Predator-prey interactions between fish and insects in streams

Graham Edward Forrester

University of New Hampshire, Durham

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Predator-prey interactions between fish and insects in streams

Forrester, Graham Edward, Ph.D.
University of New Hampshire, 1992
PREDATOR-PREY INTERACTIONS BETWEEN FISH AND INSECTS IN STREAMS

BY

GRAHAM E. FORRESTER
B. Sc. University College of Wales, Aberystwyth, 1985
M. Sc. University of Sydney, 1988

DISSERTATION

Submitted to the University of New Hampshire in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
in
Zoology

December, 1992
This dissertation has been examined and approved.

[Signatures]

Dissertation director, Peter F. Sale, Professor of Zoology

Douglas F. Fraser, Professor of Biology, Sienna College

James F. Haney, Professor of Zoology

Thomas D. Kocher, Assistant Professor of Zoology

Barbara L. Peckarsky, Professor of Entomology, Cornell University

James T. Taylor, Associate Professor of Zoology

Dec 4, 1992

Date
I dedicate this work to my parents
River
Fallen from heaven, lies across
The lap of his mother, broken by world

But water will go on
Issuing from heaven

In dumbness uttering spirit brightness
Through its broken mouth.

Scattered in a million pieces and buried
Its dry tombs will split, at a sign in the sky,
At a rending of veils.
It will rise, in a time after times,

After swallowing death and the pit
It will return stainless

For the delivery of this world.
So the river is a god

Knee-deep among reeds, watching men,
Or hung by the heels down the door of a dam

It is a god, and inviolable.
Immortal, and will wash itself of all deaths.

Ted Hughes, 1983.
ACKNOWLEDGMENTS

Thanks to everyone who helped me along the way!

Firstly, thanks to my advisor, Peter Sale, who put up with me for the duration of two degrees. Peter was an excellent mentor, role model, and friend to a young chap learning to play the science game. My other committee members Doug Fraser, Jim Haney, Tom Kocher, Bobbi Peckarsky and Jim Taylor also gave generously of their knowledge and expertise. Steven Kohler and David Allan offered helpful advice during the planning stages of this project, and I followed Bruce Mapstone's lead when considering effect sizes. My committee members, as well as Scott Cooper, and Tom Dudley, criticized drafts of this document. By doing so they helped clarify my thinking tremendously. They also helped rid the thesis of logical inconsistencies, nounal adjectives, run-on sentences and other bad things what I am prone to write.

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I am grateful to Freeport Development Inc. for letting me work on their land, and for not bulldozing the stream valley until I had finished my experiments. I am also grateful to Sally Sheldon, who kindly gave me an office in which to write this thesis.

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ABSTRACT

PREDATOR-PREY INTERACTIONS BETWEEN FISH AND INSECTS IN STREAMS

by

Graham E. Forrester
University of New Hampshire, December, 1992

Some benthic insects in streams disperse by drifting short distances downstream in the water column. While drifting they are at risk from predators, such as trout, that feed in the water column. I examined prey selection by brook trout (Salvelinus fontinalis L.) in Stoney Brook, New Hampshire, U. S. A., and effects of trout on drift dispersal and benthic density of five prey taxa (mayflies: Ephemeropera).

Effects of trout on mayflies were tested by field manipulation of trout density in replicate 35 m long sections of stream. Trout consumed all five mayflies in roughly similar numbers. Feeding rates of trout (by weight) were not significantly influenced by time of day, or by trout density. However, comparison of prey consumed to prey available indicated that selection for mayflies, and for larger prey was greater during the day than at night. Benthic densities of the two mayflies drifting most frequently, Baetis and Paraleptophlebia, were reduced at high trout densities, whereas densities of the other three mayflies were unaffected by trout. Daytime drift of none of the five mayflies was affected by trout. However, nighttime drift (both drift density [no.m⁻³ water] and departure from 0.5 m² patches of substratum) of Baetis and Paraleptophlebia was increased at high trout density. Effects of trout on the density of Baetis were due primarily to increased drift dispersal from stream sections, whereas both direct predation and increased drift contributed to the reduction in density of Paraleptophlebia by trout. Nighttime drift (departure from 0.5 m² patches

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of substratum) of *Ephemera* was reduced in the presence of trout, but this reduction was not detected at a larger scale (35 m stream sections).

Trout influenced the size distribution of two of the five mayflies. The mean size of benthic *Ephemera* decreased as trout density increased, whereas the mean size of benthic *Paraleptophlebia* was increased where trout were present. The mechanism for these shifts in size distribution was uncertain, though the effect of trout on *Paraleptophlebia* was most likely due to size-specific alteration of drift dispersal.

Influences of trout on mayfly populations were thus complex. However, influences of trout on drift dispersal were important in determining the effects of trout on benthic populations, and can explain some variation among prey taxa in the effect of predators.
CHAPTER 1

SHORT TERM EFFECTS OF REMOVING PREDATORY FISH ON THE DIEL DRIFT DENSITY OF STREAM INSECTS

Summary

I tested effects of the removal of predatory fish on the drift density of stream insects in Stoney Brook, New Hampshire, U.S.A.. Four, 35 m long sections of stream were enclosed with fences and predatory fish, brook trout (Salvelinus fontinalis Mitchill) and black-nosed dace (Rhinichthys atratulus Hermann), were removed from two stream sections. Invertebrate drift was sampled in each section during both day and night, 3 and 10 days following fish removal. Daytime drift densities of blackflies (Simuliidae), and nighttime drift densities of the mayfly (Baetis) were significantly higher in areas containing fish than in areas from which fish had been removed. Densities in the drift of midges (Chironomidae) and another mayfly (Paraleptophlebia) were unaffected by trout removal. Size distributions of the two mayflies differed between areas containing or lacking fish; mean sizes of drifting Baetis and Paraleptophlebia were significantly greater in the presence of fish. The results suggest that behavioural responses to the local presence of predatory fish result in increased drift of some stream insects.

Introduction

Drift, the downstream transport in the water column of benthic invertebrates, is one of the major processes redistributing individuals within streams (Townsend & Hildrew, 1976; Williams & Hynes, 1976; Bird and Hynes, 1981). It is thus important to the dynamics of benthic communities (Waters, 1972; Brittain and Eikeland, 1988). Entry into the drift is believed to occur both through behaviour and by passive erosion (Wiley and Kohler, 1984). Many factors have been suggested to influence
patterns of behavioural drift, including predation by fishes (Waters, 1972; Statzner et al., 1984; Brittain and Eikeland, 1988).

Predatory fishes in streams include species that feed on insects while they are drifting, and others that feed on the benthos. One way that drift-feeding fishes can affect the density of drifting invertebrates is by consuming prey. Both drift-feeding and benthivorous fishes can potentially influence the drift density of invertebrates by inducing changes in drift behaviour. For example, laboratory studies have shown that some insects drift following encounters with benthic fishes (Kohler and McPeek, 1989; Culp et al., 1991). In addition, chemical extracts from both benthic and drift-feeding fishes cause reduced drift by amphipods (Williams and Moore, 1985).

Field studies testing for effects of predatory fishes on drift dispersal have produced varying results. Allan (1982) and Flecker (1992) detected no effects of removing drift-feeding fishes on the density of drifting invertebrates. Williams (1990) also found no effects of drift-feeding fish on the drift of most taxa, but did report increased daytime drift densities of a few taxa in the presence of fish. Andersson and co-workers (1986), in contrast, noted a decrease in the abundance of drifting amphipods following the introduction of a benthic fish into a section of stream from which these fish were previously absent. The disparate results of these studies suggest the need for more field experiments testing for effects of fish on the drift of stream invertebrates.

In this study, I observed the response of stream invertebrates to the removal of fish from sections of a small cold-water stream where drift-feeding fish were the dominant predators. I tested the following two hypotheses: (1) the density and (2) the size distribution of invertebrates in the drift differs between sections of stream where fish are present and where they have been removed.
Methods

The study was done during August and September, 1989 in Stoney Brook, New Hampshire, U.S.A. (43°23'N, 72°01'W). This is a second order stream, 6 km long, which drains into Lake Sunapee, New Hampshire. The stream was shaded by riparian vegetation, consisting of mostly of mixed deciduous trees. The mean width of the stream at the study site was 2.3 m, the mean discharge was 2.91 m$^3$.min$^{-1}$, and the elevation was 300 m. The study site was composed mostly of riffle and run habitat, and the sediment was gravel and rock. Fish species present at the study site were brook trout (*Salvelinus fontinalis*) and black-nosed dace (*Rhinichthys atratulus*). Their mean densities were 33 and 0.35 fish per 35 m of stream respectively (n = 7 sections). Brook trout feed predominantly on drifting invertebrates (e.g. Allan, 1981; McNicol et al., 1985; Grant & Noakes, 1986). whereas black-nosed dace feed on invertebrates on the substratum (Johnson & Johnson, 1982; Fuller & Hynes, 1987).

On August 29, four contiguous sections of stream, each 35 m long, were enclosed using fences made of hardware cloth with 3 mm mesh. The fences extended 10 cm deep into the sediment and reached 30 cm above the water's surface. Each enclosed section ended in a riffle area. The sections second and farthest from the upstream end of the study area were designated for fish removal. Fish were removed from these sections on August 30, by making four passes through each with a pulsed direct-current electrofisher (Smith-Root model 12). I made one pass with the electrofisher through the non-removal sections to control for possible effects of electrofishing on the drift.

I sampled the drift in the four sections of stream on two dates following the fish removal, September 2 and 9. On both of these dates I hung nylon mesh (0.15 mm mesh) over each of the fences and pressed it into the substratum to a depth of 3-5 cm. This was done before drift sampling commenced in order to ensure
that all drift collected in a given section originated from within it. The nylon mesh was
cleaned with a brush every 6 hours to reduce clogging. Drift sampling was
interrupted during cleaning, and for 15 min afterwards, to prevent capture of
invertebrates disrupted by the cleaning process. The nylon mesh was removed at
the end of each drift sampling date to permit replenishment of benthic populations
from upstream.

The nets used to sample the drift had a square opening of 0.09 m², were
conical in shape, 1 m long, with a mesh size of 0.3 mm. One net was placed to
intercept the flow close to the end of each section of stream. I measured the depth
of water and current velocity (using a pygmy meter, Gurley Instruments) at the
entrances to the nets to allow calculation of the volume of water they sampled. The
mean depth at the entrance to the nets was 9.6 cm and the mean current velocity
was 0.26 m.s⁻¹. On September 2, drift was sampled from 1300-2300 h and the nets
were emptied every 2 hours. On September 9-10, sampling was done from 1200-
0130 h. On this date the nets were emptied every hour, except between 1800-2030 h
when they were emptied every half hour. In order to minimize disturbance to the
fish, I approached the sections of stream where fish were present carefully from
downstream, and only to empty the drift nets. The contents of the nets were
emptied into 250-500 ml jars containing stream water and immediately refrigerated.
The invertebrates in each sample were identified and counted under a dissecting
microscope within four days of being collected. Identification was to either family or
genus.

I measured the head capsule widths of two mayflies collected in the drift
samples, *Baetis* and *Paraleptophlebia*. Approximately 75% of the captured
individuals of each taxon were selected haphazardly for measurement. Their heads
were removed, placed on slides in glycerine and viewed using a microscope. The
microscope images were filmed, displayed on a video monitor and the head widths
measured from the monitor using a digitizing pad interfaced with computer image-
analysiss software (Sigma Scan, Jandel Inc.).

Results

Twenty eight taxa were identified in the drift samples. Drift densities of most
individual taxa were low. Therefore present analyses for only the four most
common taxa: blackflies (Simuliidae), midges (Chironomidae), and two mayflies
(Baetis and Paraleptophlebia). Drift of most taxa was low during the day, increased
markedly after dark and remained at a fairly constant higher level throughout the
night. Therefore pooled the samples into two groups, day and night, for analyses of
effects of fish on drift. For September 2, I defined day samples as those taken from
1300-1700h and night samples as those from 1900-2300h. For September 9-10. day
samples were defined as those taken from 1200-1830h and night samples defined as
those taken from 1930-0130h. Drift samples straddling the dusk period were not
used because their day/night status was uncertain. I tested for differences in drift
densities between fish removal and control sections using repeated measures
analyses of variance, where the samples from September 2 and 9 were considered
repeated measures (Winer et al., 1991). Separate analyses were performed for day
and night drift densities.

Chironomids drifted in roughly equal numbers during day and night (Fig. 1).
Their density in the drift was unaffected by the presence of fish (Table 1). The other
three taxa examined drifted more frequently at night than during the day (Fig. 1).
Drift densities of Paraleptophlebia were not significantly affected by fish removal
(Table 1, Fig. 1). The drift density of Simuliidae was significantly higher in the
presence, than in the absence, of fish during the day, but drift of this taxon was
unaffected by fish at night (Table 1, Fig. 1). Densities of Baetis in the drift were also
significantly increased in the presence of fish, but for this taxa the increase occurred
at night rather than during the day (Table 1, Fig. 1)
Size measurements of mayflies were pooled into four groups: (1) day, with fish (2) day, without fish (3) night, with fish (4) night, without fish. I then tested effects of fish presence and time of day (night and day) on size distributions of mayflies using two factor model I analyses of variance (Underwood, 1981), where individual measurements were used as replicates. Size distributions of drifting *Baetis* were significantly influenced by the presence of fish (*F*<sub>1,141</sub> = 4.64, *P* = 0.033). The mean size of *Baetis* was greater where fish were present than where fish were absent (Fig. 2). The effect of fish was not dependent on the time of day (*F*<sub>1,141</sub> = 0.546, *P* = 0.461), and *Baetis* drifting during the day were not significantly different in size from those drifting at night (*F*<sub>1,141</sub> = 0.01, *P* = 0.993) (Fig. 2). No *Paraleptophlebia* were collected in the absence of fish, during the day. At night, however, the average size of drifting *Paraleptophlebia* was significantly greater in the presence of fish, than in their absence (*F*<sub>1,140</sub> = 17.2, *P* < 0.0005) (Fig. 2).
Table 1. Summary of results of repeated measures analyses of variance testing effects of fish removal (Fish) and differences between sampling dates (Date) on the drift density of four stream insects.

