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Rapid size-specific changes in the drift of *Baetis bicaudatus* (Ephemeroptera) caused by alterations in fish odour concentration

Abstract Chemical cues from fish can alter the behaviour of stream invertebrates in experimental tanks but their effect in natural streams has received little attention. By adding brook trout (*Salvelinus fontinalis*) odour to a trout stream in the Rocky Mountains of Colorado, USA, we tested whether changes in the concentration of chemical cues from visually feeding predatory fish would alter the drift of mayfly nymphs (Ephemeroptera). Stream water was piped from streamside tanks with (odour) and without (control) three brook trout to two locations in the stream 3.5 m upstream of drift nets at six replicate sites. Five-minute drift samples were collected downstream from odour and control pipes before, during and after the release of water from the tanks into the stream during both the day and night. Almost all drift occurred at night and consisted predominantly of *Baetis bicaudatus* nymphs. The odour manipulation had no measurable effect on *Baetis* drift during the day but statistical power was low. During the night, however, the drift of large (> 0.65 mm head capsule width, HCW) *Baetis* nymphs decreased significantly during the odour addition compared to control drift. In contrast, the drift of small nymphs (≤0.65 mm HCW) increased both during and after the odour addition in comparison to control drift. Since the stream contains brook trout (0.04–0.18 m^{-2}), and water from the stream (presumably containing fish odour) altered the behaviour of fishless-stream *Baetis* nymphs in another experiment, we conclude that the changes in *Baetis* drift density were a response to an increase in the concentration of fish odour in the stream. Furthermore, we were able to detect the effect within 5 min. of odour addition, indicating that mayfly behavioural response to trout odour was rapid. These results suggest that mayflies can distinguish different concentrations of trout odour in natural streams and that the response is size-specific, according to the relative risk of predation of large and small *Baetis*.

Key words Chemical cues · Brook trout · Prey size · Odour concentration · Stream predator-prey interactions

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Introduction

The movement of macroinvertebrates in the water column of streams (drift) plays an important role in stream communities (Hynes 1970; Brittain and Eikeland 1988; Allan 1995). Drift is the primary mode of movement for many stream organisms and is involved in the colonisation of new habitat, predator avoidance, foraging success, escape from unfavourable conditions and delivering food for fishes (Townsend and Hildrew 1976; Peckarsky 1980; Kohler 1985; Brittain and Eikeland 1988; Poff and Ward 1991; Rader 1997). Visually feeding fish present a high predation risk to organisms travelling in the water column of streams during the day (Jenkins 1969; Wilzbach et al. 1986; Walsh et al. 1988; Angradi and Griffith 1990; McIntosh and Townsend 1995). Thus predatory fish, such as trout, may exert considerable selection pressure shaping the drift behaviour of stream macroinvertebrates, especially mobile taxa like mayflies (Allan 1995; Wooster and Sih 1995).

In streams with trout, large mayflies drift primarily at night, but in streams without trout, mayflies drift during both day and night (Flecker 1992; Douglas et al. 1994; McIntosh and Townsend 1994). Although changes in

light intensity regulate the onset of drift in trout streams (Elliott 1965; Anderson 1966; Holt and Waters 1967; Bishop and Hynes 1969), chemical cues also influence patterns of nocturnal drift. The nocturnal drift periodicity of mayflies from trout streams is usually retained under experimental conditions even when predators are absent (e.g. Kohler 1985; McIntosh and Peckarsky 1996; McIntosh and Townsend 1996; Peckarsky and McIntosh 1998), but nocturnal periodicities can be induced in mayflies from fishless streams when exposed to chemical cues from trout (Cowan and Peckarsky 1994; Douglas et al. 1994; Tikkanen et al. 1994; but see McIntosh and Townsend 1994). Furthermore, the magnitude of nocturnal drift can be altered by chemical cues from trout. In stream channels, the drift of large larvae of the mayfly *Baetis bicaudatus* at night was reduced when chemical cues from brook trout were present (McIntosh and Peckarsky 1996; Peckarsky and McIntosh 1998). However, none of those studies have determined how alterations in the concentration of chemical cues from predatory fish affect drift in real streams.

