

Diel Patterns of Drift by Five Species of Mayfly at Different Levels of Fish Predation

Graham E. Forrester¹

Department of Zoology, University of New Hampshire, Durham, NH 03824, USA

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Stream insects that drift downstream in the water column are at risk from fishes that feed visually in mid-water, and the restriction of drifting to nighttime is hypothesized to have evolved as an avoidance response to this type of predator. I tested the hypothesis that low daytime drifting is a proximate response to the presence of drift-feeding fishes by manipulating fish density (brook trout, *Salvelinus fontinalis*) in two field experiments. Daytime drift activity of five prey taxa (all mayflies: Ephemeroptera) was low in both experiments and did not change following fish removal. By night, however, nighttime drift activity of two mayflies, *Baetis* and *Paraleptophlebia*, was increased in areas containing fish. The other three mayflies, *Ephemerella*, *Stenonema*, and *Eurylophella*, which showed less drift activity overall, displayed no consistent responses to fish presence. The original hypothesis predicts that risk from drift-feeding fishes should result in reduced daytime drifting. The increases in nighttime drifting away from patches dense with trout were not predicted by the original hypothesis, but may be an additional avoidance response to reduce long-term predation risk in streams where trout are distributed patchily in space.

Les insectes des cours d'eau qui dérivent en descendant le courant dans la colonne d'eau sont exposés aux poissons qui se nourrissent par repérage visuel dans les eaux intermédiaires et l'on suppose que le fait que les insectes ne dérivent que la nuit constitue une réaction d'évitement de ce type de prédateurs. Pour vérifier l'hypothèse voulant qu'une faible dérive diurne soit une réaction immédiate à la présence de poissons qui se nourrissent dans le courant, nous avons manipulé la densité du poisson (omble de fontaine, *Salvelinus fontinalis*) dans deux expériences sur le terrain. L'activité de dérive diurne de cinq taxons-proies (tous des éphéméroptères) était faible dans les deux expériences et n'a pas changé à la suite du retrait des poissons. La nuit, cependant, l'activité de dérive de deux éphéméroptères, *Baetis* et *Paraleptophlebia*, était accrue dans les zones poissonneuses. Les trois autres éphéméroptères, *Ephemerella*, *Stenonema* et *Eurylophella*, dont l'activité de dérive globale était moindre, n'ont montré aucune réaction constante à la présence du poisson. Selon l'hypothèse de départ, le risque lié aux poissons se nourrissant dans le courant aurait dû provoquer une diminution de la dérive diurne. Les augmentations de dérive nocturne hors des zones densément peuplées par l'omble de fontaine n'étaient pas prévues par l'hypothèse de départ, mais elles peuvent constituer une réaction d'évitement additionnelle visant à réduire le risque à long terme de la prédation dans les cours d'eau où l'omble est inégalement distribuée dans l'espace.

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Predators have important influences on behavioural decisions made by their prey, including decisions about when and where to engage in activities such as feeding, mating, and dispersal (Edmunds 1974; Sih 1987; Lima and Dill 1990). Prey often limit their activities to places and times which reduce their frequency of encounters with predators. Many taxa vulnerable to visual predators, for example, tend to enter areas containing these predators only at night because these predators usually feed ineffectively, or not at all, after dark. (e.g., Gentry 1974; Nelson and Vance 1979; Ohlhorst 1982; Edwards 1983; Holomuzki 1986; Haney 1988). Many benthic stream insects, including mayflies (Order Ephemeroptera), disperse by drifting short distances downstream in the water column (Waters 1972). Drifting insects are at risk from predatory fish that hunt by sight in

midwater, and feed mostly during the day (Walsh et al. 1988; Angradi and Griffith 1990). Fish predation should select against behaviours that result in daytime drifting and, for this reason, the widespread pattern of concentrating drift activity in the hours of darkness (Waters 1972; Müller 1974) is hypothesized to have evolved as an avoidance response to drift-feeding fishes (Allan 1978).

Support for the predator-avoidance hypothesis comes from the observation that larger individuals of some insect species are more nocturnal than smaller ones (they show a greater ratio of night:day drift density) (Allan 1978, 1984; Skinner 1985). This supports the hypothesis because fish tend to select larger prey (e.g., Ringler 1979; Newman and Waters 1984); larger insects are therefore more at risk and so should be more nocturnal than smaller ones. More direct evidence for the hypothesis is that drift is less nocturnal in streams naturally lacking water-column predators than in streams where these predators are present (Malmqvist 1988; Flecker 1992; Douglas et al. 1994).

¹Present address: Department of Biological Sciences and Marine Sciences Institute, University of California, Santa Barbara, CA 93106, USA.

Behaviours that evolved because they result in predator avoidance may be either fixed (*sensu* Stein 1979), where the prey no longer respond to present-day variation in predator density, or phenotypically plastic, in which case prey behaviour is varied according to the current risk. Diel behavioural shifts in other systems can be the result of either fixed or plastic responses to predators (e.g., Fawcett 1984; Neill 1992; Semlitsch and Reyer 1992). Early work on the drifting and activity patterns of stream invertebrates implicated light cues as regulators of nocturnal periodicity (Elliott 1965; Müller 1966; Holt and Waters 1967; Bishop 1969), suggesting that stream insects would not respond to present-day variation in the density of water-column predators (Allan 1978). More recent studies indicate, however, show that diel periodicity in feeding and positioning on the substratum can be the result of facultative responses to drift-feeding fishes (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994). Further, several studies have demonstrated that stream insects alter their drift rates in response to predatory invertebrates (Corkum and Pointing 1979; Peckarsky 1980; Walton 1980; Malmqvist and Sjöström 1987) and benthic-feeding fish (Kohler and McPeck 1989; Culp et al. 1991); suggesting a potential for plastic drift responses to water-column predators.