(a) Daytime drift density

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Baetis</th>
<th>Paraleptophlebia</th>
<th>Simuliidae</th>
<th>Chironomidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td>1</td>
<td>0.090</td>
<td>0.335</td>
<td>0.036*</td>
<td>0.247</td>
</tr>
<tr>
<td>Error</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>0.258</td>
<td>0.555</td>
<td>0.06</td>
<td>0.778</td>
</tr>
<tr>
<td>Date * Fish</td>
<td>1</td>
<td>0.307</td>
<td>0.507</td>
<td>0.127</td>
<td>0.634</td>
</tr>
<tr>
<td>Error          w</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(b) Nighttime drift density

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Baetis</th>
<th>Paraleptophlebia</th>
<th>Simuliidae</th>
<th>Chironomidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td>1</td>
<td>0.020*</td>
<td>0.114</td>
<td>0.962</td>
<td>0.246</td>
</tr>
<tr>
<td>Error</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>0.022*</td>
<td>0.116</td>
<td>0.263</td>
<td>0.704</td>
</tr>
<tr>
<td>Date * Fish</td>
<td>1</td>
<td>0.177</td>
<td>0.129</td>
<td>0.82</td>
<td>0.067</td>
</tr>
<tr>
<td>Error          w</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

b and w refer to error between and within treatments respectively. * indicates significant results (P < 0.05).
Fig. 1. Drift densities of four insect taxa in sections of stream where fish were either present at natural densities (+ fish) or had been removed (- fish). * indicates significant differences between stream sections with and without fish (P < 0.05). Error bars are standard errors.
Fig. 2. Mean sizes of two mayfly taxa drifting in sections of stream with (+ fish) or without fish (- fish). Error bars are standard errors.

- + fish
- - fish

**Baetis**

- Day
- Night

**Paraleptophlebia**

- Day
- Night
Discussion

Both of the taxa whose drift densities were affected by fish removal showed increased drift densities in stream sections containing fish. Consumption of drifting prey by trout should deplete numbers of invertebrates in the drift, and lead to reduced drift densities where fish were present. My observation of higher drift density in the presence of fish must, therefore, reflect an increase in drift behaviour in the presence of fish. This increase in behavioural drift presumably overwhelmed any effect of direct predation. Williams (1990) also found higher drift densities of several insect taxa in a stream section containing trout, relative to a fishless area. Unfortunately the treatment was not replicated in Williams' experiment and so the difference in drift density he reported cannot be unambiguously assigned to an effect of trout (Hurlbert, 1984). The changes in drift density caused by fish that I observed were different to those caused by fish in a Swedish stream (Andersson et al., 1986). These researchers found that the amphipod, Gammarus, reduced its activity and drift rate in the presence of sculpins, probably in response to chemicals released by the fishes (Williams & Moore, 1985).

The increased drift densities in the presence of fish that I observed could have been caused by either the trout, or the dace, or by both fish species. Responses to either dace or trout are possible because the presence of similar species, or their chemical exudates, has induced changes in invertebrate drift behaviour in the lab (Williams & Moore, 1985; Culp et al., 1991). Whilst I cannot rule out effects of dace, the fact that they were rare in the study area suggests that the effects of fish I observed were more likely caused by the trout. If the presence of trout represents a stimulus to drift, then this is an intriguing result because invertebrates are presumably placing themselves at increased risk of being consumed while drifting by adopting this behaviour. This is particularly so for Simuliids which increased their drift density during the day in the presence of fish. An increase in nighttime drift in
the presence of fish, as shown by *Baetis*, is presumably less dangerous, because trout feed less actively at night (Walsh et al., 1988; Angradi & Griffith, 1990).

Higher drift densities of Simuliids and *Baetis* in the presence of fish could be due either to increased rates of entry into the water column, or to longer drift distances in sections with fish. Increased entry into the water column has been shown by mayflies in response to predatory invertebrates (Corkum & Clifford, 1980; Peckarsky, 1980; Walton, 1980; Malmqvist & Sjöström, 1987) and benthic fishes (Kohler and McPeek, 1989; Culp et al., 1991). However, effects of predators on the distance drifted by invertebrates are also possible though they are, as yet, unexplored.

The tendency for the sizes of *Baetis* and *Paraleptophlebia* drifting at night to be greater in the presence of fish implies that larger individuals of these taxa are more prone to drift in areas containing fish. Both trout and dace select for larger prey (Grant & Noakes, 1986; Fuller & Hynes, 1981) so this size-specific pattern of drift makes sense for mayflies drifting at night, when the risk of predation is low. However, *Baetis* drifting in the presence of fish during the day also tended to be larger than those drifting in fishless sections. A similar pattern was also noted by Williams (1990) and the reason for it is unclear.

The results of this experiment suggest that some stream insects alter their behaviour in the presence of fish in ways which affect their drift density. Uncovering the details of these responses, however, and their implications for benthic populations will require further work. Two issues of particular interest are: whether invertebrates respond differently to drift feeding and benthivorous fish, and whether changes in drift behaviour are due to changes in entry into the water column or changes in drift distance. Since the responses to fish were both species- and size-specific, generalizations about effects of fish on drift will require careful comparisons among invertebrate species.

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CHAPTER 2

CHANGES IN DIEL DRIFT BEHAVIOUR BY MAYFLIES UNDER THE RISK OF TROUT PREDATION: VARIATION IN RESPONSE AMONG TAXA

Summary

Many benthic stream insects disperse behaviourally by leaving the sediments to drift short distances downstream in the water column. Drifting insects are at risk from diurnal visual predators, primarily fishes, feeding in the water column. Predominantly nocturnal drift is a widespread pattern believed to be an avoidance response to this form of predation. I tested the hypothesis that insects adjust their diel pattern of drift behaviour according to the level of risk from water-column predators by manipulating the density of brook trout (*Salvelinus fontinalis*) in a field experiment. Trout densities within fenced 35 m sections of stream were adjusted to zero, natural, and high levels. Prey were nymphs of five common mayflies (Order: Ephemeroptera). Prey drift behaviour within the sections was measured as the rate at which benthic individuals drifted from small (0.5 m$^2$) patches of sediment. Daytime drift of all taxa was infrequent throughout, and no responses to trout were detected. The most frequently drifting mayflies, *Baetis* and *Paraleptophlebia*, showed increased nighttime drift rates as trout density increased. In contrast, nighttime drift of *Ephemera*, a mayfly drifting at an intermediate rate, was reduced where trout were present. The other two mayflies, *Stenonema* and *Euryptilus*, drifted at low rates and showed no responses to trout presence. None of the mayfly responses to trout was size-specific. Some mayflies, therefore, do adjust their drift behaviour according to the level of the risk from water-column predators. These responses are most likely due to changes in rates of nighttime entry into the water column. Variation among taxa in responsiveness to trout
correlated with their overall tendency to drift; mayflies responding to trout were those drifting more frequently.

**Introduction**

Predators have important influences on behavioural decisions made by their prey (Edmunds 1974; Sih 1987; Lima & Dill 1990). Prey often limit their activities to places and times which reduce their frequency of encounters with predators. Many taxa vulnerable to visually feeding predators tend to enter areas where the predators are present only at night, a time when these predators feed less effectively, or not at all (e.g. Gentry 1974; Nelson & Vance 1979; Ohlhorst 1982; Edwards 1983; Holomuzki 1986; Haney 1988).

Drift dispersal by benthic stream invertebrates occurs when these animals depart the sediments to travel short distances downstream in the water column. Drifting is behavioural for some taxa, in the sense that they can alter their probability of entering the water column and how far they travel whilst drifting (Wiley & Kohler 1984; Kohler 1985). Most taxa which drift, do so more frequently at night than during the day (Waters 1972; Müller 1974). It has been hypothesized that nocturnal drift evolved in response to predation by fish which feed in the water column (Anderson 1966; Allan 1978). These predators detect prey visually and so should feed more effectively during the day. Behaviours which result in drifting during the day, should increase the risk of predation from water-column predators, and thus be selected against.

Evidence supporting the predator avoidance hypothesis includes observations of aperiodic drifting in streams lacking fish, and nocturnal drifting in nearby streams where water column predators are present (Malmqvist 1988; Flecker 1992). The increasingly nocturnal pattern of drift shown by insects as they grow larger (Allan 1978; 1984; Skinner 1985) is taken as further evidence for the predator risk hypothesis because fish select larger prey (e.g. Ringler 1979; Newman & Waters

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1984), so the risk to insects should increase as they grow larger, and they should become more nocturnal.

Behaviours which evolved because they result in predator avoidance may become genetically fixed, where the prey no longer respond to present-day variation in predator density, or they may be phenotypically plastic (= reactive, sensu Stein 1979), in which case prey behaviour is varied according to the current risk. Some diel behavioural shifts in other systems can be the result of either fixed or reactive responses to predators (Gliwicz 1986a; Neill 1992). Early work on stream drift implicated light cues as regulators of nocturnal periodicity (Waters 1972; Müller 1974), suggesting that stream insects would not respond to present-day variation in the density of water-column predators (Allan 1978). However, more recently, various stream insects have been shown to alter their drift behaviour in response to the presence of other types of predators, both predatory invertebrates (Corkum & Pointing 1979; Peckarsky 1980; Walton 1980) and benthic-feeding fish (Kohler & McPeek 1989; Culp et al. 1991), suggesting a potential for reactive responses to water-column predators. Two direct tests for such responses produced different results. Flecker (1992) detected changes in neither nighttime, nor daytime, drift of the mayfly *Baetis* following removal of water-column predators (Flecker 1992). In contrast, Williams and Moore (1985) found that chemical extracts from fish reduced nighttime activity of the amphipod *Gammarus*, but they did not test for daytime responses.

The above discussion highlights a need for further tests for reactive responses of stream insects to water column predators. The aim of this study was to test the hypothesis that stream invertebrates adjust their drift behaviour according to the level of risk from water column predators. I tested this hypothesis by manipulating the density of water column predators (= risk) in a field experiment and measuring drift behaviour of five prey taxa.
More vulnerable prey are hypothesized to show more pronounced avoidance responses to predators (Stein 1979). Where the risk from predators varies among sizes of prey, avoidance responses to predators are often more pronounced in more vulnerable size classes of prey (e.g. Bertness et al. 1981; Sih 1982; Harvey 1991). Larger stream insects are at greater risk from water-column predators, so any reactive responses water column predators should be more strongly expressed in larger size classes of prey taxa. I tested this prediction by examining whether drift responses to water-column predators varied among prey of different sizes.

Methods

Study site and study organisms

The experiment was done during July and August 1990 in Stoney Brook, New Hampshire, U.S.A. (43°23’N, 72°01’W). Stoney Brook is a second order stream, elevation 300 m, with a gravel/rock substratum and a mean summer discharge of 3.74 m³/min. Brook trout (Salvelinus fontinalis Mitchell) are the only common predatory fish present (mean density = 1.2/m² (± 0.1 SE)). Brook trout feed predominantly on prey drifting in mid-water (McNicol et al. 1985, Grant & Noakes 1986; Chapter 4). The only other fish present were black nosed dace Rhinichthys atratulus Hermann, which are benthic-feeding insectivores (Johnson & Johnson 1982). Dace were rare at the study site (mean density = 0.009/m² (± 0.001 SE)) and were removed prior to the experiment. The prey were five genera of mayflies (Order: Ephemeroptera): Baetis, Paraleptophlebia, Ephemereilla, Eurylophella, and Stenonema. These five mayflies made up 29.2% by number of the benthic community in the study area and were all consumed by the brook trout.

Experimental design

The experiment was done in nine, 35 m long sections of stream, enclosed at the ends with 7mm mesh fences. Fences extended 0.1 m into the sediment and more than 0.5 m above the water’s surface; they were impermeable to trout, but did not
restrict movement of mayflies (Appendix, Fig. 13). Fenced sections were separated from one another by 17-20 m long unmanipulated areas. Trout densities in the sections were adjusted to one of three levels: (1) zero density, (2) natural density (1.1-1.3/m²), (3) high density (2.2-2.5/m²). The natural and high density treatments correspond to the mean and maximum densities of trout observed during four electrofishing surveys of the study area (during June and August of 1989 and 1990).

Three sections of stream were assigned to each treatment. Assignment of treatments to sections was done to reduce potential biases caused by the fact that mayflies drifting out of one section might enter the section(s) downstream. The assignment of treatments to stream sections, from upstream to downstream was as follows: high, high, zero, zero, natural, zero, high, natural, natural. Under this arrangement, the three sections immediately above the three zero density sections were: a high density, a medium density and a zero density section. The same was true for the other two treatments, assuming that the unmanipulated area above the section furthest upstream was equivalent to a natural density manipulated section. This should avoid any consistent bias which might have occurred if, for example, all of the zero density sections were immediately downstream of high density sections.

Trout were redistributed among the sections by electrofishing (using a Smith-Root Model 12 backpack electrofisher). Trout were removed from zero density sections by making four passes with the electrofisher, and captured trout were held in pens downstream. Two passes were made through the other sections estimate trout densities, and to control for possible electrofishing effects on prey taxa. Trout numbers in high and natural density sections were then adjusted to the appropriate levels by adding trout from the holding pens, or removing trout, as necessary.

Drift rates

Drift rates were measured as the rate of departure of mayflies from defined areas of substratum. The areas of were 0.5 m² (width at downstream end = 0.3 m,
width at upstream end = 0.2 m, length = 2 m) patches of gravel substratum over which flow was even and straight. Mayflies drifting from the 0.5 m$^2$ patch were captured in a drift net (mouth = 0.3 * 0.3 m square, net length = 1 m, mesh size 0.3 mm) placed across its downstream end. Flow rates at the mouth of the net before sampling commenced range from 21-29 cm/s. Pilot studies indicated that the net effectively sampled drifting objects originating within the 0.5 m$^2$ patch (Appendix, Fig. 14). To prevent capture in the net of mayflies from upstream, a small fence (width = 1 m, mesh size = 1 mm) was placed across the upstream end of the patch. These fences blocked drift of most (> 90%) mayflies (Appendix, Fig. 13), but did not substantially reduce flow (mean flow reduction 10 cm below the fence at the end of drift sampling = 11%).

I waited for one hour after setting up the net and fence before starting drift sampling, to reduce effects of disturbance on drift rates. Mayflies drifting from the patch were collected for 2 hours, then a benthic sample (0.09 m$^2$) was taken immediately upstream of the drift net. The proportion of mayflies in the 0.5 m$^2$ area that drifted during 2 hours ($2HDR$) was calculated as:

$$2HDR = \frac{N_{net}}{100N_s + N_{net}} \times 18$$

where $N_{net}$ is the number of mayflies caught in the drift net and $N_s$ is the number in the benthic sample.

Drift was measured on 24 and 28 August. On each date, measurements were made in two randomly selected stream sections from each treatment. I made two daytime (1100-1400 hr) and two nighttime (1930-2130 hr) measurements in each section on each date. Each measurement was made at a different, randomly selected location within the stream section. Daytime and nighttime drift rates were analyzed separately. Effects of trout density, sampling date, and stream sections on
drift rates were tested with three factor analyses of variance where fish density (a fixed factor) and sampling dates (a random factor) were orthogonal. Stream sections (a random factor) were nested within the fish by date interaction (Underwood (1981) describes this model in more detail).

