaines des espèces de proies; les plécoptères du Colorado n'ont entraîné que des diminutions non significatives des densités de certaines espèces et leur action s'est manifestée significativement sur toute la communauté dans son ensemble. Les prédateurs n'affectaient pas la richesse en espèces et ne modifiaient pas la composition taxonomique (addition ou élimination d'espèces) des communautés dans les enceintes. Cependant, l'abondance relative des espèces de proies différait significativement d'une cage à l'autre, en présence ou en l'absence des prédateurs. La structure des populations de proies quant à la taille des individus ne différait pas d'une enceinte à l'autre en présence ou en l'absence des prédateurs, sauf dans quelques cas. La sédimentation du limon éliminait les effets des prédateurs sur la densité des proies et a entraîné, par action directe, des réductions considérables de plusieurs populations benthiques du ruisseau du Colorado. Ce résultat démontre que des bouleversements abiotiques peuvent entraver périodiquement les effets de la prédation sur les communautés d'insectes aquatiques en voie de coloniser des enceintes.

[Traduit par le journal]

Introduction

Benthic invertebrate communities of stream riffles can be characterized by large temporal and spatial variability (Ulfstrand 1967; Allan 1975; Winterbourn 1978) and high rates of colonization and dispersal (Fisher et al. 1982; Waters 1972; Williams and Hynes 1976; Sheldon 1977; Williams 1980). The substrate may be viewed as a mosaic of more or less habitable space, depending on the morphology and behavior of different species, resulting in contagious or patchy invertebrate distributions (Needham and Usinger 1956; Chutter 1972; Resh 1979). A common feature of riffle ecosystems is disturbance by unpredictable storms or predictable seasonal fluctuations in flow regimes (Hynes 1970). Such disturbances may open space for colonization or redistribute habitable patches of substrate (Leopold et al. 1964; McAuliffe 1984). The periodicity of such disturbances, and therefore the frequency of new habitat availability for colonists, varies among streams. These features suggest that stream riffle ecosystems are open (a collection of patches connected by migration), nonequilibrium systems (sensu Caswell 1978).

Colonization by benthic invertebrates of experimentally introduced bare patches of substrate has been studied by many investigators, primarily from the perspective of abiotic effects (Allan 1975; Minshall and Minshall 1977; Williams 1980) and food effects (detritus: Egglishaw 1964; periphyton: McAuliffe 1984; prey: Peckarsky and Dodson 1980b). These studies have shown that such factors as substrate particle size, current regime, and food levels can influence the rate of colonization and the particular species succession in newly available habitats. Biological interactions such as predation and competition have been classically thought to operate only when communities are approaching equilibrium and to maintain rather than establish community structure (Paine 1966; Connell 1975; Hall et al. 1976; Glasser 1979; Schoener 1982).

Most theory on predator effects on prey communities has been developed for closed, equilibrium systems (Slobodkin 1961; Yodzis 1976, 1977). Recently, however, Caswell (1978) developed a model that predicts predator-mediated, long-term,

TABLE 1. Summary of dates, water temperatures, current velocities, and predaceous stonefly species used in experiments

| | Six Mile Creek | | East River | | | | | |
| | 1981 | 1982 | 1980 | | 1981 | | 1982 | |
	7–28 May	22 April–13 May	7–16 July	6–15 August	11–19 June	7–13 July	15–24 June	3–9 August
Water temperature (°C, minimum–maximum)	5.6–15.6	3.0–17.0	5.0–15.0	7.5–22.0	1.0–16.0	6.5–19.0	2.0–10.0	5.0–16.5
Range of current velocity (cm/s)	36–81	63–87	61–116	38–56	66–126	32–38	118–134	27–102
Predaceous stonefly species	Ac. carolinensis (4.82±0.23)[a] Ag. capitata (3.58±0.18)	Ac. carolinensis Ag. capitata	M. signata (3.98±0.16)[b] P. badia (2.81±0.07)[b]	K. modestus (2.73±0.11)[b]	M. signata P. badia	K. modestus	M. signata P. badia	K. modestus

[a]Values in parentheses are mean head capsule width (millimetres) ±95% confidence interval.
[b]Averaged over 1980–1982.

nonequilibrium coexistence of prey populations in open systems. He suggests that predation may be of major importance in such open, nonequilbrium systems. Given this theoretical framework, it is important to examine the impact of predation on the colonization of available substrate patches in streams.

Peckarsky and Dodson (1980a) demonstrated experimentally that predaceous stoneflies affected the invertebrate upstream colonization of, and downstream dispersal from, enclosures placed in the riffle sections of two streams. That study looked only at total prey density and did not examine other aspects of prey community structure, such as species diversity, relative species abundances, or body size. The objectives of the present study were to evaluate predaceous stonefly effects on five structural components of the prey community colonizing enclosures over the short term from upstream and downstream, (i) density of total prey, (ii) density of individual prey taxa, (iii) prey taxonomic richness, (iv) relative abundance of prey taxa, and (v) size composition of individual prey taxa; and to document effects of unpredicted siltation on benthic colonization of enclosures. Results of this study should allow the development of hypotheses concerning the relative effects of predaceous stoneflies and siltation on the prey community establishment in enclosures within stream riffles.

Materials and methods

Study sites

Experiments were conducted during spring and summer 1980–1982 in riffle sections of two streams, the East River, Gunnison County, CO, and Six Mile Creek, Tompkins County, NY. The East River site is a third-order, high-elevation (3100 m) stream with an open canopy, coarse-cobble substrate, and high levels of diel and seasonal fluctuations in current velocity and water temperature. Table 1 summarizes the range of temperature and flow conditions that were measured during the experiments. This stream was described in more detail by Peckarsky (1979a, 1983).

Six Mile Creek is also a third-order stream, but it is largely covered by beech–maple forest canopy. The bedrock is Devonian shale and siltstone, with soils derived from glacial till. The substrate consists of flat shale slabs with diameters ranging from a few centimetres to 1 m, underlain by gravel and silt. The stream flows beneath intermittent ice and snow during winter. Water temperatures and current velocities measured during the experimental periods are given in Table 1.

Predators

The dominant East River predaceous invertebrates are two univoltine stonefly species of the family Perlodidae: *Megarcys signata* (Hagen), which emerges in late June to early August (depending on temperature and flow regimes), and *Kogotus modestus* (Banks), which emerges at a smaller final size in late July to early September. The *Megarcys* nymphs used in experiments were larger than the *Kogotus* nymphs, since *Megarcys* is larger than *Kogotus* during the experimental period (Table 1). Another large stonefly, *Pteronarcella badia* (Hagen) (Pteronarcydae) inhabits the East River site, and has a life cycle similar to that of *M. signata*. However, *P. badia* is an omnivore that consumes primarily detritus (Fuller and Stewart 1977); late-instar nymphs also consume small mayflies and chironomids (Peckarsky 1980). Its head capsule width (Table 1) overlaps with that of *K. modestus*, although its length and robustness are more like that of *M. signata* (Peckarsky 1980; Peckarsky and Dodson 1980a). The benthic densities of these stoneflies range from 8.3 to 33.3/m² (B. L. Peckarsky, unpublished data).