Water from trout streams elicits behavioural changes in mayflies (Cowan and Peckarsky 1994), indicating that chemical cues from fish are found at some background concentration in streams where trout are present. However, if organisms can only detect the presence or absence of a predator cue, their behavioural responses should be all or nothing, since they are constrained to detecting whether or not a threat is present. In contrast, if stream macroinvertebrates can detect and respond to spatial and temporal variations in the concentration of chemical cues from fish in stream water, which correspond to variations in the threat of predation, they could adjust their behaviour according to the magnitude of the predation threat. Many aquatic organisms respond to the presence or absence of chemical cues (e.g. Crowl and Covich 1990; Larsson and Dodson 1993; Dodson et al. 1994; Feminella and Hawkins 1994; Scrimgeour et al. 1994), but few studies have reported responses to changes in their concentration in natural situations (but see Parejko and Dodson 1990; Williams 1990; Hazlett 1997).

If prey do have a flexible response to changes in predation risk mediated by the concentration of chemical cues, this should convey considerable fitness benefits (Sih 1987). If an area with a high predator density can be avoided, or vulnerable behaviour curtailed when a predator is present, the prey's risk of predation should be reduced. Since predator avoidance behaviour also frequently involves trade-offs with foraging (Cerri and Fraser 1983; Fraser and Huntingford 1986; Gilliam and Fraser 1987; Kohler and McPeek 1989; Lima and Dill 1990; Peckarsky et al. 1993; Werner and Anholt 1993), potential losses in foraging opportunities due to unnecessary predator avoidance should be minimised. Furthermore, to be effective, a flexible predator avoidance response would need to occur relatively quickly.

Often the risk of predation depends on the size of the prey animal (Brooks and Dodson 1965; Malmqvist and Sjöström 1980; Zaret 1980; Allan et al. 1987), in which case the prey sizes at greater risk to predation should show more pronounced responses to predators. For example, when visually feeding fish are present, large, more vulnerable mayflies drift only at night whereas smaller, less vulnerable individuals have more aperiodic drift behaviour (Allan 1978, 1984; Skinner 1985; Poff et al. 1991). Thus, we might also expect the response of mayflies to variations in the concentration of chemical cues from trout to be size-dependent.

In this study, we determined whether the drift density of mayflies in a Colorado trout stream changed in response to manipulations of the spatial and temporal distribution of chemical cues (fish odour) from brook trout. We tested the following hypotheses: (1) drift density of mayfly nymphs should be different in locations with elevated fish odour concentration compared to control locations with background trout odour concentration; (2) response of mayflies to elevated fish odour concentration should be rapid (<5 min), and (3) the response to elevated fish odour concentration should be dependent on mayfly size.

Materials and methods

Experimental design

Fish odour concentration was manipulated by piping stream water from tanks containing brook trout back into a trout stream with background levels of trout chemicals. Six sites located along a 1-km stretch of the East River, a high-altitude (2450 m) stream in the Colorado Rocky Mountains (see Peckarsky 1983) were chosen as replicate sampling locations. Sites were riffle and run reaches more than 75 m apart, wider than 8 m, and with comparable depths (mean $\pm$ SE = 25 ± 1 cm) and current velocity (mean $\pm$ SE = 64 ± 3 cm s^{-1}). This section of the East River has a predominately cobble substrate and flows through spruce-fir forest at the Rocky Mountain Biological Laboratory. At this altitude, the East River contains only salmonid fishes at moderate densities (range = 0.04–0.18 m^{-2}), predominantly ($>95\%$) introduced brook trout (*Salvelinus fontinalis*), but occasionally introduced brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) or native cutthroat trout (*O. clarki*).

At each site, control and treatment drift sampling locations were situated downstream of the outlets from pipes that carried water from two polyethylene plastic tanks (rubbish bins) located on the stream bank. The tanks were filled with stream water and drained into each site during the experiment. The odour treatment tank contained three brook trout in 84 l of East River water and the control tank contained the same amount of East River water, but no fish (Fig. 1). Both tanks had a mesh- (1 mm) covered outlet standpipe controlled by a valve that allowed water to drain from the tanks but maintained a water depth in the tanks of 10 cm (20 l) after draining. The flow out of each tank was adjusted with the valve so that each tank took 5 min to drain its contents into the water upstream of the sampling location. Water was delivered from the tanks using a 6-m-long section of 20-mm-diameter polyethylene pipe to the middle of the water column an arbitrary distance of 3.5 m upstream of the drift sampling locations.

