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The influence of predatory fish on mayfly drift: extrapolating from experiments to nature

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SUMMARY

1. A knowledge of how individual behaviour affects populations in nature is needed to understand many ecologically important processes, such as the dispersal of larval insects in streams. The influence of chemical cues from drift-feeding fish on the drift dispersal of mayflies has been documented in small experimental channels (i.e. < 3 m), but their influence on dispersal in natural systems (e.g. 30 m stream reaches) is unclear.
2. Using surveys in 10 Rocky Mountain streams in Western Colorado we examined whether the effects of predatory brook trout (*Salvelinus fontinalis*) on mayfly drift, that were apparent in stream-side channels, could also be detected in natural streams.
3. In channel experiments, the drift of *Baetis bicaudatus* (Baetidae) was more responsive to variation in the concentration of chemical cues from brook trout than that of another mayfly, *Epeorus deceptivus* (Heptageniidae). The rate of brook trout predation on drifting mayflies of both species in a 2-m long observation tank was higher during the day (60–75%) but still measurable at night (5–10%). *Epeorus* individuals released into the water column were more vulnerable to trout predation by both day and night than were *Baetis* larvae treated similarly.
4. Drift of all mayfly taxa in five fishless streams was aperiodic, whereas their drift was nocturnal in five trout streams. The propensity of mayflies to drift was decreased during the day and increased during the night in trout streams compared with fishless streams. In contrast to the channel experiments, fish biomass and density did not alter the nocturnal nature nor magnitude of mayfly drift in natural streams.
5. In combination, these results indicate that mayflies respond to subtle differences in concentration of fish cues in experimental channels. However, temporal and spatial variation in fish cues available to mayflies in natural streams may have obscured our ability to detect responses at larger scales.

Keywords: chemical cues, diel periodicity, Ephemeroptera, predation, streams

Introduction

Mayfly larvae are ubiquitous components of stream communities (Allan, 1995) and, for many species, movement in the water column, or 'drift', is their main form of dispersal. The rate of drift is closely related to mayfly foraging (Kohler, 1985) and can influence the fitness of individuals (Peckarsky & McIntosh, 1998), population abundance (Forrester, 1994), and the structure of communities (Diehl *et al.*, 2000). Mayfly movement also affects the apparent impact of predators on their abundance (Cooper, Walde & Peckarsky, 1990; Sih & Wooster, 1994; Englund, 1997; Dahl & Greenberg, 1999; Forrester, Dudley & Grimm, 1999; Diehl *et al.*, 2000).

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The density of mayflies in the drift is frequently low during the day but may increase dramatically after dusk (Elliott, 1967; Waters, 1972; Müller, 1974). Although other explanations have been proposed (see review by Brittain & Eikeland, 1988), the risk of predation imposed by fish that feed visually during the day is a well-documented cause of this observed nocturnal activity (Allan, 1995; Giller & Malmqvist, 1998; Huhta, Motka & Tikkanen, 2000). By reducing movement in the water column during the day, mayflies can reduce the risk of predation by visually feeding fish. However, the relationship between visually feeding fish and mayfly drift is complicated by the influence on drift of chemical cues from the predator, previously studied primarily in small experimental channels or over short distances in natural streams. Chemical cues from predatory trout can affect the periodicity of mayfly drift and its magnitude, and the effect differs according to mayfly size (McIntosh & Peckarsky, 1996; Tikkanen, Muotka & Huhta, 1996; McIntosh, Peckarsky & Taylor, 1999). If mayflies adjust their behaviour according to changes in the concentration of chemical cues, then drift density at night in natural streams should vary with the abundance of trout. To predict the effect of drift on a wide range of processes in streams, it is necessary to determine whether factors affecting mayfly drift in these small experimental channels also operate in natural systems.

Some mayfly behaviour observed in experimental channels or microcosms may not be important or detected in more complex natural systems (Peckarsky, Cooper & McIntosh, 1997; Cooper, Diehl & Sarnelle, 1998). First, fewer replicates and more variability because of uncontrolled environmental factors may reduce statistical power to detect effects in natural systems (Allan, 1982; Townsend *et al*., 1997). Secondly, the effects of behavioural interactions may be swamped by other factors, making them less obvious and important when considered in natural systems. Thirdly, observations at larger scales inevitably include a wider pool of potentially interacting species. Thus, the outcomes of behavioural interactions may be altered by higher-order interactions (Billick & Case, 1994) involving species not considered in microcosm experiments. Finally, interactions among animals need to be studied at the spatial scales over which they move and interact (Carpenter, 1996; Peckarsky *et al*., 1997; Cooper *et al*., 1998). Experiments examining the behaviour of freshwater insects, for example, are frequently conducted at spatial scales of 0.1–5 m. However, some larvae are capable of drifting longer distances (> 6 m; McLay, 1970; Elliott, 1971). Small-scale channel experiments are useful for determining the mechanisms controlling mayfly dispersal. However, their relevance to processes in natural systems must also be evaluated. Moreover, there is a general need to determine the extent to which observations from small experimental systems can be extrapolated to natural systems (Carpenter, 1996; Lodge, Stein & Klosiewski, 1998).

In this study we examined how visually feeding brook trout, *Salvelinus fontinalis* (Mitchell), affected the drift of the mayflies *Baetis bicaudatus* Dodds and *Epeorus deceptivus* (McDunnough) in experimental channels and in Colorado Rocky Mountain streams. Specifically, we addressed the following questions: (1) Are differences in the vulnerability of mayfly larvae to visually feeding fish reflected in their drift behaviour? (2) Are the responses of mayflies to variation in the concentration of chemical cues from fish observed in stream channels matched by variation in their drift behaviour in natural streams? (3) Are the predator-induced changes in mayfly behaviour observed in stream channels overshadowed by other factors that affect drift in natural streams?

Methods

Study system and animals

The study was conducted in streams of the East River catchment near the Rocky Mountain Biological Laboratory (altitude 2900 m) in Western Colorado, U.S.A. The long history of stream research in this catchment enabled us to identify sufficient replicate streams with and without drift-feeding fish (Peckarsky *et al*., 2001). Furthermore, the predator–prey interactions affecting drift of mayfly species in the catchment have been well-documented in small scale experiments (see Peckarsky, 1996). The proximity of the field station to the study streams also enabled us to run these experiments in stream-side channels using natural stream water and lighting, together with animals from the study streams.

Streams in the East River catchment are dominated numerically by mayflies. *Baetis bicaudatus* (Baetidae) is the most abundant and widespread species, but

heptageniid mayflies are also abundant, and *E. deceptivus* (Heptageniidae) is the most common species of that family (Peckarsky, 1991). Late instar *E. deceptivus* are larger than equivalent *B. bicaudatus* and have dorsoventrally flattened bodies, whereas *B. bicaudatus* has a cylindrical profile. *Baetis bicaudatus* is more prone to drift after encounters with predatory stoneflies and generally more mobile than the heptageniid mayflies present in the East River catchment (Peckarsky, 1996).

Cutthroat trout, *Oncorhynchus clarki* (Richardson), is the only native salmonid in this area; but the introduced brook trout now dominates most streams in the East River catchment and *O. clarki* is rarely encountered in high altitude tributaries. Brown trout, *Salmo trutta* L., live at lower altitude in the East River, but no other fish are present in this system.