All of these stoneflies consumed a wide variety of prey, the relative abundances of which are given in Table 2. The foreguts of each predator collected for these and other experiments during the periods shown in Table 1 were examined for recognizable prey parts. Prey were identified to species (except for chironomids and simuliids) from whole prey and fragments (claws, mandibles, and head capsules). The

TABLE 2. Relative abundances of prey species in the stomachs of stoneflies in cages during the period of experimentation. Species comprising less than 2% (Six Mile Creek) or 1% (East River) of the stoneflies' diets are not listed

Predator species	Most abundant prey taxa	% of total no. of prey in stonefly stomachs	No. of predators examined	No. with recognizable prey parts
Six Mile Creek				
Ac. carolinensis	Chironomidae	32	82	39
(2.56 prey/gut)	Paraleptophlebia	19		
	Baetis tricaudatus	14		
	Simuliidae	12		
	Epeorus	6		
	Ephemerella invaria	4		
	Stenonema	2		
	Sweltza	2		
	Rhyacophila	2		
Ag. capitata	Chironomidae	24	84	44
(2.98 prey/gut)	Baetis tricaudatus	21		
	Simuliidae	15		
	Paraleptophlebia	11		
	Epeorus	10		
	Ephemerella invaria	8		
	Sweltza	2		
	Stenonema	2		
East River				
M. signata	Chironomidae	49	320	190
(4.22 prey/gut)	Simuliidae	37		
	Baetis bicaudatus	7		
	Podmosta deliculata	4		
	Cinygmula sp.	1		
	Epeorus spp.	1		
	Ephemerella infrequens	1		
P. badia	Baetis bicaudatus	39	428	100
(0.89 prey/gut)	Chironomidae	31		
	Cinygmula sp.	7		
	Simuliidae	4		
	Arctopsyche grandis	4		
	Ephemerella infrequens	3		
K. modestus	Chironomidae	71	258	180
(6.07 prey/gut)	Simuliidae	17		
	Baetis bicaudatus	6		
	Cinygmula sp.	2		
	Ephemerella infrequens	1		
	Epeorus spp.	1		
	Podmosta deliculata	1		

NOTE: Numbers in parentheses beneath each predator species are the mean numbers of prey per predator stomach with recognizable prey parts.

minimum number of each prey species recovered from each predator stomach was extrapolated and totaled over all predator individuals to calculate relative importance (percentages) in the stonefly diets. Rare taxa were not included, and the species shown in Table 2 comprised over 95% of the prey found in all predator stomachs. These data illustrate relative frequencies of each prey species in predator stomachs during the experimental period. They do not show seasonal or ontogenetic changes, nor do they consider the detritus fraction of stonefly diets, but only indicate prey eaten during the experimental period.

Six Mile Creek has a more abundant predaceous stonefly fauna (16.7−83.3/m²; B. L. Peckarsky, unpublished data), dominated by two species of the family Perlidae with 2- to 3-year life cycles. Acroneuria carolinensis (Banks) emerges in early to mid-June at a larger final size than late June to mid-July emerging Agnetina (formerly Phasganophora) capitata (Pictet) (Bukantis and Peckarsky 1985).

Head capsule widths of nymphs used in experiments are given in Table 1. As late instars, both species consumed a wide variety of benthic prey species. The stoneflies in both streams consumed primarily Chironomidae, Simuliidae, and Ephemeroptera during the experimental periods (Table 2).

Experiments

Stainless steel screen cages filled with natural substrates were used in all experiments (Peckarsky 1984). Cages are similar to those shown in Peckarsky (1979b), but were reduced in size (30 × 20 × 10 cm) for more practical handling and to approximate more closely the space occupied by one stonefly (determined from benthic density estimates for late instar stoneflies). Lids were hinged, and removable baffles were inserted on two sides, which allowed prey colonization from upstream and downstream. Solid baffles were inserted at both ends before retrieval of cages.

The duration of experiments was 3 days (for consistency with earlier experiments in Colorado) or 7 days (in New York), which allowed examination of early colonizer assemblages. Colonization of experimental and control cages was assumed to be unaffected by any variables other than the treatment variable, since cages were placed deliberately in riffle sections with similar physicochemical regimes (water depth, stream width, current velocity).

Enclosure experiments have a number of advantages and disadvantages (Hulberg and Oliver 1980). Since cages are artificial habitats in a natural setting, observed effects may be artifacts of their presence. Cage effects can be minimized by the design and implementation of enclosures with as many natural features as possible. For example, all walls of these cages were mesh, allowing flow (though reduced) of water, chemicals, and dissolved and fine particulate organic matter. Also, the use of natural substrate arrays with associated aufwuchs approximated conditions outside the enclosures. Cages were filled with a standard number, particle-size distribution, and texture of stones cleaned of all fauna. Cages were placed in the stream essentially flush with the substrate surface with a thin cover of stones to camouflage them and discourage vandalism.

The experimental design of enclosure experiments can also minimize erroneous interpretation of results. If treatments and controls are in identical cages (enclosure−exclosure experiments) rather than in different kinds of cages (exclosure − "open" cage experiments or exclosure − uncaged controls), the same error exists in both treatments and controls. (See Walde and Davies 1984 for a demonstration of this phenomenon.) Also, cage conditions must fall within the range of natural habitat conditions, and results are technically applicable only to that subset of the stream's physicochemical conditions represented by the cage.

During the summers of 1980−1982, replicate enclosures containing subterminal instars of *M. signata*, *P. badia*, or *K. modestus* were placed in the East River. Stoneflies were stocked in natural densities (one per cage) and confined to cages by end baffles with mesh sizes that allowed prey to migrate freely (3 mm for *M. signata* and *P. badia*, whose thoraxes are wider than their heads, and 2 mm for *K. modestus*). It was assumed that the restriction of entry by very large potential prey species (e.g., *Drunella doddsi*) and access to cages by small predators (e.g., Chloroperlidae) were unimportant to the results of the experiment. Large potential prey species were always very rare (less than one per volume of substrate equivalent to the cage habitat) and were not recovered from stomachs of predators in or outside of cages. Small predators that prey on chironomids and simuliids did colonize cages, but with the same potential effect in all cage treatments.