The control and odour drift sampling locations were parallel and situated at least 3 m apart to eliminate the possibility that water from an odour treatment pipe could influence drift sampled in the adjacent control site or vice versa (Fig. 1). Visual examination of dye released into the water plumes emanating from the pipe outlets indicated that plumes were narrow (<1 m wide) at the drift sampling sites and that leaves and pieces of cork that we released in
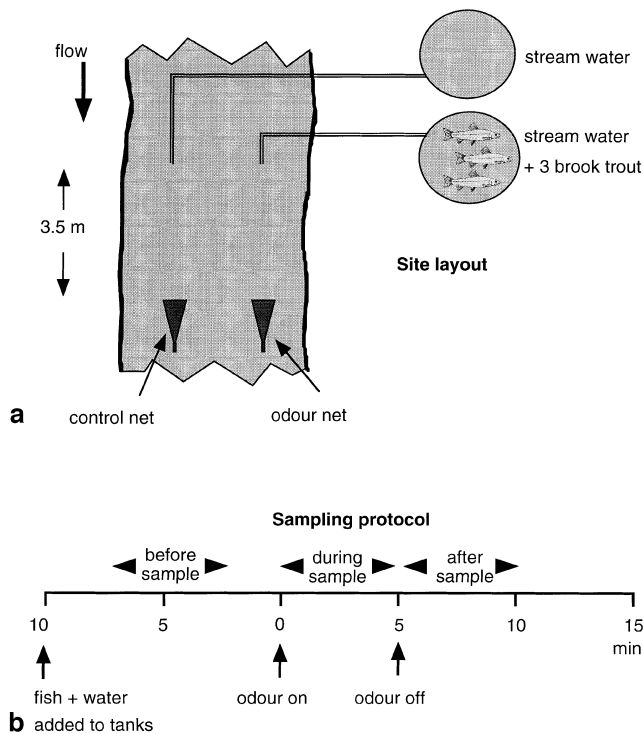
Fig. 1 Diagrams depicting the general site layout (**a**) and the sampling protocol (**b**) for the fish odour manipulation. The site layout diagram shows the location of odour and control water delivery pipes upstream of the control and odour sampling locations (not to scale). The sampling protocol shows the timing of the three, 5-min, drift samples, the addition of fish and water to the tanks, and odour release from the pipes

the plume of each tank did not float through the other sampling location. Drift was measured at sampling locations using six Wildco drift nets with a 20 × 30 cm rectangular opening and 1-m long 202-μm mesh nets, secured to metal stakes with the long axis vertical in order to sample the entire water column.

Sampling protocol

Brook trout used in the experiments (mean ± SE fork length = 179 ± 7 mm) were collected from the East River by electrofishing and held in a large tank (approx. 400 l) for between 2 and 5 days before being used in the experiment. During this time they were fed ad libitum on stream macroinvertebrates (mainly *B. bicaudatus* nymphs) obtained from the East River. Different fish were used for each trial.

Replicate sites were sampled in separate 24-h periods between 3–21 August 1996. Drift was collected for 5 min during the day (1300–1600 hours mountain daylight saving time, MDST) and night (2100–2400 hours MDST) before, during and after the release of water from the tanks. While a longer sample duration would have increased statistical power (Culp et al. 1994), we chose a shorter sample duration to enable us to identify the speed of response to the odour addition. The protocol for sampling at each site (Fig. 1) started with filling both control and treatment tanks with water bucketed directly from the stream downstream of the nets and adding the fish to the treatment tank. The 5-min "before" drift sample was then taken from both control and treatment locations and the nets replaced. Ten minutes after the fish were added to the treatment tank, the water flow from the tanks was started, releasing fish odour or control water, and the "during" sample was collected from both sampling locations. After the 5-min "during"

sample was completed, and the water flow from the tanks ceased, the drift nets were immediately replaced and a 5-min "after" sample was collected from the control and treatment locations. After drift sampling, water depth and current velocity were measured for calculation of drift densities.

After collection, drift samples were washed from nets and preserved in 90% ethanol with rose bengal dye. Mayfly nymphs were sorted from detritus, identified using Peckarsky et al. (1985) and Merritt and Cummins (1996), and head capsule widths (HCWs) were measured under ×25 magnification.

