

AN EXPERIMENTAL ANALYSIS OF BIOLOGICAL FACTORS CONTRIBUTING TO STREAM COMMUNITY STRUCTURE¹

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Abstract. Densities of invertebrates were manipulated within stony substrate filled cages in a Wisconsin and a Colorado stream to test the effects of prey densities on colonization of the cages by invertebrate predators and potential competitors. There was no difference between the number of predators colonizing cages with high initial prey densities and that colonizing cages with zero initial prey density, for any trial, during any season, in either stream. This observed lack of predator response to prey density has been termed a "null numerical response," characteristic of predator populations limited by factors other than prey availability. Food resource, then, was not responsible for the observed distributions of invertebrate predators in these two streams. Physical habitat cues or mutual interference among predators may explain the observed colonization pattern of these predators. Wisconsin stream prey preferentially colonized cages with zero initial densities compared to cages with potential competitors, but only when those cages excluded predators. The presence of spatial refuges from predators enhanced the effect of potential competitors upon prey colonization in this stream. The cage colonization by prey populations in the Colorado stream was reduced by the presence of potential competitors regardless of the availability of spatial refuges. Possible reasons for differences between the responses in the two streams are discussed.

Key words: *Colorado; competition; experimental manipulation; mayflies; mutual interference; numerical response; predator-prey interactions; spatial refuges; stoneflies; Wisconsin.*

INTRODUCTION

Factors that determine abundance and distribution of species in lotic ecosystems have not been clearly identified. The relative importance of biological and physical factors, and the relative roles of predation and competition in influencing stream community structure remain to be tested experimentally.

Results of manipulations within marine rocky intertidal systems suggest that the importance of biological interactions in determining community structure varies with the physical harshness of the environment (Connell 1975, Menge 1976). The distribution and abundance of species are ultimately determined by tolerances to extremes of physical conditions. However, species are limited to even smaller ranges of habitats and population sizes by biological interactions. In benign physical conditions, predation is more intense and may prevent prey competition from occurring by maintaining prey populations at low densities. If some factor, such as harsh physical conditions, prey ref-

uges, or prey defense, reduces the effectiveness of the predator, the structure of rocky intertidal communities is influenced more by competition. The harsher the physical conditions, the more directly they affect species distributions.

Such statements cannot be made concerning the structure of stream communities due to the lack of complete experimental studies (Fox 1977, Friberg et al. 1977). Most manipulations have tested hypotheses concerning the influence of such physical factors as current and substrate, food, or detritus upon stream distributions (Egglisshaw 1964, Cummins and Lauff 1969, Rabeni and Minshall 1977). Some investigators have suggested competition as a determinant of stream community structure, on the basis of descriptive data on spatial or temporal overlap of closely related species (Hynes 1961, Grant and Mackay 1969, Allan 1975). Nilsson and Otto (1977) reported laboratory evidence of exploitative competition between stream detritivores. Hildrew and Townsend (1976) and Siegfried and Knight (1976a) discussed the possible relationship between predator-prey interactions and benthic distributions, but provided no direct evidence in support of such a relationship. Allan (1978) suggested a significant effect of trout predation on the activity pattern

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TABLE 1. Summary of experiments.