A second treatment involved further confinement of one *M. signata* or *K. modestus* in a 1 cm height × 3 cm diameter mesh (300 μm) container placed at the upstream center of the cages (see Peckarsky and Dodson 1980a). This treatment was used to prevent the predators from feeding on or touching colonizing prey, and thus to measure noncontact predator avoidance effects. Control cages contained no predators. Treatments were randomly assigned to cages. All cage treatments received a small predator-solitary-confinement cage and the same restrictive end baffles to prevent colonization by other large predators. Stonefly mortality was very low (one *Megarcys* over 3 years), but occasionally predators were missing from the cages. Results from those cages were not included in the analysis.

Table 1 summarizes the dates over which these experiments were replicated. Numbers of replicates per treatment are given with the results. Sequential treatments were combined as replicates because of the expense of cages and the impracticality of handling more than 20 cages per day. Therefore, results reported are average effects over two 3-day periods per summer.

During the spring of both 1981 and 1982, similar experiments were conducted at Six Mile Creek with *Ac. carolinensis* and *Ag. capitata*, using end baffles with 3-mm mesh size. Results represent average effects over three 7-day periods per spring.

Current velocity was measured at half the water depth at each cage with a Marsh−McBirney model 201 electronic current meter. Tem-

peratures were monitored with maximum−minimum thermometers on cage placement and retrieval days. A record of the depth of the water at each cage was also kept.

Statistical analysis

Total prey community density differences were analyzed by Kruskal−Wallis rank sums with distribution-free multiple comparisons for unequal sample sizes (Hollander and Wolfe 1973). Densities of individual taxa within cages were compared using Wilcoxon's signed rank paired tests. Because species richness is dependent on sample size (Peet 1974), the number of prey taxa were compared between treatments by analysis of covariance between slopes and intercepts of species abundance curves (Sokal and Rohlf 1981). The relative abundances of taxa were compared between treatments using chi-square analysis, and size distributions were compared between treatments using Kolmogorov−Smirnov two-sample tests (Siegel 1956). When multiple comparisons were made, null hypotheses were rejected at reduced alpha levels to correct for experiment-wise error (Bonferroni's inequality: $\alpha = 0.05/n$, $n =$ number of experiment-wise comparisons; Snedecor and Cochran 1980). Data were analyzed using statistical programs available for the IBM/370 computer at Cornell University (SAS, SPSS, Minitab). Null hypotheses tested were that prey colonization of cages with and without predators would not differ with respect to (*i*) total density, (*ii*) density of individual taxa, (*iii*) species richness, (*iv*) relative species abundances, and (*v*) body size distributions.

Results

Total prey density

Prey density for all trials combined was significantly reduced by both perlid predators (free) in Six Mile Creek, and by both perlodid predators and the large stonefly omnivore (free) in the East River (Table 3, Kruskal−Wallis test). Therefore, as in Peckarsky and Dodson (1980a), the presence of free stonefly predators significantly affected the rate of establishment of prey communities in cages in both streams. Cages with confined predators showed colonization levels intermediate between those of cages with free predators and those of control cages, though not generally significantly different from either.

Mechanisms causing prey density reductions could be predator feeding, prey avoidance of predators before contact encounter, or escape from predators after contact. Experiments using confined predators allowed the effects of avoidance before contact (difference between controls and confined predator cage densities) to be separated from effects of feeding and escape after contact (difference between free and confined predator cage densities). Table 3 shows that different predators varied in the relative contribution of the contact and noncontact components to the total reduction in prey, with *Agnetina* (Six Mile Creek) being the only predator causing significant effects without contacting prey.

Effects of siltation

In all three summers, unexpected increases in East River flow rates caused massive deposition of inorganic silt filling the interstitial spaces of some cages and the surrounding natural substrate. In 1980, cages were silted when the current rose to a mean of 116 cm/s, then dropped to 104 cm/s; in 1981, siltation occurred when average flow over the cages rose to 126 cm/s, then fell to 86 cm/s during the trial periods. Siltation persisted for 6 days during 1982 when current fluctuated between averages of 118 cm/s and 134 cm/s. Although there was no correlation between the specific current velocity or depth at each cage site and the amount of sediment deposition, some cages were more heavily silted than others; also, the amount of

TABLE 3. Median density (lower and upper limit within which 50% of the data lie, nonparametric 95% confidence interval) of the prey per cage for predator treatments in Six Mile Creek and the East River

Predator treatment	Median density
Six Mile Creek	
Agnetina	
Free (n = 14)	51 (39, 84)a
Confined (n = 23)	55 (50, 85)a
Acroneuria	
Free (n = 18)	58 (44, 83)b
Confined (n = 22)	72 (57, 100)b,c
Control (n = 24)	95.5 (61, 115)c
East River	
No silt	
Megarcys	
Free (n = 14)	16.5 (8, 24)d
Confined (n = 14)	24 (7, 34)d,e
Pteronarcella	
Free (n = 14)	18 (7, 24)d,e
Control (n = 14)	32.5 (26, 41)
Kogotus	
Free (n = 20)	17 (12, 22.5)f
Confined (n = 27)	23 (18.5, 29.5)f,g
Control (n = 28)	27.5 (18.5, 31.5)g
Silt	
Megarcys	
Free (n = 6)	2 (2, 8)h
Confined (n = 15)	11 (9, 20)h
Pteronarcella	
Free (n = 9)	7 (4, 10)h
Control (n = 15)	8 (4, 15)h

NOTE: Median values followed by the same letter are not significantly different (distribution-free multiple comparisons based on Kruskal–Wallis test, $p > 0.05$). Separate analysis was done for silted cages, East River. Number of cages (n) differs between treatments because some predators were damaged or lost during trials.

siltation was random with respect to predator treatments. This variable was taken into account in the following analysis. Cages were classified into those with heavy silt quantities (filling greater than half of the interstitial spaces) and those with little to no siltation (less than half the interstitial spaces obstructed). Hereafter, these two classes are referred to as silted and unsilted cages.

The heavy silt deposition in cages overrode the prey density differences between predator treatments and controls (no significant differences, Kruskal–Wallis test, Table 3). Prey numbers in silted cages were significantly less than those in unsilted cages for each predator treatment except the confined *Megarcys* treatment (Mann–Whitney U-test). These data show that siltation effects masked or eliminated predaceous stonefly effects. Because of this siltation effect, only the results of the unsilted cages were included in the following analyses of predator effects on other community structure parameters; the siltation effects on colonization were considered separately.

