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## INFLUENCES OF PREDATORY FISH ON THE DRIFT DISPERSAL AND LOCAL DENSITY OF STREAM INSECTS<sup>1</sup>

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**Abstract.** Researchers have recently suggested that frequent prey dispersal into and out of an area can swamp the local effect of predation. Where prey are mobile, the extent of prey movement can therefore explain variation in the apparent effect of predators on local prey density. I compared the effect of the dominant predator in a temperate stream (brook charr, *Salvelinus fontinalis* Mitchell) on five insect prey taxa (mayflies: Ephemeroptera), to test the prediction that the extent of density reduction should be less for prey taxa dispersing more frequently.

The propensity of the mayflies to disperse by drifting downstream in the water column was measured in unmanipulated areas of the stream. Relative propensity to drift of the five mayflies was, from greatest to least: *Baetis*, *Paraleptophlebia*, *Ephemerella*, *Eurylophella*, *Stenonema*. I then tested effects of charr on the mayflies by manipulating charr density in fenced 35-m sections of the stream. Charr densities were adjusted to zero, medium, and high levels relative to natural densities. Rates of predation by charr in stream sections did not vary among the five mayfly taxa. Charr caused a large reduction in the density of *Baetis*, had a smaller effect on *Paraleptophlebia*, but had no detectable effect on the density of the other mayflies. Drift dispersal into the stream sections did not differ among charr densities. Effects of charr on prey densities could thus have been caused by direct predation or by increases in emigration from areas containing charr. Charr caused increased drift dispersal of *Baetis* and of *Paraleptophlebia*, but had no influence on drift of the other three mayflies. The reduction in density of *Baetis* by charr was due more to the charr-induced increase in drifting of *Baetis* than to direct predation on *Baetis*.

The hypothesis that frequent prey dispersal swamps the effects of predators assumes that predators influence prey density primarily by consuming prey. In this system charr also influenced prey densities by causing increases in prey drift rates, affecting the mayflies that drifted most frequently. For this reason, the mayflies drifting less frequently were not, as predicted, the ones most strongly affected by charr. Variation in the effect of predators on prey density may thus be partially explained by both (1) changes in prey dispersal not related to predators, as proposed in the initial hypothesis, and (2) influences of predators on prey dispersal.

**Key words:** *behavioral responses; brook charr; drift dispersal; mayflies; New England; power analysis; predation; streams; sublethal effects.*

### INTRODUCTION

Experimental manipulation of predator density in the field has been a powerful technique for testing the effects of predators on prey populations. Such manipulations have produced varying results (Sih et al. 1985, Wilson 1990). Predator manipulations in streams, for example, have led to effects on prey density in some studies (Flecker 1984, Walde and Davies 1984, Pekkarsky 1985, Feltmate and Williams 1989, Gilliam et al. 1989, Koetsier 1989, Schlosser and Ebel 1989, Lancaster 1990, Holomuzki and Stevenson 1992) but have

had no effects on prey density in other studies (Allan 1982, Flecker and Allan 1984, Culp 1986, Reice and Edwards 1986, Lancaster et al. 1991).

Recent theoretical studies have indicated that, where prey are mobile, the apparent effect of predators on prey density (the difference in prey density between areas with and without predators) can depend on the extent of prey mobility (Cooper et al. 1990, Hall et al. 1990, Lancaster et al. 1991). For a given rate of predation, as prey dispersal increases, the ratio of predator-induced mortality within manipulated areas to prey movement into and out of the areas decreases. When prey dispersal is frequent, the apparent effect of predators thus tends to be swamped and is unlikely to be detected, because rapid movement by prey tends to equalize prey density among areas.

It has been suggested that the swamping hypothesis might explain variation in the perceived effects of pred-

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ators in both stream (Allan 1982, Flecker 1984, Culp 1986, Gilliam et al. 1989) and marine benthic systems (Wilson 1981, Frid and James 1988, Frid 1989, Hall et al. 1990, Wilson 1990) where many prey taxa are mobile. To date, however, the only tests of the hypothesis have been done in streams. A survey of predator manipulations done in cages of varying mesh size indicated that predators reduced prey density to a greater extent when enclosed in fine-meshed cages (assumed to reduce prey movement) than in cages of larger mesh (assumed to allow freer movement of prey) (Cooper et al. 1990). Experiments varying cage mesh size in combination with manipulation of predator density produced similar results (Cooper et al. 1990, Lancaster et al. 1991). The swamping hypothesis can therefore explain variation in the apparent effect of predators on individual prey taxa as conditions influencing dispersal vary. In other experiments, the effect of a predator was less significant on prey taxa ranked as highly mobile than on prey taxa considered more sedentary (Cooper et al. 1990), suggesting that the hypothesis may also explain variation in the effect of predators among prey taxa that vary in their propensity to disperse.

I present the results of a field experiment designed to test whether the swamping hypothesis can predict differences among prey taxa in the apparent effect of predators. I manipulated the density of predatory fish in a New England stream and measured their effects on the local density of five insect prey taxa (all mayflies: Ephemeroptera), which varied in their propensity to disperse. Most dispersal by mayflies occurs by drifting downstream in the water column (Townsend and Hildrew 1976, Williams and Hynes 1976, Bird and Hynes 1981, Bergey and Ward 1989). The swamping hypothesis therefore predicts that the predators will have stronger effects on the density of prey taxa that drift less frequently.