Experiment 1: Effect of odour concentration on mayfly drift

To determine whether variation in the concentration of chemical cues from brook trout affected drift behaviour of *B. bicaudatus* and *E. deceptivus*, we conducted a stream channel experiment. The concentration of fish chemical cues was manipulated by piping water from holding tanks containing different numbers of brook trout to small stream channels containing mayflies.

The stream channels were circular (15 cm diameter), plexiglass, flow-through chambers housed in a translucent greenhouse beside the East River (see Peckarsky & Cowan, 1991; for a full description of the channels). Filtered stream water (temperature ranges: 5–7 and 3–5 °C during the day and night, respectively) was gravity fed from a fishless stream to 60 channels that had a velocity of 9–11 cm s^{-1} and a depth of 3–4 cm. Two periphyton-covered rocks (≈ 5 cm diameter) from a fishless stream were placed in each channel. Four 96-L tanks were located on a hill above the greenhouse and received 6.7 L min^{-1} of the same fishless water. Four brook trout density treatments (given below) were randomly assigned to the tanks and water from these large tanks was piped to the greenhouse and dripped into the stream channels at a mean (±SE) rate of 9.2 ± 1.0 mL s^{-1}.

We tested the effect of the four odour concentrations (0, 1, 2 and 4 fish per tank) on the drift of *B. bicaudatus*, and of two odour concentrations (zero and two fish) on *E. deceptivus* drift. In addition, we compared the responses of different sized larvae of each mayfly species (mean ± SE head capsule width = 0.90 ± 0.01 and 1.08 ± 0.01 mm for small and large *B. bicaudatus*, respectively, and 1.45 ± 0.02, 1.71 ± 0.02 mm for small and large *E. deceptivus*, respectively). Each of the four *Epeorus* treatments (two odours × two sizes) and eight *Baetis* treatments (four odours × two sizes) was replicated five times for a total of 60 experimental channels. Each channel was stocked with 15 mayfly larvae captured by electrobugging (Taylor, McIntosh & Peckarsky, 2001) from the East River, a stream with brook trout present. Brook trout (162–200 mm fork length, FL) were also captured from the East River by electrofishing and held for 24 h before the experiment in a large holding tank, where they were fed *ad libitum* on mayflies.

Mayflies were introduced to the channels between 13:00 and 15:30 hours mountain daylight saving time (MDST) on 31 July 1997 and the fish were added to the odour tanks at 16:00 hours on the same day. Counts of larvae drifting past a fixed transect during 1 min were made by two observers on three occasions at night (21:30, 22:00, and 22:30 hours MDST on 7 July 1997) and at 09:30, 10:00, and 10:30 hours the next day. Observers used a dim red light to make night observations.

Drift rates of small and large larvae were analysed by ANCOVA, where fish odour concentration was used as a covariate. Separate analyses were completed for *B. bicaudatus* and *E. deceptivus*.

Experiment 2: Vulnerability of drifting mayflies to predatory brook trout

We compared the vulnerability of drifting *B. bicaudatus* and *E. deceptivus* larvae to brook trout predation in a large observation tank during day and night. The tank (internal $L \times W \times H = 1.98 \times 0.45 \times 0.42$ m) was constructed from 5 mm clear acrylic plastic, positioned 5 m from the East River, and covered by a translucent white tarpaulin suspended 1 m above it. Water from the East River was pumped through the tank at a rate of 5.0 L s^{-1}. A 1.2-m long observation area was delineated within the tank by plastic mesh (2-cm diameter) that prevented fish from moving out of it. The observation area was isolated from observers by opaque plastic screens. By arranging rocks in the observation area we manipulated the behaviour of

fish so that they chose to hold station about 80 cm downstream from four feeding tubes used to release prey into the water column. The tubes rose 10 cm from the gravelled tank-bottom and were arranged in a diamond formation near the upstream part of the observation area. Current velocity and depth varied from 5 to 18 cm s^{-1} and 16–30 cm, respectively, within the tank; but where the fish generally chose to hold station they were 15 cm s^{-1} and 24 cm, respectively.

Brook trout were captured from the East River by electrofishing and held in a large holding tank (1.5 × 0.8 × 0.8 m) for up to 3 days before an observation trial while being fed mayflies *ad libitum*. Twenty-four hours before a trial, a fish was placed in the observation area to acclimate. During acclimation, fish were fed mayflies through the feeding tubes in daylight until at least 10 larvae had been eaten. To ensure that each fish was actively foraging before starting a feeding trial, mayflies were released into the water column until the fish had attempted to consume at least two larvae. Apart from these food items, fish were starved while in the observation tank prior to a trial. Fish that did not acclimate to feeding were replaced.

Replicate trials were run during day (10:30–14:30 hours) and night (20:40–22:20 hours) with a total of six brook trout (mean ± SE, 197 ± 3 mm FL; range, 206–188 mm FL), four in August and September 1996 and two in July 1997. One day and one night trial were run with each fish and the order of trials (day first or night first) was randomised. Water temperature in the tank ranged from 5 to 11 °C during the day and 4–7 °C at night. During each trial 10 large and 10 small larvae of each mayfly species (i.e. a total of 40 larvae) were fed to each fish (mean ± SE head capsule width was 0.77 ± 0.01 and 0.95 ± 0.01 mm for small and large *B. bicaudatus*, respectively; 1.28 ± 0.02 and 1.56 ± 0.03 mm for small and large *E. deceptivus*, respectively). Larvae were flushed through the feeding tubes at a rate of approximately 1 min^{-1} so they entered the water column upstream of the fish. The different mayfly species and sizes were presented in random order and larval delivery was rotated among the four feeding tubes. The passage of each prey item and the resulting response of fish were recorded using an infrared light-sensitive video camera (Sony SSC-M359, Tokyo, Japan) and a Hi8 video recorder (Sony EVC200). Light filtering through the white tarpaulin provided illumination during the day (1000–9000 lux at the water surface depending on cloud cover). At night, illumination was provided by two 50-W bulbs housed in a light-proof housing covered with a plastic infrared filter (Farnell Electronics, Leeds, UK). The lights produced < 0.1 lux of light in the visible range (< 720 nm), but the infrared light, which is generally invisible to fish (Allen & Muntz, 1983), enabled activity in the tank to be recorded by the camera.

Results of trout foraging are reported in terms of the number of prey detected and captured. Reaction distance to prey was calculated as the linear distance between the prey item and the snout of the fish when the prey was first detected. The time of detection was easily determined because, when fish detected a mayfly, they orientated directly towards it and formed a curved or s-shaped attack body form.

We tested the effects of prey species and prey size on prey consumption rate and predator reaction distance using factorial repeated measures ANOVA with time as the repeated measure. Variation between individual fish was included as a blocking factor in the ANOVAS to improve the power of the analyses. However, because some fish did not eat some types of prey there were not enough degrees of freedom to test the full model on fish reaction distance. Thus, we conducted separate ANOVAS on day and night fish reaction distances. Prey consumption rate was square-root transformed to normalise the data.