Densities of individual prey taxa

Comparisons between predator treatments were made of the number of individuals per cage for the 12 and 11 most abundant taxa in Six Mile Creek and the East River cages, respectively

(Wilcoxon's signed rank test, Table 4). Cages with free predators showed significant reductions in the number per cage of 5 of the 12 taxa tested in Six Mile Creek. Also, one mayfly species, *Ephemerella invaria* (Walker), showed significantly lower densities in cages with confined *Agnetina capitata* than in control cages. Densities of all other taxa did not differ among predator treatments. Thus, the significant total prey community response was not distributed evenly across all taxa.

In contrast, East River predators did not significantly reduce densities of any of the 11 prey species tested (Wilcoxon's signed rank test, Table 4). In cages with free *M. signata*, one taxon showed an increase in the number per cage (*Epeorus deceptivus* [McDunnough] and *Epe. longimanus* [Eaton] combined), and one taxon (Simuliidae) showed increased density in cages with confined *K. modestus*. Therefore, the East River stoneflies caused slight reductions in the densities of most taxa, the composite effect of which was the significantly lower density of the entire prey community (Table 3).

Wilcoxon's signed rank analysis was also performed on the number per cage of the 11 most abundant taxa in silted versus unsilted cages in the East River. Results (Table 4) demonstrate that densities of 6 of the 11 taxa were significantly reduced by silt.

Taxonomic richness

The numbers of prey taxa (richness) in unsilted cages with different predator treatments were analyzed by comparing slopes and intercepts of species-abundance curves using semi-$\log_e$ transformed data (Figs. 1, 2, 3). Taxonomic richness did not differ between treatments with and without predators in Six Mile Creek (Fig. 1) or the East River (Figs. 2, 3). Closer inspection of these data also showed that the prey species in cages with predators were essentially the same as those in control cages: predators caused no eliminations or additions of common species (Table 4).

Relative species abundance

Indices of community association based on presence and absence of taxa were not used to determine whether the relative abundance of prey taxa differed between predator treatments, because the previous analysis showed little or no differences in numbers and kinds of species among treatments. Instead, a chi-square analysis was applied to the data from only unsilted cages to determine whether the observed distribution of individuals among taxa was homogeneous with respect to predator treatment. Contingency tables of 2 (predator treatments) × S (number of taxa with high enough numbers to satisfy the assumptions necessary for inclusion in the analysis) were cast with total numbers per treatment entered in cells. A significant χ^2 indicates that the distribution of individuals among taxa was not homogeneous with respect to the predator treatments.

Results of this analysis are given in Table 5. Six Mile Creek cages with predators showed significant differences in the distribution of individuals among taxa between all treatment comparisons. Cages with free *M. signata* and confined *K. modestus* showed a significant prey community response in the East River. These data indicate that although the presence of predators did not eliminate species, some shifts in community composition did occur.

I similarly compared the species composition between East River cages with and without silt for all predator treatments combined. A very high χ^2 value indicates that the distribution of individuals among taxa was significantly different between silted and unsilted cages (Table 5).
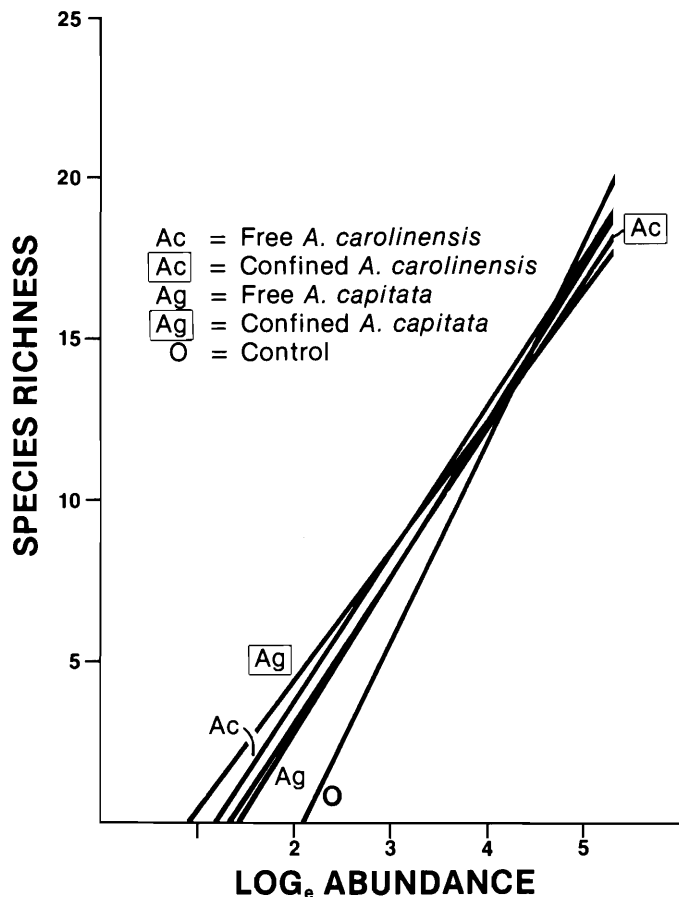
FIG. 1. Plots of taxonomic richness per cage as a function of the $\log_e$ of the number of individuals per cage (abundance) for five predator treatments, Six Mile Creek. Analysis of covariance showed no significant differences among slopes or intercepts.
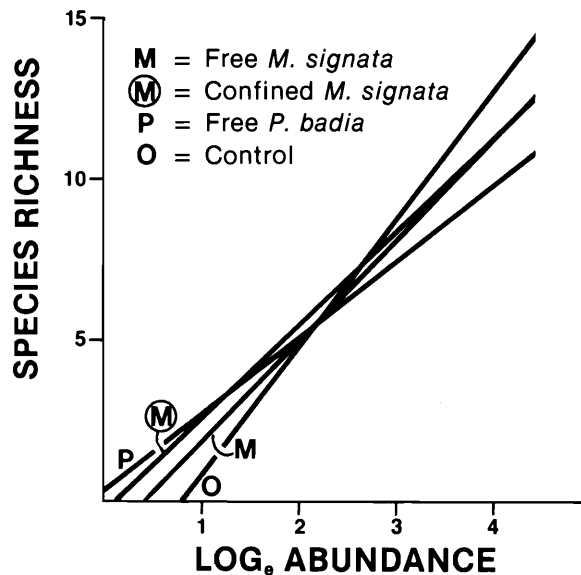

FIG. 2. Plots of taxonomic richness per cage as a function of the $\log_e$ of the number of individuals per cage (abundance) for four predator treatments, East River. Analysis of covariance showed no significant differences among slopes or intercepts.

Size composition of the prey community

Head capsule widths of all potential prey individuals colonizing cages were measured for comparison of prey community size composition between treatments. A Kolmogorov–Smirnov two-sample test was used to compare the shapes of cumulative relative frequency curves over a set of specified size intervals for individuals of all prey taxa with numbers adequate for analysis (e.g., Figs. 4, 5, 6). This statistical analysis was not applied to determine whole-community size shifts, since different species have different body shapes (head capsule : biomass ratios). However, qualitative inspection of data on relative abundance of individual taxa (Table 4) suggests that neither primarily small nor primarily large taxa were differentially affected by predation.