Experiment 1					
Cage treatments: (1) mayflies present, predators excluded; (2) mayflies present, predators not excluded; (3) no mayflies, predators excluded; (4) no mayflies, predators not excluded.					
Location	Otter Creek			East River	
	Spring 1976	Fall 1976	Spring 1977	Summer 1976	Summer 1977
Season					
Range of dates	10 May–24 June	13 September–15 November	18 April–6 June	13 July–9 August	29 June–29 July
Temperature range (°C)	10.5–17.2	0.0–20.0	9.4–18.9	5.6–22.8	6.1–19.4
Current velocity range (cm/s)	9.7–17.7	4.7–7.0	7.0–24.0	18.0–31.0	7.3–15.0
Mayfly prey species	<i>Baetis phoebus</i> , <i>Ephemerella subvaria</i> , <i>Stenonema fuscum</i> , <i>Heptagenia hebe</i> (spring only), <i>Paraleptophlebia</i> sp.			<i>Baetis bicaudatus</i> , <i>Cinygmula</i> sp., <i>Ephemerella infrequens</i> , <i>Epeorus longimanus</i> , <i>Rhithrogena hageni</i>	
Prey head capsule widths (mm)		(1–3)		(1–3)	
Number of mayflies per cage	15	10	15	15	20
Number of replicates per cage treatment	11	9	9	9	9
Experiment 2—(prey species same as above) (all cages, 1-cm mesh end baffles)					
Cage treatments: (1) 1 predator + 10 prey; (2) 1 predator + 0 prey; (3) 10 prey; (4) 0 prey.					
Location	Otter Creek		East River		
	Spring 1978		Summer 1978		
Season					
Range of dates	3 April–6 June		12 July–2 August		
Temperature range (°C)	1.6–16.7		3.3–16.1		
Current velocity range (cm/s)	14.0–45.0		41.0–90.0		
Predator species	<i>Acroneuria lycorias</i> (Plecoptera: Perlidae)		<i>Megarctys signata</i> (Plecoptera: Perlodidae)		
Predator head capsule width (mm)	3.5–5.3		3.5–5.0		
Number of replicates per cage treatment	20		9		

of one species of mayfly, and Hildrew and Townsend (1977) reported an effect of invertebrate predators on prey distribution.

Peckarsky (1979a) introduced an experimental approach to testing hypotheses involving the biological factors that determine stream distributions. By maintaining nearly constant physical factors such as current, substrate, and temperature regimes, and varying one biological factor, hypotheses concerning the role of biological interactions in structuring stream communities were tested.

The purpose of this study was to provide information about the roles of specific invertebrate interactions in determining the abundance and distribution of stream benthos. Experiments described here represent a first step in the application and documentation of some aspects of predator-prey and competition theory in lotic ecosystems. The results of this study provide basic information at the community level, on mechanisms controlling community structure in streams.

The following questions were considered:

- 1) How do invertebrate predators respond to the presence or absence of prey?
- 2) How do invertebrate predators respond to the presence or absence of other predators?

- 3) How do prey respond to the presence or absence of other prey?

MATERIALS AND METHODS

Experiments were conducted in two streams, Otter Creek, Sauk County, Wisconsin, and the East River, Gunnison County, Colorado. Otter Creek is a small, relatively benign stream, subject to a narrower range of daily and seasonal physical fluctuations than the high-altitude, montane East River (Table 1). Both streams have been described in detail elsewhere (Peckarsky 1979a).

Twelve to 16 stainless steel screen cages (Peckarsky 1979a) containing similar natural substrates standardized by numbers, sizes, and textures of particles were buried simultaneously within the substrate of each stream. Twenty-eight stones ranging from 2 to 12 cm in smallest diameter and from smooth to rough texture were placed in each cage. These cages provided a heterogeneous substrate with interstitial spaces similar to adjacent substrate conditions. Current and temperature regimes were held constant among replicate cages. Cages were buried 10 cm beneath the surface of the substrate of riffles with the removable baffle end facing downstream. The probability of passive colo-