Drift patterns in the field

We investigated the drift behaviour of mayflies in response to spatial variation in fish abundance and other biological and physical factors in natural streams by conducting a survey of five fishless and five trout streams in the East River catchment (Table 1), and an additional six sites in the East River itself. The six additional East River sites were sampled to bolster the comparison of reaches with different fish abundance. Two Wildco® (Wildlife Supply Company, Saginaw, USA) drift nets (30 × 20 cm front opening, 1 m long, 200 μm mesh) were placed in riffles at each sampling site for 10 min during the day (starting 10:00 hours) and night (starting 22:00 hours). Sampling took place between 21 July and 4 August 1997 with one fishless stream and one fish stream being sampled each day. Water velocity through the drift nets was measured by timing the passage of fluorescein dye through the net. Current velocities

Table 1 The habitat and faunal characteristics of fish and fishless streams used in the field drift survey

Site name	Brook trout biomass ($g\ m^{-2}$)	Night *Baetis* drift density (no. m^{-3} water)	Day *Baetis* drift density (no. m^{-3} water)	*Baetis* benthic density (no. m^{-2})	Altitude (m)	Channel width (m)	Mean depth (cm)	Mean current velocity ($cm\ s^{-1}$)	Discharge ($0.1\ m^3\ s^{-1}$)	Conductivity ($\mu S\ cm^{-1}$ at 25 °C)	Median substratum particle size (cm)
Avery Creek	13.64	5.170	0.943	280	2940	1.4	12	68	0.39	196	6.9
Copper Creek	1.13	6.353	1.166	143	2860	8.9	24	73	10.67	190	13.3
East River	0.80	8.668	0.822	467	2890	10.5	22	43	12.21	155	14.4
Rustlers' Gulch Creek	1.28	2.316	0.386	172	2950	4.7	22	57	4.32	270	17.2
Lower Rock Creek	0.67	4.135	0.943	157	2930	5.0	9	22	0.37	181	8.9
Upper Benthette Brook	0	1.700	2.731	383	2930	0.8	8	68	0.13	126	5.9
Upper Rock Creek	0	1.768	2.652	89	2990	5.0	14	56	0.38	187	17.8
Snodgrass Creek	0	0.038	0.096	7.4	2940	0.9	4	38	0.02	150	12.8
Lower Benthette Brook	0	2.256	0.684	139	2910	2.0	6	25	0.24	130	5.6
Billy's Brook	0	–	–	26	2920	0.9	5	20	0.10	151	9.4

– Indicates *Baetis* was not present in the drift.

were moderately fast (mean ± SE, 51 ± 4 $cm\ s^{-1}$; range, 33–79 $cm\ s^{-1}$), and sampling locations were relatively shallow (mean ± SE, 18 ± 2 cm; range, 27–7 cm). Invertebrates were removed from the nets and preserved in 90% ethanol with rose bengal dye added to aid sample sorting. All invertebrates were identified to the lowest taxonomic level possible under 25× magnification (using Peckarsky, Dodson & Conklin, 1985; Merritt & Cummins, 1995). The head capsule widths (HCWs) of *B. bicaudatus* were measured to the nearest 0.1 mm. Drift density was calculated using Equation 1 of Allan & Russek (1985) and expressed as numbers m^{-3} of water.

The day after drift sampling we also measured several biotic and abiotic variables that could potentially explain variation in mayfly drift at each site (Table 1). Fish density and biomass per unit area were estimated by electrofishing with depletion sampling between stop nets in a 20–30 m reach using a backpack electrofishing machine (Smith-Root Model 15-C, Vancouver, USA). Fish were weighed to the nearest mg, measured (FL) to the nearest mm and then released. Fish density was calculated using the maximum likelihood equations for three-pass depletion sampling (Cowx, 1983), and biomass was estimated by summing the mass of captured fish. Benthic invertebrate density was estimated using electrobug sampling inside a modified Hess sampler (30.5 × 30.5 cm, area = 0.09 m^2) with clear plastic sides, 280-μm mesh on the upstream end and a Wildco® 30 × 25 cm drift net (200 μm) on the downstream end (Taylor *et al*., 2001). Invertebrates inside the sampler were induced to drift into the downstream net with 90 s of electroshocking using standard settings (60–80 pulses s^{-1} and a pulse width of 6 ms) and a 15-cm electrode (Smith-Root, Vancouver, part no. APA83-6). Algal standing crop was estimated by measuring chlorophyll *a* from the upper surface of 10 randomly selected cobbles (70–120 mm maximum diameter) using the method of Flecker & Townsend (1994). Mean depth, velocity using a Flo-mate® current meter (Marsh-McBirney, Frederick, MD, USA), and discharge were estimated on three transects at each site. Substratum particle size distribution was assessed by measuring the maximum diameter of 30 randomly selected particles from each site. Conductivity was measured with a YSI model 30 m (YSI Incorporated, Yellow Springs, USA) and altitude was obtained from topographic maps.

The relationship between the propensity of mayflies to drift and fish biomass was examined using least-squares regression on the data from the 11 reaches that contained fish. We used drift propensity (drift density/benthic density) as the response variable in these analyses to eliminate the possibility that the observed patterns simply reflected variations in benthic density. Differences in the drift propensity of mayflies in fish and fishless streams during the day and night were analysed using repeated measures ANOVA (with time as the repeated measure). We also tested for differences in the diel periodicity (the ratio of night/day drift densities; Flecker, 1992) of drift in the five fish and five fishless streams and in relation to fish biomass using *t*-tests and regression, respectively, on the $\log_e$-transformed ratio of night drift density/day drift density. Analyses were only conducted on taxa present in at least three of the replicate fishless streams.

All habitat variables measured from the five fish and five fishless streams were subjected to principal components analysis (PCA) using the correlation matrix to extract components that described the habitat in terms of a limited number of easily comparable independent variables. Habitat variables were transformed where necessary to satisfy the assumptions of this analysis. Components explaining > 5% of the variance in the habitat measurements were used in subsequent analyses. We tested for differences in physical variables of the fish and fishless streams using MANOVA followed by ANOVA on individual response variables. Relationships between mayfly drift and all variables measured (including the habitat PCA) were investigated with stepwise multiple regression using the Systat 5.2 forward stepping procedure. Drift propensity (drift density/benthic density) was also used as the response variable in these analyses to ensure that relationships were not the result of differences in benthic density.

Results

Experiment 1: Effects of fish odour concentration

In the stream channel experiment, no drift was observed during the day and fish odour concentration altered the nocturnal drift rate of *B. bicaudatus* but not that of *E. deceptivus* (Fig. 1). The ANCOVA indicated that fish density had a significant effect on *B. bicaudatus* drift ($F_{1,37} = 4.95$, $P = 0.03$) whereas mayfly size did not affect the drift rate ($F_{1,37} = 0.34$, $P = 0.56$), and there was no mayfly size × fish density interaction ($F_{1,36} = 0.72$, $P = 0.40$). The response of *B. bicaudatus* to odour concentration was not linear, however, and was probably best described by a threshold response where only the odour concentration from at least two fish was sufficient to reduce nocturnal drift rate. A *posthoc* contrast, comparing the effects of one or zero fish vs. the effects of two or four fish, was significant ($F_{1,36} = 7.01$, $P = 0.01$), whereas the effect of one fish was not significantly different from that of no fish ($F_{1,36} = 0.001$, $P = 0.99$).