When taxa were considered individually (Table 6), 15 of 20 taxa showed no shift in size distribution with predators (e.g., Chloroperlidae, East River, Fig. 4; plots of size distributions of all other species are available from the author). Two species showed reduced size in cages with predators (e.g., *Baetis bicaudatus* Dodds, East River, Fig. 5) compared with the size distribution in control cages and cages with confined predators, while three species showed increased size in cages with predators (e.g., *Ephemerella invaria*, Six Mile Creek, Fig. 6). These results suggest that, in general, the presence of predaceous stoneflies did not affect the size distribution of individual prey species.
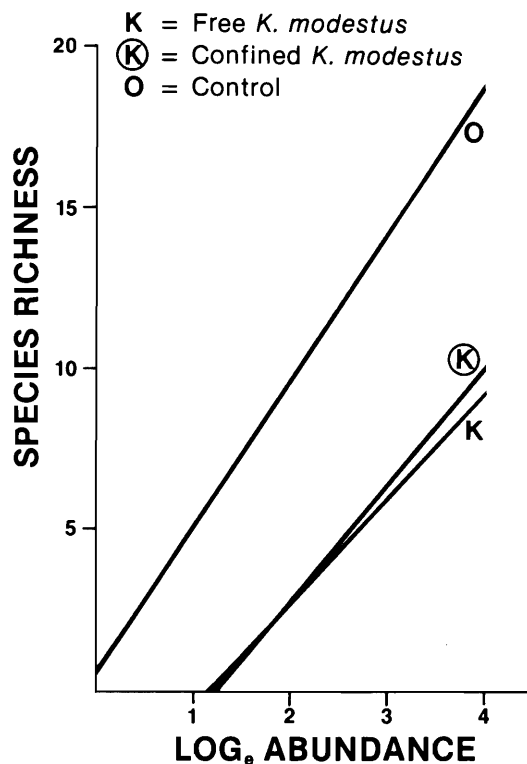

FIG. 3. Plots of taxonomic richness per cage as a function of the $\log_e$ of the number of individuals per cage (abundance) for three predator treatments, East River. Analysis of covariance showed no significant differences among slopes or intercepts.

Discussion

Density effects

This study suggests that predators can have significant effects in nonequilibrium open systems, such as stream riffle communities, as predicted by Caswell (1978). Predaceous

TABLE 4. Average density (number per cage) of the most abundant taxa colonizing cages of each treatment in Six Mile Creek and the East River (*Ag*, *Agnetina*; *Ac*, *Acroneuria*; *M*, *Megarcys*; *Pt*, *Pteronarcella*; *K*, *Kogotus*; 0, no predator (control)). Circles around symbols indicate confined predator treatments. Prey taxa were lumped where numbers of individual taxa were not adequate for analysis

(A) Six Mile Creek

	Ag	Ⓐ𝓰	*Ac*	Ⓐ𝓬	0
Baetidae spp.[a]	11.7*	15.3	9.7*	17.8	14.3
Ephemerella invaria	10.3*	11.0*	11.7*	14.0	18.0
Epeorus sp.	2.9	1.2	2.4	1.5	2.9
Other Heptageneidae[b]	0.9	1.8	2.2	2.0	2.4
Paraleptophlebia sp.	10.6*	11.5	12.6*	14.5	18.8
Chloroperlidae	1.2	1.3	1.9	1.5	2.1
Isoperla sp.	2.4	1.7	1.4	2.2	3.0
Amphinemura sp.	4.3	4.8	6.6*	6.6	7.9
Hydropsychidae[c]	2.9	2.3	3.5	3.4	3.6
Caseless Trichoptera[d]	0.6	0.6	1.0	1.0	2.5
Chironomidae	5.9*	6.5	6.9*	6.8	10.4
Simuliidae	1.9	2.3	1.5	1.4	3.5
Total no. of cages[e]	14	23	18	22	24

(B) East River

	Unsilted					Silted total	Unsilted		
	M	Ⓜ	*Pt*	0	Total		*K*	Ⓚ	0
Baetis bicaudatus	3.6	3.9	1.2	4.1	3.2	1.2*	0.6	1.3	1.5
Ephemerella infrequens	0.9	1.7	1.3	2.7	1.7	0.6	0.8	1.3	1.0
Epeorus spp.[f]	1.2*	0.4	0.5	0.2	0.6	0.4*	0	0.4	0.1
Cinygmula sp.	4.9	2.9	3.1	7.1	4.5	2.5*	1.5	2.5	2.6
Rhithrogena spp.[g]	1.4	0.4	0.2	0.5	0.6	0.4	3.6	4.6	3.6
Ameletus velox	0.1	0.8	0.5	0.3	0.4	0.1	0.3	0.4	0.5
Chloroperlidae	1.9	2.1	1.9	3.6	2.4	1.6	7.2	8.9	9.6
Podmosta deliculata	2.6	5.7	5.0	8.1	5.4	0.7*	0	0	0
Zapada haysi	0.6	1.3	0.9	1.8	1.1	0.2*	1.0	1.2	1.5
Perlodidae[h]	0.4	0.5	0.4	0.5	0.5	0.4	0.4	0.1	0.4
Pteronarcella badia[h]	0	0.2	0.6	0.1	0.3	0.1	0.1	0.2	0.4
Chironomidae	1.2	1.2	1.1	3.4	1.7	1.0	1.0	1.5	1.8
Simuliidae	0.9	1.1	0.9	2.4	1.3	0.1*	0.4	1.2*	0.2
Turbellaria	0.2	0.4	0.1	0.6	0.3	0.3	0.4	0.3	0.5
Total no. of cages[e]	14	14	14	14	56	45	22	28	31

[a] *Baetis tricaudatus* and *Pseudocloeon* sp.
[b] *Heptagenia, Leucrocuta, Stenonema, Stenacron, Rhithrogena* spp.
[c] *Cheumatopsyche, Hydropsyche* spp.
[d] *Dolophilodes, Rhyacophila, Polycentropus* spp.
[e] Total number of cages differed between treatments because some predators were lost or killed during trials.
[f] *Epe. longimanus* and *Epe. deceptivus*.
[g] *R. hageni* and *R. robustus*.
[h] Small instars of these taxa colonized cages.
*Significantly different number of individuals per cage compared with control cages (Wilcoxon sign rank test). Silted cages were compared with unsilted cages.

stoneflies in two streams reduced the density of prey colonizing enclosures over the short term, thereby potentially affecting the rate of prey community establishment on substrate patches, and, therefore, the microdistribution patterns of prey. These results are consistent with those of Peckarsky and Dodson (1980*a*), and those of other workers examining predator effects on longer-term benthic colonization or on the maintenance (rather than establishment) of stream community structure. Oberndorfer et al. (1984) recorded a significant effect of enclosed predaceous stoneflies (*M. signata*) on the population levels of a leaf-shredding prey species and, consequently, on the leaf decomposition rate over 8 weeks in a Utah stream. Walde and Davies (1984) demonstrated that predaceous stoneflies (*Kogotus nonus*) altered densities of various chironomid prey species in enclosures placed in an Alberta stream for 10 days. These three studies, therefore, documented significant prey density reductions in enclosures containing predaceous stoneflies.