Data analysis

Drift densities (DDs) for each sample were calculated using Eq. 1 of Allan and Russek (1985) and expressed as numbers m^{-3} of water. Although control and treatment samples were collected at the same time, they included different animals coming from separate sections of stream. Thus, measurements from control and treatment locations at the same site were treated independently in the analysis. To assess changes in drift at replicate control and treatment sampling locations during and after the water addition, we compared the change in ln-transformed before and during DDs (i.e. ln during DD − ln before DD) and the change in ln-transformed before and after DDs (i.e. ln after DD − ln before DD). We tested for significant differences ($\alpha = 0.05$) in this parameter between times (during vs after) and treatments (control vs fish odour) using two-way ANOVA (Systat 1992). Differences in the response of different-sized mayfly nymphs were assessed by examining size-frequency histograms to identify size classes, dividing the data into two equal size classes, and analysing them separately. The power of tests was assessed using Eq. 13.30 of Zar (1984).

Results

Large numbers of mayfly nymphs were caught during the 5-min drift samples at night, but relatively few were caught during the day. Both day and night drift densities were highest for *B. bicaudatus* nymphs (Mean ± SE number m^{-3} for day and night, respectively = 0.25 ± 0.02, 4.04 ± 0.24), followed by *Epeorus deceptivus* (0.04 ± 0.004, 1.79 ± 0.13), *Rhithrogena robusta* (0.05 ± 0.01, 0.59 ± 0.04) and *Cinygmula mimus* (0.005 ± 0.001, 0.29 ± 0.02) nymphs. *Ameletus velox*, *Drunella* spp., and *Ephemerella infrequens* nymphs occurred in samples, but at low densities (night mean number m^{-3} < 0.25). Only the analysis of *B. bicaudatus* provided satisfactory statistical power to detect treatment effects and hence avoid type II statistical errors. *B. bicaudatus* was the only species for which the probability of detecting a difference among the population means was > 0.4 for both size classes and in both day and night samples. *Baetis* is bivoltine at this elevation, and drift samples included individuals of both summer and winter generations. However, the responses to treatments are most representative of the summer generation, because 92% of the individuals caught in drift nets were summer generation nymphs.

A wide size range of *B. bicaudatus*, including both summer and winter generation nymphs, was caught in drift nets from the start to the end of sampling (Fig. 2a–f) with a mean (± SE) number of 50 (± 5) nymphs caught per sample. The median HCW of nymphs caught was 0.65 mm. This is the same size at which Allan (1978)

Fig. 2 The size frequency distribution of the head capsule widths of the "before" sample *Baetis bicaudatus* nymphs from each of the replicate sites (**a–f**) and the combined size frequency distribution (**g**) for all sites. **a–f** Samples are arranged in the chronological order of sampling from 3 August (**a**) to 21 August (**f**)
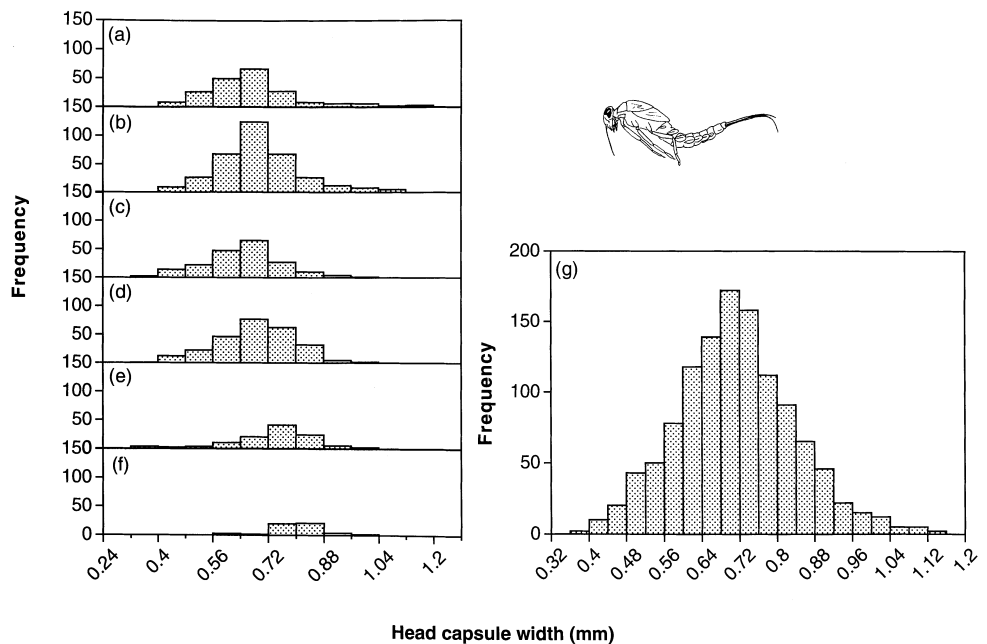