The swamping hypothesis assumes that predators influence prey density only by consuming prey. Predators have a variety of sublethal effects on prey behavior, however, including behaviors which influence dispersal (Sih 1987, Lima and Dill 1990). Predators can, therefore, alter prey density by inducing changes in dispersal behavior as well as by consuming prey. Several stream invertebrates exert some control over entry in the water column and the distance they drift (e.g., Kohler 1985, Allan and Feifarek 1989) and show altered drift rates depending on the density of predators (Peckarsky 1980, Walton 1980, Kohler and McPeck 1989, Peckarsky and Penton 1989, Culp et al. 1991, Forrester 1992). Differential effects of predators on prey dispersal are, therefore, an alternative mechanism that may cause differences among prey in the apparent effect of predators. I measured both direct predation rates and changes in drift dispersal caused by predators in an attempt to separate their relative contributions to overall effects on prey densities.

## METHODS

### *Study site and initial charr densities*

The experiment was conducted in a 0.6-km section of Stoney Brook, a second-order stream in New Hampshire, USA (43°23' N, 72°01' W, elevation 300 m). Fish in the study area were surveyed by electrofishing (pulsed direct current [DC], 7–900 V) during August 1989 and June and August 1990, using the removal method (following Bohlin et al. 1989). Unblocked 5–16 m long sections of stream were fished three times, 2–3 h apart, working upstream. Most fishing was done from the bank, or while standing on rocks in the stream, to reduce disturbance to the benthos. The number of fish present in each section was estimated from the numbers captured during the three passes (following Bohlin et al. 1989). Brook charr, which feed mostly on drifting prey (McNicol et al. 1985, Grant and Noakes 1986, Forrester et al., *in press*), were the only common fish in the stream (density =  $1.2 \pm 0.1$  fish/m<sup>2</sup> [mean  $\pm$  1 SE], range = 0.6–2.4 fish/m<sup>2</sup>). The size distribution of charr at the time of the experiment was bimodal, with peaks around 55–60 and 80–110 mm fork length. A few black-nosed dace, *Rhinichthys atratulus* Hermann, were also present (mean density =  $0.009 \pm 0.001$  fish/m<sup>2</sup>), but were removed when the experiment was set up.

### *Mayfly drift propensity and benthic density in unmanipulated areas*

To predict the relative effects of charr on the five mayflies, I estimated their propensity to drift in unmanipulated areas of the stream. Drifting mayflies were censused using stationary nets placed in the stream (square-mouth nets: mouth area = 0.09 m<sup>2</sup>, net length = 1 m, mesh size = 0.3 mm). Drift was sampled at 20 different locations, spread over 390 m of stream and over three dates (2 and 10 August 1989 and 27 June 1990). A single net was placed at each location. Nets were in place for 24 h, but were emptied every 2 h. After drift sampling I took four randomly located benthic samples (Surber samples, 0.09 m<sup>2</sup>) 5–16 m upstream of each net. All samples were preserved in 70% ethanol and counted in the laboratory.

For each location I estimated the drift propensity of each mayfly as the number of mayflies collected in the drift net in 24 h ( $N_{\text{net}}$ ) divided by the mean number in benthic samples upstream. For comparison with experimental values I also calculated benthic densities (number per square metre) and the number of mayflies drifting past the stream cross section per day (24-h drift rate) at each location. Twenty-four-hour drift rates were estimated as  $N_{\text{net}}$  multiplied by the stream discharge and divided by the discharge through the net. Drift propensities of the five mayflies were compared using analysis of variance, with drift-net locations as a blocking factor.

TABLE 1. Characteristics of stream sections stocked with different densities of brook charr. Values are means  $\pm$  1 SE.

Treatment	Zero	Medium	High
Charr density (no./m <sup>2</sup> )	0	0.88 $\pm$ 0.02	1.56 $\pm$ 0.12
Charr size (g)	0	7.67 $\pm$ 1.30	6.90 $\pm$ 0.90
Canopy (%)	67 $\pm$ 4	74 $\pm$ 6	72 $\pm$ 8
Habitat type			
% riffle	55 $\pm$ 6	50 $\pm$ 4	60 $\pm$ 7
% pool	5 $\pm$ 2	10 $\pm$ 7	10 $\pm$ 5
% run	45 $\pm$ 5	40 $\pm$ 4	30 $\pm$ 4
Depth (cm)	25 $\pm$ 7	21 $\pm$ 9	26 $\pm$ 7
Width (m)	2.7 $\pm$ 0.2	2.6 $\pm$ 0.2	2.9 $\pm$ 0.5

#### Experimental manipulation of charr density

To test effects of charr on mayfly densities and drift rates and to measure predation rates on the mayflies, I manipulated charr density in 35 m long stream sections enclosed at the ends with fences (mesh size = 7 mm). Fences were constructed on 6–7 July and extended 0.1 m into sediment and 0.5 m above the water's surface. Fences did not restrict drift of mayflies (Forrester 1992).

Charr densities within the sections were adjusted to three levels: (1) zero (few or no charr), (2) medium density (mean  $\pm$  1 SE = 0.88  $\pm$  0.02 fish/m<sup>2</sup>), and (3) high density (1.56  $\pm$  0.12 fish/m<sup>2</sup>). Three sections of stream were assigned to each treatment. To reduce potential biases due to transport of mayflies or trout odors from upstream sections to those downstream I separated sections with 17–20 m long unmanipulated areas. In addition, the sections were arranged systematically to guarantee interspersed of the treatments. The order of sections, from upstream to downstream, was: high, high, zero, zero, medium, zero, high, medium, medium. Physical characteristics of stream sections did not vary significantly among treatments (Table 1).