I used hierarchical pooling procedures to remove the nested term and the fish by date interaction from the model in order to generate more powerful tests for effects of fish density (Underwood 1981). Terms were removed only if $P$ was $> 0.25$ (Winer et al. 1991) and if they explained less than three percent of the total variation in the data (calculated following Vaughan & Corballis 1969; Dodd & Schulz 1973). Where significant responses to fish density were detected, I estimated the magnitude of the response as the proportion of variation in drift rate that was explained by fish density (Vaughan & Corballis 1969). Where responses to fish were not detected, I calculated the power of the tests to detect responses of the magnitude shown by other mayflies (following Cohen 1977).

**Size-related patterns of drift**

I measured the head widths (maximum distance across the eyes) of preserved mayflies using a computerized measuring system. Microscope images of mayflies were filmed and displayed on a computer monitor and their head widths measured from the screen using a digitizing pad interfaced with image analysis software (Sigma Scan, Jandel Inc.). I only measured insects sampled during nighttime on 24 August. For each mayfly taxa, I randomly picked one pair of samples, consisting of mayflies that drifted from the patch (= drifting), versus those remaining in the sediment (= benthic), from each of the stream sections sampled on that date. I usually measured all of the mayflies in the chosen samples, excepting some large benthic samples, from which I measured 10 randomly selected individuals. In a few cases, I also measured mayflies a second pair of samples (drifting and benthic) to equalize sample sizes among treatments.
Measurements on individual mayflies were used as replicates in statistical analyses. I pooled all of the measurements of drifting and benthic individuals from each fish density treatment, assuming that the randomized subsampling procedures I used generated representative samples. Differences in sizes of benthic and drifting mayflies under different fish densities were tested using two factor model I analyses of variance.

Results

Drift rates

Overall, *Baetis* and *Paraleptophlebia* drifted most frequently, followed by *Ephemerella*, whereas *Eurylophella* and *Stenonema* drifted relatively rarely (Fig. 3). Most drift occurred at night (Fig. 3).

*Baetis*, *Paraleptophlebia* and *Ephemerella* showed significantly altered nighttime drift rates in response to change in trout density (Table 2, Fig. 3). Drift rates of both *Baetis* and *Paraleptophlebia* increased as the density of trout increased (Fig. 3). The magnitude of this response was greater for *Baetis* than for *Paraleptophlebia*, explaining 35 and 22 per cent of the total variation in drift rate respectively. *Ephemerella* drifted at a lower rate in the presence of trout (Fig. 3, Table 2). This response was of a similar magnitude to that shown by *Paraleptophlebia*, also explaining 22 percent of the variation in drift rate.

I detected no effects of trout density on drift rates of *Eurylophella* and *Stenonema* (Table 2, Fig. 3). If these two taxa had shown a response of the magnitude observed for *Baetis* then I would very likely have detected it (power = 0.86). If they had shown a weaker response, of the size observed for *Paraleptophlebia* and *Ephemerella*, then my chance of detecting it was slightly less (power = 0.58). Overall, however, I conclude that trout density did not influence drift rates of *Eurylophella* and *Stenonema*. 

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Very few mayflies, of any taxa, drifted during the daytime and no changes in drift rate in response to fish density were detected (Table 2, Fig. 3). The tests had the same statistical power as those for nighttime drift, so if mayflies had changed their behaviour as much in the daytime as they did at night, I had a reasonable chance of detecting it.

**Size related patterns of drift**

Size-related variation in drift rates that was caused by trout would be indicated by a difference in size between drifting and benthic mayflies that was conditional on the density of trout (i.e. a significant interaction in the ANOVA; Table 3).

*Paraleptophlebia* varied in size according to trout density (Table 3). A multiple comparison test indicated that *Paraleptophlebia* were larger on average in areas lacking trout, than in areas where fish were present at either natural or high density (Tukey's HSD, $P < 0.01$; Fig. 4). However, I found no significant differences in size between drifting individuals and individuals that remained in the sediment (Table 3). *Ephemera* tended to decrease in size as the density of trout declined, but again mayflies that drifted did not differ in size from those in the sediment (Table 3; Fig. 4). Overall size distributions of *Paraleptophlebia* and *Ephemera* were, therefore, affected by trout, but this was not due to size-related variation in the tendency to drift.

Drifting *Baetis* tended to be larger than those remaining in the benthos, at all levels of fish density (Table 3, Fig. 4). Individuals of *Stenonema* covered a far greater range of size than the other taxa (Fig. 4), and there was a weak overall tendency for *Stenonema* that drifted to be smaller than those remaining behind. As for *Baetis*, however, size distributions of *Stenonema* were not significantly affected by trout density (Table 3, Fig. 4). *Baetis* and *Stenonema*, thus, both showed size-related variation in drift behaviour that was not influenced by trout density.
Sizes of *Eurylophella* that drifted were not different from those remaining in the sediment (Table 3, Fig. 4), nor was there any variation in size among areas containing different densities of trout.
Table 2. Summary of results of ANOVA testing effects of trout density on daytime and nighttime rates of drift from small (0.5 m²) patches of substratum by five mayflies.

<table>
<thead>
<tr>
<th>Prey taxa</th>
<th>Nighttime F</th>
<th>Nighttime P</th>
<th>Daytime F</th>
<th>Daytime P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baetis</td>
<td>6.93</td>
<td>0.005</td>
<td>0.79</td>
<td>0.469</td>
</tr>
<tr>
<td>Paraleptophlebia</td>
<td>3.66</td>
<td>0.044</td>
<td>0.17</td>
<td>0.891</td>
</tr>
<tr>
<td>Ephemera</td>
<td>3.48</td>
<td>0.050</td>
<td>0.19</td>
<td>0.830</td>
</tr>
<tr>
<td>Eurylophella</td>
<td>1.54</td>
<td>0.238</td>
<td>0.71</td>
<td>0.584</td>
</tr>
<tr>
<td>Stenonema</td>
<td>0.08</td>
<td>0.925</td>
<td>1.00</td>
<td>0.386</td>
</tr>
</tbody>
</table>

Tests were done using pooled ANOVA models with terms for fish density, and sampling date, df for all tests were 2 and 20, sampling date was always non-significant (P > 0.05); b the complete ANOVA model was used for this test, df = 2 and 2; c variances unequal.
Table 3. Results of ANOVA comparing the sizes of mayflies that drifted from patches of substratum to those remaining in the sediment (Type) at different fish densities (Fish).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>P</th>
<th>df</th>
<th>P</th>
<th>df</th>
<th>P</th>
<th>df</th>
<th>P</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type (T)</td>
<td>1</td>
<td>0.0004</td>
<td>1</td>
<td>0.559</td>
<td>1</td>
<td>0.568</td>
<td>1</td>
<td>0.643</td>
<td>1</td>
<td>0.049</td>
</tr>
<tr>
<td>Fish (F)</td>
<td>2</td>
<td>0.111</td>
<td>2</td>
<td>0.007</td>
<td>2</td>
<td>0.013</td>
<td>2</td>
<td>0.557</td>
<td>2</td>
<td>0.543</td>
</tr>
<tr>
<td>T * F</td>
<td>2</td>
<td>0.349</td>
<td>2</td>
<td>0.180</td>
<td>2</td>
<td>0.096</td>
<td>2</td>
<td>0.136</td>
<td>2</td>
<td>0.072</td>
</tr>
<tr>
<td>Error</td>
<td>103</td>
<td>185</td>
<td>75</td>
<td>200</td>
<td>52</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a variances unequal; b analysis on log_{10}(x + 1) transformed data.
Fig. 3. Nighttime and daytime rates of drift from small patches of substratum by five mayfly taxa exposed to different densities of trout.
Fig. 4. Size-related patterns of drift for five mayfly taxa exposed to different densities of trout. Drifting mayflies are those departing from small patches of substratum at night, benthic ones are those remaining in the sediment. Other symbols on plot are as for Fig. 3. Mean sample size per point = 24.
Discussion

Under the hypothesis that nocturnal drift functions to avoid diurnal predators that feed in the water column (Allan 1978), the most likely reactive response following removal of these predators is an increase in daytime drifting. This is because daytime feeding by water-column predators should select against drifting during daylight hours (it does not select for drifting at night). Daytime drift by all five mayflies I studied was low, and did not change significantly following manipulation of trout density. Flecker (1992) also found no changes in daytime drift density of mayflies following exclusion of water column predators from areas of a stream in Venezuela. Williams (1990) detected no effects of trout removal on drift densities of mayflies and most other taxa, but did detect reduced daytime drift of amphipods, chironomids and dipterans in the absence of trout. Unfortunately, the treatment was not replicated in Williams' experiment, so these changes cannot be reliably attributed to trout removal. The lack of daytime drift responses to water column predators in my study, and Flecker's (1992) study, are therefore consistent with the hypothesis that low daytime drift is a fixed avoidance response to water-column predators.

Nighttime drift rates of three of the mayflies I tested, *Baetis*, *Paraleptophlebia* and *Ephemera*, differed among areas of varying trout density. There are several potential mechanisms for these effects of trout on drift rates. Firstly, they might reflect effects of trout on the rate at which mayflies entered the water column, or effects on the average distance drifted by mayflies. Trout can also affect drift rates by consuming drifting mayflies. Field studies testing effects of fish on drift have often not effectively isolated which of these mechanisms cause differences (or no differences) in drift net catches between areas with and without fish (Allan 1982, Andersson et al. 1986, Williams 1990, Flecker 1992, Chapter 1). This difficulty is
shared by the present study, but I can make some inferences about likely mechanisms for changes in drift rates caused by trout.

The length of the patches from which drift was measured (2 m) was chosen to be as short as possible, and still provide enough area to generate reasonable sized drift samples. If few mayflies entering the water column from the patch reentered the substratum before reaching the net, then the drift rate from the patch is a measure the rate of entry into the water column. Published estimates of drift distances for mayflies range from tens of centimetres to tens of metres and vary depending on factors such as flow rate, body size and species (Brittain & Eikeland 1988). Most estimates at the range of flow rates over the patches (21-29 cm/s) are in the order of 1-4 m (Elliott 1971, Larkin & McKone 1985, Otto & Sjöström 1986, Allan & Feifarek, 1989). This suggests that changes in drift rate from the patches were more likely the result of changes in entry into the water column than changes in drift distance.

Mean nighttime drift rates of Baetis, Paraleptophlebia and Ephemera from the 0.5 m² patches were always greater than 5% of the benthic population per 2 hours (Fig. 3). Trout consume less than 0.15% of the benthic population of each mayfly in each 35 m section per 2 hours (unpublished data). Whilst I did not directly measure the extent of depletion of drifting mayflies by trout predation, the low predation rate suggests that it is extremely unlikely that direct predation had a measurable impact on the nighttime drift rates of these three mayflies.

The above reasoning suggests that Baetis, Paraleptophlebia, and Ephemera showed reactive responses to the density of water-column predators at night, by altering their rates of entry into the water column. Two other experiments manipulating the density of water column predators detected no changes in nighttime drift of mayflies (Williams 1990, Flecker 1992), whereas Williams and Moore (1985) demonstrated reduced nighttime drift of a crustacean amphipod,

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**Gammarus**, in response to extracts from several fishes, including water-column feeders.

The changes in nighttime rates of water column entry I observed were measured in the field using a natural prey community. I will assume that the changes in mayfly behaviour are direct responses to trout, though, because all prey taxa were tested together it is also conceivable that they are the result of other interactions mediated by the presence of trout (e.g. Holt 1977; Schmitt 1987; McNeely et al. 1990). Circumstantial evidence for direct responses comes from observation of similar responses by these mayflies to other types of predator. *Baetis* and *Paraleptophlebia*, which showed increased drift rates in the presence of trout, have been observed to enter the water column upon encountering predatory stoneflies (Corkum & Pointing 1979; Peckarsky 1980, for *Baetis*) and benthic fishes (Kohler and McPeek 1989, for *Baetis*; Culp et al. 1991, for *Paraleptophlebia*). *Ephemera*, drifted at reduced rates in the presence of trout, responds to some stoneflies by reducing its activity (Peckarsky 1980).

Changes in nighttime drift behaviour following manipulation of trout density indicate that mayflies can detect variation in trout density in the dark over tens of metres (the scale of the manipulation). *Baetis* and *Paraleptophlebia* were sensitive to the actual number of trout in the vicinity, whereas *Ephemera* responded only to the present and absence of trout. The cue(s) they use to detect trout remains unclear however, since mayflies respond to other types of predator using a range of cues, including pressure waves (Peckarsky & Wilcox 1989; Culp et al. 1991), visual cues (Malmqvist 1988), long range chemicals (Peckarsky, 1980) and chemotactile cues (Peckarsky 1980; Peckarsky & Penton 1989).

Predator avoidance behaviours are often size-specific when the risk of predation varies among prey size classes (Bertness et al. 1981; Sih 1982; Harvey 1991). None of the changes in drift rates of mayflies at different trout densities were
size-specific. There was also no tendency for mayfly taxa that were larger to be the ones which responded to trout. This was perhaps not surprising, since the mayfly responses to trout all occurred at night. Selection by trout for larger prey is strong during the day, but is weak or non-existent at night (Allan 1978; Chapter 4) and so nighttime responses would not be expected to be size-specific.

The adaptive significance, if any, of the nighttime responses to trout is unclear. Stomach content analyses indicate that, while salmonids feed mostly by day, a low level of nighttime feeding does occur (Allan 1981; Walsh et al. 1988; Sagar & Glova 1988; for an exception see Elliott 1973). Trout, then, do present some risk to their prey at night. The nature of this risk is uncertain, because, while trout are capable of feeding on drifting prey at night (Jenkins 1969), whether they feed only in the water column or switch to some degree of benthic foraging is not known. Reduced drift by *Ephemerella* in the presence of trout may reduce their risk of being preyed upon while in the water column at night. Increased nighttime drift of *Baetis* and *Paraleptophlebia* at higher trout densities implies that the benefits of this behaviour outweigh the immediate risk of being consumed by trout while drifting. Entry into the water column might be an effective response to encounters with trout if a high proportion of nighttime feeding was on benthos. If most nighttime feeding by trout is in the water column, then this behaviour would seem to be maladaptive. Direct observation of interactions between trout and mayflies at night would be a useful first step toward clarifying these issues.

Another form of nighttime drift response shown by several stream insects is a reduction of nocturnal drift activity during full moon periods (Anderson 1966, Hynes 1975). Some vertically migrating zooplankton and marine infauna show a similar response, reducing the extent of their upward migration into areas containing fish during full moon (Alldredge & King 1980; Gliwicz 1986b). Both responses are hypothesized to occur because bright moonlight during full moon allows visual
predators to feed more effectively at night, but it is not known whether reduced drift
during full moon is due to increased predation rates by fish or due to reduced drift
behaviour.