Specific tests for flexibility of drift periodicity in response to the presence of drift-feeding fishes have produced varying results. Gammarid amphipods have shown both reduced (Williams and Moore 1985, 1989; Holomuzki and Hoyle 1990) and increased (Andersen et al. 1993) drift density and overall activity in the presence of midwater predators. Drift densities of insects have, however, usually been unaffected by manipulations of the density of drift-feeding fishes (Allan 1982; Williams 1990; Flecker 1992). Exceptions to this pattern are Williams' (1990) report that a few insect taxa increased their daytime drift density in response to trout removal, and Douglas et al.'s (1994) finding that a baetid mayfly reduced its daytime drift rate following trout addition. The varying results of these studies, and the lack of replication of the treatment in two of them (Allan 1982; Williams 1990), suggests a need for further tests for plastic responses of stream insects to drift-feeding fishes.

The aim of this study was to test whether drift periodicity is a fixed or plastic response to drift-feeding fishes by manipulating the density of drift-feeding fish in two field experiments and observing any resulting changes in the drift activity of five prey taxa. Specifically, the first experiment tested the combined effect of brook trout (*Salvelinus fontinalis*) and black-nosed dace (*Rhinichthys atratulus*) on drift densities of five mayflies, whereas the second experiment isolated the effect of brook trout on the propensity of mayflies to drift, measured as the rate of departure from a patch relative to benthic density within it. During both experiments, I also tested whether drift responses to fish were more strongly expressed in larger size classes of prey taxa, because larger insects are more vulnerable to drift-feeding fishes.

Methods

Study Site and Study Organisms

The experiments were done in Stoney Brook, New Hampshire, (43°23'N, 72°01'W), a second-order stream, 6 km long, which drains into Lake Sunapee, New Hampshire. The 0.6-km study section was located 3 km above the lake outlet (elevation = 300 m; mean summer discharge = 3.74 m³·min⁻¹)

and was shaded by riparian vegetation, consisting mostly of eastern hemlock (*Tsuga canadensis*) and mixed deciduous trees. Habitat in the experimental section was composed mostly of flowing riffles and runs, with a gravel and cobble substratum.

Fish populations were surveyed by electrofishing (pulsed direct-current, Smith-Root model 12) during August 1989, and June and August 1990 using the removal method (following Bohlin et al. 1989). Unblocked sections of stream (5–16 m long) were fished three times, 2–3 h apart, working upstream. The number of fish present (\hat{y}) was estimated as

$$(1) \quad \hat{y} = \frac{C_T}{1 - (C_T - C_1 / C_T - C_3)^3}$$

where C_T , C_1 , and C_3 represent the total, first, and third catches respectively. Brook trout were present at densities ranging from 0.6 to 2.4·m⁻² (mean = 1.2 ± 0.1·m⁻² (SE)). The trout size distribution 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. During the day, brook trout feed predominantly on invertebrate prey drifting in midwater (McNicol et al. 1985; Grant and Noakes 1986; Forrester et al. 1994). The only other fish present were a few black-nosed dace (mean density = 0.009 ± 0.001·m⁻², which feed on benthic invertebrates (Johnson and Johnson 1982; Fuller and Hynes 1987).

The prey were five genera of mayflies (Ephemeroptera): *Baetis*, *Paraleptophlebia*, *Ephemerella*, *Eurylophella*, and *Stenonema*, the first two of which are bivoltine in Stoney Brook, whereas the last three are univoltine (G.E. Forrester, unpublished data). These mayflies constituted 29% of the benthic community in the study area and were all consumed by the brook trout (Forrester et al. 1994; Forrester 1994).

Experiment 1

The hypothesis that mayflies adjust their drift density according to the presence of fish was tested in a preliminary experiment in September 1989. Fish presence was manipulated in 35-m-long sections of stream, enclosed at the ends with mesh fences. Brook trout and black-nosed dace were present at natural densities in two stream sections, but were removed from two other sections. Drift densities of the five mayfly prey taxa were measured at the downstream end of each stream section 3 and 10 d after the fish manipulation.

Manipulation of fish density was done on 29–30 August by fencing the ends of the four contiguous sections of stream with hardware cloth (mesh size = 3 mm) that extended 10 cm into the sediment and 30 cm above the water's surface. Fish were removed from the sections second and furthest downstream by making four passes through each with an electrofisher. One pass was also made through the nonremoval sections to control for possible effects of electrofishing on drift rates.