These experiments did not, however, conclusively elucidate the mechanisms producing the observed responses. Predator confinement to small mesh containers as in the present study and an earlier study (Peckarsky and Dodson 1980*a*) allows some partitioning of effects into density reductions caused by prey avoidance of predators without contact and those caused by predator feeding and prey escape on contact. Behavioral experiments (Peckarsky 1980) showed that some mayfly species respond to predators given only noncontact, nonvisual cues. The enclosure experiments corroborate that
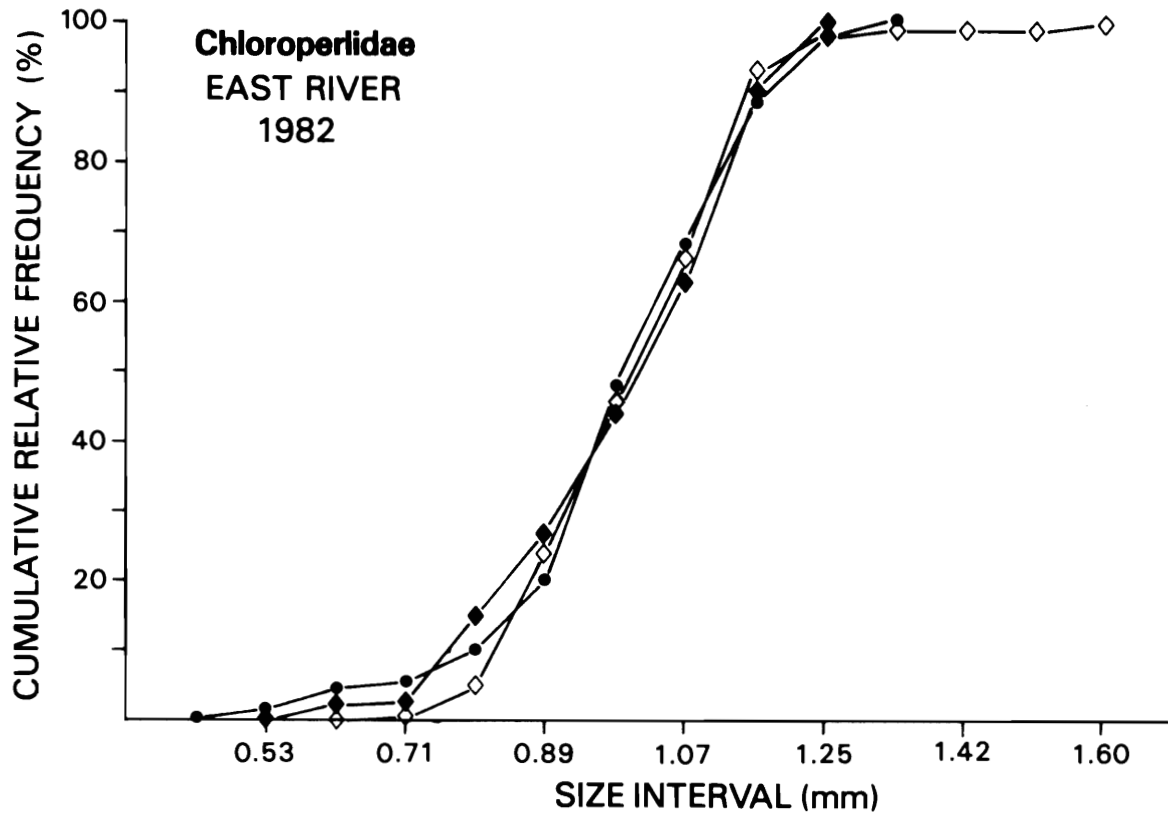
FIG. 4. Cumulative relative frequencies (percent) over the given size intervals (head capsule widths) of Chloroperlidae in cages of different predator treatments. ◆, *K. modestus* free; ◇, *K. modestus* confined; ●, control. Sample sizes were 41, 154, and 143, respectively.
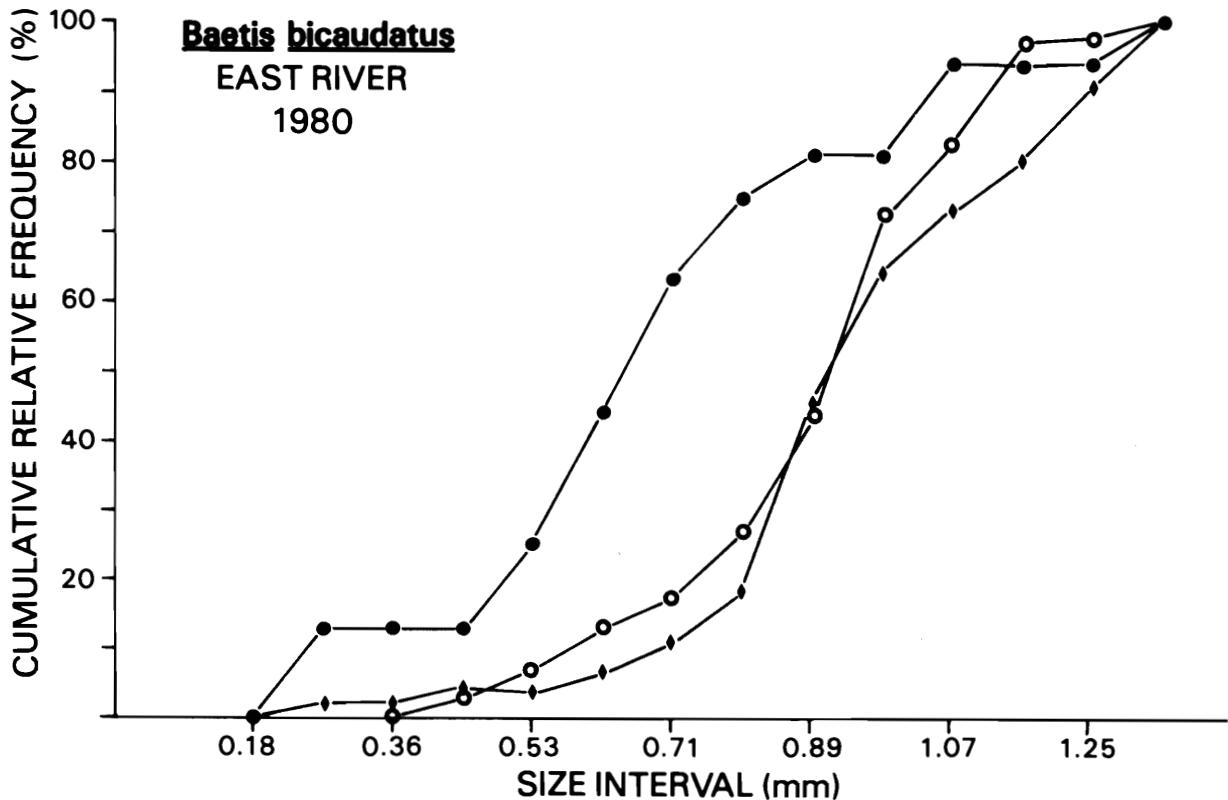

