Ecology, 71(4), 1990, pp. 1503–1514

PREY EXCHANGE RATES AND THE IMPACT OF PREDATORS ON PREY POPULATIONS IN STREAMS[1, 2]

SCOTT D. COOPER[3] AND SANDRA J. WALDE[3, 4]
Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, California 93106 USA

BARBARA L. PECKARSKY
Department of Entomology, Cornell University, Ithaca, New York 14853 USA

Abstract. We present four lines of evidence that the magnitude of prey exchange (=immigration/emigration) among substrate patches has an overwhelming influence on the perceived effects of predators on prey populations. (1) An extensive review of the literature on predation effects in benthic and littoral freshwater habitats revealed a significant relationship between prey exchange rate and observed predator impact. In streams, studies showing significant predator effects used cages with smaller mesh sizes than studies showing nonsignificant effects. Similarly, there was a highly significant correlation between cage mesh size and the magnitude of predator impact on common prey. Large-scale stream studies indicated that prey drift and colonization rate were inversely related to predator impact on benthic prey. (2) These patterns were confirmed by field experiments and observations where mesh size was directly manipulated or where exchange rates varied among taxa. In Colorado streams we saw greater predator impacts on *Baetis* prey when immigration/emigration was restricted vs. when the mesh size of the cage was relatively large. Similarly, the effects of trout in California stream pools were greater when prey turnover rates were low. (3) A re-analysis of Peckarsky's (1985) data shows an inverse relationship between predator impact and prey mobility within a field experiment. (4) Finally, a model that incorporates both predation and exchange of prey indicates that we ought to expect a lower magnitude of predator effects when exchange rates are high. These results suggest that some discrepancies in past studies may be explained by differences in the exchange rates of prey, and that differences in predator effects across different systems or habitats may be related to variation in the rates of prey dispersal and colonization.

Key words: cages; colonization; emigration; field experiments; freshwater habitats; immigration; predation; prey exchange rates; streams.

INTRODUCTION

At present there is little consensus regarding the effects of predators on prey populations in freshwater benthic or littoral habitats (see reviews in Allan 1983, Healey 1984, Sih et al. 1985, Hixon 1986, Thorp 1986, Northcote 1988). Some studies find depressions in prey density owing to predators (Crowder and Cooper 1982, Walde and Davies 1984*b*, Peckarsky 1985, Cooper 1988, Mittelbach 1988, Osenberg 1988, Gilliam et al. 1989), while others find none (Thorp and Bergey 1981*a*, *b*, Allan 1982, Reice 1983, Flecker and Allan 1984, Culp 1986). Some studies have shown the effect of predators to depend on season, substrate characteristics, and current regime (Gilinsky 1984, Hershey 1985, Walde 1986, Schlosser and Ebel 1989), and many studies find effects on some but not all potential prey species. Discrepancies in the results of field experiments on predation can probably be attributed to one of two possible causes: (1) Experiments vary widely in design, analysis, and interpretation, affecting the confidence with which we accept the validity of their conclusions. (2) Systems vary in the strength of predator effects on prey assemblages.

In this paper we focus on one factor that can influence the observed effects of predators on prey populations: the rate of prey immigration and emigration (=exchange). The rate of prey exchange between the inside and outside of experimental units is affected by mesh size and spatial scale of experimental containers, and in natural situations, by the extent of refuge space, prey mobility, and physical processes. Although a number of researchers have suggested that rapid prey colonization may overwhelm the local effects of predators on prey populations (Allan 1982, 1983, Flecker 1984, Culp 1986, Gilliam et al. 1989), there has been no rigorous, quantitative examination of this idea. We use a survey of the literature, some new empirical data, and a model that incorporates predation and coloni-

[1] Manuscript received 26 October 1988; revised 30 September 1989; accepted 27 October 1989.

[2] Address reprint requests to S. Walde or B. Peckarsky.

[3] Present address: Department of Biological Sciences, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1.

[4] The order of the first two authors was determined by the flip of a coin.

zation dynamics to argue that exchange rates may play a key role in determining the perceived impact of predators on their prey. Although our emphasis is on freshwater ecosystems, any general conclusions about the relationship between prey mobility and predator effects should apply to other systems.

Prey Exchange Rates: Literature Survey

Cage studies

As part of a survey of the literature on freshwater predation experiments, we examined the relationship between impact of the predator and the mesh size of cages used to manipulate predator density. We used two measures of predator impact: (1) the author's conclusion of an important predator effect, and (2) the negative natural logarithm of the ratio of densities of prey in cages with predators (N_p) to the density of prey in cages without predators (N_0, control). The logarithm is hereafter called the PI (predator impact) index. The experiments included both enclosure/exclosure experiments, where predators were present in some cages and absent in others, and exclosure-only experiments, where cages excluding predators were compared to open cages or areas to which predators had access. The PI index is derived from a simple model that assumes that the per capita effect of predators on prey populations is a constant. We use this measure of predator impact because it removes the potentially confounding influence of prey density on the magnitude of predator impact (Osenberg 1988).

In all studies that we examined, prey densities in control and manipulated arenas were shown or assumed to be initially similar. In this survey we examined all papers that we could find that contained predation experiments in freshwater benthic or littoral habitats, scanning the last 25 yr of English-language journals containing papers on freshwater ecology. We also conducted a less comprehensive survey of foreign language journals. The criteria that we used for including studies in our analyses were that predators be directly manipulated and that experiments include concurrent controls so that we could quantitatively compare prey densities in areas with and without predators. We analyzed the results for lentic and lotic systems, and those for cage vs. large-scale (whole lake, pond, pool, divided lakes and ponds, stream section) manipulations separately. Of the >250 papers that we examined, we found that 14 stream cage, 32 lake cage, 5 stream section or pool, and 13 large-scale lake or pond studies could be included in our analyses.

Investigators have very different criteria for concluding that predator effects are important. For example, Reice and Edwards (1986) reported that brook trout generally had little effect on prey assemblages in two streams, despite the fact that, in one stream, 75% of the 65 recorded taxa and all of the 10 most common taxa showed declines in mean abundance, and overall invertebrate abundance was significantly reduced when

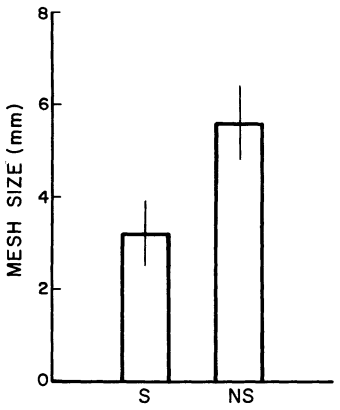

FIG. 1. Average mesh size of cages used in stream studies showing significant (S) vs. nonsignificant (NS) effects of predators on prey assemblages. Studies showing significant effects: Peckarsky and Dodson (1980), Flecker (1984), Oberndorfer et al. (1984), Walde and Davies (1984*b*), Peckarsky (1985), Walde (1986), Gilliam et al. (1989), Schlosser and Ebel (1989). Studies showing nonsignificant effects: Reice (1983), Flecker and Allan (1984), Reice and Edwards (1986), Culp (1986). Inclusion of Schofield et al. (1988) as showing either significant or nonsignificant effects (see *Prey exchange rates: Literature survey: Cage studies*) did not change the results. In this analysis Walde (1986) and Walde and Davies (1984*b*) were treated as one study because both studies deal with the same experiments. Peckarsky (1985) was treated as two studies since 2-mm mesh was used in one set of experiments and 3-mm mesh was used in another. Heights of bar graphs are means, vertical lines are ±1 SE.

trout were present. On the other hand, Schofield et al. (1988) found that trout had a significant effect on the abundance of only one, relatively rare, prey taxon. They, however, emphasized this effect, probably because this prey item was large, conspicuous, and the dominant invertebrate predator in their stream. Similarly, although included as a study showing significant predator effects on prey populations, Schlosser and Ebel (1989) reported important predator impacts in only one of four habitat types.