Whilst water column predators may present most risk to drifting insects during
the day, my results suggest that they also influence the nighttime behaviour of some
taxa. These influences are not well understood and there is a need for further
studies of nighttime interactions between predatory fish and stream insects.
CHAPTER 3

INFLUENCES OF PREDATORY FISH AND DRIFT DISPERSAL ON INSECT PREY POPULATIONS IN STREAMS

Summary

I tested effects of field manipulation of the density of predatory fish (brook trout, *Salvelinus fontinalis*) on the local density and size distribution of five insect prey taxa (mayflies: Ephemeroptera) in a temperate stream. Stream researchers have recently suggested that frequent prey dispersal, by drifting downstream in the water column, can overwhelm effects of predation on local prey populations. This hypothesis predicts that effects of trout should be greater on mayflies that disperse less frequently.

Trout densities in fenced 35 m sections of the stream were adjusted to zero, average natural, or twice natural levels. Benthic densities of the two mayflies drifting most frequently, *Baetis* and *Paraleptophlebia*, were significantly reduced in the presence of trout. Effects on trout on prey densities could have been caused by direct predation, or by increases in emigration from areas containing trout. Trout caused increased drift of *Baetis*, and probably also of *Paraleptophlebia*, though the effect on *Paraleptophlebia* was difficult to corroborate statistically. Effects of trout on the density of *Baetis* were primarily the result of increased drift dispersal out of areas containing trout, whereas both direct predation and increased drift dispersal contributed to the reduction in density of *Paraleptophlebia* by trout. Trout did not influence the densities of the three remaining mayflies, *Ephemerella*, *Eurylophella* and *Stenonema*, nor did trout influence the rate at which these mayflies drifted out of the enclosures. Trout had significant effects on the size distributions of
Paraleptophlebia and Ephemera, most likely by inducing size-specific changes in drift behaviour.

The hypothesis that frequent prey dispersal swamps the effects of predators assumes that predators influence prey density primarily by consuming prey. In this system trout also influenced prey densities by causing changes in prey dispersal rates, and these influences were on the mayflies that drifted most frequently. For this reason, the mayflies drifting less frequently were not, as predicted, the ones most strongly affected by trout.

Introduction

Predators have important effects on the density and size structure of prey populations in many aquatic systems (Brooks and Dodson 1965, Zaret 1980, Sih et al. 1985, Kerfoot and Sih 1987). There is, however, still little agreement concerning the effects of predators on prey communities in streams (Cooper et al. 1990). This is, in part, because experimental manipulations of predator density in streams have produced varying results. For example, predator manipulation led to effects on the density of some, or all, prey species in some studies (Flecker 1984, Walde and Davies 1984, Peckarsky 1985, Feltmate and Williams 1989, Gilliam et al. 1989, Koetsier 1989, Schlosser and Ebel 1989) but had no effects on prey in other studies (Allan 1982, Flecker and Allan 1984, Culp 1986, Reice and Edwards 1986, Lancaster et al. 1991). There is similar variation in the influence of predators on prey size distributions (Peckarsky 1985, Schlosser and Ebel 1989, Cooper et al. 1990, Gilliam et al. 1989, Lancaster 1990). A greater understanding of the role of predation in organizing prey communities in streams may come through attempting to determine why effects are found in some situations, but not others.

Benthic stream insects are often distributed patchily in space at small spatial scales (tens of metres and less) (Malmqvist and Sjöström 1984, Bowlby and Roff 1986, Resh and Rosenberg 1989, Schlosser and Ebel 1989). Some taxa redistribute
themselves primarily by departing the sediment to drift short distances downstream in the water column (Townsend and Hildrew 1976, Williams and Hynes 1976, Bird and Hynes 1981, Bergey and Ward 1989). Local densities of these taxa will thus be influenced by drift dispersal into the patch from upstream and drift out of the patch to downstream areas. Several workers have suggested that variation in prey dispersal is an important reason why effects of predators on local prey density were detected in some stream studies, but not others (Allan 1982, Flecker 1984, Culp 1986, Gilliam et al. 1989). Recent evidence which supports this hypothesis includes a negative correlation between the extent of prey reduction by predators and the rate of prey dispersal. This correlation holds for experiments done in cages of varying mesh size (where finer mesh size is assumed to be a greater barrier to dispersal) and for experiments done on prey with varying mobility (Cooper et al. 1990). Further support for the hypothesis is provided by findings of increased impact of predators where prey dispersal was experimentally reduced by reducing the mesh size of cages (Cooper et al. 1991, Lancaster et al. 1991).

Size-selective predators may alter the size composition of prey populations (references in McQueen et al. 1989). Reasons for variation in effects of predators on size distributions of prey in streams are not well explored. In principle, however, variation in prey dispersal could mediate predator effects on the size-distributions and density of prey in similar ways. Size distributions of prey might, therefore, be altered less as prey dispersal decreases.

I present the results of a field experiment designed to test a prediction of the hypothesis that predators will have greater effects on prey populations when prey dispersal is lower. I manipulated the density of predatory fish in a New England stream and measured their effects on the local density and size distributions of five closely related prey taxa, which varied in their frequency of drift dispersal. The
hypothesis predicts that the predators will have stronger effects on prey taxa that disperse less frequently.

Drifting is behavioural for some stream invertebrates (Kohler 1985) and several taxa alter their rate of entering the drift according to the density of predators (Peckarsky 1980, Walton 1980, Kohler and McPeek 1989, Peckarsky and Penton 1989, Culp et al. 1991). Predators might, therefore, alter prey density by inducing changes in dispersal behaviour as well as by consuming prey. Likewise, patterns of drift behaviour resulting in the avoidance of predators are often expressed more strongly in more vulnerable size classes of prey (Allan 1978, 1984), so effects of predators on the size distributions of prey might be caused by direct size-selective predation, or by size-specific drift responses to predators. I measured both direct predation rates and changes in prey dispersal caused by predators in order to separate their relative contributions to overall effects on prey densities and size distributions.

Methods

Study site, predators and prey

The experiment was conducted during July and August 1990 in Stoney Brook, a second order stream in New Hampshire, U. S. A. (43°23'N, 72°01'W, elevation 300 m). The study area was 0.6 km long, and was comprised mostly of flowing riffle and run habitat with few pools (mean stream width = 2.8 m, mean summer discharge = 3.74 m³/min). Riparian vegetation consisted of hemlock and mixed hardwood trees.

The stream supports a population of brook trout (Salvelinus fontinalis Mitchell) from April to early November. The only other fish present are a few black nosed dace (Rhinichthys atratulus Hermann) (mean density = 0.009/m² (± 0.001 SE)). The brook trout were used as predators in the experiment, dace were removed from the experimental area by electrofishing when the experiment was set up, and were not included in the manipulation of fish density.
Brook trout are usually sit-and-wait predators, feeding mostly in the water column on drifting prey (Keensleyside 1962, McNicol et al. 1985, Grant and Noakes 1986, Chapter 4). They select larger prey (Allan 1981, Grant and Noakes 1986) and often also select prey by taxa (Allan 1981, Johnson and Johnson 1982, Hubert and Rhodes 1989). Details of prey selection by trout in the study stream are presented in Chapter 4. The prey for the experiment were five mayfly taxa (Order Ephemeroptera), which were common prey of the trout and made up 29% by number of the invertebrate community in the study area (unpublished data).

Experimental design

Trout density was manipulated in 35 m long sections of stream, enclosed at the ends with fences. Trout densities within the sections were adjusted to three levels: (1) zero (no trout), (2) natural density (1.1-1.3/m²), and (3) high density (2.2-2.5/m²). The natural and high density treatments correspond to the mean and maximum densities of trout observed during electrofishing surveys of the study area during June and August of 1989 and 1990.

Three sections of stream were assigned to each treatment. Contiguous sections of stream are non-independent because prey dispersing out of one section would enter sections downstream. In an attempt to reduced this problem, experimental sections were separated by unmanipulated, 17-20 m long, buffer zones. If sections influenced one another by drift dispersal or transmission of chemical cues from trout, the strongest influence on a section was probably from the section immediately upstream. The longitudinal arrangement of treatments was designed to equalize any such influences among treatments. The arrangement of treatments, from upstream to downstream, was: high, high, zero, zero, natural, zero, high, natural, natural. Under this arrangement the three sections immediately above the three zero density sections were: a high density, a medium density and a zero density section. The same was true for the other two treatments (assuming that the
unmanipulated area above the high density section furthest upstream was equivalent to a natural density section. This arrangement should reduce any consistent bias which might have occurred if, for example, all of the zero density sections were downstream of high density sections.

**Experimental enclosures**

Experimental sections were enclosed with fences across the stream made of hardware cloth (mesh size = 7 mm). The fences extended at least 0.1 m into sediment and 0.5 m above the water's surface. Mesh of this size prevents movement by trout, but pilot studies indicated that it is not a barrier to drift dispersal (Appendix, Fig. 13). Trout densities were adjusted by electrofishing (using a Smith-Root model 12 backpack electrofisher). Trout were removed from zero density sections by making four passes with the electrofisher. No trout were captured on the fourth pass. Captured trout were held in pens downstream. Two passes were made through the other sections to estimate trout densities (> 85% of trout present are captured in the first two passes, unpublished data) and to control for possible electrofishing effects on prey taxa. Trout numbers in high and natural density sections were then adjusted to the appropriate levels by adding trout from the holding pens, or by electrofishing to remove trout, as necessary. The fences were constructed on 13-14 August, and the electrofishing was done from 16-18 August.

**Benthic densities of prey**

Benthic densities of prey were sampled on 27 and 29 August. On each date I took five randomly located Surber samples (0.09 m^2) in each stream section. Samples were preserved in 70 percent alcohol, and mayflies were later sorted and enumerated in the lab. Individual Surber samples were used as replicates in statistical analyses.
Rates of prey drift dispersal into and out of stream sections

I estimated the numbers of mayflies drifting into and out of the stream sections using drift nets with square mouths (0.09 m$^2$), 1 m long with 0.3 mm mesh. Nets sampling drift into and out of a section were placed immediately (10-20 cm) below the fence at the upstream and downstream end of the section respectively. A single net was placed at each sample location and, since the net did not sample the entire stream flow, the total number of organisms drifting in or out of the section per day (24 hour drift rate) was estimated as,

$$24 \text{ hour drift rate} = \frac{24 \text{ hour count} \times \text{stream discharge}}{\text{discharge through the net}}$$

where the 24 hour count is the number of mayflies collected in the net in 24 hours.

The 24 hour drift rate out of the sections was measured on three dates. On 21 August, nets were in place continuously for 24 hours and emptied every 3.5 hours. Four 3.5 hour samples were lost, and mean counts for the section and time of day (night or day) were inserted when calculating 24 hour counts. On 29 August, nets were in place for six, 1.5-2 hour periods spaced evenly over 24 hours. I interpolated between the six sample counts to estimate the 24 hour count for each section. On 24 August, nets were in place for a single 2-3.5 hour nighttime sample between 2300 and 0230 hr. Twenty four hour counts were estimated from the 2 hour counts using previously constructed regression equations (Appendix, Table 10) (following Allan and Russek 1985).

On 22 August, I estimated the 24 hour drift rate into each section. Nets were in place for three, 3 hour periods over 24 hours. Twenty four hour counts for each section were estimated by interpolating between the three sample counts. Twenty four hour drift rates for stream sections were used as replicates in statistical analyses.
Rates of prey drift dispersal from small patches within stream sections

I also measured drift rates from small patches of substratum within the 35 m stream sections. Drift rates were measured from 0.5 m² areas of gravel/cobble substratum with uniform flow. The areas were 0.3 m wide at the downstream end, 2 m long, tapering to be 0.2 m wide at the upstream end. Mayflies drifting from the 0.5 m² patch were captured in a drift net placed at the downstream end of the area. Pilot studies indicated that the net effectively sampled drifting objects originating within this area (Appendix, Fig. 14). A small fence (mesh size = 1 mm, width = 1 m), flush with the substratum and reaching above water surface, was placed across the upstream end of the area to ensure that mayflies from upstream did not enter the net. Collections were made for 2 hours, starting one hour after the net and fence were set up. The fences did not clog during this period, but reduced water flow slightly (mean reduction after 2 hr = 11% [± 1.3% SE], n = 6). Immediately after the drift collection, a benthic sample, comprising 18 per cent of the 0.5 m² area was taken just upstream of the drift net. The percentage of benthic individuals that drifted in two hours (2HDR) was then estimated as:

\[
2\text{HDR} = \frac{N_{\text{net}}}{100.N_s + N_{\text{net}}} \times \frac{18}{18}
\]

where \( N_{\text{net}} \) is the number of mayflies caught in the drift net and \( N_s \) is the number in the benthic sample.

Drift from small patches was measured in two randomly selected stream sections from each treatment, on both 24 and 28 August. I made two daytime (1100-1400 hr) and two nighttime (1930-2130 hr) measurements in each section on each date. Each measurement was made at a different location within the stream section.

Drift rates in Stoney Brook are usually low during the day, and higher at night, there are no distinct dusk or dawn increases (unpublished data). I therefore
multiplied the 2 hour rates by the duration of daytime (14 hr) or nighttime (10 hr), divided them by two, and then pooled them to give an estimate of the percentage of the benthic population in each section that drifted per 24 hours on each date. These 24 hour rates were used as replicates in statistical analyses.

**Prey consumption by trout**

Prey consumption by trout was estimated in two high density and two natural density sections on 29 August. Six trout were captured in each section every four hours for 24 hours. Trout were captured by electrofishing. Electrofishing was interspersed between the drift sampling also done on this date. Fishing was started at the downstream end of each section, and proceeded upstream. Areas were not revisited once they had been fished. The captured trout were killed, preserved in formalin and prey items in their stomachs later enumerated.

The number of prey consumed per day in each section (C24) was estimated as:

\[ C_{24} = P \times N \times 6 \]

where, \( P \) = the mean number of prey per stomach, \( N \) = the number of trout in the section. Estimates of gastric evacuation rates, and of prey consumption by weight suggest this calculation slightly overestimates the actual number of prey consumed (Chapter 4, unpublished data). The percentage of the benthic population consumed by trout per day in each section was then estimated by dividing the number of mayflies consumed by the total number present (the mean benthic density multiplied by the area of the section).

**Size distributions of prey**

I measured the head widths of preserved mayflies using a computerized measuring system. Microscope images of mayflies were filmed and displayed on a video monitor and their head widths measured from the screen using digitizing software (Sigma Scan, Jandel Inc.). I measured mayflies in two benthic samples and all of the drift samples from each of two sections per treatment on 29 August.
sometimes measured mayflies from extra benthic samples to increase sample sizes, but always measured all of the mayflies from a chosen sample to avoid bias which might occur if I subsampled mayflies from samples. Measurements on individual mayflies were used as replicates in statistical analyses.