Charr were removed from all sections by making four passes with the electrofisher through each section on 9–10 July; they were held in pens downstream and later returned to their sections, with the exception of charr from zero-density sections, which were distributed among the high-density sections. When adding charr, care was taken to keep size distributions similar among sections. Small floods on 17 and 30 July and on 12 August undermined some or all of the fences. The fences were repaired or replaced within 2 d following each flood and the sections were electrofished (2–3 passes per section) to check charr densities and reestablish the treatments. Charr appeared to move little during the floods; few charr were captured in the zero-density sections (mean  $\pm$  1 SE = 0.04  $\pm$  0.004 fish/m<sup>2</sup>) and numbers in high-density sections remained high (1.41  $\pm$  0.07 fish/m<sup>2</sup>). After the third flood, a fourth pass with the electrofisher was made through the zero-density sections to ensure that all fish had been removed.

#### Rates of predation by charr

Rates of predation by charr were estimated in two high-density and two medium-density sections on 29 August. Six charr were captured in each section every 4 h for 24 h by electrofishing. Two zero-density sections were also fished to control for effects of electrofishing. Electrofishing was done after the benthic sampling and interspersed between the drift sampling also done on this date (see *Section-specific effects of charr*). Fishing proceeded upstream, without revisiting areas, and captured charr were immediately killed and preserved in 10% formalin. I later dissected the stomach contents of the charr and stored them in 70% alcohol. Prey items were enumerated, dried at 60°C for 24–48 h, and weighed to the nearest 0.001 mg.

The dry mass of food consumed per section in 4 h ( $C_4$ ) was calculated (following Elliott and Persson 1978) based on the mean dry mass of food in charr stomachs at the beginning and end of the interval and the exponential rate of gastric evacuation (Forrester et al., *in press*). The number of each mayfly taxon ( $x$ ) consumed in a section in 4 h ( $N_{4,x}$ ) was estimated based on  $C_4$ , the mean prey mass in charr stomachs, and the proportion of prey items that were mayfly  $x$ . I calculated the percentage of the mayfly population in each section consumed per day as the number consumed (the sum of the six  $N_{4,x}$  values) divided by the number present (the mean benthic density multiplied by the area of the section).

#### Section-specific effects of charr

To test effects of charr on benthic density of mayflies, I took five randomly located Surber samples (area = 0.09 m<sup>2</sup>, depth = 10 cm) in each stream section on each of two dates (27 and 29 August). Approximately 80% of mayflies occurred in the top 10 cm of substratum (G. E. Forrester, *unpublished data*). I pooled the samples from the two dates to calculate an overall mean density of each mayfly in each stream section and used these section means as replicates in statistical analyses.

Effects of charr on daily drift rates of mayflies were tested by placing single drift nets immediately (10–20 cm) downstream of the fence at the upstream or downstream end of each section. Drift out of the sections

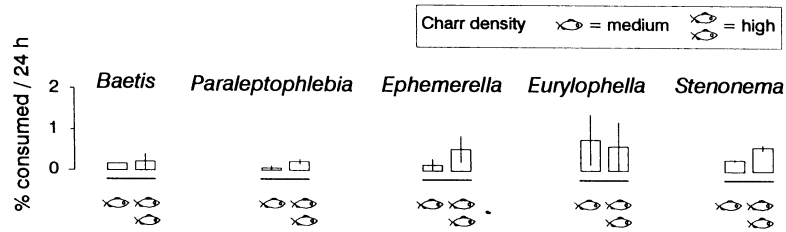


FIG. 1. Percentage daily losses of mayflies from experimental stream sections due to predation by brook charr. Horizontal lines under bars indicate means not significantly different at  $P = 0.05$  (Tukey's hsd test). Error bars are  $\pm 1$  SE.

was sampled on three dates. On 21 August, nets sampled the flow for 24 h and were emptied every 3.5 h. Four 3.5-h samples were lost, however, and mean counts for the section and time of day (night or day) were inserted when calculating 24-h counts. Logistical constraints prevented sampling continuously for 24 h on the other dates. On 24 August, drift out of the sections was sampled for 2–3.5 h starting at 2300. Twenty-four-hour drift rates were estimated using relationships between 2- and 24-h drift rates derived from the survey in unmanipulated areas ( $r^2 = 0.65\text{--}0.88$ ,  $n = 20$ ) following Allan and Russek 1985). On the last date, 29 August, drift out of the sections was sampled for six 1.5–2 h periods spaced evenly over 24 h. I estimated 24-h drift rates by interpolating between the six sample counts.

Drift into the sections was sampled on 22 August by taking three 3-h samples starting at 1500, 2000, and 2300 h. Twenty-four-hour drift rates were again estimated by interpolation, assuming that the samples were representative of their time of day (day or night).

#### Habitat-specific effects of charr

In addition to testing effects of charr over entire stream sections, I also assessed their effect on mayfly drift rates and benthic densities in small patches of run habitat within sections (flowing areas with gravel substrata; water velocity = 21–29 cm/s). A drift net sampled mayflies departing the patch, while a block fence (width = 1 m, mesh size = 1 mm) placed 2 m above the net prevented capture of mayflies from upstream (Forrester 1992). Block nets also reduced flow slightly (mean reduction = 11%). Drift was sampled for 2 h, commencing 1 h after setting up the block fence. A benthic sample (0.09 m<sup>2</sup>) was then taken immediately upstream of the net.