To avoid relying on the subjective judgments of individual researchers, we examined the relationship between the magnitude of predator impact (PI) and the mesh size of experimental cages. Common prey were defined as those that occured at densities greater than 10 prey/cage, and were commonly found in predator diets. Where there was no direct information on predator diets we relied on diet data from the literature. We used data on total prey abundances if these were the only data presented. In most cases where data on both total prey abundances and the densities of the component taxa were compared, results for common prey were similar to those for total prey. For each experiment, the PI index was determined for the dominant prey in each predator treatment (i.e., different densities, species, or combinations of predators constitute different treatments within an experiment). We conducted a second analysis using studies rather than individual treatments as replicates. Here, PI value for

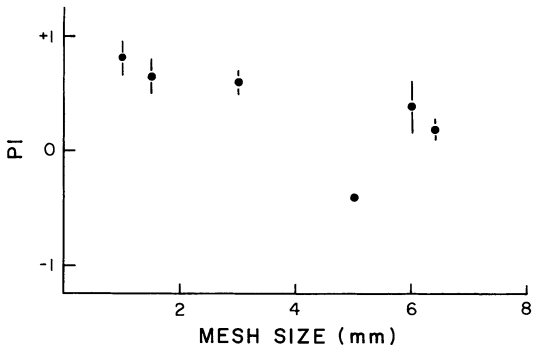

FIG. 2. Relationship between predator impact (PI) for common prey and the mesh size used in cages. PI = $-\log_e(N_p/N_0)$, where N_p = density of prey in cages with predators and N_0 = density of prey in cages without predators. Data for calculations were from the studies listed in Fig. 1 legend. The number of replicate treatments (n) per mesh size was: 1 mm: 10; 1.5 mm: 8; 3 mm: 17; 5 mm: 1; 6 mm: 4; 6.4 mm: 12; total n = 52. There was a highly significant correlation between PI and mesh size (Spearman's $r_s = -0.50$, $P < .0001$, $n = 52$).

common prey was calculated using all treatments within a study.

Mesh size of cages was significantly greater in lotic studies reporting no significant effects of predators on prey than in those reporting significant effects (Mann-Whitney U test, $P < .05$, Fig. 1). In addition, there was a highly significant negative relationship between PI and mesh size (Spearman's $r_s = -0.50$, $P < .0001$, $n = 52$, Fig. 2). When studies rather than predator treatments were used as replicates, the same result was obtained (PI vs. mesh size: Spearman's $r_s = -0.52$, $P < .05$, $n = 14$). Cage size did not differ significantly between studies reporting significant vs. nonsignificant predation effects (mean ± SE: 2570 ± 820 cm² vs. 2130 ± 880 cm²), duration of experiment (23 ± 10 d vs. 25 ± 11 d), and predator density (166 ± 98 predators/m² vs. 11 ± 4 predators/m²) (Mann-Whitney U tests, $P > .05$ in all cases). The high mean number of predators present in the studies showing significant predator effects was primarily owing to two studies where invertebrate predators were added to cages at densities ranging from 222 to 778 predators/m² (Oberndorfer et al. 1984, Walde and Davies 1984*b*, Walde 1986). However, the biomass of predators in one of these studies (Walde and Davies 1984*b*: 2.3–6.9 g/m²) was actually less than the fish biomass added to channels in a study not showing significant predator effects (Culp 1986: 25–101 g/m²). In the other studies showing significant predator effects (Peckarsky and Dodson 1980, Flecker 1984, Peckarsky 1985, Gilliam et al. 1989, Schlosser and Ebel 1989), predators were added at densities comparable to those added to cages not showing significant predator effects (i.e., 8–17 predators/m²).

We also attempted to examine relationships between prey mobility and PI values for lotic systems. We could find only one study that had sufficient replication for rigorously quantifying predator effects (Peckarsky 1985), and only five taxa in that study occurred at densities ≥8 individuals/cage. These five common taxa were also the only taxa showing significant responses to predator manipulations. We calculated PI values for predatory stoneflies in Six Mile Creek resulting in the following ranking of prey taxa from low to high PI (least to greatest impact): Baetidae < *Amphinemura* < *Paraleptophlebia* = Chironomidae < *Ephemerella*. To obtain estimates of the relative colonization abilities or mobilities of prey taxa, we examined literature data describing the colonization trajectories of taxa invading empty substrate trays or cages (Allan 1975, Townsend and Hildrew 1976, Shaw and Minshall 1980, Ciborowski and Clifford 1984, Peckarsky 1986). We compared short-term (3-d) colonization rates to benthic densities (=% moving each day, Townsend and Hildrew 1976), or densities in trays or cages after short time intervals (1–6 d) to asymptotic or peak densities recorded for the entire colonization period (Allan 1975, Shaw and Minshall 1980, Peckarsky 1986). In the latter case we also noted the time required for populations to reach asymptotic or peak densities. Finally, in one case we used data on the proportion of animals leaving a tray each day as calculated from an "equilibrium colonization model" (Ciborowski and Clifford 1984). We obtained rankings of the relative mobilities of prey taxa for each study, then calculated an average ranking for each taxon over all studies. Based on these analyses, we ranked the colonization ability of Peckarsky's common prey taxa as (low to high): *Ephemerella* < Chironomidae = *Paraleptophlebia* < *Amphinemura* < Baetidae. Although the colonization abilities of chironomids will depend on the exact species present, most studies report relatively low colonization rates for this group (Townsend and Hildrew 1976, Shaw and Minshall 1980). Despite the low number of taxa, there was a significant relationship between PI values and colonization ability (Spearman's $r_s = -0.90$, $P < .05$). These results indicate that the magnitude of predator impact was negatively correlated with prey mobility.