Head capsule width (mm)

Table 1 Results of ANOVA testing for differences in the mean change in *Baetis* drift densities from sites where either stream water or stream water with fish odour was added (odour treatment) during or after the odour addition (time treatment). Data for different times were calculated by subtracting ln-transformed drift densities from the during or after samples from drift densities recorded from the before sample (see Materials and methods and legend to Fig. 1 for a more detailed explanation). ANOVA results are for large (>0.65 mm HCW) and small (≤ 0.65 mm HCW) nymphs from the night experiment and for all sizes of nymphs from the day experiment

	Source	*df*	MS	*F*	*P*
Night					
Large nymphs	Time	1	0.0091	0.126	0.73
	Odour	1	0.3211	4.43	0.05
	Time × odour	1	0.7793	10.7	<0.01
	Error	16	0.0725		
Small nymphs	Time	1	0.0124	0.417	0.53
	Odour	11	0.3125	10.5	<0.01
	Time × odour	1	0.0004	0.012	0.91
	Error	16	0.0297		
Day					
All nymphs	Time	1	0.0028	0.232	0.64
	Odour	1	0.0478	3.899	0.06
	Time × odour	1	0.0093	0.761	0.39
	Error	20	0.0123		

observed brook trout selection of *Baetis* prey to change from negative (avoidance) to positive (preference). Thus, we calculated and analysed drift densities for small (≤ 0.65 mm) and large (>0.65 mm) nymphs separately. Unfortunately, a fish escaped from an odour tank at some stage during the night sampling at one site, so data from that replicate were excluded from the analysis leaving a total of five replicates.

The response of *Baetis* to the fish odour manipulation depended on the size of the nymph (Fig. 3, Table 1) and the time of the sample (Fig. 4, Table 1). At night, drift

densities of large nymphs downstream of fish odour declined compared to control samples during the water addition, but were similar to those recorded in control samples after the water addition (Fig. 3a). Thus, large *Baetis* responded to the elevated fish odour concentration by decreasing their nocturnal drift, but only if the concentration remained high (during the trout odour addition), resulting in a significant odour × time interaction (Table 1). In contrast, the night drift density of small *Baetis* increased significantly when fish odour was added and remained high for at least 5 min after the concentration of odour returned to normal (Fig. 3b), as indicated by a significant odour treatment term in the ANOVA, but no other significant effects (Table 1).

Since small and large *Baetis* responded similarly to the manipulation during the day, data for small and large nymphs were combined for the analysis. There were no significant differences in drift density between locations receiving fish odour and controls, during or after the addition, although there was a trend toward reduced drift during and after addition of trout odour (Fig. 4, Table 1). These results indicate that fish odour concentration may affect the daytime drift of both small and large *Baetis*, but we have insufficient statistical power to reject the null hypothesis that odour concentration has no effect during the day (power of the test ≈ 0.4).