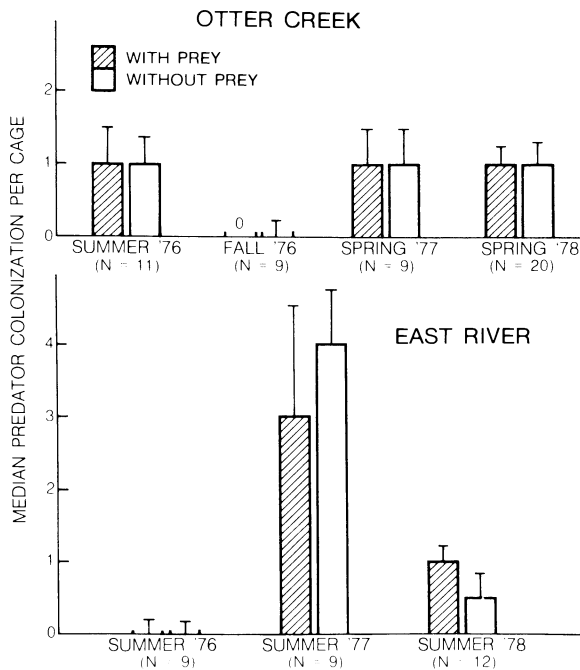


FIG. 1. Median number of predators colonizing each cage. Histograms represent colonization of invertebrates that consume mayflies. Vertical bars = 1 SE (Wilcoxon and Wilcoxon 1964). N = number of replicate cages per treatment.

nization of cages was reduced by orienting cages in this direction, because the cage mesh (813 μ m) prevented drifting benthos from entering cages (Peckarsky 1979a). The 10- to 20-cm cage depth, and a 4-d duration for experiments were identified from preliminary trials as appropriate for adequate cage colonization (Peckarsky 1979b). The cage depth also reduced passive colonization of macrobenthos. Animals present in the cages after each experiment were preserved in 70% ethanol for counting and identification.

To address the questions stated in the introduction, two types of experimental design were implemented during different sampling seasons in each stream (Table 1). Experiment 1 tested the responses of invertebrate predators to local concentrations of prey density. The design also allowed the measurement of effects of prey density upon colonization of other prey. Experiment 2 provided further information regarding responses of predators to prey density. It also tested the influence of stonefly predators on colonization by other invertebrate predators. For each experiment, replicate cages containing different densities of predators or prey were introduced into the stream. Further colonization was either restricted by a small-mesh end baffle (3.0 mm), or unrestricted (1-cm mesh end baffle). Cage treatments, dates of trials, locations, organisms used, numbers of replicates, current, and temperature regimes are summarized in Table 1.

Because all the mayfly species tested have been re-

ported in the gut contents of the dominant stonefly predators in each stream (Fuller and Stewart 1977, Peckarsky 1980, J. D. Allan, *personal communication*) we stocked combinations of prey species. Species and densities of prey were chosen on the basis of their seasonal abundance within the substrate of each stream, and to approximate natural cage densities (Peckarsky 1979a). Stonefly predators used were the dominant invertebrate predators in each stream during the sampling periods, in terms of numbers and range of prey consumed (Peckarsky 1980). They were marked by placing identifying dots on their ventral surfaces with Liquid Paper® correction fluid before introducing them into the cages. Current velocity was determined at the surface of the substrate at each cage using a Marsh-McBirney current meter (model 201). Water temperatures were monitored continuously with a maximum-minimum thermometer.

For experiment 1, comparison of predator colonization in cage treatments (2) and (4) showed the responses of predators to local concentrations of prey density (Table 1). Comparison of prey colonization in cage treatments (1) vs. (3) and (2) vs. (4) showed the effect of potential competitors upon prey colonization. Net prey colonization of cages with initial prey densities other than zero was calculated by comparing initial numbers to final numbers of prey per cage (Peckarsky 1979a). Comparison of the differences in prey colonization between cages from which predators were excluded [(1) and (3)] and those from which predators were not excluded [(2) and (4)] provided information regarding the effect of spatial refuges from predators on colonization by prey.

For experiment 2, comparison of predator colonization between cages (3) vs. (4) and of attrition of predators from cages (1) vs. (2) further documented the response of predators to areas of higher prey density. Comparison of colonization by other predators between cage treatments (1) and (2) in which marked stoneflies emigrated or remained provided information regarding the effect of stonefly presence on colonization by other predators.