Drift was sampled at the downstream end of each stream section on 2 and 9 September using a stationary drift net (mouth = 0.3 × 0.3 m square, net length = 1 m, mesh size = 0.3 mm). Drift was sampled from 13:00 to 23:00 on the first sampling date and the nets were emptied every 2 h. On the second date, however, sampling was done from 12:00 to 01:30 and the nets were emptied every hour, except between 18:00 and 20:30 when they were emptied every

half hour. To calculate the volume of water sampled by the nets, I measured the depth of water and current velocity at the net entrance before and after sampling (using a pygmy meter, Gurley Instruments). The drift samples were stored in refrigerated stream water after removing any large predatory invertebrates, and the mayflies were counted under a dissecting microscope within 4 d.

To ensure that all drift collected in a given section originated from within it, nylon mesh (mesh size = 0.15 mm) was placed over each of the fences 1 h before sampling started and then removed after sampling ceased. The mesh reduced flow in the upstream 1–2 m of the stream sections, but the drift measurements at the downstream end of the sections (33–34 m away) were unlikely to have been affected by the flow reduction. The mesh was cleaned with a brush halfway through the sampling interval to reduce clogging. Drift sampling was interrupted during cleaning, and for 15 min afterwards, to prevent capture of invertebrates disrupted by the cleaning process.

Mayfly drift densities were consistently low during the day, increased markedly after dark and remained at a fairly constant higher level throughout the night (Forrester 1992). I, therefore, pooled the samples into two groups, day and night, for statistical analyses. For 2 September, day samples were defined as those taken from 13:00 to 17:00 and night samples as those from 19:00 to 23:00. For 9–10 September, day samples were defined as those taken from 12:00 to 18:30 and night samples defined as those taken from 19:30 to 01:30. Drift samples straddling the dusk period were not used because their day–night status was uncertain. Differences in daytime and nighttime drift densities between fish removal and control sections were tested using repeated measures analyses of variance (ANOVA), with sample date as the repeated measure (Winer et al. 1991).

To test effects of fish on the size of drifting mayflies, I measured the head-capsule widths of the two most common mayflies, *Baetis* ($n = 143$) and *Paraleptophlebia* ($n = 152$). Measurements were made from a video display of a microscope image using a computerized image-analysis system. Measurements were pooled to calculate a mean size for each time of day (day and night), in each stream section, on each sampling date. These means were used as replicates in a repeated measures ANOVA to test effects of fish on the size of mayflies drifting during the day and at night. Sample sizes for *Paraleptophlebia* during the day were too small to permit analysis, so a test was performed only on the nighttime data.

Experiment 2

A second experiment was done in August 1990 to test the hypothesis that mayflies adjust their propensity to drift according to the density of brook trout. I manipulated trout density in fenced 35-m-long stream sections and removed all dace from the study area to isolate whether effects of fish in the first experiment were due to trout or dace. Trout densities in the stream sections were adjusted to one of three levels: (1) zero (no trout), (2) medium density (mean = $0.88 \pm 0.02 \cdot \text{m}^{-2}$), and (3) high density (mean = $1.56 \pm 0.12 \cdot \text{m}^{-2}$), with three replicate stream sections assigned to each treatment. Changes in drift of the five mayflies in response to trout manipulation were measured 6 and 10 d following the manipulation. Drift was quantified as the proportion of mayflies that drifted from small patches of

substratum. This drift measure was adopted because it provides a better indication of mayfly behaviour than drift density, the measure used in the first experiment.

Experimental stream sections were enclosed at each end with a mesh fence made of hardware cloth (mesh size = 7 mm), and separated from one another by 17–20 m long unmanipulated areas. Trout-density treatments were established on 16–18 August by removing trout from zero-density sections with the electrofisher (four passes) and holding them in pens downstream. The remaining sections were also electrofished (three passes) to estimate trout densities, and to control for possible electrofishing effects on prey taxa. Trout numbers in high- and medium-density sections were then adjusted to the appropriate levels by adding trout from the holding pens, or removing trout, as necessary. Assignment of fish to sections was done so that different trout size-classes were roughly equally represented in each section.

Treatments were interspersed among sections in a way designed to reduce biases that might arise because a given stream section may receive trout cues and/or drifting mayflies from neighbouring upstream section(s). The assignment of treatments to stream sections, from upstream to downstream was as follows: high, high, zero, medium, zero, high, medium, medium. 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 medium-density manipulated section. This should avoid any consistent bias that might have occurred if, for example, all of the zero-density sections were immediately downstream of high-density sections.

The propensity of mayflies to drift was measured from 2-m-long patches of gravel substratum with uniform flow (range of velocities = $21\text{--}29 \text{ cm} \cdot \text{s}^{-1}$). A small fence (width = 1 m, mesh size = 1 mm) was placed across the upstream end of the patch to prevent sampling of mayflies drifting from upstream. The fence blocked drift of over 90% of mayflies (Forrester 1992), but reduced flow over the patch only slightly (mean reduction = 11%). Mayflies drifting from the patch were collected in a drift net placed across its downstream end for 2 h, starting 1 h after the fence was set up. A benthic sample (0.09 m^2) was then taken immediately upstream of the drift net. The drift propensity of mayflies was calculated as the number caught in the drift net divided by the number in the benthic sample. This calculation may be biased by variation in the area of substratum from which mayflies caught in the net originated, but any biases should be consistent among treatments so effects of trout can be tested.