These analyses suggest that the observed results of predation experiments depend on prey immigration and emigration rates. Mesh size will undoubtedly affect the rate of exchange of prey between the inside and outside of cages, and this, in turn, may affect the degree to which predators can locally depress prey densities. Mesh size will, of course, affect a number of other factors, but most of these would be expected to have the opposite effect on predator impact. For example, decreased mesh size probably increases sedimentation inside cages; however, increased sedimentation generally reduces rather than enhances predator effects (Peckarsky 1985, Walde 1986). Prey exchange rates will also be affected by factors other than mesh size, such as prey mobility and flow regimes. However, prey assemblages were quite similar among studies, and differences among study sites in flow regime would tend

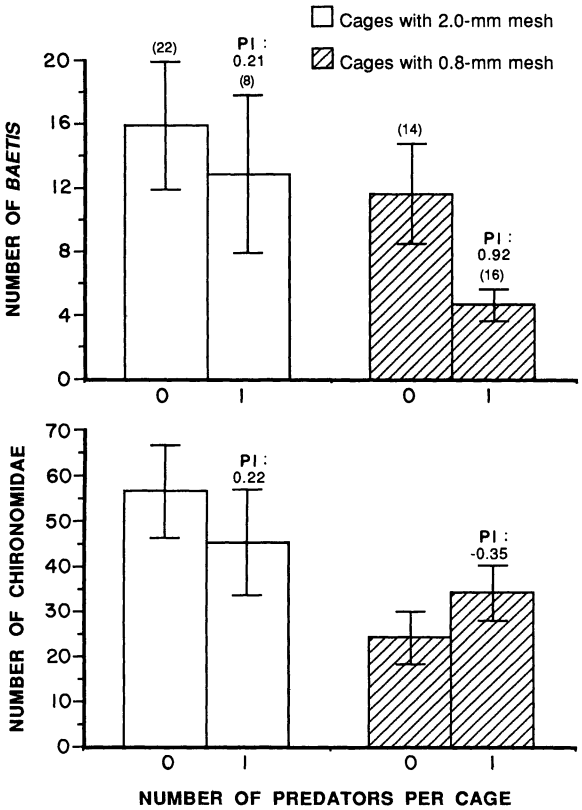

FIG. 3. Comparison of predator impact in fine vs. coarse-meshed cages (1985 and 1987 experiments). Shown are number of prey in cages (mean ± SE) with 0 or 1 *Megarcys* after 3 d. Numbers of replicates are in parentheses. PI values are indicated above the "predator impact" bar of each related pair in the histogram. PI = $-\log_e(N_p/N_0)$, where N_p = density of prey in cages with predators and N_0 = density of prey in cages without predators.

to accentuate the influence of prey exchange on observed predator impacts. For example, most of the studies showing significant predator effects on prey were conducted by placing fine-mesh cages in interstitial or slow-flowing habitats, whereas studies not showing predator effects were conducted with coarse-mesh cages in fast-flowing zones (see Fig. 1 legend).

Large-scale fish manipulations

The results of large-scale experiments in streams also emphasize the overwhelming influence of prey exchange rates on perceived predator effects in streams. Prey drift rates were one to two orders of magnitude lower in studies showing significant effects of predatory trout on invertebrate assemblages (Griffiths 1981, Cooper et al. 1986, Cooper 1988) than in studies not showing significant reductions by trout (Zelinka 1974, Allan 1982). Drift densities (per unit volume of water) for mayfly nymphs averaged 3.4–5 nymphs/100 m^3 where trout had a significant impact (Griffiths 1981, Cooper et al. 1986, Cooper 1988), as compared with 50 and 1300 nymphs/100 m^3 where trout had no effect (Zelinka 1974, 1976, Allan 1982). Average discharge was also much lower in the former three studies 4–40 L/s) than in the latter two (140 and 630 L/s). The exchange rate of prey due to drift between areas with and without predators was thus much lower in studies showing significant predator effects than in studies showing nonsignificant predator effects.

Although the invertebrate predator *Plectronemia* is extremely vulnerable to predatory trout, its total numbers were not significantly different in an 8-m section of stream to which trout were added vs. a control, downstream stretch where trout were absent (Schofield et al. 1988). The lack of response could be due to the high dispersal and colonization rates of *Plectronemia* (Townsend and Hildrew 1976, Schofield et al. 1988). At the extreme of little or no emigration, Reimers (1958) reported that epibenthic invertebrates were eliminated and infaunal invertebrates drastically reduced when trout were introduced into an isolated montane lake, and Macan (1977) reported a variety of significant prey responses to trout introductions in a small pond.

Although these results certainly suggest that exchange rates are important in modifying predator impacts on prey populations, differences in the effects of invertebrate vs. fish predators or in the effects of drift vs. benthic-feeding predators could possibly account for some of the observed patterns (see *Discussion*). Given these complications, it is necessary to assess more directly the effects of prey exchange rates on predator effects on prey. We report the results of some relevant field experiments and observations in the next section.

PREY EXCHANGE RATES: FIELD EXPERIMENTS AND OBSERVATIONS

Experiments on stonefly predation

The first set of experiments used a factorial design, manipulating both mesh size and the density of a predatory stonefly (*Megarcys signata*) in Benthette Brook, a first-order tributary of the East River in Colorado. Preliminary experiments were conducted in 1985 and 1987 using small plastic containers (10 × 10 × 10 cm) with 8 × 8 cm windows of 0.80- or 2-mm mesh on the upstream, downstream, and top sides. Cage size was chosen to approximate the amount of space occupied by one stonefly in Benthette Brook. Cages were filled with standardized natural substrates colonized with periphyton, and each received a subsample of the benthic prey community, approximating the natural density of prey, as well as 0 or 1 *Megarcys*. Cages were buried in the stream and retrieved after 3 d. Invertebrates in the cages were filtered through a 400-μm net, preserved in 70% ethanol, and counted under a dissecting microscope. Cages from which predators were lost during the experiments were not included in the analyses. Because the results of the experiments in 1985

TABLE 1. Summary of two-way ANOVAs testing the effects of mesh size (F [fine] = 0.8 mm and C [coarse] = 2 mm) and predator density (0*M*, 1*M*, 2*M* = 0, 1, or 2 *Megarcys*) on the transformed [$\log(x + 1)$] abundances of two common prey (1988 data).

Prey species	Source	ss	df	*F*	*P**
Baetis	Model	25.4	5	15.9	.0001
	Mesh size	10.4	1	32.4	.0001
	Predation	13.1	2	20.5	.0001
	Interaction	1.9	2	3.0	.05
	Error	26.2	82	···	···
Chironomids	Model	0.6	5	0.7	.65
	Mesh size	0.04	1	0.2	.65
	Predation	0.3	2	0.7	.49
	Interaction	0.3	2	0.8	.43
	Error	14.9	81	···	···

t tests for *Baetis*:	0*M*: C	0*M*: F	1*M*: C	2*M*: C	1*M*: F	2*M*: F
Means:	10.6	8.2	6.0	5.8	3.2	1.3

* When results were significant, ANOVAs were followed by a posteriori *t* tests with alpha levels adjusted for number of comparisons (*n*) (Bonferroni's adjustment: $\alpha = .05/n$). Treatments (predator code: mesh size) connected by an underline are not significantly different.

and 1987 were similar, the composite results of those experiments are presented here.

In these trials mesh size did affect the magnitude of the predator's impact on one of the two prey types (Fig. 3). Predatory stoneflies significantly reduced population densities of *Baetis* in cages with a mesh size of 0.8 mm ($P < .05$, Mann-Whitney *U* test), but had no effect in cages with a mesh size of 2 mm (Fig. 3). Mean predator impact (PI) in the fine-meshed cages was significantly larger than in the coarse-meshed cages (Mann-Whitney *U* test, $P < .005$). There was no effect of mesh size on predator impact on chironomids; the presence of predatory stoneflies did not affect the density of chironomids in cages of either mesh size (Fig. 3).