We used an application of chi-square analysis that is sensitive only to differences between treatments rather than to seasonal changes in physical factors, prey sizes, or prey species between dates of replicate trials. The within-treatment (between-sampling-date) marginal totals were not included in the calculation 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 invertebrates among all treatments, and between specific pairs of treatments within each sampling date. Those from each date were added to determine a total effect for replicate trials within each season. A median test was used for comparisons shown in Fig. 3 because of unequal sample sizes. A Wilcoxon signed rank test was used to determine

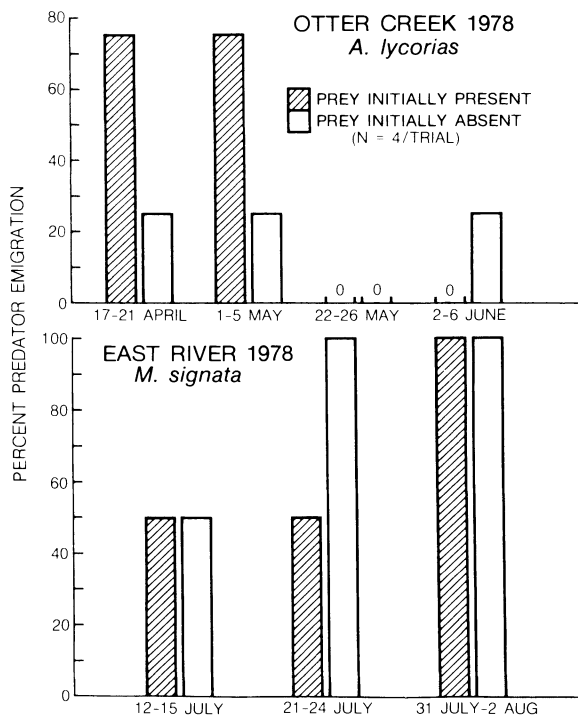


FIG. 2. Percent per trial of marked predators that emigrated. N = number of replicate cages.

whether initial differences in cage prey densities remained at the end of the experiment (Wilcoxon and Wilcox 1964). Spearman rank correlation coefficients were calculated to determine whether final predator densities were correlated with final prey densities.

RESULTS AND DISCUSSION

Responses of predators to prey density

If predators in either stream responded positively to prey density, we would expect: (a) increased predator colonization where prey were present compared to where prey were absent [Experiment 1, cage treatment (4) > (3), and Experiment 2, cage treatment (3) > (4)]; and (b) decreased emigration of predators where prey were present compared to where prey were absent [Experiment 2, cage treatment (1) < (2)] (Table 1).

Colonization by predators that prey on mayflies in both streams is illustrated in Fig. 1. Otter Creek predators included the perlid stoneflies *Acroneuria lycorias* and *Paragnetina media*, the megalopteran *Nigronia serricornis*, and turbellarians. Occasional odonate predators were also included in the analysis. East River predators of mayflies recovered within cages were the perlid stoneflies *Megarcys signata* and *Kogotus modestus*, *Pteronarcella badia*, a pteronarcid stonefly that occasionally consumes mayflies, and turbellarians.

The number of predators colonizing cages with high initial prey densities did not differ from that colonizing

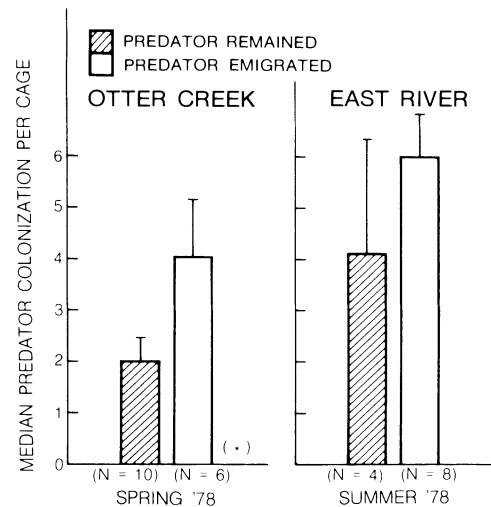


FIG. 3. Median number of predators colonizing each cage. Vertical bars = 1 SE. N = number of replicate cages per treatment. * = $P < .05$, level of significance (median test).

cages with zero initial prey for any trial, during any season, in either stream. These results indicated a lack of aggregative response of predators to centers of higher prey density. Wilcoxon rank sum tests showed that initial differences in prey densities were maintained over the 4-d experiment period ($P < .005$), although the magnitude of difference became smaller due to prey migration. Spearman rank correlation coefficients showed no significant association between predator colonization and final prey density for any trial, during any season in either stream.