Statistical analyses

Effects of trout density on dependent variables were tested using analyses of variance (ANOVA). Data were tested for homoscedasticity prior to analyses, and transformed, if necessary, to equalize variances (Underwood 1981). Where significant effects of trout density were detected, I estimated their magnitude by calculating the strength of association ($\hat{\nu}^2$) between trout density and the dependent variable (following Vaughan and Corballis 1969, and Dodd and Schulz 1973). Association strength values are measures of the proportion of the total variation in the data attributable to a given factor, and can be interpreted similarly to $r^2$ values from regression analyses.

Hierarchical post-hoc pooling procedures were used to remove non-significant interaction and nested terms from ANOVA models to allow more powerful significance tests for treatment effects (Winer et al. 1991). Terms were pooled only if they explained less than three percent of the total variation in the data and if $P$ was $> 0.25$ (following Winer et al. 1991). Association strength was always calculated using the complete ANOVA model (Vaughan and Corballis 1969).

In some cases where I did not detect effects of trout density, I calculated the power of the test, i.e. my ability to detect an effect of trout density if, in fact, one existed (following Cohen 1977). Power calculations of this sort are conditional on $P$ (set at 0.05), the sample size, and the size of the effect to be detected. Cohen (1977) uses a dimensionless index ($f$) as the measure of effect size. The effect size index $f$ is related to the strength of association measure $\hat{\nu}^2$ as:
\[ f = \frac{\hat{\omega}^2}{1-\hat{\omega}^2} \]

(Cohen 1977). Thus the greater the percentage of variation explained by the effect of trout density (\(\hat{\omega}^2\)), the greater the index (f) of effect size. Where I removed terms from ANOVA models, power calculations were made on pooled models because these were the ones used for significance testing.

**Results**

**Benthic densities of prey**

None of the mayflies varied in density between the two sample dates (Table 4). Two of the five mayflies were affected by the presence of trout (Table 4, Fig. 5). Both *Baetis* and *Paraleptophlebia* were reduced in density as trout density increased, but the pattern of differences between means was slightly different (see comparison of means, Fig. 5). *Baetis* were much more strongly affected by trout than *Paraleptophlebia*, the effect of trout explaining six times as much of the variation in benthic density (41\% for *Baetis* and 7\% for *Paraleptophlebia*).

I detected no effects of trout on benthic densities of *Ephemera*, *Eurylophella* or *Stenonema* (Table 4, Fig. 5). If these taxa had been impacted as strongly as *Baetis*, I would almost certainly have detected effects on their density (Cohen's f = 0.83, power > 0.995). I was less likely to detect a smaller effect, of the size found for *Paraleptophlebia* (Cohen's f = 0.27, power = 0.61) but, overall, I conclude that trout did not influence benthic densities of these prey taxa.

**Rates of prey drift dispersal into and out of stream sections**

Twenty four hour rates of drift dispersal into the sections showed no consistent variation between treatments (one way ANOVAs, df 2 and 6, P always > 0.363; Fig. 6). These tests were, however, weak. Their power to detect the largest observed effects on benthic density (f = 0.830) and entry into the water column (f = 0.95) was low (power = 0.39 and 0.49 respectively). While these results suggest there were no
dramatic biases in the supply of drifting immigrants to the experimental sections, I cannot rule out the possibility that smaller differences occurred.

Because benthic densities varied among treatments, I expressed rates of drift dispersal out of sections as per-capita rates. The percentage of the benthic population drifting out of each section per day was calculated by dividing the average 24 hour drift rate by the mean benthic population size (both sample dates pooled). Per-capita drift of *Baetis* increased with increasing trout density (one way ANOVA, df 2 and 6, P = 0.059; Fig. 7), but trout had no significant effects on the per-capita drift rates of any of the other mayflies (one way ANOVAs, df 2 and 6, P always > 0.23; Fig. 7). The nonsignificant results are again inconclusive, however, because the tests were weak (power to detect an effect of the size shown by *Baetis* = 0.39).

Rates of prey drift dispersal from small patches within stream sections

Trout had significant effects on per-capita drift rates from small (0.5 m$^2$) patches of substratum of three of the five mayflies. Drift rates of *Baetis* generally increased with increasing trout density (Fig. 8). The pattern of difference between means differed slightly among sampling dates, however, indicated by a significant interaction term in the ANOVA (Table 5), and by comparison of means (Fig. 8). The interactive effect of trout and sampling date explained 18 percent of the variation in drift rate. *Paraleptophlebia* also drifted at higher rates as the density of trout increased (Table 5, Fig. 8); this response explained 40 percent of the variation in drift rate. Per-capita drift by *Ephemerella* was significantly reduced in the presence of trout (Table 5, Fig. 8) and trout density explained 78 percent of the variation in drift rate at this scale. *Eurylophella* and *Stenonema* drifted less frequently than the other three mayflies (Fig. 8). Neither of the two showed significant responses to trout density (Table 5). For *Eurylophella*, the power of the analysis to detect a response to trout density as large as that shown by *Ephemerella*
was reasonable (Cohen’s $f = 0.95$, power = 0.68). I therefore conclude that
Eurylophella did not alter its drift rate in the presence of trout. I cannot make a
similar conclusion for Stenonema. My chances of demonstrating a response of the
magnitude displayed by Ephemera were slight (Cohen’s $f = 0.95$, power = 0.17).

Prey consumption by trout

Estimates of the numbers of mayflies of each taxon consumed per day ranged
from 31 to 201 per section. Trout at high densities consumed significantly greater
percentages of the benthic population per day than those at natural density only for
Paraleptophlebia and Ephemera (t-tests, $P < 0.05$; Fig. 7).

Size distributions of prey

For Paraleptophlebia and Ephemera, the mean size of benthic individuals
differed from those drifting in the water column. These differences were, however,
conditional on trout density, indicated by significant interactions in the ANOVAs
(Table 6). The size distributions of drifting and benthic Paraleptophlebia were not
significantly different in sections where trout were present (Tukey’s HSD, $P > 0.05$),
but where trout were absent the mean size of drifting Paraleptophlebia was
significantly lower than the mean size of benthic individuals (Tukey’s HSD, $P < 0.05$) (Fig. 9). The mean size of benthic Ephemera was greater in areas of high
tROUT density, than in areas of natural or zero trout density (Tukey’s HSD, $P < 0.05$).
The mean size of drifting individuals, in contrast, did not differ significantly among
tROUT densities (Tukey’s HSD, $P > 0.05$) (Fig. 9).

Mean sizes of drifting Baetis were larger than the mean sizes of benthic
individuals at all levels of trout density (Table 6, Fig. 9). For Stenonema the
opposite was true, benthic individuals always tended to be larger than drifting ones
(Table 6, Fig. 9). Size distributions of benthic and drifting Eurylophella did not
differ significantly, nor were they significantly influenced by trout density (Table 6,
Fig. 9).
Table 4. Summary of ANOVAs testing for effects of trout density and sampling date on benthic densities of five mayfly taxa.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Baetis P</th>
<th>Paraleptophlebia P</th>
<th>Ephemera P</th>
<th>Eurylophella P</th>
<th>Stenonema P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trout</td>
<td>2</td>
<td>&lt;0.005</td>
<td>0.019</td>
<td>0.962</td>
<td>0.151</td>
<td>0.509</td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>0.496</td>
<td>0.819</td>
<td>0.465</td>
<td>0.132</td>
<td>0.953</td>
</tr>
<tr>
<td>Error</td>
<td>86</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes:
- Analysis performed on square root \((x+1)\) transformed data.
- Trout is a fixed effect and date a random effect. Presented are results of tests using pooled ANOVA models after removal of non-significant terms. Initial ANOVA models also contained terms for a date * trout interaction, differences between experimental enclosures (a random effect nested within the effect of trout density), and a date * enclosure interaction (nested within the effect of trout density).
Figure 5. Mean benthic density of five prey taxa at different densities of trout. Horizontal lines under bars indicate means not significantly different at P = 0.05 (Tukey’s HSD test).
Figure 6. Mean 24 hour drift rates of five prey taxa into stream sections containing different densities of trout. Symbols are as for Fig. 5.
Figure 7. Rates of per-capita emigration by drifting and per-capita loss to predation for five prey taxa in experimental stream sections containing different densities of trout. Presented are percentages of benthic prey populations drifting out of sections per day and percentages consumed by trout per day. Symbols are as for Fig. 5.
Table 5. Summary of ANOYAs testing for effects of trout density and sampling date on 24 hour drift rates from small (0.5 m²) patches of substratum by five mayflies.

<table>
<thead>
<tr>
<th>Source</th>
<th>Baetis(^a)</th>
<th>Paraleptophlebia</th>
<th>Ephemera</th>
<th>Eurylophella</th>
<th>Stenonema</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df  P</td>
<td>df  P</td>
<td>df  P</td>
<td>df  P</td>
<td>df  P</td>
</tr>
<tr>
<td>Trout</td>
<td>2  &lt;0.005</td>
<td>2  0.037</td>
<td>2  0.024</td>
<td>2  0.482</td>
<td>2  0.823</td>
</tr>
<tr>
<td>Date</td>
<td>1  0.101</td>
<td>-</td>
<td>-</td>
<td>1  0.031</td>
<td>1  0.677</td>
</tr>
<tr>
<td>Trout * Date</td>
<td>2  0.037</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Error</td>
<td>6  0.037</td>
<td>9</td>
<td>9</td>
<td>8</td>
<td>6</td>
</tr>
</tbody>
</table>

Trout is a fixed effect and Date is a random effect. \(^a\) analysis performed on arcsine transformed data. - indicates terms removed by pooling.
Figure 8. Rates of per-capita drift dispersal from 0.5 m² patches of substratum by five mayfly taxa. For *Baetis*, a and b refer to two different sampling dates. Horizontal lines under bars indicate means not significantly different at P = 0.05 (Tukey's HSD test). Other symbols are as for Fig. 5.
Table 6. Results of factorial model I ANOVA comparing the sizes of mayflies in the benthos to those drifting out of the experimental stream sections (Location) at different trout densities (Trout).

<table>
<thead>
<tr>
<th>Source</th>
<th>Baetis&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Paraleptophlebia</th>
<th>Ephemera&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Eurylophella</th>
<th>Stenonema&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>df</td>
<td>P</td>
<td>df</td>
<td>P</td>
<td>df</td>
<td>P</td>
</tr>
<tr>
<td>Location</td>
<td>1 0.0004</td>
<td>1 0.532</td>
<td>1 0.326</td>
<td>1 0.727</td>
<td>1 0.025</td>
</tr>
<tr>
<td>Trout</td>
<td>2 0.142</td>
<td>2 0.240</td>
<td>2 0.032</td>
<td>2 0.500</td>
<td>2 0.714</td>
</tr>
<tr>
<td>L*T</td>
<td>2 0.481</td>
<td>2 0.006</td>
<td>2 0.004</td>
<td>2 0.174</td>
<td>2 0.246</td>
</tr>
<tr>
<td>Error</td>
<td>223 225</td>
<td>137</td>
<td>288</td>
<td>88</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Variances unequal, not correctable by transformation.
Figure 9. Mean sizes of five prey taxa in experimental stream sections stocked with different densities of trout. Open squares indicate benthic prey and filled circles indicate prey drifting out of the sections. Mean sample size per point = 33.0. Other symbols are as for Fig. 5. Standard error bars are shown, but often do not extend beyond the points.
Discussion

Variation in the effect of predators on prey populations: correlation with prey dispersal frequency

Several workers have recently presented models predicting changes in the effect of predators on prey density as prey dispersal into and out of the population varies (Cooper et al. 1990, Hall et al. 1990, Lancaster et al. 1991). The models assume that predators do not influence prey dispersal, and that predators deplete prey populations within patches only by consuming prey. The models all predict that the impact of predators decreases as migration increases, because the ratio of predator-induced mortality to migration among patches decreases.

The models predict that the effect of trout on the five mayflies in this experiment should depend on their dispersal rates, and the rate at which they were preyed upon by trout. For mayflies, much dispersal occurs by drifting (Townsend and Hildrew 1976, Williams and Hynes 1976, Bird and Hynes 1981, Bergey and Ward 1989). I therefore, used drift rates as measures of prey dispersal to predict relative effects of trout on the five mayflies. I acknowledge, however, that dispersal may occur by other means (by crawling or by swimming upstream). Drift rates of the mayflies (drift rate relative to benthic density) were measured before the experiment in unmanipulated areas of stream (Appendix, Fig. 15). The rate of predation on each mayfly was estimated by combining the average predation rates at high and natural density to calculate an overall average rate of predation on each mayfly (Appendix, Fig. 15). This gives an estimate of the rate of loss from the population due to predation (comparing all sections where predators were present to sections where they were absent). The predicted order of effect of trout was estimated as the drift dispersal rate relative to the predation rate and was (from greatest to least effect): Stenonema, Eurylophella, Ephemeraella, Paraleptophlebia, Baetis (Appendix, Fig. 15).
My results do not conform to the predicted pattern of predator impact. The taxon most strongly affected by trout, *Baetis*, had the highest rate of drift relative to predation. *Paraleptophlebia*, the only other taxa affected by trout, had the second highest rate of drift relative to predation (Fig. 15). Thus, the two taxa whose densities were significantly reduced by trout were those predicted to be least affected by trout predation.

Where predators selectively remove certain size classes of prey, prey size distributions in areas containing predators will tend to diverge from areas where they are absent. The extent of the divergence will depend on the rate of predation and the degree of size selection. There are no formal models of the influence of prey dispersal on this process but, the prey dispersal hypothesis (Cooper et al. 1990; Hall et al. 1990, Lancaster et al. 1991) should also apply to effects of predators on size distributions of prey. The hypothesis predicts that predators should alter size distributions of prey to a lesser extent as prey dispersal increases. Trout in the study area showed significant size-selective predation on only two of the mayflies, *Stenonema* and *Ephemerella* (Chapter 4). This prevents a thorough test of the prediction. However, one of the two mayflies whose benthic size distribution was influenced by trout was *Paraleptophlebia*, a mayfly which trout did not consume size-selectively. A significant effect of trout on the size distribution of this mayfly is therefore not consistent with the prediction.

**Partitioning effects of direct predation and predator-induced drift on prey populations**

Trout are unlikely to be able to influence the number of mayflies drifting into a stream section from upstream, and I detected no differences among treatments in the rate of drift into stream sections. Reduced densities of *Baetis* and *Paraleptophlebia* at higher trout densities may thus have been caused by direct
predation within enclosures, or by an increase in drift dispersal out of enclosures containing trout.