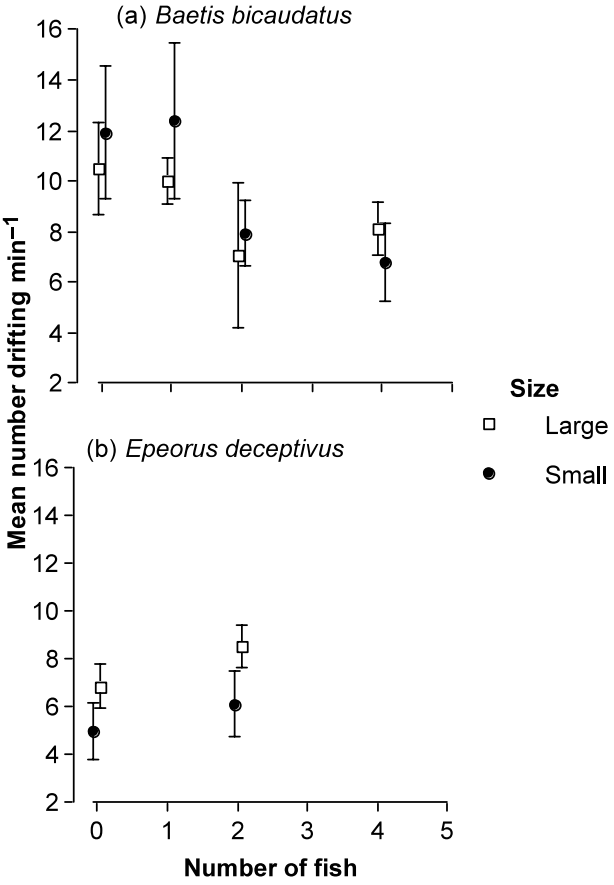


Fig. 1 Mean (±SE) drift rate of (a) small and large *B. bicaudatus* and (b) small and large *E. deceptivus* in stream channels receiving water from tanks containing different numbers of brook trout during Experiment 1. Drift was measured between 21:00 and 22:30 hours MDST. See Methods text for mayfly sizes.

Experiment 2: Vulnerability of drifting mayflies to capture by predatory brook trout

Brook trout, once acclimated to the observation tank, held station and attempted to capture prey by day and

night. We observed large diel variation in their ability to detect and capture prey. Drifting mayflies were four to five times more likely to be consumed during the day than at night, but night predation rates were still measurable (Fig. 2, Table 2). *Epeorus* larvae released into the drift by observers were more vulnerable to trout predation than *Baetis* larvae, and large larvae of both species were more vulnerable than small both by day and night (Fig. 2). These effects were indicated by significant main effects of prey species and size in the ANOVA, but no significant interactions between prey species and prey size (Table 2).

Brook trout captured almost all the prey detected; however, the proportion detected but not captured was generally higher at night (Fig. 2). Trout reaction distance was significantly shorter at night (repeated measures ANOVA, time effect: $F_{1,12} = 134.19$, $P < 0.0001$; Fig. 2). When separate ANOVAS were conducted on day and night reaction distances, significant effects of prey species and size were found during the day, but not during the night (Table 2). This result indicates that prey species and size had important effects on the ability of fish to detect prey during the day, but not at night.

Drift patterns in the field

We observed a wide range of fish biomass and density in natural streams, but no significant relationship (regression: $P > 0.1$) was found between fish biomass and the drift propensity of any taxon in the 11 reaches sampled (Fig. 3, Table 3).

In contrast, the presence or absence of predatory brook trout had a large influence on the diel drift patterns of mayfly larvae in the streams surveyed. Drift was consistently nocturnal in streams with fish, but aperiodic in streams lacking fish (Figs 4 and 5). The analysis of drift propensity (Table 4), which standardised for differences in benthic density, indicated that the effect of predatory fish was different during the day and night. During the day, drift propensity of all taxa in trout streams was lower than

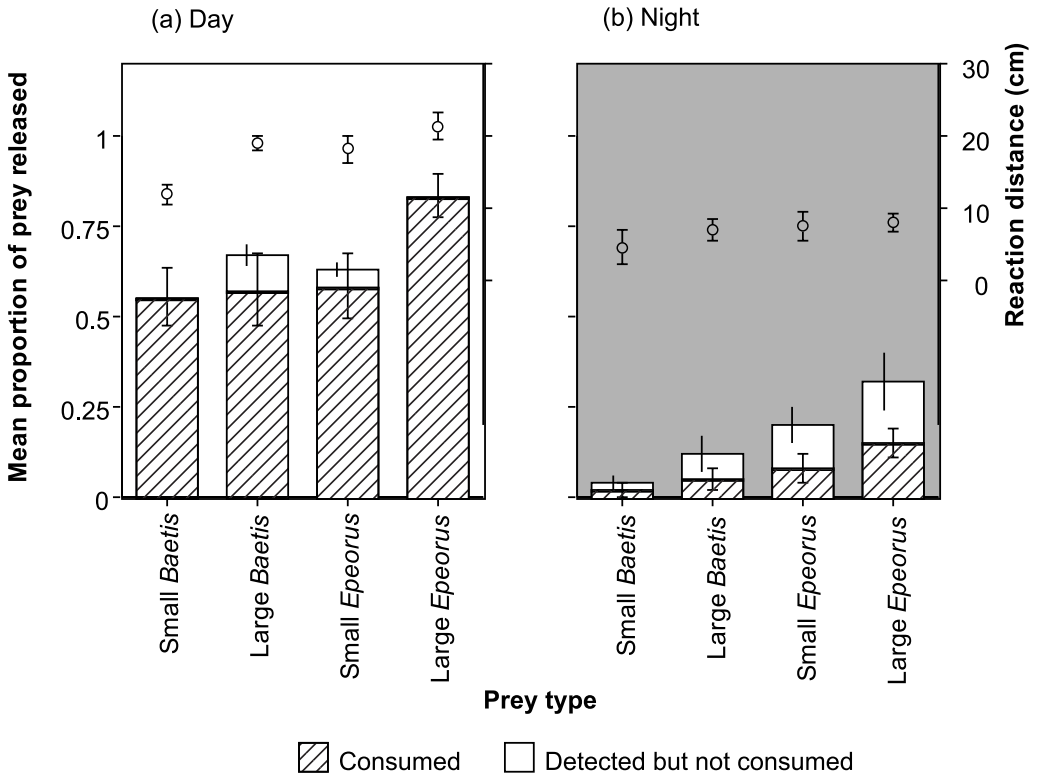


Fig. 2 The capture rate of prey by brook trout in an observation tank during the day (a) and the night (b) measured as the mean (±SE) proportion of prey released that were consumed (hatched bars), mean (±SE) proportion detected but not captured (white bars), and mean (±SE) reaction distance (white circles) in Experiment 2. The prey were small and large *B. bicaudatus* and *E. deceptivus* mayfly larvae. See Methods for mayfly sizes.

Source	d.f.	MS	*F*-ratio	*P*-value
(a) Number consumed				
Between subjects				
Size	1	0.704	4.95	0.04
Species	1	2.506	17.60	< 0.001
Fish	5	0.611	4.29	0.01
Size × species	1	0.080	0.56	0.46
Error	15	0.142		
Within subjects				
Time	1	41.214	178.91	< 0.001
Time × size	1	0.010	0.045	0.83
Time × species	1	0.301	1.30	0.27
Time × fish	5	1.126	4.89	< 0.01
Time × size × species	1	0.298	1.29	0.27
Error	15	0.230		
(b) Reaction distance				
Day				
Size	1	153.520	22.21	< 0.001
Species	1	111.370	16.11	< 0.01
Fish	5	39.722	5.75	< 0.01
Size × species	1	23.800	3.44	0.08
Error	15	6.912		
Night				
Size	1	8.169	0.66	0.31
Species	1	13.602	1.10	0.43
Size × species	1	2.771	0.23	0.64
Error	12	12.309		

Table 2 Repeated measures ANOVA on the results from Experiment 2: (a) the mean number of small and large (size) *B. bicaudatus* or *E. deceptivus* (species) consumed by brook trout in an observation tank during the day and night (time) and (b) ANOVAs on the reaction distance of brook trout during the day and night. For fish consumption, data were square root transformed counts. Variation between individual fish (fish) was included as a blocking variable to improve the power of the analysis

that in fishless streams. At night, drift was increased in trout streams in comparison with that in fishless streams (Fig. 4). Mayfly drift was significantly more nocturnal in streams with predatory fish than in streams without fish (*B. bicaudatus*: $t_{5,4} = 4.46$, $P = 0.002$; total heptageniids: $t_{5,3} = 4.26$, $P = 0.005$; *Cinygmula* spp. $t_{5,3} = 3.20$, $P = 0.019$). However, there was no effect of fish biomass on the tendency towards nocturnal drift (*Baetis* regression: $F_{1,9} = 0.61$, $P = 0.46$; Heptageniidae regression: $F_{1,9} = 0.66$; $P = 0.44$; Fig. 6).