Further substantiation of the lack of aggregative response by predators in these two streams appears in Fig. 2. The emigration of experimentally introduced predators based on the recovery of marked individuals showed no consistent relationship to the initial prey density. Some trends in predator emigration were present, but none were dependent on initial prey density. From early to late spring in Otter Creek, *A. lycorias* tended to emigrate less frequently. Stomach content analysis showed that those nymphs remaining in cages ceased feeding toward the end of May, as is typical of pre-emergent stoneflies (Peckarsky 1979c). The trend toward reduced emigration throughout the spring could reflect a reduction in foraging intensity, or it could reflect declining current velocity. As *Megarcys signata* neared its emergence time, its frequency of emigration from East River cages increased (Fig. 2). Movement out of cage microhabitats was related neither to prey availability, nor to foraging intensity of these predators as indicated by gut content analysis (Dodson and Peckarsky, *personal observation*). Search for emergence sites is a possible explanation.

We see, then, a failure of invertebrate predators to enter or remain in cages of high prey density rather

than cages of zero initial prey density. These results are in contrast to the aggregative responses of two invertebrate stream predators to regions of high prey density, as reported by Hildrew and Townsend (1976). However, their conclusions were based on an observed association of high predator and prey densities rather than experimental evidence. The remarkably constant median number of predators that colonized experimental cages here, regardless of initial prey density, is similar to that reported by Peckarsky (1979a), in which final cage densities of predators did not vary consistently over a broad range of initial benthic densities.

The responses of invertebrate predators to prey density have been discussed by numerous authors (Holling 1961, 1966, Beddington et al. 1976, Hassell et al. 1976, Hassell 1978). Some empirical evidence exists for responses of aquatic invertebrate predators to changes in prey density. The "functional response" is the change in the number of prey eaten by a predator as prey density changes (Hildrew and Townsend 1977, Fox and Murdock 1978, Thompson 1978). The "numerical response" is a change in predator density with changes in prey density (Crawley 1975). The "developmental response" is a long-term change in attack rate by predators over developmental time (Murdock 1973, 1977).

The experiments presented here tested the numerical response of invertebrate predators to prey in each stream. The resultant lack of predator response to prey density has been termed a "null numerical response" (Holling 1961, Crawley 1975), in which predators showed no change in density with changes in prey density. A null numerical response is characteristic of predator populations that are limited by factors other than prey availability. Food resource, then, was not responsible for the observed distributions of invertebrate predators in these two streams.

A numerical response is considered the result of a balance, specific to each situation, between the effect of prey density and the effect of mutual interference among predators (Hassell 1978). Aggregation of searching predators within a patch (or cage) increases the probability of encounters between them, and, in some cases, reduces their search efficiency and increases their dispersal (Hassell et al. 1976, Murdock and Sih 1978). A null numerical response or an inverse numerical response might reflect a disproportionate effect of mutual interference as opposed to prey density upon predator distribution. Walton et al. (1977) suggested that nymphs of *Acroneuria abnormis* demonstrated intraspecific competition for space within a stream-tank system. Single nymphs occupied interstitial spaces that could accommodate more than one stonefly. The authors concluded that *A. abnormis* densities were influenced by a combination of space limitation and interference competition. The obser-

vations presented here are consistent with their interpretation.

Responses of invertebrate predators to a stonefly predator

If *A. lycorias* or *M. signata* affected colonization by other predators of the same and other species, we would expect their continued presence within a cage habitat to depress colonization by other predators. To test this expectation, we compared cage colonization by invertebrate predators (stoneflies, caddisflies, megaloptera, odonates, and flatworms) of cages in which a marked stonefly was recovered, to those in which it was not recovered.