Drift was measured in two randomly selected stream sections from each treatment on each of two dates (24 and 28 August). Two daytime (11:00–14:00) and two nighttime (19:30–21:30) measurements were made in each section on each date and the daytime and nighttime averages were used as replicates in analyses. Effects of trout density and sampling date on daytime and nighttime drift propensity were tested using ANOVA, where data from different dates were not considered repeated measures because they were taken in different stream sections.

To test for size-specific drift from the patches of substratum, I compared the head widths of mayflies that drifted

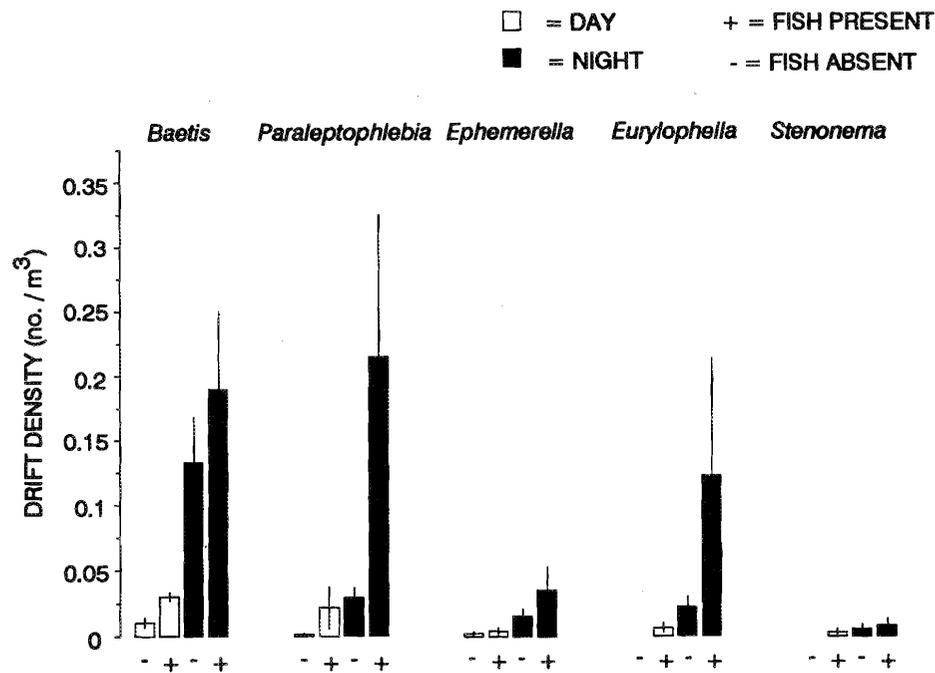


FIG. 1. Daytime and nighttime drift densities of five mayfly taxa in sections of stream where fish were either present at natural densities or had been removed (experiment 1). Error bars are standard errors.

during the night on 24 August with those that remained in the substratum (measurement technique described above). One pair of samples, consisting of mayflies that drifted from the patch (= drifting) versus those remaining in the sediment (= benthic), was picked from each of the stream sections. All of the mayflies in the chosen samples were measured, except some large benthic samples from which I measured only 10 individuals. In a few cases, mayflies from a second pair of samples were also measured to increase sample sizes. Measurements were pooled to generate a mean size for the benthic and drifting mayflies from each section and these section means were used as replicates in analyses. Effects of trout density and source (benthic vs. drifting) on the size of mayflies were tested using ANOVA.

As a second test for size-specific drifting, I compared the sizes of mayflies captured in drift nets placed at the downstream end of the sections with the size of mayflies collected in benthic samples randomly located within the sections. Drift was sampled for six, 1.5 to 2 h periods spaced over 24 h on 29 August by placing a drift net at the downstream end of each stream section. Two randomly located benthic samples (Surber samples; 0.09 m²) were taken in each section after drift sampling ended. Samples were preserved in 70% alcohol and later sorted in the laboratory. Intact mayflies in the samples were measured (using the method described above). I pooled individual measurements to generate mean sizes of both benthic and drifting mayflies for each section. Effects of trout density and source (benthic versus drifting) on mayfly sizes were tested using ANOVA with section means as replicates.

Statistical Analyses

Most drift measurements involved subsampling within the replicate stream sections, but I always pooled subsamples and used stream sections as replicates when testing for effects of fish density to avoid inappropriately inflating the

degrees of freedom for tests (see Hurlbert 1984). In addition to calculating the statistical significance of effects, I also calculated the proportion of the total variation in the data attributable to each term in the ANOVA models (following Vaughan and Corballis 1969; Dodd and Schulz 1973). Non-significant terms were removed from ANOVA models by pooling to allow more powerful tests for effects of fish density, but terms were pooled only if they explained less than 5% of the total variation in the data and if P was >0.25 (following Winer et al. 1991). When effects of fish density were not detected, I calculated the power of the test, i.e., my ability to detect an effect if, in fact, one existed. Power calculations were done following Cohen (1988) and Koele (1982), and are conditional on P (set at 0.05), the sample size, and the size of the effect to be detected. When I removed terms from ANOVA models by pooling, power calculations were made on pooled models because these were the ones used for significance testing.

The two experiments can be considered independent tests of the biological hypothesis that fish affect mayfly drift activity. P values from the two experiments can, therefore, be combined using Fisher's method to generate an overall P value for the hypothesis (Sokal and Rohlf 1981). I used this method when P values for effects of fish in both experiments were low ($P < 0.15$) but not conclusive individually, and the difference between means was in the same direction in both experiments.