Three components that collectively explained 96% of the variance among streams in the habitat variables measured were identified by PCA (Table 5). Component 1 was correlated with stream size, component 2 with altitude and component 3 with stream current velocity (Table 5). Although fish and fishless streams overlapped in their physical characteristics, univariate ANOVA indicated that streams with fish were on average larger than fishless streams (Table 5). However, when mayfly drift propensity was used as the dependent variable in stepwise multiple regression models using other biotic and abiotic measurements as the independent variables, the models generally explained small proportions of variation in mayfly drift and no significant regressions were obtained. Correlation coefficients are reported in Table 6. Thus, the primary influence on mayfly drift at the reach scale appeared to be the presence or absence of fish, which affected the tendency to be nocturnal.

Discussion

In these Rocky Mountain streams, drift of all mayfly taxa examined was nocturnal where drift-feeding predatory brook trout were present. Previous studies suggest that nocturnal drift by mayflies reduces the risk of predation by drift feeding fish (Flecker, 1992; Douglas, Forrester & Cooper, 1994; McIntosh & Townsend, 1994). The results from our brook trout feeding study (Experiment 2), which demonstrated that drifting mayflies were four or five times more vulnerable to trout predation during the day than at night, strongly support this hypothesis.

Streams containing fish tended to be larger than fishless streams. Nonetheless, observed differences in drift periodicity between fish and fishless streams

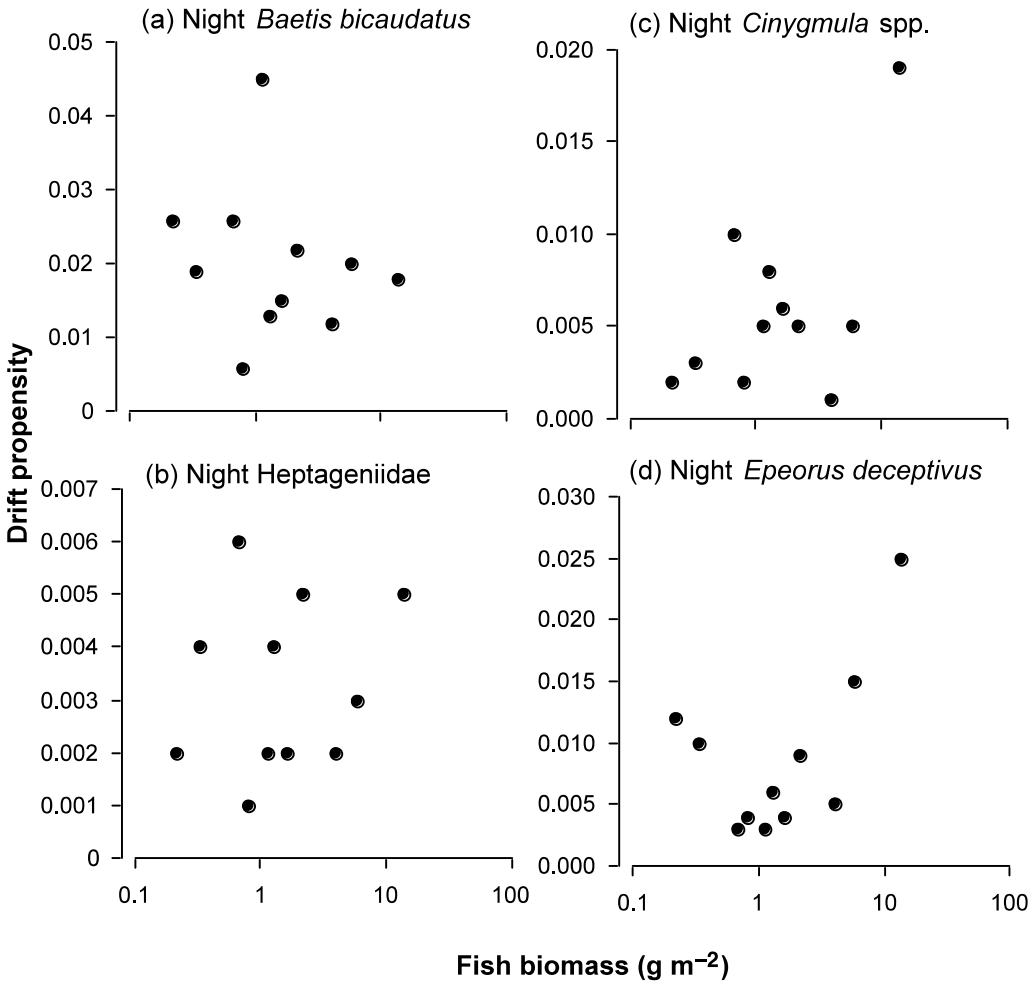


Fig. 3 The relationship between fish biomass per unit area of stream and the night drift propensity (calculated as drift density/benthic density) of (a) *B. bicaudatus*, (b) total Heptageniidae, (c) *Cinygmula* spp. and (d) *E. deceptivus* mayfly larvae in streams with fish. Data plotted come from those sites used in the comparison between fish and fishless streams and six additional sites in the East River. Note different scales of Y-axes used for different taxa of mayflies, because of higher drift propensity of *Baetis* compared with the Heptageniidae.

could not be attributed to physical differences between them, because nocturnal drift was observed in all fish streams, including two small trout streams that were the same size as most fishless streams (Table 1). Moreover, no significant correlations between the drift density of any taxa and other biotic and abiotic variables measured were detected. Thus, the major factor influencing drift at the reach scale appeared to be the presence or absence of drift-feeding fish.