The drift propensity of mayflies in a patch (DP) was calculated as the number collected in the drift net divided by the number in the benthic sample. The drift propensity in a given section over 24 h was estimated by calculating average daytime and nighttime DPs for the section. The averages were extrapolated to the duration of day (14 h) and night (10 h) by multiplying them by 7 and 5, respectively. The two extrapolated

averages were then summed to give a 24-h drift propensity for each section.

#### Statistical analyses

Effects of charr density on all mayfly responses were tested using multivariate analyses of variance (MANOVA). Data were transformed prior to analyses, if necessary to meet the assumptions of normality and equal variances. The magnitude of effects was calculated as the proportion of the total variation in the data attributable to charr density ( $\hat{\omega}^2$  = strength of association), following Vaughan and Corballis (1969) and Dodd and Schulz (1973). To allow more powerful significance tests for treatment effects, nonsignificant ( $P > 0.25$ ) interaction terms that explained <5% of the variation in the data were removed by post-hoc pooling, following Mapstone (1988) and Winer et al. (1991). Where I did not detect effects of charr density, I calculated the power of the test following Koele (1982), Cohen (1988), and Winer et al. (1991). These power calculations are conditional on  $P$  (set at 0.05), the sample size, and the size of the effect to be detected ( $\hat{\omega}^2$ ).

## RESULTS

#### Rates of predation by charr

Rates of predation on mayflies measured during the experiment were generally low (Fig. 1). There were no significant differences among mayflies in the rate at which they were consumed by charr (MANOVA;  $F_{4,8} = 0.86$ ,  $P = 0.527$ ). There was also no significant difference in predation rates by charr at different charr densities (MANOVA;  $F_{1,2} = 3.75$ ,  $P = 0.192$ ). Based solely on predation rates, there should not, therefore, be major differences among mayflies in the extent to which their densities were reduced by charr.

#### The propensity to drift of mayflies in unmanipulated areas

The five mayflies did, however, differ significantly in their propensity to drift when surveyed in unmanipulated areas (ANOVA;  $F_{4,95} = 4.57$ ,  $P = 0.002$ ; log-transformed data) (Fig. 2). *Baetis* showed a significantly greater tendency to drift than did *Eurylophella* and *Stenonema* (Tukey's hsd,  $P < 0.01$ ), with *Paralepto-*

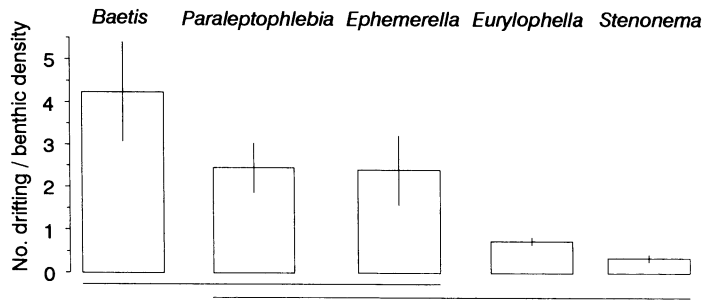


FIG. 2. Propensity to drift ([no. nymphs passing a stream cross section per 24 h]/[benthic numbers/m<sup>2</sup>]) of five mayfly taxa in unmanipulated areas of Stoney Brook. Horizontal lines under bars indicate means not significantly different at  $P = 0.01$  (Tukey's hsd test). Error bars are  $\pm 1$  SE.

*phlebia* and *Ephemerella* intermediate between these taxa. The swamping hypothesis predicts that, given similar predation rates, predation by charr should cause greater reductions in density of mayflies that disperse less frequently.

*Section- and habitat-specific effects of charr*

*Effects of charr on mayfly benthic density.*—The actual impacts of charr do not, however, conform to this prediction. The mayfly with the greatest propensity to drift, *Baetis*, was significantly reduced in mean density as charr density increased. This was true both when samples were located randomly throughout sections (one-way MANOVA;  $F_{2,6} = 25.8, P = 0.001$ ) and when samples were restricted to run habitats within sections (two-way MANOVA;  $F_{2,6} = 6.73, P = 0.029$ ) (Fig. 3). At the scale of whole stream sections, charr also re-

duced the density of *Paraleptophlebia* (one-way MANOVA;  $F_{2,6} = 5.53, P = 0.043$ ). *Baetis* was more strongly affected by charr than was *Paraleptophlebia*, the effect of charr explaining a higher percentage of the variation among stream sections in benthic density (84% for *Baetis* and 50% for *Paraleptophlebia*). No reduction of *Paraleptophlebia* density by charr was detected in run habitats (two-way MANOVA;  $F_{2,6} = 0.76, P = 0.51$ ) (Fig. 3). This apparent difference in the effect on *Paraleptophlebia* at different spatial scales may, however, be due to low statistical power of the test in run habitat (power using size of effect on *Paraleptophlebia* in stream sections was 0.45).