Results

Effects of Fish on Drift Activity of Mayflies

Nighttime drift of *Baetis* was consistently increased by the presence of fish. During the first experiment, *Baetis* drifting at night were at higher densities in stream sections containing fish than in sections lacking fish ($F_{1,2} = 48.3$, $P = 0.02$) (Fig. 1). During the second experiment, nighttime

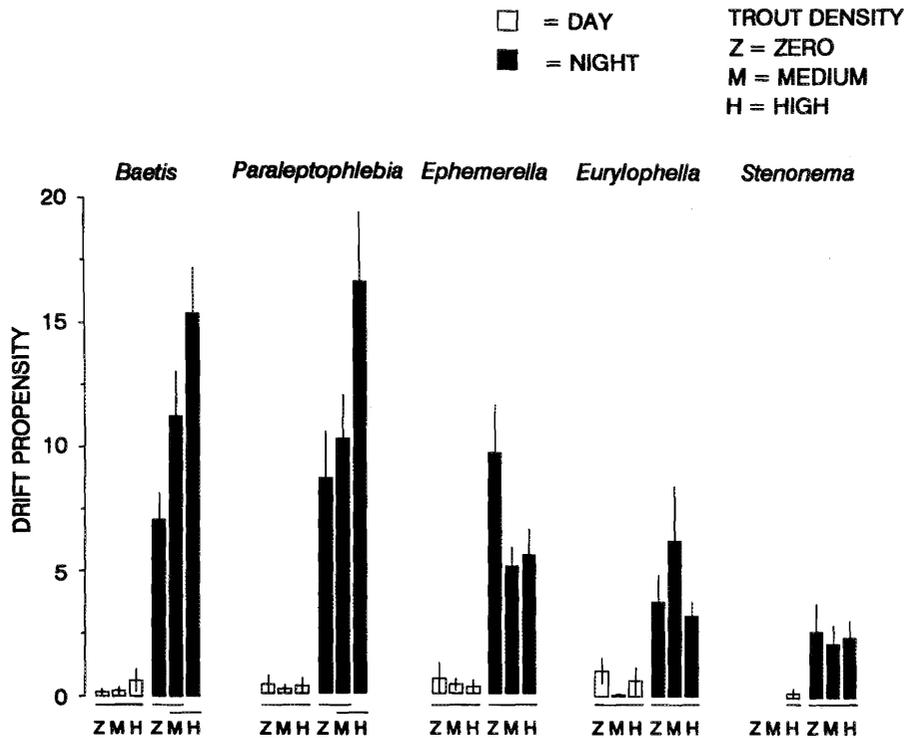


FIG. 2. Daytime and nighttime propensities to drift (drift rate divided by benthic density) from small (2-m-long) patches of substratum for five mayfly taxa exposed to different densities of trout (experiment 2). Error bars are standard errors. Horizontal lines underneath bars indicate means not significantly different at $P < 0.05$ (Tukey's HSD test).

drift propensity of *Baetis* increased with increasing trout density ($F_{2,8} = 17.3$, $P = 0.001$) (Fig. 2). The effect of trout in the second experiment was greater than that of fish in the first experiment, and explained 63% compared with 6.5% of variation in drift activity. Nighttime drift of *Paraleptophlebia* also increased at higher fish densities during both experiments (Fig. 1 and 2), but P values were too high individually to allow firm rejection of the null hypothesis (experiment 1: $F_{1,2} = 7.31$, $P = 0.11$; experiment 2: $F_{2,8} = 4.61$, $P = 0.046$). Combining the P values from the two experiments to calculate an overall P value for the effect of fish density on drift activity strengthens the conclusion that the presence of fish increases nighttime drift of *Paraleptophlebia* ($\chi^2 = 12.68$, $df = 4$, $P = 0.013$). The magnitude of response to fish was more consistent among experiments than for *Baetis*; fish density explained 31 and 47% of variation in drift of *Paraleptophlebia* during the first and second experiments, respectively.

Ephemerella showed a lower propensity to drift at night in stream sections containing trout than in sections without trout during the second experiment ($F_{2,8} = 7.81$, $P = 0.013$) (Fig. 2). Nighttime drift density was, in contrast, unaffected by fish in the first experiment ($F_{1,2} = 2.19$, $P = 0.28$), but the power of the test to detect an effect of the magnitude observed in the second experiment was low (power = 0.36). The weak test provided by the first experiment, and the fact that the difference between means was in the opposite direction in the two experiments (Fig. 1 and 2) precludes any firm conclusion about the effect of fish on *Ephemerella*.

I detected no influences of fish density on nighttime drift density or drift propensity of *Eurylophella* (experiment 1: $F_{1,2} = 0.85$, $P = 0.45$; experiment 2, analysis on log transformed data: $F_{2,8} = 2.70$, $P = 0.13$) and *Stenonema*

(experiment 1: $F_{1,2} = 0.10$, $P = 0.79$; experiment 2: $F_{1,2} = 0.07$, $P = 0.94$) (Fig. 1 and 2). If *Eurylophella* had responded to trout to the same extent as *Baetis*, the response would probably have been revealed by the analyses (power = 0.44 and 0.83 for the first and second experiments respectively). For *Stenonema*, my chances of demonstrating a response of the strength exhibited by *Baetis* were slightly less (power = 0.44 and 0.66 for the first and second experiments, respectively) but, overall, I conclude that *Eurylophella* and *Stenonema* did not alter their drifts rates according to the local density of fish.