Despite there being substantial variation in the size and morphology of different mayfly taxa, their diel periodicity was remarkably similar. That is, night to day drift ratios in fish streams were all around 10 : 1. This finding suggests that all of these Ephemeroptera species have fixed behavioural responses to trout presence. Once nocturnal behaviour is established after contact with fish, most mayflies continue to avoid daytime drift even when returned to a fishless habitat (Ciborowski, 1983; Kohler, 1985; McIntosh & Townsend, 1994; Peckarsky & McIntosh, 1998; Drinnan, 2000). This result is logical from an evolutionary perspective; once a mayfly drifts from a fishless stream to one with fish, there is a high probability that it will be in a fish stream for the rest of its larval life. The high daytime predation risk associated with drift-feeding fish also affects a large number of behaviours that can reduce drift density in streams (e.g. avoidance of the substratum surface, McIntosh & Townsend, 1994;

Source	d.f.	MS	*F*-ratio	*P*-value	r^2
(a) *Baetis bicaudatus*					
Day					
Fish biomass	1	0.010	0.014	0.91	0.02
Error	9	0.759			
Night					
Fish biomass	1	0.00003	0.294	0.60	0.03
Error	9	0.00011			
(b) Total Heptageniidae					
Day					
Fish biomass	1	0.583	1.37	0.27	0.13
Error	9	0.425			
Night					
Fish biomass	1	0.9×10^{-7}	0.326	0.58	0.04
Error	9	0.27×10^{-5}			
(c) *Cinygmula* spp.					
Night					
Fish biomass	1	1.12	1.48	0.25	0.14
Error	9	0.758			
(d) *Epeorus deceptivus*					
Night					
Fish biomass	1	0.655	1.36	0.27	0.13
Error	9	0.481			

Table 3 Tests using regression of the relationship between fish biomass and the drift propensities (drift density/benthic density) of (a) *Baetis bicaudatus* (day $\log_e$ transformed), (b) total Heptageniidae (day $\log_e$ transformed), (c) *Cinygmula* spp. ($\log_e$ transformed), and (d) *Epeorus deceptivus* ($\log_e$ transformed). There was insufficient day drift to complete the analysis for some taxa

reduction in encounters with predatory invertebrates, McIntosh & Peckarsky, 1996).

Interestingly, the match between the effect of fish on mayfly drift periodicity in the experimental channels and in natural streams was not consistent. No drift was observed during the day in the channels. Nevertheless, we consistently measured small amounts of daytime drift in all taxa during the field sampling. This daytime drift was not because of small larvae, invulnerable to predation (Allan, 1978), drifting during the day, because almost all *Baetis* larvae drifting (> 95%) were relatively large (i.e. > 0.65 mm HCW). Mayfly larvae in natural streams which experience higher current velocities than those in our channels, are exposed to predatory invertebrates **(**stoneflies**)**, and may suffer from food shortage, all of which are known to induce mayfly drift (Ciborowski, 1983; Kohler, 1985; Lancaster, 1990). Thus, the wider range of field conditions may make some daytime drift inevitable, despite the presence of visually feeding fish.

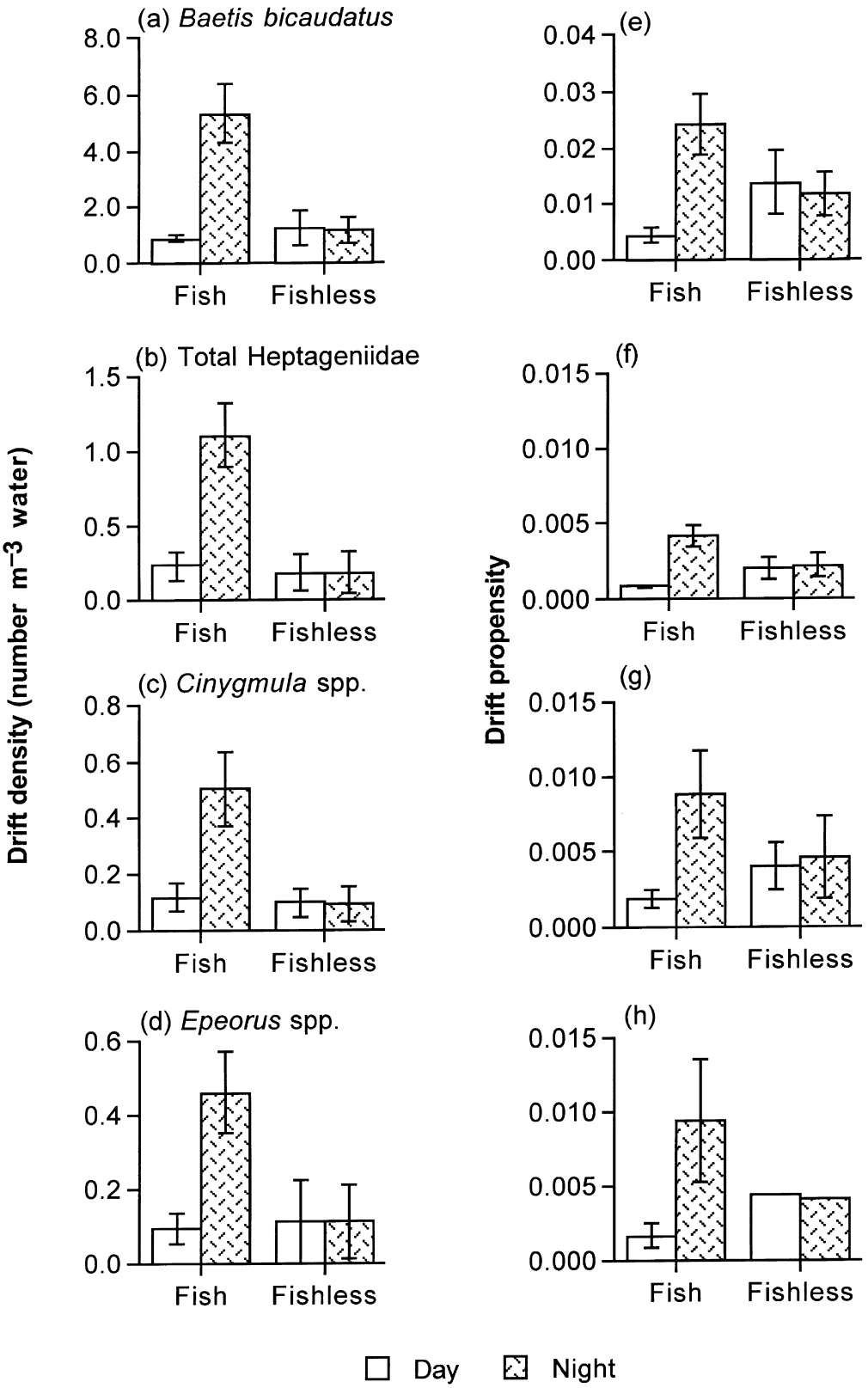
Mayfly responsiveness to different concentrations of fish odour

In the stream channel experiments, we observed that *B. bicaudatus* nymphs changed their behaviour in response to the concentration of brook trout odour. Such a response is consistent with the results of previous experiments, in which large *B. bicaudatus* reduced the magnitude of their nocturnal drift in mesocosms (0.8 m^2) when fish odour from two brook trout was present, and when encountering plumes of a similar concentration of fish odour (approximately 3.5 m in length) in natural streams (Peckarsky & McIntosh, 1998; McIntosh *et al*., 1999).

It seems reasonable that large mayfly larvae should avoid daytime drift if they are four or five times more vulnerable to trout predation by day than by night. It is less clear why mayflies should alter their behaviour

►

Fig. 4 Mayfly drift density (mean ± SE) during the day (10:00 hours) and night (22:00 hours) from streams with and without fish for (a) *B. bicaudatus*, five fish and four fishless streams; (b) total Heptageniidae, five fish and four fishless streams; (c) *Cinygmula* spp., five fish and three fishless streams; (d) *Epeorus* spp., five fish and one fishless and mayfly drift propensities (mean ± SE, calculated as drift density/benthic density) for the same times and taxa (e–h respectively). The number of replicate streams included in the comparisons varies for each taxon, because some taxa were not present in all streams. Note different scales of *Y*-axes used for different taxa of mayflies, because of higher drift densities of *Baetis* versus the heptageniids.