The three mayflies with the lowest propensities to drift, *Ephemerella*, *Eurylophella*, and *Stenonema*, were not reduced in density by charr at the scale of entire stream sections (one-way MANOVA;  $F_{2,6} = 0.02, P =$

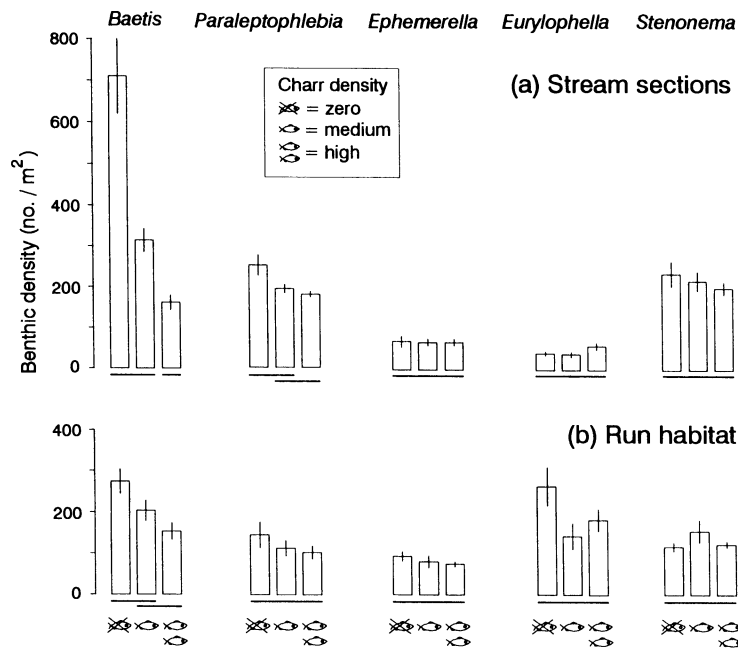


FIG. 3. Effects of brook charr density on benthic densities of five mayfly taxa (a) in 35-m stream sections and (b) in patches of run habitat within stream sections. Horizontal lines under bars indicate means not significantly different at  $P = 0.05$  (Tukey's hsd test). Error bars are  $\pm 1$  SE.

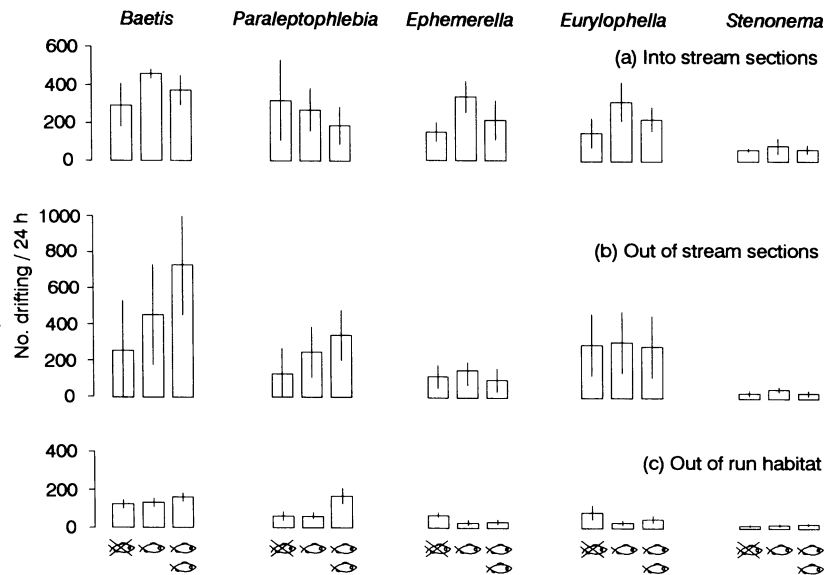


FIG. 4. Effects of brook charr density on 24-h drift rates (a) into and (b) out of 35-m stream sections, as well as (c) out of patches of run habitat within sections. Symbols are as for Fig. 3. Error bars are  $\pm 1$  SE.

0.98 for *Ephemerella*;  $F_{2,6} = 2.54$ ,  $P = 0.26$  for *Eurylophella*;  $F_{2,6} = 0.54$ ,  $P = 0.61$  for *Stenonema*) (Fig. 3). If these taxa had been affected as strongly as *Baetis*, I would almost certainly have detected changes in their density (power  $> 0.995$ ). I also had a reasonable chance of detecting smaller effects, of the size seen on *Paraleptophlebia* (power = 0.64). *Ephemerella*, *Eurylophella*, and *Stenonema* were also unaffected by charr density in patches of run habitat (two-way MANOVA;  $F_{2,6} = 0.87$ ,  $P = 0.47$  for *Ephemerella*;  $F_{2,6} = 2.19$ ,  $P = 0.19$  for *Eurylophella*;  $F_{2,6} = 1.34$ ,  $P = 0.38$  for *Stenonema*) (Fig. 3). The power of these tests was moderate (power using effect of the size for *Baetis* = 0.58). I therefore conclude that charr had no impact on the densities of *Ephemerella*, *Eurylophella*, or *Stenonema* at either of the spatial scales examined.

Overall, the relative effects of charr on the five mayflies were not as predicted by the swamping hypothesis because the two taxa drifting most frequently were the ones whose density was reduced by the predator. I therefore considered other mechanisms for differences in predator impacts among mayflies.

*Effects of charr on mayfly drift rates.*—One potential mechanism is bias in the supply of drifting immigrants into the stream sections. Drift rates into sections, however, showed no consistent variation between treatments for any of the mayflies (one-way MANOVA;  $df = 2$  and  $6$ ,  $P$  always  $> 0.363$ ) (Fig. 4). These results suggest there were no dramatic biases in the supply of drifting immigrants to the experimental sections, but I cannot rule out the possibility that smaller differences occurred because the tests had modest power (power to detect the largest observed effect on per-capita drift out of the stream sections was 0.47).