Daytime drifting by all five mayflies was low throughout (Fig. 1 and 2). *Baetis* tended to drift more frequently in the presence of fish in both experiments (Fig. 1 and 2), but the response was not significant in either experiment separately (experiment 1: $F_{1,2} = 9.62$, $P = 0.09$; experiment 2: $F_{2,8} = 0.93$, $P = 0.43$), nor when the two tests were combined ($\chi^2 = 6.50$, $df = 4$, $P > 0.1$). No significant responses to fish density were detected for any of the other four mayflies (P always > 0.30) and the tests generally had reasonable power to detect effects of the magnitude shown by *Baetis* at night in the second experiment. For the first experiment power was 0.44 for *Baetis*, *Paraleptophlebia*, and *Eurylophella*, and the other two mayflies were too rare to test. For the second experiment power was 0.66 for *Eurylophella* and 0.83 for the other four mayflies. Overall, these results suggest that fish density does not influence the daytime drift activity of any of the five mayflies.

Effects of Fish on Size-Specific Drifting by Mayflies

Size distributions of *Baetis* were not influenced by the presence of fish in the first experiment (daytime: $F_{1,2} = 0.51$, $P = 0.51$; nighttime: $F_{1,2} = 1.34$, $P = 0.37$) (Fig. 3)

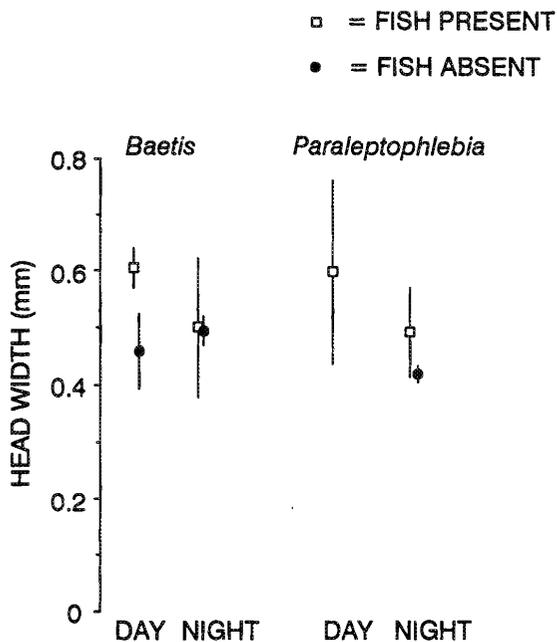


FIG. 3. Mean sizes of two mayfly taxa drifting in sections of stream containing or lacking fish (experiment 1). Error bars are standard errors.

nor by trout in the second experiment ($F_{2,5} < 1.49$, $P > 0.31$). *Baetis* that drifted in the second experiment were, however, significantly larger than those that remained in the substratum at all levels of trout density. This was true when mayflies were sampled from small (0.5 m^2) patches of substratum ($F_{1,5} = 12.5$, $P = 0.017$) (Fig. 4) and from 35-m stream sections ($F_{1,5} = 45.8$, $P = 0.001$) (Fig. 5), suggesting that larger *Baetis* were generally more prone to drift than smaller ones. Fish had no effect on the size distributions of *Stenonema* during the second experiment ($F_{2,5} < 0.79$, $P > 0.50$), but *Stenonema* drifting from small patches of substratum ($F_{1,5} = 7.20$, $P = 0.044$) and from entire stream sections ($F_{1,5} = 4.92$, $P = 0.077$) tended to be smaller than those that remained in the sediment at all levels of trout density. Drift of *Stenonema*, thus also appears to be size specific, but the pattern is in the opposite direction to that displayed by *Baetis*.

The average size of *Paraleptophlebia* drifting at night during the first experiment did not vary significantly according to the presence of fish ($F_{1,2} = 0.78$, $P = 0.47$) (Fig. 3). Trout density also had no influence on the size distribution of *Paraleptophlebia* during the second experiment ($F_{2,5} < 1.08$, $P > 0.40$), nor did drifting *Paraleptophlebia* differ in size from those that remained in the sediment ($F_{1,5} < 0.17$, $P > 0.69$) (Fig. 4 and 5). The mean sizes of the remaining mayflies, *Ephemera* and *Eurylophella*, were similar in the drift and benthos ($F_{1,5} < 0.09$, $P > 0.78$) and were also uninfluenced by the density of trout ($F_{2,5} < 3.3$, $P > 0.12$) (Fig. 4 and 5).

Discussion

Daytime feeding by predatory fish in the water column should select against drifting during daylight hours. Surveys of streams naturally varying in predator presence (Malmqvist 1988; Flecker 1992; Douglas et al. 1994) and

ontogenetic changes in drift periodicity (Allan 1978, 1984; Skinner 1985) provide good evidence that nocturnal drifting evolved because it results in the avoidance of drift-feeding fishes. If nocturnal drifting is a plastic response to fish presence, then drift should become less nocturnal (more evenly divided between day and night) following experimental fish removal. On the other hand, a lack of change in drift periodicity following predator manipulation supports the hypothesis that nocturnal drifting is a fixed avoidance behaviour.