(a) Baetis bicaudatus
8.0
6.0
4.0
2.0
0.0
Fish
Fishless
(b) Total Heptageniidae
1.5
1.0
0.5
0.0
Fish
Fishless
(c) Cinygmula spp.
0.8
0.6
0.4
0.2
0.0
Fish
Fishless
(d) Epeorus spp.
0.6
0.4
0.2
0.0
Fish
Fishless
(e)
0.04
0.03
0.02
0.01
0.00
Fish
Fishless
(f)
0.015
0.010
0.005
0.000
Fish
Fishless
(g)
0.015
0.010
0.005
0.000
Fish
Fishless
(h)
0.015
0.010
0.005
0.000
Fish
Fishless
Drift density (number m−3 water)
Drift propensity
Day
Night

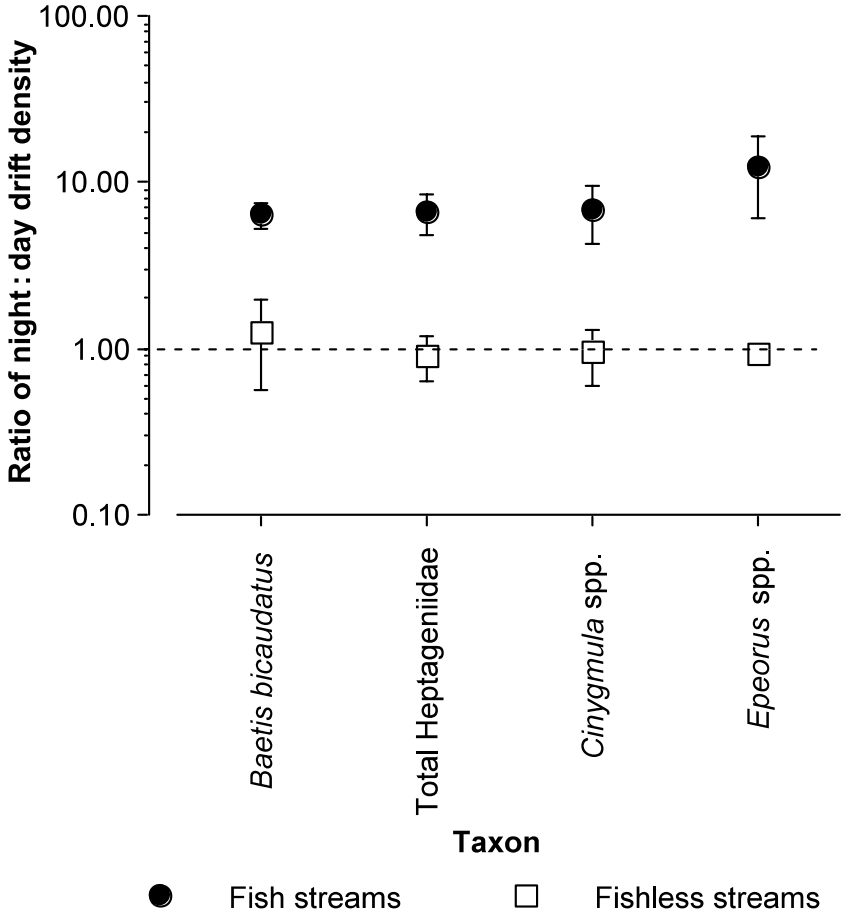


Fig. 5 The ratio of night to day drift density for streams with (solid circles) and streams without (open squares) predatory fish. The number of replicate streams included varies for each taxon, because of low numbers or taxa absent from some streams: *B. bicaudatus*, five fish and four fishless; total Heptageniidae, five fish and three fishless; *Cinygmula* spp., five fish and three fishless; *Epeorus* spp., five fish and one fishless.

to avoid drift-feeding fish at night. Our observations of brook trout foraging provide a possible explanation. Under relatively natural lighting conditions, fish were able to consume 5–10% of the larvae released into the water column during the night. Consistent with this, local anglers have reported catching trout at night, most trout stomachs contain prey at night (e.g. Allan, 1981; Angradi & Griffith, 1990; Glova & Sagar, 1991), and other experiments have demonstrated that salmonid fishes are capable of nocturnal foraging (Jenkins, 1969; McIntosh & Townsend, 1995; Giroux, Ovidio & Baras, 2000). Atlantic salmon, *S. salar* L., and brown trout, *S. trutta* L., even switch to predominantly nocturnal foraging at low environmental temperatures (Fraser, Metcalfe & Thorpe, 1993; Heggenes *et al*., 1993). Thus, although drift-feeding fish present a higher predation risk during the day, the risk to large drifting mayfly larvae at night is still measurable. Thus, there is some adaptive advantage for mayflies to avoid drift in areas where drift-feeding trout are present, even at night.

Streams inhabited by drift-feeding fishes probably contain some background concentration of fish odour. Interestingly, *B. bicaudatus* larvae from fishless streams changed to nocturnal behaviour when exposed to fish stream water of unknown fish odour concentration (Cowan & Peckarsky, 1994). However, the reduction in nocturnal drift of *B. bicaudatus* reported here from the experimental channels receiving odour from two or more fish, but not in the one fish treatment, indicates that *B. bicaudatus* may respond to fish odour above some threshold concentration. *Baetis* larvae may therefore exhibit increased predator-avoidance behaviour (reduced drift) when fish odour concentration is sufficient to indicate the proximity of a fish.

In contrast to *B. bicaudatus*, fish odour concentration had no effect on the drift of *E. deceptivus* (Experiment 1), despite our finding that *E. deceptivus* was more vulnerable than *B. bicaudatus* to trout predation (Experiment 2). However, the different responses of *Baetis* and *Epeorus* are consistent with their resource

Table 4 Repeated measures ANOVA on the drift propensity (drift density/benthic density) of (a) *B. bicaudatus* [ln(x) transformed], (b) total Heptageniidae [ln(x + 1) transformed], in streams with and without predatory brook trout (Fish) during the day and night (Time, the repeated measure). There were insufficient data to analyse individual heptageniid taxa separately

Source	d.f.	MS	*F*-ratio	*P*-value
(a) *B. bicaudatus*				
Between subjects				
Fish	1	0.050	0.075	0.80
Error	7	0.662		
Within subjects				
Time	1	3.04	14.22	< 0.01
Time × Fish	1	4.25	19.85	< 0.01
Error	7	0.214		
(b) Total Heptageniidae				
Between subjects				
Fish	1	5.0×10^{-5}	0.191	0.68
Error	7	2.5×10^{-4}		
Within subjects				
Time	1	0.0014	16.2	< 0.01
Time × Fish	1	0.0011		< 0.01
Error	7	0.8×10^{-4}		