Fig. 3 illustrates a significant depression by *A. lycorias* of cage colonization by other predators, regardless of the initial presence of prey ($P < .05$). The same trend occurred in East River trials, but it was not statistically significant. The tendency of other predators to colonize preferentially cages from which a dominant predator emigrated may indicate mutual interference among predators. However, other predators may appear in lower numbers because they were eaten by *A. lycorias* or *M. signata*. Benke (1978) reported an increase in the production of one species of insect predator upon the removal of another predator species within experimental enclosures in ponds. He attributed this response to predation by the removed species on the remaining species rather than to competition. Direct evidence must be obtained to differentiate the effects of interference competition from predation in producing the observed reduction of cage colonization by predators.

In summary, we observed a null numerical response to changes in initial prey density within cage microhabitats. The most probable explanation is that the distribution of invertebrate predator species in these streams is limited by factors other than prey density, such as space-limited competition or mutual interference among foraging predators. Results are consistent with the interpretation that predators search randomly for prey, given habitat cues held constant among cage replicates, rather than prey density cues that varied (Siegfried and Knight 1976b).

Responses of prey to other prey

If prey responded negatively to the presence of other prey within cage microhabitats, we would expect a decrease in net colonization of prey within cages of high initial prey density compared to those with zero initial prey. During spring trials in Otter Creek a significantly greater number of prey colonized cages with no mayfly prey initially present, but only where large predators were excluded (Fig. 4) ($P < .05$ spring 1976, $P < .001$ spring 1977). The inhibitory effect of initial prey upon the colonization of cage habitats by subsequent prey individuals was damped or eliminated

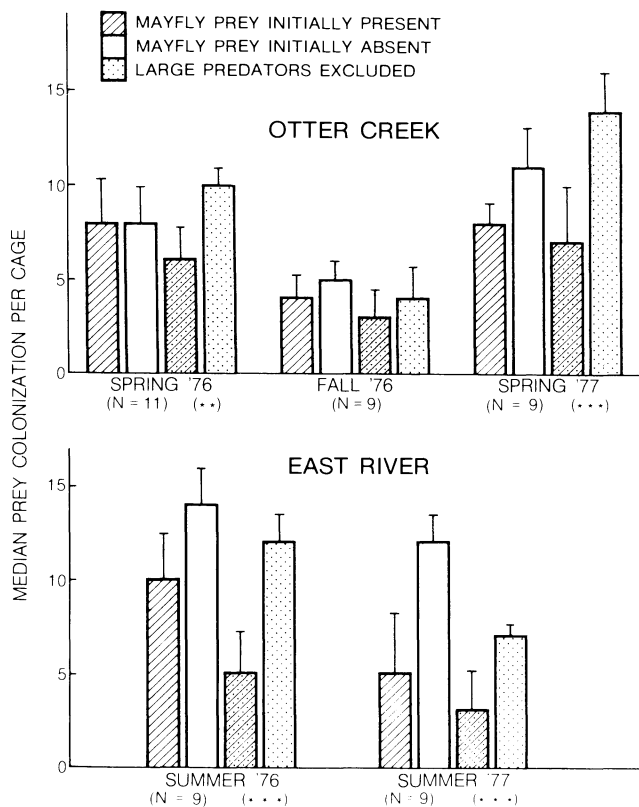


FIG. 4. Median net number of prey colonizing each cage. Vertical bars = 1 SE. N = number of replicate cages per treatment. ** = $P < .01$. *** = $P < .001$, levels of significance of differences among all treatments (chi square). Discussion of pairwise comparisons appears in the text. Note that histograms with dots represent results of cages from which predators were excluded, with (striped) and without (not striped) mayfly prey.

when cages were subject to invasion by predators. In other words, the distribution of prey was influenced by the presence of potential competitors only in the absence of predation. The lack of a significant effect during fall trials may be due to the failure of generally low benthic densities and levels of activity within the substrate to reveal differences in colonization among cage treatments.

East River prey significantly preferred cages with initial mayfly densities of zero to those of high prey density over all trials in both summers ($P < .001$). This result indicates that prey distribution was influenced by the presence of potential competitors whether predators were excluded or not.