FIG. 5. Cumulative relative frequencies (percent) over the given size intervals (head capsule widths) of *Baetis bicaudatus* in cages of different predator treatments. ●, *M. signata* free; ○, *M. signata* confined; ◆, control. Sample sizes were 16, 30, and 45, respectively.
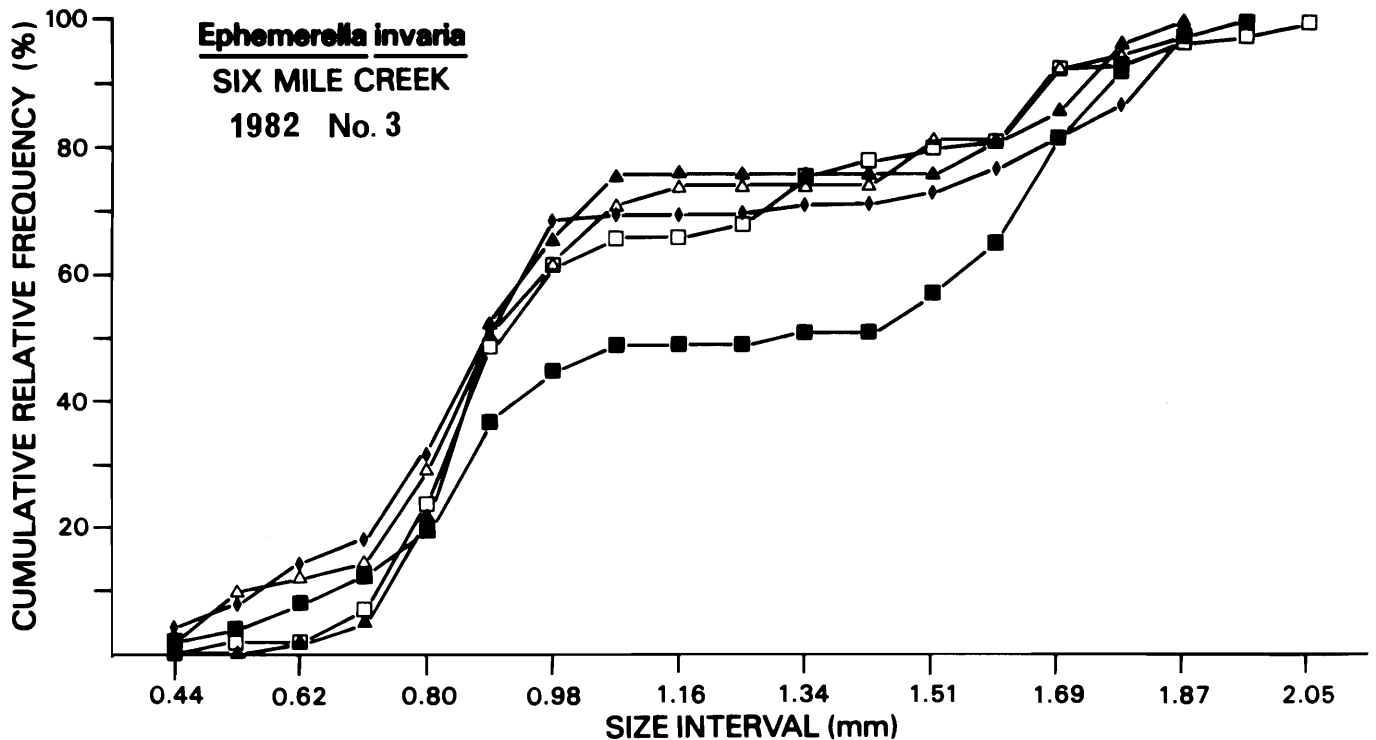
FIG. 6. Cumulative relative frequencies (percent) over the given size intervals (head capsule widths) of *Ephemerella invaria* in cages of different predator treatents. ■, *Ac. carolinensis* free; □, *Ac. carolinensis* confined; ▲, *Ag. capitata* free; △, *Ag. capitata* confined; ◆, control. Sample sizes were 49, 59, 58, 42, and 84, respectively.

TABLE 5. Summary of χ^2 values for comparisons made of the relative species abundances between predator treatments in Six Mile Creek and the East River (only unsilted cages)

Predator species	Free predator vs. no predator	Free predator vs. confined predator	Confined predator vs. no predator
Ag. capitata	34.90, 11 df, $p < 0.01$	34.05, 11 df, $p < 0.01$	53.89, 11 df, $p < 0.01$
Ac. carolinensis	23.84, 11 df, $p < 0.01$	43.40, 11 df, $p < 0.01$	55.98, 11 df, $p < 0.01$
M. signata	62.14, 11 df, $p < 0.013$	44.79, 10 df, $p < 0.013$	16.26, 10 df, NS
K. modestus	18.42, 11 df, NS	23.69, 11 df, $p < 0.017$	37.96, 12 df, $p < 0.017$
P. badia	12.49, 9 df, NS	—	—

Silted vs. not silted cages; East River: 122.59, 13 df, $p < 0.05$

NOTE: NS, no significant difference; —, experiment not conducted. Analysis of silted versus unsilted cages is also given. Rejection of null hypotheses based on Bonferroni's inequality; $\alpha = 0.05/n$; n = number of pairwise comparisons per experiment.

this avoidance component may be an important mechanism explaining prey reductions and, in some cases, may be more important than the feeding component (see Table 3). These experiments did not allow separation of the feeding and escape-upon-contact mechanisms reducing prey densities. Behavioral experiments indicate that both mechanisms are probable (Peckarsky 1980; Peckarsky and Penton 1985).