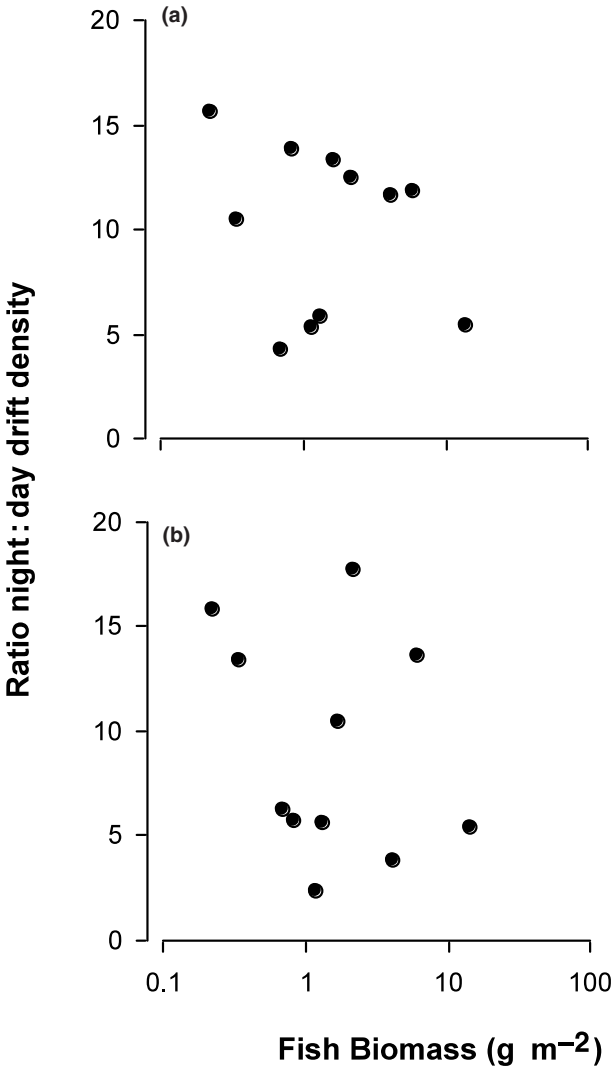


Fig. 6 The relationship between fish biomass per unit area of stream and the ratio of night to day drift density for (a) *Baetis bicaudatus* and (b) total Heptageniidae. Note that only values for streams containing fish are shown. See Fig. 5. for a comparison of fish and fishless streams.

acquisition and predator avoidance behaviours. Peckarsky (1996) argued that heptageniid mayflies such as *Epeorus* maximised their fitness by avoiding energetically costly and conspicuous swimming, and rather crawled within and between food patches. The high mortality rate suffered by *Epeorus* when drifting would provide strong selection for a less mobile lifestyle. *Epeorus* has little to gain by modifying its behaviour according to a chemical cue concentration because it drifts so infrequently. Moreover, heptageniids may be physically incapable of quickly settling out of the water column after detecting fish cues, because they have a dorsoventrally flattened body that is less suited to swimming. In contrast *Baetis*, which maximises its fitness by being highly mobile, could decrease its mortality rate considerably by avoiding drift or reducing drift distance in risky situations.

Effects of fish odour in natural streams

As *B. bicaudatus* has responded to changes in the concentration of fish chemical cues, we suspected here that stream reaches containing a higher abundance of fish may have a lower drift density of *B. bicaudatus*. In the stream channel experiments reported here, *B. bicaudatus* altered their behaviour in response to water piped from a tank with two fish per ~100 L, but not to one fish per ~100 L, although the actual concentration of chemicals experienced by the mayflies when diluted in channels was unknown. Nevertheless, we detected no effect of fish biomass on the drift of any mayfly taxon at the reach scale. One possible explanation is that, despite the large range of fish biomass in the reaches sampled, the concentration of fish chemicals in the streams sampled did not

Table 5 Multivariate and univariate analysis of variance (ANOVA) using the scores for the three factors extracted by PCA (explaining >5% variance) from habitat measurements to test for differences in the physical conditions found in streams with and without fish

Source	Factor correlations*	Eigen value	Percentage variance explained	Cumulative percentage variance explained	d.f.	MS (effect)	MS (error)	*F*-ratio	*P*-value
MANOVA					3, 6	0.509		1.93†	0.22
Factor 1	+: Depth, width, discharge	3.51	58.6	58.6	1, 8	4.141	0.6.7	6.82	0.03
Factor 2	+: Altitude	1.34	22.4	81.0	1, 8	0.246	1.094	0.22	0.65
Factor 3	−: Current velocity	0.87	14.5	95.5	1, 8	0.031	1.121	0.02	0.30

* Variables listed correlate with a PCA axis at absolute values ≥0.7.
† Wilks' Lambda.

Table 6 Pearson correlation coefficients for the relationship between mayfly drift propensity (drift density/benthic density) and various physical and biotic variables that could potentially affect mayfly drift. $n = 9$, correlations with absolute values > 0.60 are significant at alpha = 0.05(*)

Response variable	PCA 1 (Depth, width and discharge)	PCA 2 (Altitude)	PCA 3 (Current velocity)	Predatory stonefly density (no. m^{-2})	Algal chl *a* ($\mu g\ cm^{-2}$)	Grazer density (no. m^{-2})
Night *B. bicaudatus*	0.05	−0.72*	−0.46	−0.32	−0.27	0.61*
Day *B. bicaudatus*	−0.40	−0.02	−0.30	−0.05	−0.54	0.01
Night Heptageniidae	−0.14	−0.14	−0.31	−0.05	−0.07	0.15
Day Heptageniidae	−0.46	0.28	−0.10	0.01	−0.29	−0.08

consistently surpass the threshold at which large *B. bicaudatus* larvae reduce their nocturnal drift.

We have previously observed *B. bicaudatus* responding to brook trout odour piped into natural streams over scales ranging from 3.5 m (McIntosh *et al.*, 1999) to 30 m (Peckarsky *et al.*, 2002). We also know that naive *B. bicaudatus* from a fishless stream become nocturnal when presented with water from the East River, a stream with a relatively low biomass of fish (Cowan & Peckarsky, 1994). However, the reductions in nocturnal drift observed in our experimental systems are responses to continuously delivered doses of high odour concentrations, and measured in close proximity to the odour source. We may not have observed responses of mayflies to variation in trout biomass in natural streams because the exact locations of the fish, and thus the fish chemical cues, are temporally and spatially variable within each reach. Moreover, it is possible that the higher flows and variable currents of natural streams dilute fish odour more quickly than in our experimental channels.

Other studies have reported increases in baetid drift propensity (or *per capita* emigration rates) in response to manipulations of predatory trout density in fenced stream reaches or large channels (Forrester, 1994; Diehl *et al.*, 2000). Besides chemical cues, the effect of predatory trout on baetid drift propensity probably involves indirect effects of predatory fish on algal food supply (Forrester *et al.*, 1999; Diehl *et al.*, 2000), interactions with predatory invertebrates (Wooster & Sih, 1995; Huhta *et al.*, 1999; McIntosh & Peckarsky, 1999), and will also depend on *Baetis* size (Huhta *et al.*, 1999; McIntosh *et al.*, 1999). Diehl *et al.* (2000) also observed that *per capita* emigration of baetid mayflies from 50-m long stream channels was positively related to trout density at high trout density, but negatively affected by trout at low trout density. Thus, it is possible that simultaneous variations in several factors, such as the physical conditions, algal food availability, and the density of predatory invertebrates and fish, obscure the relationship between *Baetis* drift propensity and any single factor (Table 6).

The relationship between observations from small-scale experiments and natural systems

To enhance knowledge of the mechanisms structuring freshwater communities, ecologists must determine over what scales, and to what extent the interactions they study will influence the distribution and abundance of organisms (Peckarsky *et al*., 1997; Cooper *et al*., 1998; Downes & Keough, 1998). There has been some controversy regarding the usefulness of experimental observations from small microcosms, such as the stream-side channels we have used in this study (Carpenter, 1996). Collectively, our results indicate the value of linking studies in microcosms and natural systems to test whether phenomena observed at small scales have important influences on patterns and processes in natural systems. Controlled releases of chemical cues from brook trout do influence the drift and life history of *Baetis* mayflies in natural streams (McIntosh *et al*., 1999; Peckarsky *et al*., 2002), but variation among streams in trout density (odour concentration) appears not to affect drift rates measured at larger scales under natural stream conditions.

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