Per-capita drift dispersal out of stream sections tended to increase with increasing trout density for both *Baetis* and *Paraleptophlebia*. The increase was marginally significant for *Baetis*. Drift of *Baetis* from small (0.5 m²) patches within the sections was also increased in the presence of trout, as was drift dispersal out of 35 m stream sections in a pilot experiment at the study site in 1989 (Chapter 1). In combination, these data provide good evidence that drift rates of *Baetis* are increased from areas of higher trout density. The increase in drift out of stream sections with higher trout densities by *Paraleptophlebia* was not statistically significant. The non-significant result for *Paraleptophlebia* reflects an inability to detect an effect because of low statistical power, rather than the absence of an effect. Two lines of evidence suggest there may have been a small increase in emigration due to trout, even though I did not detect it. Firstly, significant increases in drift in the presence of trout were detected when dispersal was measured at a smaller scale (from 0.5 m² patches). Secondly, the presence of trout in 35 m stream sections resulted in increased drift densities of *Paraleptophlebia* during a pilot study at the study site in 1989 (Chapter 1). The similar trend all three cases is suggestive of an effect of trout.

Assuming drift of *Baetis* and *Paraleptophlebia* increased at higher trout densities, how important was it relative to direct predation in reducing the densities of these mayflies? Direct predation removed 0.36% and 0.57% of *Baetis* per day, at natural and high trout densities respectively (Fig. 7), whereas trout increased mean drift by 1.05% per day (at natural densities) and 3.75% per day (at high densities) (Fig. 7). Loss of *Paraleptophlebia* due to direct predation was 0.29% per day at natural trout densities, and 0.66% per day at high trout densities (Fig. 7). Corresponding increases in loss by drifting due to trout were 0.77% per day and
0.80% per day (Fig. 7). Consumption of drifting prey by trout would decrease emigration rates, so the increase in drift dispersal in the presence of trout is due to increased drift behaviour. These are rough comparisons of the magnitude of effects, and do not take into account variation around the means being compared. They do suggest, however, that trout reduce the density of *Baetis* primarily by causing an increase in emigration by drifting. Both prey consumption and increased drift in the presence of trout seem to have contributed to the effect of trout on the density of *Paraleptophlebia*.

Changes in drift behaviour may also be important to effects of trout on size distributions of prey. The mean size of *Paraleptophlebia* in the benthos was lower in the presence of trout, than in their absence. In contrast, drifting *Paraleptophlebia* tended to increase in size as trout density increased. Size-selective predation on drifting *Paraleptophlebia* was not detected (Chapter 4), but if trout did selectively consumed larger drifting *Paraleptophlebia*, then drifting individuals should be smaller on average than benthic ones in the presence of trout. Observation of the opposite pattern suggests that any effect of size-selective predation was overwhelmed by a countervailing increase in the drift of larger individuals in the presence of trout.

Benthic *Ephemera* were larger on average, at higher trout densities, whereas drifting individuals tended to be smaller in areas containing more trout. Trout did selectively prey on larger *Ephemera* in the drift and this pattern in the relative sizes of benthic and drifting prey could be the result of this size-selective predation. This pattern of differing size distributions could, however, also be the result of reduced drift of larger *Ephemera* in the presence of trout. Distinguishing between these mechanisms will require direct observation of the drift behaviour of mayflies in the presence and absence of trout.
Variation in the effect of predators: influences of predator-induced and other types of variation in drift dispersal

Models predicting how the impact of predators is altered by varying prey dispersal (Cooper et al. 1990, Hall et al. 1990, Lancaster et al. 1991) assume that prey dispersal is not influenced by the presence of predators. The rates of prey dispersal into and out of patches of prey are therefore similar, and high prey dispersal acts simply to swamp effects of predators due to prey consumption within the patch. In this study, drift dispersal of two of the five prey taxa increased as trout density increased. Increased drift resulted in increased dispersal out of the enclosures, which contributed to an overall reduction of prey density at high trout densities. Interestingly, where predators influence prey dispersal, those influences should lead to greater changes in prey density in situations where prey dispersal is greater overall.

Prediction of variation in predator impacts may therefore be improved by separating the influence of two sources of variation in dispersal: (1) variation in dispersal caused by predators and (2) variation in dispersal not related to predators. For stream insects, the second type of variation includes that due to differences in physical parameters like flow, resistance to accidental dislodgment, and other influences on drift behaviour like food availability.

Predator-induced increases in dispersal behaviour will tend to reduce prey densities in areas containing predators and enhance any impacts due to direct predation. Increased emigration in response to predators is shown by stream insects (Walton 1980, Peckarsky 1980 Culp et al. 1991), salamanders (Sih et al. 1992), small fish (Schlosser 1987, Fraser and Gilliam 1992), and marine amphipods (Ambrose 1984). Local densities of several of these prey were reduced following experimental manipulation of predator density (Ambrose 1984, Peckarsky 1985, Feltmate and Williams 1989, Lancaster 1990, Fraser and Gilliam 1992, Sih et al. 1992) and
increased behavioural dispersal contributed to the overall effect of predators in all of these studies except one (Sih et al. 1992). In contrast, reduced dispersal behaviour in the presence of predators should tend to negate or even override effects of prey consumption. Reduced emigration in response to predators is shown by stream amphipods (Williams and Moore 1985, Andersson et al. 1986), and isopods (Holomuzki and Hoyle 1990). The consequences for prey distributions of reduced emigration by prey in the presence of predators have, however, not yet been examined.

Only one earlier study has examined the consequences of size-related bias in drift dispersal in the presence of predators. Lancaster (1990) found that larger Baetis drifted more than small Baetis in the presence of predatory stoneflies, and this was the probable reason why the mean size of benthic Baetis was reduced in the presence of stoneflies. These data, along with mine for Paraleptophlebia, indicate that size-specific biases in prey dispersal behaviour can affect the size composition of prey populations, but further studies are needed to identify patterns in their influence.

Overall, these results suggest that, where prey dispersal is influenced by predators, the direction of these behavioural responses may partially explain effects of predators on prey densities. There is, however, also evidence that variation in dispersal not related to predators also explains variation in predator impacts. For example, predators caused greater reduction in prey density, and alteration of prey size-composition, when enclosed in fine meshed (low permeability), rather than coarse meshed (high permeability) cages (Cooper et al. 1990, Lancaster et al. 1991). Given that both predator-induced and other sources of variation in prey dispersal influence the outcome of predator manipulations it would be beneficial in future to separate their relative contributions to overall predator impacts. This could be achieved experimentally by manipulating predator density and overall dispersal.
frequency, and then measuring direct predation rates and prey dispersal behaviour in addition to local prey density and size composition.

**Scaling, and the influence of predators on prey populations**

Experimental manipulations of predator density create patches, within which the density of predators is varied. The scale of these patches in this, and most other, studies has been chosen arbitrarily. Where predators deplete prey populations within patches only by consuming prey, as in the simple models of predation and prey dispersal (Cooper et al. 1990, Hall et al. 1990, Lancaster et al. 1991), the impact of predators will be greater in larger patches because the ratio of within-patch processes to dispersal among patches decreases (a simple perimeter-area effect). For the same reason, where predators enhance or suppress prey emigration, predator impacts should decrease in larger patches. Where variation in prey dispersal is not caused by predators, the role it plays in mediating the impact of predators how dispersal and predator density vary in space relative to each other. The overall effects of spatial scale on predator impacts within patches may thus be complex, and more systematic replication of predator manipulations at different scales would be informative.

In order to interpret experimental results for natural situations it will be also be useful to identify scales of patchiness of predator distributions in real streams and of spatial patterns in factors influencing prey dispersal rates. While there is some information on patchiness in both predator and prey distributions, there is very little information on relationships between the two (for an exception see Malmqvist and Sjöström 1984). In addition, there is almost no data on spatial variation in drift dispersal (for an exception see Baker and Hawkins 1990).

Prey dispersal between local patches may also be important to the dynamics of prey populations at larger scales, such as in entire streams. Most models for the global dynamics of sub-divided populations have assumed all that all sub-
populations are connected equally by dispersal (Chesson 1978, Metz and Diekman 1986, Hastings and Wolin 1990). Empirical studies on terrestrial insects suggest that details of migratory behaviour have important impacts on dynamics of terrestrial predator-prey systems (Huffaker 1958, Kareiva 1986, 1987). Models where patches are connected unequally, as they are in streams, also predict that the details of connections between patches will be important determinants of overall population dynamics (Fahrig and Paloheimo 1988). Streams will be useful systems for the further development of these models and for the study of the interaction between the local and global dynamics of sub-divided populations.
CHAPTER 4

DIEL AND DENSITY-RELATED CHANGES IN FOOD CONSUMPTION AND PREY SELECTION BY BROOK TROUT IN A NEW HAMPShIRE STREAM

Summary

I report the results of a field study testing influences of both trout density and changes over the diel cycle on food consumption and prey selection by brook trout (Salvelinus fontinalis). Trout density in replicate 35 m long sections of a New Hampshire stream was adjusted to either average or maximum natural levels. Diets of trout and the availability of drifting prey were then sampled every four hours for 24 hours. There were no significant diel changes in the weight of prey consumed by trout per four hours, though there was some indication of reduced feeding at night. Trout fed selectively on different prey taxa, showing most preference for cased caddis larvae. Several taxa of mayflies and stoneflies were selected more strongly during the day than at night. Trout fed selectively on larger prey during the daytime but showed no size-selection at night. The density of trout had no significant effects on either their rate of food consumption or on selection for prey of different taxa or sizes.

Introduction

Many studies have sought to determine mechanisms by which stream-dwelling salmonids select prey by comparing the composition of the diet to the composition of prey available. One important aspect of the feeding behaviour of salmonids which has received limited attention is changes in feeding and prey selection over the diel cycle. Feeding might be expected to differ between day and night because salmonids feed visually (Robinson & Tash 1979, Tanaka 1970), and so should feed less efficiently, and perhaps also less selectively after dark. In addition, there are
marked diel changes in the availability of their prey. Prey, in the form of drifting invertebrates, are usually more abundant at night than during the day (Waters 1972). A few studies suggest that salmonids take advantage of this nocturnal increase in prey availability by increased feeding at night (Jenkins et al. 1970, Elliott 1973), but the majority of studies suggest that most feeding occurs during daylight (Bisson 1978, Allan 1981, Walsh et al. 1988, Angradi & Griffith 1990). Studies of prey selection by trout done during the day have demonstrated selection for different prey taxa (Cada et al. 1987) and also for larger prey (Irvine & Northcote 1983, Newman & Waters 1984, Grant & Noakes 1986). The few diel studies of prey selection indicate that selection for larger prey may be relaxed at night (Allan 1978, 1981, Sagar & Glova 1988) but there are no clear diel patterns in selection of prey by taxa (Angradi & Griffith 1990).

A second potentially important factor influencing feeding and prey selection by salmonids is their local population density. Both growth and survival of salmonids are often reduced at high population densities (Fraser 1969, Mortensen 1977, Elliott 1984, Wentworth & LaBar 1984). Populations of salmonids also show reduced growth (Mason & Chapman 1965, Mason 1976, Wilzbach et al. 1986) and production (Warren et al. 1964) in areas of low food availability. There is no direct evidence that trout at elevated densities experience reduced food availability, but one possible mechanism for reduced growth at high density is a shortage of prey. Optimal foraging theory predicts that animals feed less selectively when food becomes scarce (Pyke et al. 1977). Despite the possibility for influences of population density on feeding rates and prey selection in stream salmonids, there have been no attempts to test for this.

I present a field study of brook trout (*Salvelinus fontinalis* Mitchill) designed to answer two questions: (1) does the feeding rate of trout, and selection for prey of
different taxa and size change with time of day, and (2) does the rate of feeding and prey selection by trout depend on their local population density.

**Methods**

**Study site**

The study was conducted during July and August 1990 in Stoney Brook, a second order stream in New Hampshire, U. S. A. (43°23'N, 72°01'W, elevation 300 m). The study area was 0.6 km long, and was comprised mostly of flowing riffle and run habitat with few real pools (mean stream width = 2.8 m, mean summer discharge = 3.74 m³.min⁻¹). Riparian vegetation consisted of hemlock and mixed hardwood trees. Daytime water temperature during the study ranged from 16-18°C. The stream supports a population of brook trout from April to early November (mean density at the study site = 1.2 m⁻²); the trout appear to overwinter in the lake into which the stream drains. The size distribution of trout during the study was bimodal, with one peak around 55-60 mm fork length (FL) representing young-of-the-year trout and a broader, shallower, peak around 80-110 mm FL representing older trout. The only other fish present at the study site were a few black nosed dace, *Rhinichthys atratulus* Hermann (mean density = 0.009 m⁻²). All dace captured while setting up the study were removed and placed in areas downstream of the study site.

**Experimental procedures**

Trout density was manipulated in 35 m long sections of stream, enclosed at the ends with 7 mm mesh fences. The fences were constructed on 13-14 August, and extended at least 0.1 m into sediment and 0.5 m above the water’s surface. Trout densities within the sections were adjusted to three levels: (1) zero (no trout), (2) average density (1.1-1.3 m⁻²), and (3) high density (2.2-2.5 m⁻²). The average and high density treatments correspond to the mean and maximum densities of trout observed during four electrofishing surveys of the study area done in June and
August of both 1989 and 1990. Three replicate sections were assigned to each treatment.

Densities of trout were adjusted by electrofishing from 16-18 August, using a Smith-Root model 12 backpack electrofisher. I made four passes through zero density sections to remove all trout. Captured trout were held in pens downstream. Two passes were then made through the other sections to estimate trout densities, and to control for possible electrofishing effects on prey taxa. Numbers of trout in average and high density sections were then adjusted to the appropriate levels by adding trout from the holding pens, or removing trout, as necessary.

Sampling trout for prey consumption

Trout for diet analysis were captured by electrofishing on 29 August. Two high density and two average density sections were electrofished every four hours over 24 hours. Start times of sampling were: 1400 hr, 1800 hr, 2200 hr, 0200 hr, 0600 hr, and 1000 hr. Each collection took less than one hour. Electrofishing was started at the downstream end of each section, proceeding upstream until six trout had been captured. Areas within sections were not revisited once they had been fished.

Captured trout were immediately killed and preserved in 10% formalin. Their stomachs were later dissected and the contents stored in 70% alcohol. Prey items in the stomachs were later enumerated under a dissecting microscope. All mayfly and stonefly nymphs (Ephemeroptera and Plecoptera) encountered were measured (maximum head width) using an eyepiece graticule. Stomach contents were then dried at 60° C for 24-48 hr and weighed using a microbalance (Cahn model 27). Non-prey items in stomachs, primarily cases of caddis larvae, were not weighed.

Sampling prey availability

Drifting prey were sampled at the downstream end of each section on 29 August using drift nets with square mouths (area = 0.09 m²), 1 m long with 0.3 mm mesh. Nets were in place for six, 1.5-2 hour periods spaced over 24 hours. Drift
sampling was interspersed between the electrofishing also done on this date. The start times of the samples were: 1600 hr, 2000 hr, 0000 hr, 0400 hr, 0800 hr. Disturbance from wading was minimized, both during electrofishing and prey sampling, by walking on the banks or on rocks in the stream.