Another potential mechanism for reduction in prey density by charr is a predator-induced increase in emigration by drifting. Twenty-four-hour drift rates out of stream sections were not significantly influenced by charr density (repeated-measures MANOVA;  $df = 2$  and  $6$ ,  $P$  always  $> 0.19$ ) (Fig. 4). For all five mayflies there was significant variation in drift rates, however, among the three sample dates (repeated-measures MANOVA;  $df = 2$  and  $12$ ,  $P$  always  $< 0.036$ ) that was independent of brook charr density (repeated-measures MANOVA;  $df = 4$  and  $12$ ,  $P$  always  $> 0.10$ ). As was the case for drift out of entire stream sections, daily drift rates out of run habitats were not significantly altered by the density of charr (two-way MANOVA;  $df = 2$  and  $8$ ,  $P > 0.25$  for *Baetis*, *Eurylophella*, and *Stenonema*;  $df = 2$  and  $2$ ,  $P > 0.23$  for *Paraleptophlebia* and *Ephemerella*) (Fig. 4). Drift from run habitats did not, however, differ significantly among sample dates (two-way MANOVA,  $df = 1$  and  $6$ ,  $P$  always  $> 0.13$ ). The nondetection of effects of charr on mayfly drift rates does not eliminate the possibility that there were effects because all of the tests were weak (power to detect the largest effect on per-capita drift out of stream sections was always  $< 0.47$ ).

*Effects of charr on the propensity of mayflies to drift.*—By the time drift measurements were made, benthic densities of mayflies had diverged among the treatments. I therefore analysed drift rates relative to local benthic density as a better indicator of changes in dispersal induced by brook charr than absolute drift rates. The propensity of *Baetis* to drift from run habitats increased sharply as charr density increased (two-way MANOVA on log-transformed data;  $F_{2,8} = 18.4$ ,  $P < 0.001$ ) (Fig. 5). This effect explained 69% of variation

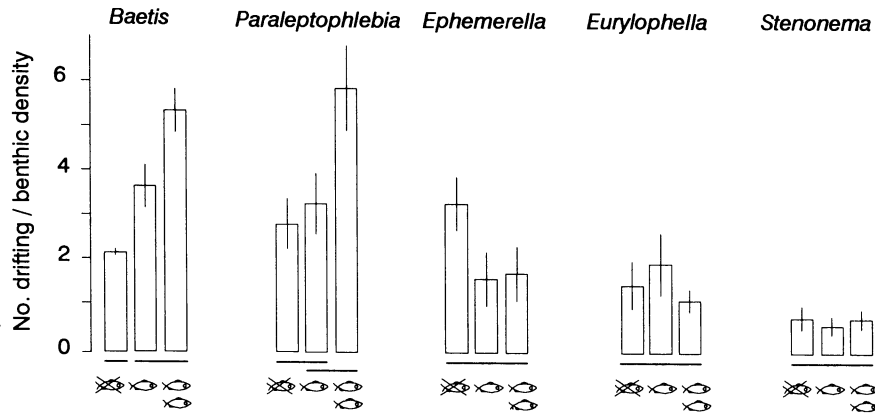


FIG. 5. Effects of brook charr density on propensity of mayflies to drift ([no. nymphs caught in a 0.3 m wide drift net per 24 h]/[benthic numbers/0.09m<sup>2</sup>]) from small (2 m long) patches of run habitat within 35-m stream sections. Symbols are as for Fig. 3. Error bars are ± 1 SE.

in drift propensity of *Baetis*. The drift propensity of *Paraleptophlebia* was also increased at higher charr densities (two-way MANOVA;  $F_{2,8} = 4.88, P = 0.037$ ) (Fig. 5), but the effect was smaller than that on *Baetis* and explained only 39% of variation in drift propensity (Fig. 5). Drift rates of the other three mayflies, relative to their benthic densities, were not significantly affected by charr density (two-way MANOVA;  $F_{2,2} = 7.0, P = 0.12$  for *Ephemerella*;  $F_{2,2} = 0.68, P = 0.59$  for *Eurylophella*;  $F_{2,2} = 0.07, P = 0.94$  for *Stenonema*) (Fig. 5). The tests were fairly powerful (power using effect size on *Baetis* = 0.87), so I concluded that these three mayflies did not alter their propensity to drift from patches of run habitat in response to charr.

The percentage of mayflies drifting out of entire stream sections per day was calculated by dividing the

mean 24-h drift rate (all dates pooled) by the mean benthic population size. The daily percentage drift of *Baetis* may have increased at higher charr densities (one-way MANOVA;  $F_{2,6} = 4.71, P = 0.059$ ; log-transformed data) (Fig. 6). This effect explained 45% of the variation in drift out the stream sections. Charr had no significant effects on the per-capita drift rates of any of the other mayflies (one-way MANOVA on log-transformed data;  $df = 2$  and  $6, P$  always  $> 0.23$ ) (Fig. 6) but these results are ambiguous because responses to charr of the magnitude displayed by *Baetis* were unlikely to be detected (power = 0.47).

Overall, the analyses of drift rates relative to benthic densities suggest that charr caused increases in drifting by *Baetis* and *Paraleptophlebia*, though the effect on *Paraleptophlebia* was not detectable at the scale of en-