To corroborate these results, we conducted a second set of experiments in summer 1988. These experiments were identical in design to the 1985/1987 experiments except that we used cylindrical plexiglass enclosures (10 cm high × 10 cm diameter) with 5 × 10 cm windows of 0.80- or 2-mm mesh. In 1988 we also measured the size distributions (head capsule widths) of prey in control and predator cages using a dissecting microscope. Predator effects on *Baetis* were again influenced by mesh size, as indicated by the significant ANOVA interaction term (Table 1). As in the previous trials, predator impact on *Baetis* was much more pronounced in the smaller meshed (0.8-mm) cages (Fig. 4). Mesh size did not affect *Baetis* density when predators were absent, but fine-meshed cages had significantly lower densities than coarse-meshed cages when predators were present (Table 1). Mean PI was again significantly larger in the fine-meshed cages than the coarse-meshed cages for both one *Megarcys* (*t* test, $P < .05$) and two *Megarcys* (*t* test, $P < .001$).

Predators also significantly altered the size structure of *Baetis* populations in fine-meshed, but not in coarse-meshed, cages (Fig. 5). Again, there were no significant effects of predator manipulations on either chironomid density (Table 1) or chironomid size structure (Fig. 5) at either mesh size. Chironomids are consumed in greater numbers than *Baetis* (Peckarsky 1985), so the absence of a measurable predation effect may be due to high turnover rates (chironomids are small enough to pass readily through the fine mesh).

Observations on trout predation

We then examined the relationships between trout effects on individual prey taxa and the drift rates of these taxa out of pools in Rattlesnake Creek, Santa Barbara County, California.

Estimates of the densities of 22 taxa of invertebrates were obtained from benthic samples taken with an 0.09-m^2 box sampler (1-mm mesh size) (Hemphill and Cooper 1984) in 11 trout and 11 troutless pools. Four box samples were taken from each pool and combined into one composite sample per pool. For each pool, the number of individuals of each taxon was deter-

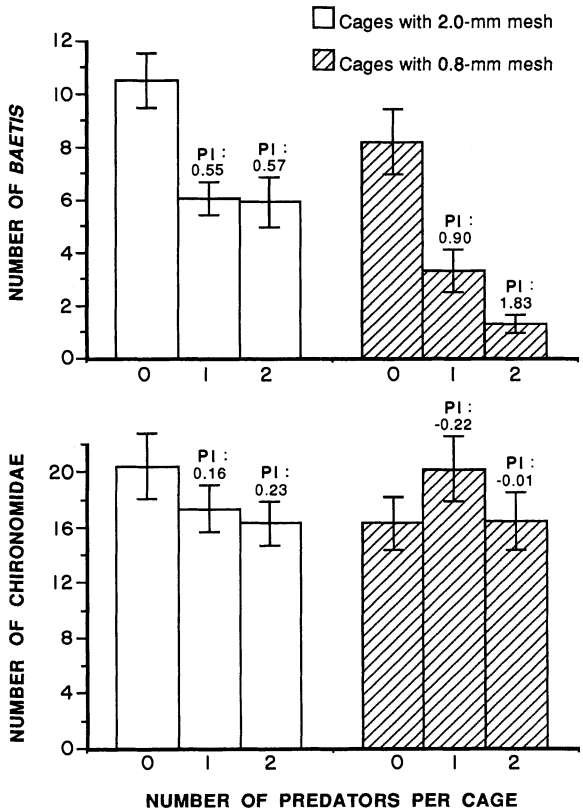

FIG. 4. Comparison of predator impact in fine vs. coarse-meshed cages (1988 experiments). Number of prey in cages (mean ± SE) with 0, 1, or 2 *Megarcys* after 3 d. Number of replicates was 15. PI values are shown above the "predator impact" bar of each related pair in the histogram. PI = $-\log_e(N_p/N_0)$, where N_p = density of prey in cages with predators and N_0 = density of prey in cages without predators.

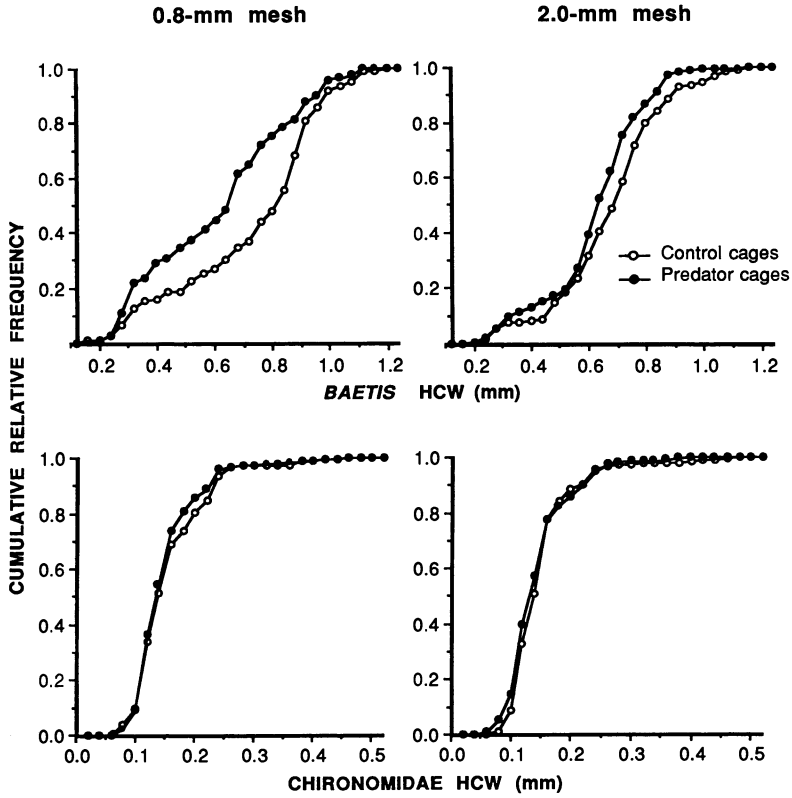

FIG. 5. Cumulative relative frequencies of prey sizes (HCW = head capsule widths) in control and predator cages in 1988. Data for treatments with 1 and 2 *Megarcys* were pooled since abundances and sizes of prey did not differ significantly. There were significant differences in the size distributions of *Baetis* populations in control vs. predator treatments for 0.8-mm mesh cages ($P < .05$, two-sample Kolmogorov-Smirnov test). The presence of the predator did not affect the size distribution of *Baetis* in the 2-mm mesh cages, and neither predator presence nor mesh size influenced the size distribution of chironomids ($P > .05$, two-sample Kolmogorov-Smirnov tests).

mined from these estimates of benthic density and measurements of pool area. Predator impact, or PI index, was calculated as above: the negative natural logarithm of the ratio of invertebrate densities in trout vs. troutless pools. Field experiments manipulating trout in Rattlesnake Creek have shown that observed differences in benthic densities between trout and troutless pools are, in fact, owing to the direct effects of trout (Cooper et al. 1986, Cooper 1988).

Drift rates of the same 22 taxa were measured in 4 trout and 2 troutless pools using drift nets with mouth dimensions 46 × 30 cm, mesh size 250 μm. Trout (T) and troutless (TL) pools were similar in area (mean ± SE: T = 14.2 ± 3.9 m², TL = 12.8 ± 1.3 m²), maximum depth (T = 70 ± 14 cm; TL = 60 ± 25 cm), and flow rate (T = 3.7 ± 0.7, L/s, TL = 4.1 ± 0.1 L/s). Pool outlets were narrow (<40 cm) and shallow (<20 cm) and discharge was low (2–5 L/s). Drift nets sampled the entire water column, were left in place for 24 h, and were emptied at dusk and dawn. To calculate drift density (numbers per cubic metre) we measured the width, depth, and velocity (with Bentzel tubes, Everest 1967) of the water flowing through nets at the beginning and end of each sampling period.