Benthic prey were sampled by taking five Surber samples (0.09 m$^{-2}$) within each section after all drift and fish sampling was completed. Benthic samples were taken at random locations within the sections, except that I avoided taking samples in areas where I had walked in the stream whilst electrofishing. Samples were preserved in alcohol and later sorted and enumerated using a dissecting microscope. The microscope image was filmed and displayed on a video monitor. Head widths of mayflies and stoneflies in the drift samples were measured from the screen image using a digitizing pad and computerized image analysis software (Sigma Scan, Jandel Inc.).

Patterns of prey consumption

The dry weight of prey consumed by the trout in each section of stream, during each of the six, four hour sampling intervals was calculated, following Elliott and Persson (1978) as

$$C_t = \frac{(S_t - S_0 e^{-Rt})Rt}{1 - e^{-Rt}}$$

where $C$ is the dry weight of food consumed per trout in a sample interval of $t$ hours, $S_0$ and $S_t$ are the mean dry weights of food in trout stomachs at the beginning and end of the interval respectively, $e$ is the exponent of natural logarithms, and $R$ is the exponential rate of gastric evacuation.

I had previously estimated $R$ as 0.51 from a field pilot study done immediately downstream of the study site in June 1990. Thirty trout for the pilot study were captured by electrofishing at 1200 hr and placed in a plastic holding tank, filled with approximately 50 L of stream water. The stream water had previously been filtered.
through 0.3 mm mesh to remove any food items. The holding tank was placed in the stream to keep it at the same temperature as the stream water (16° C). Five of the trout were then killed every 2 hours, and the prey in their stomachs were later dried at 60° C for 48 hr and weighed (as described above). The rate of gastric evacuation (R) was estimated as the slope of the regression of the logarithm of prey dry weight against time since feeding ceased (following Elliott 1972).

I tested effects of trout density and time of day on food consumption using analysis of variance (ANOVA), where stream sections were replicates and samples over 24 hours were considered repeated measures.

Patterns of prey selection by taxa

Prey selection was evaluated by comparing the relative abundances of prey consumed to the relative abundances of prey available. Prey selection was measured using the rank preference index which provides measures of relative preference for different prey items, and has the advantage over other commonly used indices of being relatively unbiased by the inclusion or exclusion of rare prey items from the analysis (Johnson 1980). To calculate this index, prey available and prey consumed are ranked from most to least abundant. The rank preference index for a given prey item is the rank of consumption minus the rank of availability, so higher index values indicate lower selection for a given prey item.

The drift samples were used as measures of prey available, because observations of trout of a range of sizes (roughly 40-120 mm FL) in Stoney Brook indicated that most daytime feeding attempts are directed at drifting prey (mean (± SE) = 84% (± 3.5%), n = 30, 5 min observations of different fish). Other studies also found most daytime feeding (> 80%) by brook trout to be on drifting prey (McNicol et al. 1985, Grant & Noakes 1986). I also used drift samples as measures of prey available at night, but note that whether trout continue to feed primarily on drift at night is unknown. Our estimates of the availability of prey were for each
stream section, rather than for each trout. I therefore used the mean number of prey per stomach for each section as our measure of prey consumed, and calculated rank preference indices for each stream section, rather than for each trout individually.

To compare diel and density-related changes in prey selection, I pooled the samples collected during the daytime (2200, 0200 and 0600 hr) and nighttime (1400, 1800, and 1000 hr) within each section. I pooled the samples this way because daytime and nighttime represent periods of distinctly different prey abundance, and of visual conditions for feeding. Separate rank preference indices were then calculated for daytime and nighttime feeding by the trout in each section. Selection indices provide measures of relative, rather than absolute, selection for different prey items and so effects of time of day and trout density on prey selection cannot be tested statistically. However, because stream sections contain replicate groups of trout, I present information on variability in preferences and use this information to make some inferences about diel and density-related changes in prey selection by trout.

Patterns of prey selection by size

Selection for prey of different sizes was tested using mayflies and stoneflies. These taxa were used because they were common prey, and relatively easy to recognize and measure in stomach contents. If there was no selection by size, then the average sizes of consumed and available prey should be the same. I tested this null hypothesis by comparing the sizes of prey consumed to those available in the drift. Measurements of mayflies and stoneflies from different sections at different times of day were pooled into day or night, and average or high density. To test for diel and density-related changes in prey selection I compared the sizes of mayflies consumed versus available, during both day and night, and at high and average trout densities using a 3-way factorial ANOVA.
Results

Patterns of prey consumption

Trout had on average 8.4 prey in their stomachs (± 22.4 SD), weighing 72.8 mg (± 24.7 SD). Contents of trout stomachs, in terms of both numbers and weight of prey, were highly variable and neither changed significantly over the 24 hour period (Table 7). There was, however, some tendency for the weight of prey in trout stomachs to be lower during the nighttime samples than during the daytime (Fig. 10). Numbers of prey per stomach showed a similar diel pattern to weights of prey and so are not presented.

Trout captured from different stream sections at different times of day did not vary significantly in size (2-factor analysis of variance, P always > 0.23) and the relationship between the size of trout and their rate of food consumption (g.4 hr⁻¹) was very weak (r² = 0.115, n = 144). For these two reasons I did not standardize estimates of food consumption rates for the size of trout, and present rates of food consumption per trout.

Food consumption estimates were highly variable, and rates of food consumption by trout did not change significantly over the diel cycle (Table 7). There was, however, some suggestion of reduced feeding between 2200 and 0200 hr (Fig. 10). The method I used to calculate food consumption assumes that food is consumed at a constant rate during the time interval (Elliott & Persson 1978). If this was not the case then the estimates will be biased. One interval where I feel this is likely was between 0200 and 0600 hr. Trout captured at 0200 hr had relatively empty stomachs, compared to those captured at 0600 hr (Fig. 10). Few prey items at 0600 showed signs of digestion, suggesting a commencement of feeding at dawn just prior to electrofishing at 0600 hr, rather than continuous feeding from 0200-0600 hr. If most of the prey in the stomachs of trout sampled at 0600 hr were consumed just prior to their capture, our estimate of food consumption from
0600 hr will be biased upwards. If the estimate of food consumption for 0200-0600 hr is biased upwards, this would add support to a nighttime decline in feeding (Fig. 10). Whether or not this the case, however, some feeding occurred at all times of night and day.

Trout at average and high densities did not have significantly different numbers and weights of prey in their stomachs (Table 7). Trout at high density contained on average 6.1 prey (± 0.2 SE), weighing 13.0 g (± 0.9 g SE), whereas mean stomach contents of trout at average density were 10.8 prey (± 1.4 SE), weighing 10.9 g (± 0.5 g SE). There were also no significant differences in the food consumption rates of trout at different densities (Table 7). Food consumption rates (g.4 hr⁻¹) were similar for trout at high (mean = 6.1 ± 0.6 SE) and average (mean = 4.9 ± 0.5 SE) densities.

Patterns of selection for different prey taxa

The overall composition of the diet of trout and of prey available is shown in Table 8. Common prey types in the diet included midges (Chironomidae), terrestrial insects, caddis larvae (Trichoptera) and mayfly nymphs (Ephemeroptera). Rank preference indices indicate that cased caddis larvae were always the most strongly selected prey taxon (Fig. 11). These animals rarely drift, so it is possible that the trout were picking them from the benthos. However, even if the benthic samples are used as measures of prey available, cased caddis larvae were still the most preferred prey taxon (data not shown).

Rank preferences for different prey taxa shown by trout feeding during day and night, and at high and average densities are shown in Figure 11. One obvious diel pattern of change in prey selection was the increase in selection for mayflies and stoneflies during the day, compared to during the night (Fig. 11). The difference in prey selection between day and night was particularly striking for Paraleptophlebia, Eurylophella and Utaperla (Fig. 11). The density of trout, however, did not appear
to affect prey selection. For all taxa there was more variation in rank preference within, rather than between, densities of trout (Fig. 11).

**Patterns of selection for different prey sizes**

Selection for prey of different sizes would be indicated by significant differences between the sizes of prey consumed and those available (a significant Location effect in the ANOVA, Table 9). Changes in size selection at different times of day, or at different trout densities would be indicated by significant interactions in the ANOVA (Location by Time, or Location by Density, Table 9).

Trout consumed **Ephemera**, **Stenonema** and **Peltoperla** selectively by size, but the extent of size-selection differed between night and day (indicated by significant Location by Time interaction terms in the ANOVAs, Table 9). Multiple comparison tests indicated that **Peltoperla** consumed by trout during the day and night did not differ significantly in size (Tukey's HSD, \( P > 0.05 \)), whereas the **Peltoperla** that drifted during the night tended to be larger than those drifting during the day (Tukey's HSD test, \( P < 0.05 \)) (Fig. 12). **Ephemera** and **Stenonema** consumed by trout during the day were significantly larger on average than those available in the drift (Tukey's HSD test, \( P < 0.05 \)), whereas at night drifting prey and prey consumed by trout were of similar sizes (Tukey's HSD test, \( P > 0.05 \)) (Fig. 12). For the remaining four mayflies and stoneflies, the mean size of prey consumed by trout during the day was larger than the mean size of prey available. In contrast, the prey consumed by trout at night tended to be either smaller or of similar sizes to prey available (Fig. 12). While none of these latter trends was significant individually, the data for all of the taxa viewed together suggest that there was a general tendency for trout to selectively consume larger mayflies and stoneflies during the day, but to show no size-selection at night.
There were no significant effects of trout density on selection for prey of different size (indicated by the absence of significant Location by Density interactions in the ANOVAs, Table 9).
Table 7. Summary of results of repeated measures ANOVAs testing for effects of trout density (Density) and changes over the diel cycle (Time) on numbers (# prey) and weight (wt. prey) of prey per trout stomach, and on the weight of prey consumed per four hours (wt. consumed).

<table>
<thead>
<tr>
<th>Source</th>
<th># prey</th>
<th>wt. prey</th>
<th>wt. consumed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>P</td>
<td>P</td>
</tr>
<tr>
<td>Density</td>
<td>1</td>
<td>0.475</td>
<td>0.804</td>
</tr>
<tr>
<td>Error*</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>5</td>
<td>0.337</td>
<td>0.577</td>
</tr>
<tr>
<td>Time * Density</td>
<td>5</td>
<td>0.460</td>
<td>0.305</td>
</tr>
<tr>
<td>Error\w</td>
<td>10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(b\) and \(w\) refer to error between and within subjects respectively.
Fig. 10. (a) The average weight of prey contained in trout stomachs at six sampling times over 24 hours and (b) estimates of food consumption during 6, 4 hour intervals over 24 hours. Horizontal bars under x axes indicate nighttime. Error bars are standard errors.
Table 8. Overall numeric composition of trout diets, and of drifting and benthic prey available. Values are percentages. Only taxa comprising more than two per cent of either drift, benthos or stomach contents were listed separately; rarer taxa were pooled into higher taxonomic units.

<table>
<thead>
<tr>
<th>Prey taxa</th>
<th>Stomach contents</th>
<th>drift</th>
<th>benthos</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aquatic prey</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ephemeroptera</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Baetis</em></td>
<td>2.23</td>
<td>8.26</td>
<td>12.28</td>
</tr>
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<td><em>Paraleptophlebia</em></td>
<td>2.16</td>
<td>6.60</td>
<td>6.46</td>
</tr>
<tr>
<td><em>Ephemerella</em></td>
<td>1.24</td>
<td>3.11</td>
<td>2.11</td>
</tr>
<tr>
<td><em>Eurylophella</em></td>
<td>0.74</td>
<td>5.64</td>
<td>1.45</td>
</tr>
<tr>
<td><em>Stenonema</em></td>
<td>2.98</td>
<td>1.85</td>
<td>6.80</td>
</tr>
<tr>
<td><em>Plecoptera</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Peltoperla</em></td>
<td>2.65</td>
<td>8.34</td>
<td>0.58</td>
</tr>
<tr>
<td><em>Utaoperla</em></td>
<td>0.83</td>
<td>9.03</td>
<td>8.66</td>
</tr>
<tr>
<td><em>Trichoptera</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Caseless</em></td>
<td>2.69</td>
<td>4.82</td>
<td>3.20</td>
</tr>
<tr>
<td><em>Cased</em></td>
<td>8.06</td>
<td>0.77</td>
<td>1.81</td>
</tr>
<tr>
<td><strong>Diptera</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chironomidae</em></td>
<td>30.0</td>
<td>12.3</td>
<td>36.9</td>
</tr>
<tr>
<td><em>Simuliiidae</em></td>
<td>0</td>
<td>7.76</td>
<td>1.39</td>
</tr>
<tr>
<td><em>Tipulidae</em></td>
<td>1.24</td>
<td>17.1</td>
<td>4.07</td>
</tr>
<tr>
<td><em>Culicidae</em></td>
<td>11.07</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Other Diptera</td>
<td>1.06</td>
<td>2.19</td>
<td>1.08</td>
</tr>
<tr>
<td><strong>Coleoptera (adults)</strong></td>
<td>0.90</td>
<td>3.66</td>
<td>6.38</td>
</tr>
<tr>
<td><strong>Oligochaeta</strong></td>
<td>0.83</td>
<td>0.24</td>
<td>5.29</td>
</tr>
<tr>
<td><strong>Other taxa</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Terrestrial prey</strong></td>
<td>15.12</td>
<td>6.53</td>
<td>0.16</td>
</tr>
<tr>
<td><strong>Unidentified</strong></td>
<td>9.10</td>
<td>0</td>
<td>0.01</td>
</tr>
</tbody>
</table>

*a* this taxon was found in the stomach of only two trout, one of which had consumed very large numbers of these prey.  
*b* Other taxa included Odonata, Megaloptera, larval Coleoptera, Hemiptera, Mollusca and other rare Ephemeroptera and Plecoptera.
Fig. 11. Patterns of selection for common prey taxa by trout feeding during the day versus at night (a) and stocked at different densities (b). More negative preference indices indicate stronger selection for a given prey item. Error bars are standard errors.
Table 9. Summary of results of 3-factor model I ANOVAs comparing the sizes of prey consumed versus available in the drift (Location), at night versus daytime (Time), and at two different trout densities (Density).