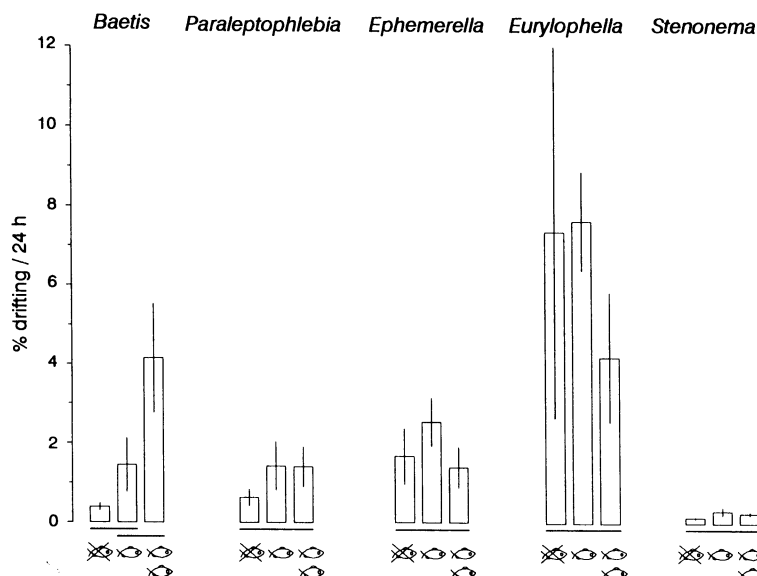


FIG. 6. Effects of brook charr on percentage daily loss from stream sections due to drifting. Symbols are as for Fig. 3. Error bars are ± 1 SE.



TABLE 2. Benthic densities and 24-h drift rates of mayflies in unmanipulated areas. Values are means  $\pm$  1 SE from 20 locations. See *Methods* for description of locations and sample collection.

	<i>Baetis</i>	<i>Paraleptophlebia</i>	<i>Ephemerella</i>	<i>Eurylophella</i>	<i>Stenonema</i>
Benthic density (no./m <sup>2</sup> )	253 $\pm$ 20	144 $\pm$ 11	87 $\pm$ 6	90 $\pm$ 7	285 $\pm$ 14
24-h drift rate (no. passing/24 h)	888 $\pm$ 158	346 $\pm$ 71	161 $\pm$ 45	62 $\pm$ 9	89 $\pm$ 18

tire stream sections. Predator-induced increases in emigration by drifting are therefore a potential mechanism for the reduction in density of these mayflies caused by charr.

#### DISCUSSION

I tested whether the swamping hypothesis (Cooper et al. 1990, Hall et al. 1990, Lancaster et al. 1991) could explain how the relative effect of a predator differed among five prey taxa that varied in their propensity to disperse. Contrary to the prediction of the hypothesis that predator impact and prey mobility should be inversely correlated, I found that the taxa affected by the predator were those dispersing most frequently.

One possible reason why my results were not as expected is that my measures of drift propensity might not reflect the actual tendency of the mayflies to disperse. Mayflies can disperse by crawling through the substratum and by swimming upstream, as well as by drifting. If these means of movement were more important than drifting, and if rates of movement by these means were inversely correlated to drift propensities, then my predictions would be incorrect. I consider this unlikely, for two reasons. First, where dispersal by drifting has been compared with dispersal by other means, drifting was the major component of movement by mayflies (Bishop and Hynes 1969, Townsend and Hildrew 1976, Williams and Hynes 1976, Bird and Hynes 1981, Benzie 1984, Bergey and Ward 1989). Second, and more important, studies measuring recolonization of denuded substrata, where colonization could occur by any means, suggested the same rank order of dispersal propensity that I measured using drift nets (Allan 1975, Shaw and Minshall 1980, Ciborowski and Clifford 1984, Peckarsky 1986, Giller and Campbell 1989).

A second potential source of bias in the results was the disturbance due to flooding and electrofishing before and during the experiment. Both these types of disturbance induce drifting and, if they did so differentially among treatments, could have caused spurious treatment effects on emigration. I consider this unlikely because differences among treatments in the extent of disturbance were slight (zero density sections were electrofished one time more than other sections). Further evidence for lack of artefacts due to disturbance is that benthic densities and drift rates in experimental sections were similar to those measured in unmanipulated areas before any flooding or electrofishing (Table 2, Figs. 2, 3, 4, 5, and 6).

A more likely reason for the pattern of my results is that the system I studied does not conform to the assumption of the swamping hypothesis that predators do not influence prey dispersal (Cooper et al. 1990, Hall et al. 1990, Lancaster et al. 1991). Given that input of drifting mayflies from upstream did not differ among treatments, effects of charr on drift dispersal out of the sections could lead to differences in benthic densities of mayflies among treatments. Increased emigration at higher charr densities would act in concert with direct predation to reduce benthic densities, and I suggest this is the most likely reason why benthic densities of *Baetis* and *Paraleptophlebia* were reduced by charr while densities of the other three mayflies were not.

In situations where prey movements were unaffected by predators, the swamping hypothesis successfully predicted the impact of predators on individual prey taxa. Larval chironomids in streams do not alter their drift rate in response to predatory stoneflies (Lancaster 1990), and Cooper and coworkers' (1990) model of predation and prey dispersal successfully predicted the extent to which chironomid density was reduced by stonefly predation in a field caging experiment. The swamping hypothesis also successfully explained changes in the apparent effect of predators on individual prey taxa as conditions affecting prey transport varied. A review of predator caging experiments showed that prey densities were reduced to a greater extent when predators were enclosed in fine-meshed cages (assumed to restrict dispersal) than in coarse-meshed cages (presumably allowing freer prey movement) (Cooper et al. 1990). In addition, experiments where predator density and cage mesh size were manipulated jointly demonstrated greater depression of prey density in fine-meshed, as opposed to coarse-meshed cages (Cooper et al. 1990, Lancaster et al. 1991).