Discussion

Our results indicate that *Baetis* drift densities were altered when chemical cues from brook trout were experimentally added to a trout stream at night. This is a particularly interesting result since some chemical cues from brook trout were already present in the stream
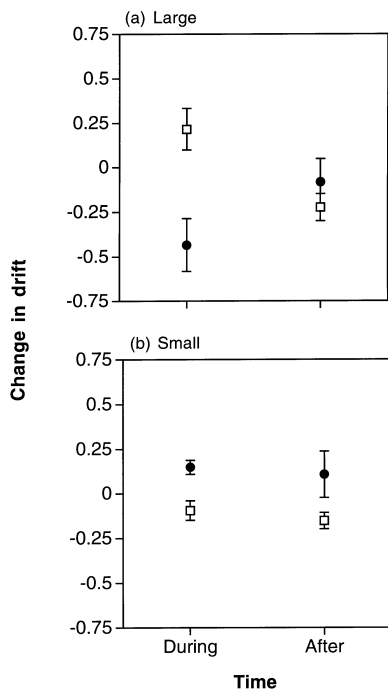
Fig. 3 The mean (±SE) change in drift densities during (ln during sample – ln before sample) and after (ln after sample – ln before sample) the addition of water from odour (*black circles*) and control (*open squares*) tanks for *Baetis* nymphs >0.65 mm head capsule width (HCW) (large) (**a**) and *Baetis* nymphs with ≤0.65 mm HCW (small) (**b**) during the night. A positive change indicates an increase in drift density, whereas a negative change indicates a decrease in drift density. The units used in the calculation of changes in drift density are ln number m^{-3}

Fig. 4 The mean (±SE) change in drift densities during (ln during sample – ln before sample) and after (ln after sample – ln before sample) the addition of water from odour (*black circles*) and control (*open squares*) tanks for all *Baetis* nymphs during the day (see legend to Fig. 3 for additional information)

before our addition. The density of brook trout in this stream ranges from 0.04 to 0.18 m^{-2} in the sections used for experiments; and it has been shown previously that water from this stream changes the behaviour of *Baetis* nymphs from a fishless stream (Cowan and Peckarsky 1994). Thus, we conclude that the change in drift found in the current experiments was a response to an increase in the concentration of fish odour. Furthermore, we were able to detect changes in drift density within 5 min of the time of trout odour addition, providing strong evidence that the response to trout odour was very fast. The specific properties of the chemical cue from trout that elicit the mayfly drift response have not been identified. The responses could involve products from both predators and prey (e.g. Crowl and Covich 1990) and multiple stimuli may be needed to elicit responses (e.g. Scrimgeour et al. 1994; Tikkanen et al. 1994; 1996). We suspect prey are not responding to excretory products, since the fish were in our tanks for <15 min and the concentration of such products would have been very low during the 5 min of the odour addition.

Diel variation in prey response to predator cues

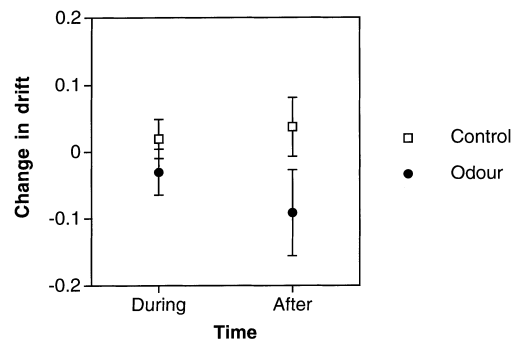Since trout present the highest risk of predation during the day when light levels are high (Jenkins 1969; Walsh

et al. 1988; Angradi and Griffith 1990; McIntosh and Townsend 1995) one might expect *Baetis* to show the greatest response to trout odour addition during the day. However, in experimental stream channels we have observed that large *Baetis* from trout streams only drift during the day when chemical cues from predatory fish are absent and stoneflies are present (Peckarsky and McIntosh 1998). Those channel experiments also show that once *Baetis* has been exposed to any concentration of trout odour, drift avoidance behaviour during the day becomes fixed. Those observations support the expectation of no response by trout stream *Baetis* to odour concentration during the day. However, we cannot rule out the possibility that low daytime drift densities may have contributed to the lack of statistical power to detect treatment effects. Future tests of daytime drift responses of stream insects to fish odour should be conducted using longer sample times to collect higher numbers of insects and provide the statistical power to detect differences among treatments. Nonetheless, our data indicate that *Baetis* mayflies used a flexible response to changes in the concentration of trout odour at night, but had an inflexible "no drift" response to trout odour during the day, regardless of its concentration.