Three of the five mayflies I studied did not alter their daytime or nighttime drift activity respond to the removal of drift-feeding fishes. Three prior studies in which drift-feeding fishes were removed also failed to detect subsequent changes in the drift periodicity of most taxa (Allan 1982; Williams 1990; Flecker 1992). The results of these experiments provide apparent support for the hypothesis that drifting has a fixed diel periodicity. Two other alternative explanations for the nondetection of plastic responses to drift-feeding fish cannot, however, be ruled out. The first is that responses to fish removal take longer to be expressed than the short duration (<2 wk) of these removal experiments (Magurran 1990; Semlitsch and Reyer 1992). The second possibility is that mayflies rely on chemical cues to assess fish presence. Water-borne chemicals may be transported large distances in streams so removal of fish from small areas of a stream might not remove these chemical cues. The experiments cannot, therefore, distinguish whether low daytime drifting is a fixed response or a plastic response to chemical cues released by fishes.

A solution to the confounding of removal experiments by chemical cues is to test for plastic responses by adding fish to areas of streams that otherwise lack fishes, or to work in laboratory streams filled with water never exposed to fish. In a recent study that adopted the former approach, trout addition caused reduced daytime drifting of *Baetis*, which suggests that the nocturnal peak in drift activity of this mayfly is a plastic avoidance response to trout (Douglas et al. 1994). Experiments using the second approach showed that the amphipod, *Gammarus pseudolimnaeus*, displayed reduced nighttime drift in laboratory streams when exposed to extracts from several fishes, including trout (Williams and Moore 1985, 1989). These results are also consistent with the predator avoidance hypothesis because prey may become more nocturnal in the presence of fish by either increasing daytime drift, reducing nighttime drift, or both.

Baetis and *Paraleptophlebia* both increased their rate of nighttime drifting at higher fish densities in my experiments, a response that does not conform to the predator-avoidance hypothesis. The response to fish density during the first experiment could have been to either the brook trout or the black-nosed dace, or both. The rarity of dace, and the similarity to the results of the second experiment, when brook trout alone were present, suggests that effects on mayfly drift propensity were due primarily to brook trout. Another study recently reported a similar response to trout by the amphipod, *Gammarus pulex*, which displayed a transient increase in nighttime drifting but no change in daytime drifting after trout were stocked in two Danish streams (Andersen et al. 1993).

The behavioural mechanisms for, and adaptive significance (if any), of the nighttime responses to trout I observed is unclear. There are three potential mechanisms for increased drift by mayflies in the presence of brook trout: (1) the

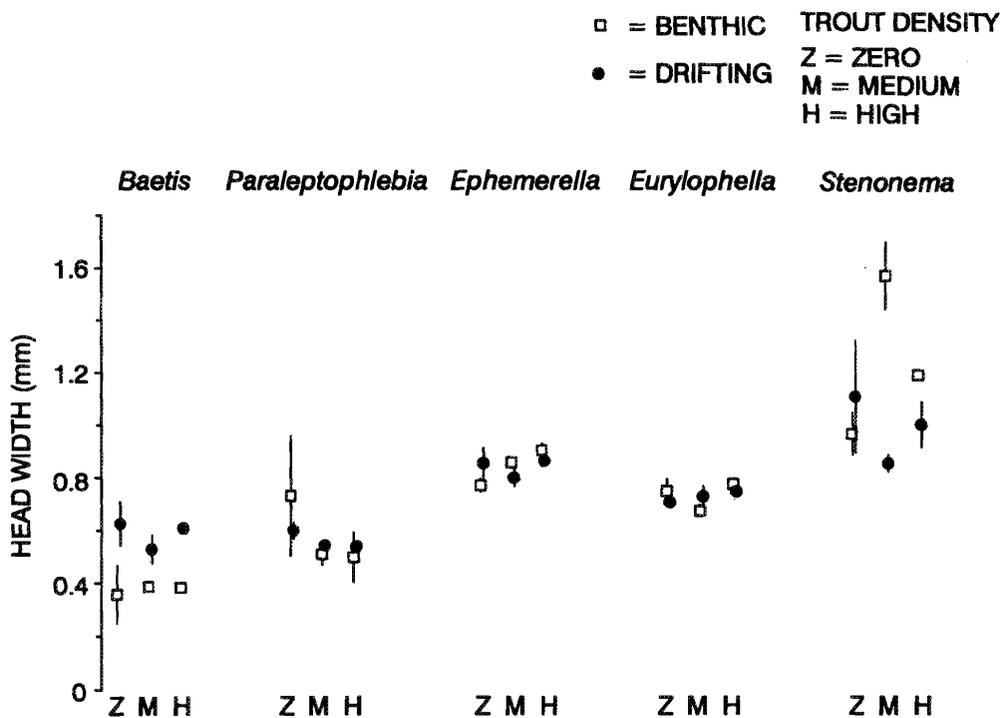


FIG. 4. Size-related patterns of drift for five mayfly taxa exposed to different densities of trout (experiment 2). Drifting mayflies are those departing from small (2-m-long) patches of substratum at night, benthic ones are those remaining in the sediment. Error bars are standard errors.