<table>
<thead>
<tr>
<th>Source</th>
<th>Bae	sis</th>
<th>Paraleptophlebia</th>
<th>Ephemera</th>
<th>Eurylophella</th>
<th>Stenonema</th>
<th>Utaperla</th>
<th>Peltoperla</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
</tr>
<tr>
<td>Time</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
</tr>
<tr>
<td>Density</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
</tr>
<tr>
<td>L * T</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
</tr>
<tr>
<td>L * D</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
</tr>
<tr>
<td>T * D</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
</tr>
<tr>
<td>L * T * D</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
</tr>
<tr>
<td>Error</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
<td>df P</td>
</tr>
</tbody>
</table>

- Indicates non-significant terms (P > 0.25) removed from the model by post-hoc pooling (Winer et al. 1991).
Fig. 12. Diel patterns of selection for different sized prey by trout feeding on five mayfly and two stonefly taxa. Plotted are mean sizes (with standard errors) of drifting prey and prey consumed by trout. Mean sample size per point = 29.3.
Discussion

Diel changes in feeding and prey selection by trout

The density of drifting invertebrates at the study site showed a pronounced increase during the night (Chapter 1, unpublished data), as it does in most streams (Waters 1972). There was, however, no corresponding increase in food consumption after dark. Other studies of brook trout found that more feeding occurred during the day than at night (Allan 1981, Johnson & Johnson 1982, Walsh et al. 1988), suggesting that brook trout are predominantly diurnal feeders. My observation of a decline in feeding at night, though non-significant, is consistent with the finding of these other studies. Studies of other salmonid species have uncovered a wider range of diel feeding patterns, including dawn, evening and daytime peaks of feeding activity (Elliott 1970, 1973, Sagar & Glova 1988). There is variation within, as well as among, species in diel feeding periodicity. Rainbow trout, for example, have been observed to feed mostly during the day in some streams (Bisson 1978, Angradi & Griffith 1989), but in other streams they show pronounced evening peaks of feeding (Elliott 1973).

Reasons for this variation in diel feeding chronicity are not clear. Salmonids detect prey visually and so are unable to feed at light levels below which they cannot see (Robinson & Tash 1979, Tanaka 1970). One reason for variation in the rate of feeding at night may, therefore, be the amount of light available, as determined by the moon phase and weather. Indirect evidence for this is that the usual increase in the abundance of drifting prey at night is suppressed during full moon periods (Anderson 1966). This alteration of prey behaviour implies that the risk of predation from fish is increased during full moon, presumably because drifting prey are more visible in bright moonlight. More systematic observations of diel feeding rates under varying moonlight conditions might therefore help to explain differences in the extent of nighttime feeding.
Brook trout during this study tended to select larger mayflies and stoneflies during the day, but showed no size-selection at night. A similar diel pattern of size-selective predation on mayflies has been reported in other streams for brook trout (Allan 1978, 1981) and Chinook salmon (Sagar and Glova 1988). Mayflies and stoneflies also seemed to be selected more strongly relative to other prey taxa during the day than during the night, a finding mirrored in Sagar and Glova's (1988) study of Chinook salmon. Diminished selection for these taxa during the night might perhaps reflect reduced ability of the trout to detect subtle differences between drifting prey at low light levels. Better understanding of selective feeding by salmonids would thus be furthered by direct observations of trout feeding behaviour in the field at night to determine where and how they feed, and by lab tests of their capabilities to detect and capture different types of prey at low light levels.

Cased caddis larvae were the most strongly selected prey during both day and night. Cased caddis larvae are large and conspicuous and field studies often find that they are selected by salmonids (Griffith 1974, McNicol et al. 1985, Hubert & Rhodes 1989). Why cased caddis larvae were strongly selected at night, while selection for mayflies and stoneflies was reduced after dark, is uncertain. Cased caddis rarely drift, and so their consumption has been inferred to be the result of benthic foraging (Bisson 1978). If trout feed on mayflies and stoneflies mostly from the drift, but on caddis larvae from the benthos, then continued selection for cased caddis at night may be because benthic foraging is more effective than drift feeding after dark.

A caveat, which must be borne in mind, is that inferences about prey selectivity from comparison of stomach contents to food availability rely on the assumption that prey are evacuated from the stomach at similar rates (Gannon 1976, Kolok & Rondorf 1987). Cased caddis larvae in stoney cases may be digested more slowly than other prey. An alternative explanation for the frequent occurrence of cased
caddis larvae in trout stomachs is, therefore, that these prey were evacuated more slowly than other prey types. Confirmation of patterns of prey selection identified in the field by this study, and others, should be corroborated in the lab, where consumption of prey can be observed directly.

Density-related changes in feeding and prey selection

Mean drift rates of prey did not differ significantly between areas containing high and average densities of trout (the one exception was Baetis, Chapter 3). The mean number of prey available per trout should, therefore, have been lower in stream sections containing high densities of trout density, than in sections with average densities. Despite this fact, I detected no effects of trout density on their feeding rate and selectivity for different prey types.

One possible reason for the apparent lack of effects of population density on food consumption is that food was available in excess and so no effects of density were likely. Brook trout in this study consumed on average 1.75% of their dry body weight per day (calculated assuming trout dry wt = 24% of wet wt, Elliott 1975). I do not have the information necessary to determine whether this rate of food consumption by the trout was adequate for them to maintain their body weight, or allow growth. This rate of food consumption is, however, at the low end of food consumption values reported by Walsh and coworkers (1988) for young-of-the-year (YOY) brook trout in Quebec (1.27-9.75%). It is also lower than values reported for other salmonids, e.g. 2.5% for juvenile sockeye salmon (Doble & Eggers 1978), 5.6% for YOY rainbow trout (Angradi & Griffith 1989), 8.3% for juvenile Chinook salmon (Sagar & Glova 1988) and 6.6-13.1% for juvenile pink salmon (Godin 1981). The fact that rates of food consumption by brook trout during our study were low, relative to most other reported values, suggests that food was not superabundant in the study area.
Another possible reason for the absence of measurable effects of trout density on feeding is high variation among individuals in feeding success. The abundance of drifting prey varies substantially at small spatial scales (e.g. Baker & Hawkins 1988), suggesting that individual trout will experience different supplies of drifting prey. In addition, most stream dwelling salmonids, including brook trout, tend to occupy small feeding territories (Dill et al. 1981, McNicol et al. 1985, Puckett & Dill 1985). Territory sites vary markedly in profitability, defined as the flow rate (= food delivery rate) relative to the energy required to maintain position (Fausch 1984) further adding to variation in food supply. It may be, then, that over the range of densities tested, variation in access to food among individual trout is much greater than any influence of population density at larger scales (35 m sections of stream).
APPENDIX

Effects of mesh fences on drift densities of stream insects

Aim

This pilot study was designed to test whether fences with different sized mesh presented a barrier to drift dispersal by stream insects.

Methods

Six mesh fences were placed in Stoney Brook, perpendicular to the direction of flow, on 20 June 1990. The fences were buried 5 cm deep into the sediment and extended above the water's surface. Two of the fences had 7 mm mesh, two fences had 3 mm mesh, and the remaining two fences had 1 mm mesh. A drift net was placed immediately upstream and immediately downstream of each fence. The mouths of the upstream nets were 1.2 m upstream of the fences, the mouths of the downstream nets were 0.2 m downstream of the fences. The downstream net was slightly to the side of, as well as downstream of, the upstream net so that the downstream net did not sample water that had already passed through the upstream net. The nets collected drifting organisms from 2000-2300 hr. Water flow at the mouth of each net was calculated before sampling commenced in order to calculate the volume of water filtered by each net. Nets did not clog during the sampling period. The six fences were then placed in different locations on June 21 1990, and drift was sampled using methods identical to those used on June 20.

Invertebrates in the drift samples were identified and counted, and their numbers converted to drift densities (Number per m$^3$ water). For each mesh size, I tested for differences in drift density upstream of and downstream of the fences using paired t-tests (where the samples upstream and downstream of each net constituted paired values).
Results

Drift densities of both mayflies and all invertebrates were significantly reduced downstream of 3 mm and 1 mm mesh fences (t-tests, $P < 0.05$), but not below 7 mm mesh fences (t-test, $P > 0.05$) (Fig. 13).
Fig. 13. Effects of mesh fences on drift densities of (a) mayflies and (b) of all invertebrate taxa combined. Plotted are mean drift densities upstream of, and downstream of, fences with different sized mesh. Error bars are standard errors. Asterisks indicate significant reductions in drift density downstream of fences (t-tests, $P < 0.05$).

(a) Mayflies

(b) Total
Sampling drift from small patches of substratum

Aim

This pilot study was designed to test the effectiveness of a method designed to measure drift dispersal from small (0.5 m²) defined areas of substratum. I tested how effectively the net sampled drifting objects (simulating insects) originating in the defined area.

Methods

Drift nets were placed in the stream. Small fences (1 m wide, mesh size = 1 mm) were placed 2 m directly upstream of them, to ensure that mayflies from upstream of this point were not captured in the net (Fig. 14). To test what area of substratum the net was likely to sample drifting insects from, I released beads into the water column at different points upstream of the net and recorded whether they were captured by the net. The beads were neutrally buoyant plastic spheres (diameter = 0.6 cm).

Preliminary tests indicated that drift nets only captured beads from a predictable area in sites where the flow was fairly even and straight, and where the substratum consisted of gravel and small cobbles. I, therefore, chose 6 such sites to conduct more quantitative tests of the method. At each of these 6 sites, beads were released one by one into the water column from each of 71 locations (shown in Fig. 14) and an observer recorded whether or not they were captured by the net. Two beads were released from each location. The data from the 6 sites was pooled to calculate overall probabilities of capture for beads released from each of the 71 locations.

Results

The results are summarized in Fig 14 (b). Ninety one per cent of beads released at locations inside the area 0.3 m wide at the net mouth, tapering to 0.2 m wide at the fence (total area = 0.5 m²) were captured by the net, whereas few beads
outside this area were caught in the net. When nets were set up under similar conditions (Chapters 2 and 3) I therefore assumed that the drifting insects captured by the nets originated from this 0.5 m² area.
Fig. 14. Diagrams of apparatus for sampling drift of mayflies from small patches of substratum (viewed from above). Diagram (a) shows locations from which beads were released into the water. Diagram (b) shows the area within which 91% of beads released were captured by the net.
Predicting 24 hr drift counts from 2 hr counts

Aim

This pilot study was done to test whether 24 hour drift rates of mayflies could be effectively predicted from 2 hour drift rates measured just after dark.

Methods

Regression equations predicting 24 hour drift counts from 2 hour nighttime counts were generated using drift collections made on three dates. These equations were used to estimate 24 hour drift counts in Chapter 3. The three sampling dates were chosen because 2 hour nighttime counts on these three dates were in the same range as 2 hour nighttime counts made for Chapter 3.

On both 2 and 10 August 1989, 4 drift nets were placed in Stoney Brook, at locations spread over 70 m. On each date, 2 nets were placed at the ends of pools, and two nets at the end of riffles. On 27 June 1990, 12 drift nets were placed at locations spread over 320 m. Six nets were placed at the ends of riffles and six nets at the end of pool or run habitats. Drift nets were placed at different locations on each date. On all 3 dates, the nets collected drifting invertebrates for 24 hours. On 2 and 10 August 1989, the nets were emptied every 2 hours, except from 1930-2130 hr when they were emptied every 15 min. On 27 June 1990, the nets were emptied every 2 hours.

Mayflies in each drift collection were counted. The number of mayflies collected in 24 hr was regressed against the number collected in 2 hours just after dark, using individual drift nets as replicates (n = 20). The 2 hours after dark were from 1930-2130 hr for August 2 and 10 1989; and from 2100-2300 hr for June 27 1990. Regression equations were constructed using both untransformed data and data transformed to $\log_{10}(x + 1)$ and 4th root $(x + 1)$ (following Allan and Russek 1985).
Results

The regression equations best predicting 24 hour counts (highest $r^2$ values) for each mayfly are shown in table 10. These equations were used to predict 24 hour counts in Chapter 3.
Table 10. Regression equations predicting 24 hour drift counts from a 2 hour nighttime count.

<table>
<thead>
<tr>
<th>Mayfly</th>
<th>Intercept</th>
<th>Slope</th>
<th>P</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baetis</td>
<td>66.4</td>
<td>4.11</td>
<td>&lt;0.0005</td>
<td>0.65</td>
</tr>
<tr>
<td>Paraleptophlebia$^a$</td>
<td>0.36</td>
<td>1.46</td>
<td>&lt;0.0005</td>
<td>0.69</td>
</tr>
<tr>
<td>Ephemereilla$^a$</td>
<td>0.41</td>
<td>1.28</td>
<td>&lt;0.0005</td>
<td>0.72</td>
</tr>
<tr>
<td>Eurylophella$^a$</td>
<td>-0.314</td>
<td>1.72</td>
<td>&lt;0.0005</td>
<td>0.882</td>
</tr>
<tr>
<td>Stenonema$^b$</td>
<td>0.667</td>
<td>0.905</td>
<td>&lt;0.0005</td>
<td>0.688</td>
</tr>
</tbody>
</table>

P-values are for F-tests of the significance of the regression, df = 1 and 18. $^a$ data transformed to 4th root (x + 1), $^b$ data transformed to log$_{10}$ (x + 1).
Predicted order of effect of predators on mayfly densities

Aim

Chapter 3 thre was designed as a test of the hypothesis that predators should have greater effects on prey taxa that show lower rates of dispersal. I used surveys of drift rates and benthic densities, independent of the experimental data, to estimate the dispersal rates of five prey taxa (mayflies) and predict the relative impact of predators on their density.

Methods

Drift of mayflies in Stoney Brook was sampled over 24 hours on each of three dates, 2 and 10 August 1989, and 27 June 1990. The drift sampling regime is described in the section above (predicting 24 hour counts from 2 hour counts). Before drift sampling commenced, I estimated the discharge through each net and the discharge of the stream at the location of each net. The twenty four hour drift rate at each net location was then calculated (following Chapter 3). On each date I took four benthic samples (Surber samples, 0.09 m²) upstream of each net, after drift sampling was completed. The distance upstream of the net within which benthic samples were taken ranged from 5-16 m. Benthic samples were taken at randomly located points within the defined area.

In order to make the drift rates comparable to data from the 35 m experimental sections (Chapter 3) I scaled the data to estimate the % of percentage of the benthic population dispersing into or out of hypothetical stream sections that were 35 m long and 2.8 m wide (2.8 m = the mean width of the experimental sections). To do this, I calculated the mean benthic density (No./m²) of each mayfly in the area above each drift net. I multiplied this mean by (35 * 2.8) to estimate the benthic population present above the net, if the net had been at the end of an experimental stream section. I then divided the 24 hour drift rate at the net location by the estimated number of mayflies in the hypothetical 35 m section and multiplied

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by 100. The resultant figure is an estimate of the % of the benthic population drifting per day from an area the size of an experimental section of stream. An estimate of drift dispersal (expressed as % dispersal from a 35 m section) was calculated for each of the twenty net locations.

Results

The overall mean rate of drift dispersal for each of the five mayfly taxa is shown in Fig. 15. The order of drift dispersal (from most to least) is as follows: *Baetis, Paraleptophlebia, Ephemerella, Eurylophella, Stenonema.*
Fig. 15. Mean rates of drift dispersal of five mayflies, and mean rates of predation on these mayflies by trout. Error bars are standard errors. (Details of calculation of dispersal rates and predation rates are presented in the Appendix above and in Chapter 3 respectively).
REFERENCES


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