In contrast to my study, the swamping hypothesis also successfully predicted differences among taxa in the apparent effect of a predator in two previous tests (Cooper et al. 1990). In one study, the extent to which densities of five insect prey were reduced by a predatory stonefly was inversely correlated to an estimate of the relative mobility of the prey. In the second example, a negative correlation was found between the effect of rainbow trout on 22 invertebrate prey taxa occupying stream pools and prey drift rate. In my experiment the discrepancy between predicted and actual results was explicable in terms of the mechanisms by which predators influenced prey density. How predators influenced prey density in Cooper and coworkers' (1990)

studies is less clear. No effects of trout on drift out of stream pools were detected in the second study (with one exception). The assumption of the swamping hypothesis, that predators do not influence prey dispersal, thus appears to be met in this situation. Predation rates by trout were not presented, however, so it is possible that the prey whose densities were reduced most were simply those that were consumed most frequently. In the first study, the prey whose density was reduced most strongly by the predatory stonefly formed the second-lowest proportion of the stonefly's diet, and reduction in density of this taxon could be accounted for almost entirely by noncontact avoidance of the predator (Peckarsky 1985). In both cases then, though variation among taxa in the effect of the predator was correlated with prey mobility, the reasons for the correlation were unclear.

Since the effect of charr on mayfly densities in my study seemed to be related to effects on prey dispersal, I considered how widespread influences of predators on prey dispersal are and how much these effects contribute to the overall impact of predators on prey density. Increased emigration in response to predators has been identified in many prey taxa. Various stream insects, including several mayflies (Peckarsky 1980, Kohler and McPeck 1989, Culp et al. 1991), herbivorous stoneflies (Walton 1980), and corixids and notonectids (Cooper 1988) increase their drift rate in the presence of predators. Larval salamanders (Sih et al. 1992) and small fish in streams also disperse away from predators (Schlosser 1987, Fraser and Gilliam 1992). Amphipods and polychaetes inhabiting marine sediments emigrate into the water column in response to benthic predators (Ambrose 1984). Local densities of many of these prey were reduced following experimental manipulation of predator density (Ambrose 1984, Peckarsky 1985, Cooper 1988, Feltmate and Williams 1989, Lancaster 1990, Fraser and Gilliam 1992, Sih et al. 1992). Reduced emigration in response to predators has been reported less often, but is displayed by stream amphipods (Williams and Moore 1985, 1989, Andersson et al. 1986) and isopods (Holomuzki and Hoyle 1990), and might be expected in other taxa that reduce activity or hide in the presence of predators. The consequences for prey density of reduced dispersal in the presence of predators have not yet been tested.

Where predators both reduced prey density and increased prey emigration, how much did these two effects contribute to the overall reduction in prey density? I cannot budget the contribution of these two mechanisms to density reduction over the course of my experiment because I only sampled near its finish. For *Baetis*, though, the extent to which loss from drifting increased at higher charr densities was much greater than the corresponding increase in loss due to direct predation (compare Figs. 1 and 6, which have the same scale on the y axes). This suggests that the increase in drifting induced by charr contributed more to the re-

duction of *Baetis* density than did direct predation, particularly since charr consume drifting prey, which means that the observed increase in drifting in the presence of charr is a conservative measure of the actual increase.

In other studies of predation in streams, several approaches for partitioning the effects of predators on prey density into components due to prey consumption and predator-induced emigration have been used (Peckarsky 1985, Feltmate and Williams 1989, Lancaster 1990, Fraser and Gilliam 1992, Sih et al. 1992). The methods used were each subject to potential biases (discussed by Sih et al. 1992). In all cases, however, increased emigration in the presence of predators contributed substantially (> 50%) to reduction of prey density. The only exception was Sih et al. (1992), where the effect of green sunfish on the density of larval salamanders in stream pools could be accounted for entirely by direct predation.

The above discussion suggests that, where prey dispersal is influenced by predators, the direction of these behavioral responses may partially explain effects of predators on prey densities. Reductions of prey density by predators should be larger and be detected more frequently, when predators cause increased prey dispersal. Though there are no observations of this as yet, we might expect that reduced prey dispersal in the presence of predators should tend to negate or even override effects of prey consumption. In summary, variation in the apparent effects of predators on prey density may be partially explained both by (1) swamping, when variation in prey dispersal is not influenced by predators and by (2) differential effects of predators on prey dispersal. Though my discussion has focused on streams, these two types of variation in prey dispersal may have a strong influence on the perceived effect of predators in any situation where prey are mobile. Experimental manipulations of predator density may therefore be difficult to interpret in the absence of knowledge of prey dispersal rates and of the extent to which they are influenced by predators.

The effects of swamping, and of predator-induced emigration, also have implications for the outcome of experiments done at different spatial scales. Where predators deplete prey populations within patches only by consuming prey, the swamping hypothesis predicts that predators should tend to reduce prey density to a greater extent in larger patches. This prediction arises because the ratio of within-patch processes to dispersal among patches decreases with increasing patch size, due to a perimeter-area effect (Frid 1989). The same perimeter-area effect, however, means that the opposite scaling effect should be observed where predators enhance or suppress prey emigration. In these cases, the impact of predators on prey density should decrease in larger patches. The notion that large-scale manipulations, such as this experiment, should be more likely to detect effects of predators than small-scale caging

experiments may not, therefore, turn out to be true. Predicting the effects of spatial scale on the outcome of experiments may, however, be more complicated than these perimeter–area effects suggest. In natural systems, prey populations are patchy in space, as are factors that influence rates of dispersal. Predator manipulation overlays an array of patches varying in predator density on an already patchy system. Understanding the consequences of varying the size of the predator patches on the effect predators have on prey populations may not, therefore, be a straightforward problem.

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