The importance of prey refuges in determining the relative influence of biological interactions in structuring communities has received the attention of numerous investigators. Woodin (1978) defined five types of refuges, the third of which is a condition of spatial non-overlap between predators and prey. This type of refuge is effective where a size or other morphological difference exists between predators and prey. The experimental cages with 3.0-mm mesh end baffles effectively excluded larger predators, providing a spatial

non-overlap refuge for prey. The result of the availability of prey refuges was a possible shift from predation to competition as the dominant biological factor structuring the resultant Otter Creek prey communities.

This concept has been theoretically developed by Comins and Blatt (1974), Comins and Hassell (1976), Roughgarden and Feldman (1975), and Vance (1978). Connell (1961a and b, 1975), Kohn and Leviten (1976), Menge (1976), and Paine (1974) demonstrated experimentally that competitive effects were enhanced in the absence of predators in the marine rocky intertidal zone. Similar damping of competition by predators was reported as a result of manipulations within freshwater zooplankton communities (Neill 1975, 1978, Maly 1976, Jacobs 1978). Hildrew and Townsend (1977) reported significantly higher mortality by predation for prey in habitats with fewer available refuges, thus indicating a selective advantage for prey in habitats providing refuge from predators.

The results of the experiments in Otter Creek are consistent with the interpretation that, in the absence of *A. lycorias* and other large predators, the colonization of prey was significantly reduced by the pres-

ence of potential competitors within cage habitats. Competitive effects may determine the abundances and distribution of Otter Creek prey within habitats that offer spatial refuge from predators. This hypothesis can be tested through more refined manipulation of potential competitors in cages that offer spatial refuge from predators.

The East River results indicate that the exclusion of predators did not alter the effect of prey density on further prey colonization. These data suggest that the presence of competitors overrode the presence of predators in determining species abundances and distributions in this stream.

In summary, in Otter Creek, access to cages by large invertebrate predators dampened the effect of potential competitors upon the migration of prey. Colonization by East River prey populations was significantly altered by the presence of potential competitors regardless of the availability of spatial refuges from predators.

Stonefly predators were shown by Peckarsky and Dodson (1980) to influence benthic distributions significantly in both streams. These effects were measured, however, while controlling for possible competitive effects. The apparent difference shown here in the relative importance of competition and predation in structuring these two stream communities may be related to their positions on a continuum of physical environmental harshness from harsh to benign (Menge 1976). The Rocky Mountain stream is harsher, that is, subject to more widely fluctuating physical conditions than the benign, temperate, woodland stream (Table 1). Perhaps this difference explains the decreased importance of competition in determining the distributions of prey in the more benign habitat. Depending upon the harshness of the conditions and the productivity of the system, the effect of competition may be more or less mitigated by predation. This hypothesis is also testable through more refined manipulations within stream ecosystems.

CONCLUSIONS

The data from experiments presented here suggest preliminary answers to the questions posed in the introduction:

1) Invertebrate predators of the two streams did not aggregate within cage habitats that were experimentally enriched with mayfly prey, given nearly identical alternative cages with no initial prey. This behavior exemplifies a null numerical response characteristic of predators that are not limited by the prey resource, or predators whose distributions are affected more substantially by mutual interference from other foraging predators. The tendency of predators to enter or remain within cage habitats may be related to physical environmental cues provided by all cages, or the intensity of foraging during different life history stages.

2) Predators preferentially colonized cages from

which an experimentally introduced stonefly had migrated in the Wisconsin stream. The presence of *Acro-neuria lycorias* effectively reduced cage colonization by other invertebrate predators, possibly through a combination of competitive and predatory effects.

3) Prey populations in the Wisconsin stream showed no preference for cages with zero initial prey densities unless those cages also excluded predators. During spring trials in the more benign, woodland stream, access to cages by predators resulted in a dampening of effects of potential competitors upon prey colonization. Where predators were excluded, colonization of spatial non-overlap refuges by prey was significantly affected by the presence of potential competitors. Prey in the Colorado stream preferred cages with zero initial prey densities, regardless of the availability of spatial refuges. Access by predators to cages did not dampen the effect of potential competitors upon cage colonization in this harsher, high-altitude, Rocky Mountain stream.

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