Density comparisons of the most abundant individual taxa colonizing cages showed that the Six Mile Creek perlids caused significant density reductions of 5 of the 12 species tested. Comparison of these results (Table 4) with those of the stomach content analysis (Table 2) reveals that most taxa showing significant declines were also abundant in the predators' diets (e.g., *Baetis*, *Ephemerella*, *Paraleptophlebia*, and Chironomidae). These experiments did not resolve the mechanisms explaining exceptions, but suggest that *Amphinemura*, rare in stonefly stomachs, avoided cages with *Acroneuria*, and other taxa common in stonefly stomachs (e.g., Simuliidae, *Epeorus*)

compensated predation rates with high immigration rates. Interestingly, relatives of the one species (*Eph. invaria*) that showed significant density reductions in cages with a confined predator have been shown to detect and avoid predators without contact (Peckarsky 1980).

The lack of significant density reductions of individual prey taxa in East River enclosure experiments may also be explained by compensatory migration. Significant density increases of some taxa in cages with East River stoneflies (e.g., *Epeorus* and Simuliidae) are suggestive of secondary interactions. In other words, these species may be responding to decreases in the colonization rates of other taxa, but this speculation needs to be tested directly.

In general, it appears that immigration rates compensated, at least in part, predation effects on population levels of most individual prey species in enclosures in both streams. Perlids in the New York stream did, however, disproportionately depress populations of some prey species, a phenomenon that could

TABLE 6. Summary of effects of predator treatments on sizes of different prey taxa

Location	Taxa showing size increase with predators	Taxa showing size decrease with predators	Taxa showing no size differences
Six Mile Creek	*Ephemerella invaria* (*A*) *Isoperla* sp. (Ⓐ)	*Baetis* sp. (Ⓐ)	*Paraleptophlebia* sp. Heptageniidae Chloroperlidae *Amphinemura* Hydropsychidae Chironomidae Simuliidae
East River	Chloroperlidae (*M*)	*Baetis bicaudatus* (*M*)	*Ephemerella infrequens* *Epeorus* spp. *Cinygmula* sp. *Rhithrogena* spp. *Podmosta deliculata* *Zapada haysi* Chironomidae Simuliidae

NOTE: Kolmogorov–Smirnov two-sample test; rejection of null hypotheses based on Bonferroni's inequality; $\alpha = 0.05/n$; n = number of pairwise comparisons per experiment. *A*, *Ac. carolinensis*; Ⓐ, *Ac. carolinensis* confined; *M*, *M. signata*. Cumulative relative frequency plots of all of these taxa are available from the author.

be due to selective feeding or differential prey avoidance of enclosures with predators.

Species diversity effects

The present study showed no difference in prey taxonomic richness between enclosures with and without predators in either stream. Examination of specific taxa reveals that species replacements did not occur in cages with predators. Only rare taxa were added or eliminated, but not consistently. Absence of any difference in taxonomic richness or composition suggests either that predaceous stoneflies did not intensely overexploit certain prey species in these two streams, or that no prey species were so vulnerable to stonefly predation as to be eliminated from communities in enclosures. Stoneflies apparently did not act as "keystone species," removing dominant competitors from the prey community and allowing competitively inferior species to invade habitats from which they were excluded in the absence of predation (Paine 1966). These results suggest that the rate of predation on each prey species was compensated (at least in part) by high rates of immigration.

Although entire species of prey were not eliminated from enclosures by predaceous stoneflies, analysis of the relative prey species abundances showed that both predaceous perlids in the New York stream altered the distribution of individuals among taxa (chi-square analysis). Only one predator in the Colorado stream (*M. signata*) produced this effect. This analysis further corroborates that *M. signata* and the perlids have some disproportionate effects on the densities of various prey taxa.

Size effects

Prey size distribution analysis suggests that during the time of year of the experiments either predators were, for the most part, not size selective, or prey immigration rates compensated for size-selective predation. Size frequency distributions of the most abundant prey taxa in both streams showed that the sizes of most species were indistinguishable between experimental and control cages (Fig. 4). This phenomenon may be a function of the synchrony of development and, therefore, the narrow range of intraspecific sizes of many stream insects. However, other species retained a wide range of sizes in cages with all

predator treatments. A few species, however, did show a size-dependent response to predators in enclosures in both streams. Prey size reductions in cages with predators (e.g., *Baetis*) suggest that predators selectively preyed on larger individuals, or that larger prey were more likely to migrate from or avoid cages with stoneflies. Laboratory studies by Malmqvist and Sjöström (1980) and Molles and Pietruszka (1983) showed that related predaceous stoneflies were not size-selective on *Baetis* prey, casting doubt on the former explanation. However, experiments conducted by J. D. Allan (unpublished data) using a wider range of *Baetis* size classes (smaller *Baetis*) have documented selection for larger prey by *Megarcys* and *Kogotus* of the same size as those used in these experiments.

Predominance of large prey individuals with predators suggests that large size may be an effective refuge and smaller individuals may be more vulnerable to stonefly predation (e.g., *Ephemerella invaria*, Six Mile Creek). Behavioral experiments have shown that this and other species of this family freeze and exhibit a defensive posture ("scorpion") more often than dispersing in response to predator encounters (Peckarsky 1980). Furthermore, the frequency of the posture is greater in larger individuals, whereas smaller prey tend more often to flee actively. These behavioral observations are consistent with the size distribution response shown in this study.

In summary, enclosure experiments showed that the major effects of predaceous stoneflies on the short-term colonization of benthic communities in cages in two streams were significant reductions in total community density and changes in the relative distributions of individuals among taxa. A few species, also common in stonefly stomachs, showed significant declines, and a few species increased, but most showed no significant differences in density or in body size in enclosures with predators. The community as a whole did not exhibit substantial shifts in species composition or changes in species richness in cages with stoneflies.

Finally, the significant siltation effects on total prey density and on many individual taxa within enclosures indicate that such abiotic perturbations have the potential to override the effects of biological interactions, such as predation, in structuring communities (Peckarsky 1983). Obviously, siltation di-

rectly reduced population densities, but it also obscured any benthic community response to predaceous stoneflies. Predators recovered from cages with silt were all still alive, but prey communities were uniformly low in all cages with silt. The taxa affected most by siltation were primarily mayflies and stoneflies (Table 4), some of which were also shown by McClelland and Brusven (1980) and Lenat et al. (1981) to be highly sensitive to siltation. Simuliidae were also significantly reduced, probably because inorganic particles interfered with their filtering processes. This unexpected disturbance exemplifies the unpredictable nature of the stream ecosystem and illustrates how periodic changes in high quality microhabitat availability might occur.

Acknowledgments

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