Drift densities and discharge rates were used to estimate the number of individuals leaving pools per day. Turnover rate was then calculated by dividing the number of invertebrates drifting out of pools per day by the number of invertebrates in the pools. Because the inlets of most pools were small waterfalls, it is unlikely that prey emigrated via upstream movement. Since trout and troutless pools did not have significantly different turnover rates or drift densities (one-way ANOVAs, $P > .05$), the six pools were combined to calculate mean turnover indices and drift densities for individual taxa. We also conducted two-way ANOVAs treating log-transformed drift density (numbers per cubic metre) or the log-transformed number caught in nets per 10-h set as the response variables, and trout presence and time of day (night vs. day) as the independent variables. Drift rates were low and variable, and, with one exception, there were still no significant differences in drift or turnover rates between trout vs. troutless pools for the most common drifting taxa, or for total invertebrates ($P < .05$). The exception was *Lepidostoma* (Trichoptera) larvae, which had significantly higher drift densities when trout were present. (This should not be taken to imply that predators such

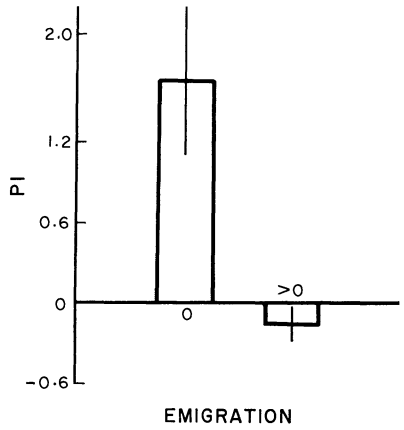

FIG. 6. Mean PI values (±1 SE) for prey taxa showing very little or no movement between stream pools (turnover index ≈0, $n = 8$) vs. taxa moving between pools ($n = 14$). PI = $-\log_e(N_P/N_0)$, where N_p = density of prey in cages with predators and N_0 = density of prey in cages without predators. PI values for emigrating vs. non-emigrating taxa were significantly different ($P < .001$, Mann-Whitney U test).

as trout do not influence the tendency of their invertebrate prey to drift, but in this case the effects were not large enough relative to other factors to be detected.)

Predator impact (PI) was negatively correlated with turnover rate for the 22 most common prey taxa (Spearman's $r_s = -0.65$, $P < .001$, $n = 22$). Taxa that had turnover indices close or equal to 0, and drift densities ≤1 individuals/1000 m³, had significantly higher PI values (high predation impact) than did taxa with high turnover rates or drift densities (Fig. 6). The presence of trout had little or no effect on the benthic densities of taxa with high turnover rates (>0) and drift densities (≥2 individuals/1000 m³), despite the common occurrence of some of these taxa in trout diets (PI for these taxa ≈0, Fig. 6).

To determine whether the observed correlations could actually have been caused by confounding factors such as prey size or microhabitat type, we estimated the average length of each taxon in each of the 22 August pool samples, and subjectively assigned each taxon to a microhabitat type based on 7 yr of sampling and observations of faunal assemblages in California stream pools. Microhabitats were ranked according to accessibility to trout predators, and categories were water column or water surface (1), epibenthic (2), and interstitial (4) microhabitats. A separate microhabitat category (3) was assigned to taxa that regularly moved between epibenthic and interstitial microhabitats.

Prey size was significantly correlated with prey turnover rate (Spearman's $r_s = -0.64$, $P < .001$, $n = 22$). To determine if this could be producing the relationship between PI and turnover rate, we regressed PI on average size (using ranked data), and then regressed the residuals on turnover rate. There remained a significant negative relationship between the residuals and turnover rate ($r^2 = 0.25$, $P = .019$, $n = 22$), indicating that size could not fully account for the original correlation between PI and turnover rate. Microhabitat type was not related to turnover rate ($r_s = +0.04$, $P > .10$, $n = 22$).

The results of these experiments and analyses are consistent with the hypothesis that the magnitude of perceived predator effects on prey is determined by prey exchange rates.

PREY EXCHANGE RATES: A DYNAMIC MODEL OF PREDATION AND COLONIZATION

To explore how immigration/emigration rates might be expected to affect the outcome of predation experiments, we developed a simple model that describes the reponse of prey population size to different rates of prey movement and predator consumption. Our model can be considered an extension of Sheldon's (1984) and Crowley et al.'s (1987) colonization models. Sheldon assumes that prey movement is essentially a diffusion process:

$$dN/dt = I - E, \qquad E = mN. \tag{1}$$

Here the change in the prey population with time (dN/dt) is the difference between the number of immigrants (I) and emigrants (E) per unit time. The number of prey emigrating is simply a constant (m) times the number of prey present (N).

Our model makes two modifications to the Sheldon model. (1) In the same way that the number of emigrants depends on interior cage density (N_i), immigration is a function of exterior prey density (N_e). So net migration $M = c(N_e - N_i)$. c is the rate at which prey move across the barrier; at $c = 0$, no prey move in or out, at $c = 1.0$, prey turn over inside cages once per unit time. This is identical with Crowley et al.'s (1987) model. (2) Predators (P) are assumed to consume prey inside the cage at a per capita rate a. Thus the complete model is

$$dN/dt = c(N_e - N_i) - aN_iP. \tag{2}$$

The equilibrium prey density then is

$$N_i^* = cN_e/(c + aP), \tag{3}$$

or, equivalently, the ratio of interior to exterior density is

$$N_i^*/N_e = c/(c + aP). \tag{4}$$

Three points are apparent here. First, if there is no migration ($c = 0$), then the equilibrium prey density inside the cage is 0, and the experiment is essentially a closed-system feeding trial. Second, increasing either the number of predators or the predator feeding rate will result in a lower prey density. The model assumes no interference between predators. Third, predator impact ($-\ln[N_i/N_e]$, which is equivalent to PI in the field experiments) decreases nonlinearly as a function of c, the immigration/emigration rate (Fig. 7).

It is clear that the amount that predators depress prey density within a localized area such as a cage, depends critically on the rate at which predators consume prey and the rate at which prey move into and out of the cage, or in a more natural setting, into and out of nonrefuge areas. This exchange rate depends, in part, on prey mobility, and thus variation in prey movement rate may explain some of the different results investigators have obtained. For a given predation rate, one should expect to see a greater local depression of sedentary prey than mobile prey, even if these benthic prey are not actively avoiding the predator. However, in the case of experimental manipulations, c may also be affected by the cage itself. If mesh size is too small to allow the prey to pass, the expected prey density is zero. Even if prey can pass through the mesh, the cage may still bias immigration/emigration rates either by reducing the permeable area or by affecting the behavior of animals that encounter it. This is a more disturbing result, since it means that practically any result can be obtained in a cage experiment, and the more restrictive the cage, the greater the expected depression of prey density. Since cage permeability is certainly affected by mesh size, this result fits well with our empirical observation that higher PI values are observed in experiments that used smaller mesh sizes.