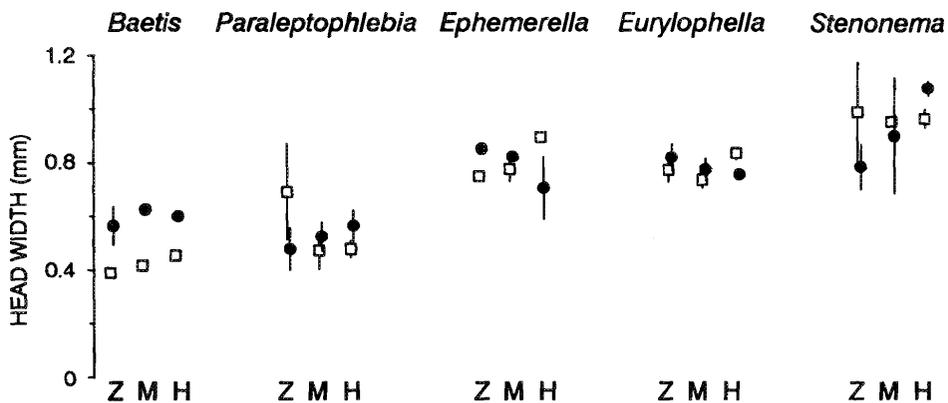


FIG. 5. Mean sizes of five mayfly taxa in 35-m-long stream sections stocked with different densities of trout (experiment 2). Open squares indicate mayflies from benthic samples within the section and solid circles indicate mayflies collected in drift nets at the downstream ends of the sections. Other symbols as for Fig. 4. Error bars are standard errors.

mayflies altered other behaviours, such as positioning on the substratum or locomotor activity, which increased their probability of being dislodged into the water column; (2) the mayflies increased their rate of entry into the water column or distance drifted directly; or (3) mayfly behaviour was unchanged and trout were physically dislodging them from the substratum.

Physical dislodgments as a result of benthic foraging by trout cannot be excluded as a possibility because, although stomach content analyses indicate that salmonids feed mostly by day, a low level of nighttime feeding does occur (Allan 1981; Walsh et al. 1988; Sagar and Glova 1988; Forrester et al. 1994; for an exception see Elliott 1973). Indirect evidence indicates that brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are capable of feeding on drifting

prey at night (Jenkins 1969), but there no direct observations of nocturnal foraging by trout, so whether they feed only in midwater or switch to some degree of benthic foraging is unknown.

Baetis and *Paraleptophlebia* show increased drifting in the presence of benthic fish (Kohler and McPeck 1989; Culp et al. 1991) and predatory invertebrates (Corkum and Pointing 1979; Peckarsky 1980; Malmqvist and Sjöström 1987). Drifting in these studies was not correlated with changes in positioning or activity, suggesting that drifting was not a byproduct of these other behaviours. *Baetis* (Charnov et al. 1976; Culp and Scrimgeour 1993; Cowan and Peckarsky 1994) and other stream invertebrates (Williams and Moore 1985, 1989; Andersson et al. 1986; Feltmate et al. 1986; Feltmate and Williams 1989; Holomuzki and Hoyle 1990) do,

however, show altered positioning and activity in the presence of drift-feeding fish, so changes in these other behaviours could also potentially account for increased nighttime drifting by *Baetis* and *Paraleptophlebia* in my experiment.

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; Culp and Scrimgeour 1993). None of the mayflies, however, showed size-specific drift responses to brook trout density. There was also no tendency for the larger mayfly taxa to be the ones that responded to trout. This result was perhaps not surprising, because the mayfly responses to trout all occurred at night. Selection by trout for larger prey is strong during the day, but is weak or nonexistent at night (Allan 1978; Forrester et al. 1994) and so nighttime responses would not be expected to be size specific.

Increased behavioural drifting at night by *Baetis* and *Paraleptophlebia* exposed to high trout densities would imply that the benefits of this behaviour outweigh the immediate risk of being consumed by trout while drifting. Increased drifting might be an effective response to encounters with trout if a high proportion of nighttime feeding is on the benthos. If, instead most nighttime feeding by trout is in the water column then this behaviour appears, at first sight, to be maladaptive. One potential explanation for such a response, however, arises from the fact that trout are often patchily distributed in space over tens of metres (e.g., Egglisshaw and Shackley 1977; Bohlin 1978; Bowlby and Roff 1986; Newman and Waters 1989). *Baetis* and *Paraleptophlebia* nymphs therefore pass through many patches of varying trout density in their several months of nymphal life. Under these circumstances, drifting more frequently at night from patches of high trout density would result in spending a greater proportion of the daytime in patches of low predator density, when summed over several months. Because risk from trout is greater during the day than at night, this strategy may reduce the long-term risk of predation by trout.

Most studies of how prey respond to risk from visual predators have focused on activities that take place during the day (Stein 1979; Sih 1987; Lima and Dill 1990). The results of my experiments, and those of Andersen et al. (1993), suggest that visual predators can also influence the nighttime behaviour of some taxa. These influences are not well understood and there is a need for further studies of the interactions between visual predators and their prey that occur after dark.

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