This model was built for the hypothetical situation where benthic predators are not present outside cages. The densities of prey inside control cages (without predators) will equal exterior prey densities. The magnitude of depression of prey densities inside predator cages (relative to exterior or control densities) will depend on predation rate and prey exchange rate, over the short term. These same kinds of considerations, however, will apply equally to situations where predators are present outside of cages. For example, if predators and prey are stocked into predator cages at natural densities (=exterior densities), then changes inside predator cages should parallel those outside cages. In contrast, control cages stocked with natural prey densities, but no predators, will increasingly diverge from exterior or predator cage densities as predators deplete prey. The greater the rate of prey exchange between the inside and outside of control cages the greater the resemblance of interior to exterior prey densities. In essence, then, prey exchange tends to homogenize patches in an environment. The greater the rate of exchange, the less the difference between manipulated (predators added or removed) and unmanipulated areas, or between manipulated units and controls.

There is a fairly straightforward link between the two empirical patterns found in our literature survey and experimental observations: high exchange rates tend to be associated with low magnitudes of predator impacts and with studies reporting nonsignificant predator effects. For a given level of variation among samples or cages (=spatial variability), the smaller the predator impact, the lower the probability of detecting the effect. Thus any factor affecting immigration/emigration rates by prey, whether it be the intrinsic mobility of the prey, discharge rates, or mesh size of cages, will affect not only the magnitude of the perceived predator impact, but also the probability of the impact being statistically significant.

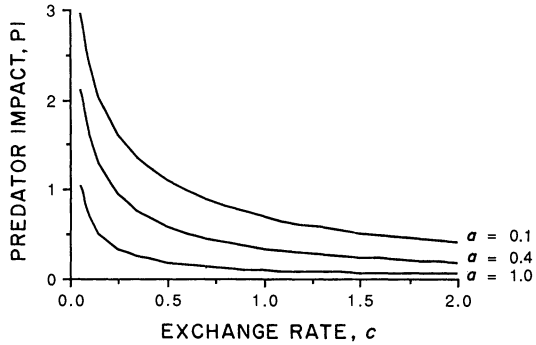

FIG. 7. Predicted relationship between exchange rate of prey (c) and predator impact (PI) for different levels of predation (a). PI $= -\log_e(N_p/N_0)$, where N_p = density of prey in cages with predators and N_0 = density of prey in cages without predators. Curves are generated from Eq. 4 in text.

Test of model on empirical data

If the above model has actually captured the essential features of a predation experiment using cages, and if we know certain parameters, such as a, c, and N_e, we should be able to predict the ratio of interior to exterior prey density. We tested the model on a set of experiments using the perlodid stonefly *Kogotus nonus* and its chironomid prey *Thienemaniella* sp. Cages were stocked with various densities of predators and background densities of prey, and left in the stream for 10 d in July 1981 and 1982, and June 1981. (Details of these field experiments have been published previously [Walde and Davies 1984b].)

Parameter values were estimated from data obtained independently of the field experiments. Benthic density was determined from samples taken from the experimental riffle at the time of the experiment and standardized for the area of the cage. The predation constant, or attack rate, a was estimated by regressing ln{[number available − (number killed/day)]/number available} on number killed per day (Thompson 1975) from 24-h functional response experiments conducted in small circular laboratory streams, using starved (48 h) *Kogotus* larvae (July 1982). (Protocol was identical to that described in Walde and Davies 1984*a*.) Our best estimate of attack rate a was 0.09.

The exchange rate, c, was obtained from colonization experiments conducted simultaneously with the predation experiments (Walde and Davies 1984*b*). Cages identical to those used for the experiment, but containing no prey, were interspersed among the treatment cages in the stream. Since the cages were initially emp-

TABLE 2. Fit of the colonization/predation model (Eq. 4 in text) to three experiments examining the impact of the predator *Kogotus* on its prey *Thienemaniella* when the two were left in cages in a stream for 10 d. Observed values are the densities ($\bar{X} \pm$ SE) of *Thienemaniella* within cages (number per cage; 4 to 6 replicates per treatment). Expected values are densities calculated using the model. (See *Prey exchange rates: A dynamic model of predation and colonization: Test of model on empirical data* for details of parameter estimation.)

Experiment		Number of predators in cage				P
		0	1	2	3	
		No. *Thienemaniella* per cage				
July 1981	Observed:	108 ± 10		34 ± 7		>.91
	Expected:	108		35		
June 1982	Observed:	54 ± 8	45 ± 9	43 ± 4		>.05
	Expected:	63	35	25		
July 1982	Observed:	151 ± 12	106 ± 15	55 ± 9	45 ± 11	>.36
	Expected:	195	101	69	52	

ty, the number moving in over a short time (5 d) was a reasonable estimate of the number moving across the barrier over that time. Our estimate of c was then the number immigrating per day divided by the benthic density, and ranged from 0.07 to 0.12 d^{-1} over the three experiments.

In both July experiments, the model provided a good fit to the observed experimental values (Table 2). There are a number of possible explanations for the poorer fit in June. The model is expected to produce a good fit when the following assumptions hold: (1) Prey movement can be represented as a diffusion process, unaffected by the presence/absence of the predators, or of the cage. The model will not predict experimental outcomes very well if there is considerable movement of prey out of the cage in response to the predator, or if the cage provides an environment for the prey that is either more or less desirable than outside. (2) The parameters have been estimated under conditions that mimic closely, or apply to the experimental conditions. (3) The duration of the experiment is short enough that the only source of prey mortality is predation, and there are no births of prey or predators. It must be of sufficient length that prey density has equilibrated. (Density should not still be increasing due to colonization.)

In general, the *Kogotus/Thienemaniella* system fits these assumptions well. These chironomids are not known to have any escape or avoidance response to *Kogotus,* the colonization estimates were determined under conditions nearly identical to the experiment, and cages were stocked with prey, so that densities began close to "equilibrium." The poorest parameter estimates were predator attack rates, since they were obtained under laboratory conditions. Discrepancies were probably exacerbated for the June experiment, since *Thienemaniella* is much smaller in June than in July (≈25% the body mass), and the functional response experiments were conducted on July-sized *Thienemaniella.* Overall, however, the fits were surprisingly good, indicating that in this system predation and exchange rates were good predictors of predator impact.

DISCUSSION

We have presented four lines of evidence suggesting that exchange rates of prey may play a major role in determining the potential impact of a given predator. (1) In a survey of the literature on predation experiments in streams, we found a negative correlation between cage mesh size and the magnitude of predator impact. There is certainly considerable noise in the relationship (Fig. 2), but we consider the fact that there is any relationship at all quite interesting, given the large number of factors that can influence the outcome of different experiments (different predators, prey communities, experimental design). Perceived impacts of predators in large-scale (non-cage) experiments were also apparently related to prey exchange rates.

There are, however, possible alternative explanations for these patterns. For example, stream caging studies using fine meshes were usually conducted with interstitial, invertebrate predators, whereas experiments using coarse meshes usually used fish; both fish and invertebrate predators were manipulated in cages with intermediate mesh sizes (3 mm). It is possible that the observed effects of mesh size reflect, at least partially, the differences between the effects of invertebrate and vertebrate predators. It may be that indirect or compensatory effects tend to obscure the direct effects of fish predators. For example, fish may remove large predatory invertebrates in cages, reducing predation rates on smaller prey. In addition, the effects of fish on large predatory invertebrates might frequently be undetected due to the low power of statistical tests when replication and densities are low (Allan 1984, Johnson et al. 1987).

Among studies examining the effects of fish predation, there was a tendency for salmonids to have few or no effects on prey (Culp 1986, Reice and Edwards 1986, Schofield et al. 1988), but for other kinds of fish (cyprinids, cottids) to reduce prey populations significantly (Flecker 1984: open vs. closed cages, Gilliam et al. 1989, Schlosser and Ebel 1989). These data suggest that drift-feeding salmonids probably have fewer

effects on benthic prey than do benthic-feeding fishes. However, there were also some studies that did not show effects of benthic-feeding fish (dace, darters, sticklebacks, sculpins) on prey (Flecker 1984 [cages with or without sculpins], Reice 1983, Reice and Edwards 1986, Flecker and Allan 1984). Similarly, the analysis of the large-scale manipulations indicates that trout have greater predatory impacts in slow- as compared with fast-flowing streams. Trout operate as ambush, drift-feeding predators in fast-flowing situations, and as searching, surface or benthic-feeding predators in slow-flowing or lentic situations (Grant and Noakes 1987); consequently, the observed patterns may have been related to differences in the impacts of trout using ambush vs. cruising foraging modes. If this is true, flow regimes and prey exchange rates still determine the impacts of predators on prey, albeit as mediated through effects on predator behavior.

Nonetheless, three other lines of evidence strongly support the hypothesis that much of the variation in the impact of predation is due to differences in prey exchange rates: (2) Significant predator impacts on the mobile *Baetis* prey in Colorado streams were observed when colonization rates were restricted, but not when mesh size of the cage was relatively large. Similarly, the effect of trout in California stream pools was greater when prey turnover rate was low. (3) Re-analysis of Peckarsky's (1985) data shows an inverse relationship between predator impact and prey mobility within one experiment using only one species of predator. (4) A model that incorporates both exchange rates of prey and predation rates suggests that these patterns are what we ought to expect. The magnitude of predator effects will be smaller when exchange rates are high, and when all else is equal, fewer significant predator effects will be obtained in manipulative experiments where exchange rates are high.

This relationship between exchange rates of prey and perceived predator impact has at least two implications. First, mesh size is an important cage artifact with the potential to affect the outcome of predation experiments. Experiments using cages fall onto a continuum from the use of barriers that completely restrict immigration/emigration to those having no effect at all on prey movement. The former is essentially a feeding trial, where, if no refuges are present, and the trial lasts long enough, the expected final prey density is zero. Clearly, this type of experiment has the highest probability of producing large predator impacts (and significant results), but the results would appear to have little relevance to real predator effects. To the extent that a cage decreases the movement of prey, it is approaching a feeding trial, and it is difficult to infer anything about predator impacts.

What mesh size should ecologists use in conducting field experiments? Cage mesh must allow the same amount of prey immigration and emigration as the natural systems to which the results are to be extrapolated, while, at the same time, retaining or excluding predators. Because they enable one to "freeze" patches with differing densities of predators in situ, cage experiments may indicate how prey populations respond to varitions in the local abundance or foraging pressure of their predators (Walde and Davies 1984*b*). Eliminating or restricting sources of recruitment and loss at local scales will provide a distorted view of how predators affect the local distribution and abundance of prey. Even with cages that provide natural levels of prey exchange, results must be extrapolated to the natural situation with caution since cages restrict predator movement, and the relative size of refuge and nonrefuge areas (inside vs. outside of cage) may be much different than that in the natural environment.

In many lake or pond experiments researchers have examined predator effects on prey in large plastic bags that eliminated prey immigration or emigration (Andersson et al. 1978, Neill 1981, Vanni 1988). In these cases, researchers were interested in extrapolating their results to whole lake or pond systems, and treated the individual bags as isolated miniature lakes or ponds. Because movement of prey into and out of isolated pond or lake systems is quite limited, prey movement within these bags simulates that within natural whole systems. Of course, cages or bags may not faithfully mimic the array of conditions and processes occurring in the natural system (Carpenter and Kitchell 1988), and since lakes and streams are a mosaic of patches of different sizes and durations connected by the exchange of organisms and chemicals, it is unlikely that cage or bag results that are specific to a given type of patch can be extrapolated with confidence to whole systems.

A second implication is of greater interest from an ecological point of view. We propose the hypothesis that prey exchange rates may actually explain a significant proportion of the variation in predator impacts seen among different communities. Within a stream, predator effects may be more pronounced in pools, where prey turnover rates are low, than in riffles or runs, where prey dispersal and colonization tend to be higher (Schlosser and Ebel 1989). Similarly, in fast-flowing streams, global exchange processes probably swamp the effects of local biological interactions, whereas in streams showing more limited prey movement among patches the effects of local biological interactions may be more manifest. Differences in prey exchange rates may also explain some of the differences in observed predator impacts in different kinds of habitats. For example, the greater proportion of lentic studies showing significant predator impacts (94%) as compared to streams (69%) might be in part attributable to differences in exchange rates mediated by differences in the flow regime. Drift in lotic habitats contributes to the continuous redistribution of invertebrates in streams, and lotic invertebrates are notorious for their rapid colonization of new habitats (Allan 1975, Townsend and Hildrew 1976, Shaw and Minshall 1980,

Peckarsky 1986, Richards and Minshall 1988). Intrinsic factors affecting prey mobility (swimming ability, wing size) as well as external factors such as water or wind current regimes will contribute to the final exchange rate of prey, and these factors might be expected to affect the relative importance of predation in any particular community. These results suggest that predators may play very different roles in closed as compared with open systems.

ACKNOWLEDGMENTS

Colin Townsend encouraged the review of predation experiments that led to this paper. We thank Ulrike Berninger for translating articles written in German and for performing library research that facilitated completion of the review. We thank M. O. G. Eriksson and Z. Kajak for information and articles, and David Allan, John Roff, Gary Sprules, Sheila Wiseman, Jill Lancaster, and Cathy Cowan for reviewing the manuscript. Cathy Cowan, Marge Penton, Darcy Tichner, Elise Jones, Alison Weller, and Nina Hemphill provided field assistance. We are also very grateful to Alison and Darcy for measuring prey sizes in Colorado experiments, and to Becky Shaw for measuring prey sizes in California experiments. We thank the following institutions for the use of library facilities: University of East Anglia, Queen Mary's College, Freshwater Biological Association at Windermere, and the British Library. This paper benefitted from discussions with Tom Dudley, Alan Hildrew, Colin Townsend, Phil Crowley, Mary Power, and Craig Osenberg. The work reported in this paper was supported by NSF grants BSR86-04808 to S. Cooper and T. Dudley and BSR 86-04921 to B. Peckarsky.

LITERATURE CITED

Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology **55**: 1040–1053.

———. 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. Ecology **63**:1444–1455.

———. 1983. Predator–prey relationships in streams. Pages 191–229 *in* J. R. Barnes and G. W. Minshall, editors. Stream ecology: application and testing of general ecological theory. Plenum, New York, New York, USA.

———. 1984. Hypothesis testing in ecological studies of aquatic insects. Pages 484–507 *in* V. H. Resh and D. M. Rosenberg, editors. The ecology of aquatic insects. Praeger, New York, New York, USA.

Andersson, G., H. Berggen, C. Cronberg, and C. Gelin. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia **59**: 9–15.

Carpenter, S. R., and J. F. Kitchell. 1988. Strong manipulations and complex interactions: consumer control of lake productivity. BioScience **38**:764–769.

Ciborowski, J. J. H., and H. F. Clifford. 1984. Short-term colonization patterns of lotic macroinvertebrates. Canadian Journal of Fisheries and Aquatic Sciences **41**:1626–1633.

Cooper, S. D. 1988. Responses of aquatic insects and tadpoles to trout. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **23**:1698–1703.

Cooper, S. D., T. L. Dudley, and N. Hemphill. 1986. The biology of chaparral streams in southern California. Pages 139–152 *in* J. DeVries, editor. Proceedings of the Chaparral Ecosystem Research Conference. Report Number 62, California Water Resources Center, Davis, California, USA.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology **63**:1802–1813.

Crowley, P. H., P. M. Dillon, D. M. Johnson, and C. N. Watson. 1987. Intraspecific interference among larvae in a semivoltine dragonfly population. Oecologia (Berlin) **71**: 447–456.

Culp, J. M. 1986. Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry. Journal of the North American Benthological Society **5**:140–149.

Everest, F. H. 1967. Midget Bentzel current speed tube for ecological investigations. Limnology and Oceanography **12**: 179–180.

Flecker, A. S. 1984. The effects of predation and detritus on the structure of a stream insect community: a field test. Oecologia (Berlin) **64**:300–305.

Flecker, A. S., and J. D. Allan. 1984. The importance of predation, substrate and spatial refugia in determining lotic insect distributions. Oecologia (Berlin) **64**:306–313.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology **65**:455–468.

Gilliam, J. F., D. F. Fraser, and A. M. Sabat. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. Ecology **70**:445–452.

Grant, J. W. A., and D. L. G. Noakes. 1987. Movers and stayers: foraging tactics of young-of-the-year brook char, *Salvelinus fontinalis*. Journal of Animal Ecology **56**:1001–1013.

Griffiths, R. W. 1981. The effect of trout predation on the abundance and production of stream insects. Thesis. University of British Columbia, Vancouver, British Columbia, Canada.

Healey, M. 1984. Fish predation on aquatic insects. Pages 255–288 *in* V. H. Resh and D. M. Rosenberg, editors. The ecology of aquatic insects. Praeger, New York, New York, USA.

Hemphill, N., and S. D. Cooper. 1984. Differences in the community structure of stream pools containing or lacking trout. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen **22**:1858–1861.

Hershey, A. E. 1985. Effects of predatory sculpin on the chironomid communities in an arctic lake. Ecology **66**:1131–1138.

Hixon, M. A. 1986. Fish predation and local prey diversity. Pages 235–257 *in* C. A. Simenstad and G. M. Cailliet, editors. Contemporary studies on fish feeding. Dr. W. Junk, Dordrecht, The Netherlands.

Johnson, D. M., C. L. Pierce, T. H. Martin, C. N. Watson, R. E. Bohanan, and P. H. Crowley. 1987. Prey depletion by odonate larvae: combining evidence from multiple field experiments. Ecology **68**:1459–1465.

Macan, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. Biological Review **52**:45–70.

Mittelbach, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. Ecology **69**:614–623.

Neill, W. E. 1981. Impact of *Chaoborus* predation upon the structure and dynamics of a crustacean zooplankton community. Oecologia (Berlin) **48**:164–171.

Northcote, T. G. 1988. Fish in the structure and function of freshwater ecosystems: a "top-down" view. Canadian Journal of Fisheries and Aquatic Sciences **45**:361–379.

Oberndorfer, R. Y., J. V. McArthur, and J. R. Barnes. 1984. The effect of invertebrate predators on leaf litter processing in an alpine stream. Ecology **65**:1325–1331.

Osenberg, C. W. 1988. Body size and the interaction of fish predation and food limitation in a freshwater snail community. Dissertation. Michigan State University, East Lansing, Michigan, USA.

Peckarsky, B. L. 1985. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? Canadian Journal of Zoology **63**:1519–1530.

———. 1986. Colonization of natural substrates by stream benthos. Canadian Journal of Fisheries and Aquatic Sciences **43**:700–709.

Peckarsky, B. L., and S. I. Dodson. 1980. Do stonefly predators influence benthic distributions in streams? Ecology **61**:1275–1282.

Reice, S. R. 1983. Predation and substratum: factors in lotic community structure. Pages 325–345 *in* S. Bartell and T. Fontaine, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan, USA.

Reice, S. R., and R. L. Edwards. 1986. The effect of vertebrate predation on lotic macroinvertebrate communities in Quebec, Canada. Canadian Journal of Zoology **64**:1930–1936.

Reimers, N. 1958. Conditions of existence, growth, and longevity of brook trout in a small, high-altitude lake of the eastern Sierra Nevada. California Fish and Game **44**: 319–333.

Richards, C., and G. W. Minshall. 1988. The influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream. Journal of the North American Benthological Society **7**:77–86.

Schlosser, I. J., and K. K. Ebel. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecological Monographs **59**:41–57.

Schofield, K., C. R. Townsend, and A. G. Hildrew. 1988. Predation and the prey community of a headwater stream. Freshwater Biology **20**:85–95.

Shaw, D. W., and G. W. Minshall. 1980. Colonization of an introduced substrate by stream macroinvertebrates. Oikos **34**:259–271.

Sheldon, A. L. 1984. Colonization dynamics of aquatic insects. Pages 401–429 *in* V. H. Resh and D. M. Rosenberg, editors. The ecology of aquatic insects. Praeger, New York, New York, USA.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics **16**:269–311.

Thompson, D. J. 1975. Towards a predator–prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. Journal of Animal Ecology **44**:907–916.

Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. Oikos **47**:75–82.

Thorp, J. H., and E. A. Bergey. 1981*a*. Field experiments on interactions between vertebrate predators and larval midges (Diptera: Chironomidae) in the littoral zone of a reservoir. Oecologia (Berlin) **50**:285–290.

Thorp, J. H., and E. A. Bergey. 1981*b*. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. Ecology **62**:365–375.

Townsend, C. R., and A. G. Hildrew. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. Journal of Animal Ecology **45**: 759–772.

Vanni, M. J. 1988. Freshwater zooplankton community structure: introduction of large invertebrate predators and large herbivores to a small-species community. Canadian Journal of Fisheries and Aquatic Sciences **45**:1758–1770.

Walde, S. J. 1986. Effect of an abiotic disturbance on a lotic predator–prey interaction. Oecologia (Berlin) **69**:243–247.

Walde, S. J., and R. W. Davies. 1984*a*. Diel feeding periodicity of two predatory stoneflies (Plecoptera). Canadian Journal of Zoology **63**:883–887.

Walde, S. J., and R. W. Davies. 1984*b*. Responses of lotic prey populations to an invertebrate predator: evaluation of in situ enclosure/exclosure experiments. Ecology **65**:1206–1213.

Zelinka, M. 1974. Die eintagsfliegen (Ephemeroptera) in forellenbachen der beskiden. III. Der einfluss des verschiedenen fischbestandes. Vestnik Ceskoslovenske Spolecnosti Zoologicke **38**:76–80.

———. 1976. Mayflies (Ephemeroptera) in the drift of trout streams in the Beskydy Mountains. Acta Entomologica Bohemoslovaca **73**:94–101.