The change in the magnitude of nocturnal drift that we observed in response to the addition of fish odour indicates that *Baetis* can adjust their behaviour according to imminent risk of predation. Trout select and defend stream microhabitats that provide the best feeding conditions and cover (Kalleberg 1958; Slaney and Northcote 1974; Fausch 1984; Hughes and Dill 1990). This inevitably results in patchy trout distributions in streams, and consequent temporal and spatial variation in the predation risk. *Baetis* are particularly vulnerable to trout (Allan 1978, 1981) and suffer considerable reduction in fitness when trout are present (McPeek and Peckarsky 1998). Both experimental and field data indicate that size of emergence, which is directly related to fecundity in females (Peckarsky et al. 1993), is reduced by the presence of trout (Peckarsky 1998; Peckarsky and McIntosh 1998; B.L. Peckarsky, unpublished data).

Thus, a flexible anti-predator strategy may have considerable fitness advantages because prey can adjust their behaviour according to spatial and temporal variation in predation risk, thereby minimising foraging losses due to unnecessary predator avoidance.

Size-dependent predator avoidance

The flexible response of *Baetis* to the increase in odour concentration at night was size-dependent, since drift densities of small and large *Baetis* changed in opposite directions. The different behaviours of small and large *Baetis* during the odour additions at night probably reflect their differential vulnerability to trout predation. Although the probability of a visually feeding fish detecting and consuming a prey item during the day is higher than at night, trout also consume prey at night (Jenkins 1969; Elliott 1970; Allan 1978; McIntosh and Townsend 1995; authors' unpublished data). Trout are more size selective during the day, but continue to preferentially consume larger prey at night (Allan 1978; McIntosh and Townsend 1995; authors' unpublished data). Experiments in an observation tank indicated that large *Baetis* (0.75–0.9 mm HCW) released into the drift upstream of a brook trout at night have a probability of being consumed between 0.03 and 0.12. This risk is sufficient to warrant large nymphs reducing their probability of capture by curtailing drift when trout are in the vicinity at night.

In comparison to that experienced by large nymphs, the risk of predation experienced by small (<0.65 mm HCW) nymphs at night is probably substantially less, because small prey should always be harder to detect than large prey. However, we were unable to estimate the probability of capture of small nymphs by trout in our observation tank because they were so difficult to see using infrared video. If the risk of predation experienced by small nymphs at night is nearly zero, we would expect no response to elevated fish cues. However, given that small nymphs are consumed by trout during the day (Allan 1978) and will be subject to substantial predation risk later in their ontogeny, we speculate that increased drift of small *Baetis* in response to elevated odour concentration indicates avoidance of areas where predation risk will be higher in the future (the next day or later in ontogeny). This explanation assumes that the spatial distribution of trout is relatively constant over time (Bachman 1984; Fausch 1984; Hughes 1992a, b).

Large and small *Baetis* nymphs also differed in their responses to removal of the additional fish odour. We suspect that large nymphs resumed "normal" drift behaviour after trout odour was turned off because the benefits of increasing movement (to resume foraging) outweigh the costs (reduced movement) once the threat of predation has decreased. In contrast, small nymphs continued to drift at higher densities for at least 5 min after the concentrations of odour had returned to normal. We speculate that once they have detected high concentrations of fish cues in that area, they continue to relocate to areas that will be less risky in the future.

The mechanism determining the observed changes in *Baetis* drift density could be a lower propensity of larvae to enter the drift, an increased propensity to exit the drift (resulting in a reduction in drift distance) or an increased propensity to stay in the drift leading to longer drift distances. An experimental examination of drift distance (Allan and Feifarek 1989) revealed that the mean distance travelled by *Baetis* nymphs under similar flow conditions (55 cm s^{-1}) was around 2 m for large nymphs (0.15 mg dry weight, DW) and around 5 m for small nymphs (0.96 mg DW). These findings indicate that a large proportion of the drift caught by our nets may have originated upstream of the odour addition. Thus, it is possible that the responses to alteration of the odour concentration are the result of behavioural decisions made by *Baetis* while in the water column. Although large *Baetis* have been reported to drift shorter distances than small *Baetis* (Malmqvist and Sjöström 1987; Allan and Feifarek 1989), drift distances have not been compared in the presence and absence of chemical cues. The size-dependent variations in prey response could also partly reflect their differential swimming abilities. For example, when *B. tricaudatus* nymphs were confronted with a predatory benthic fish, the longnosed dace (*Rhinichthys cataractae*), small nymphs took flight into the drift at longer distances from an approaching dace compared to large nymphs, which waited until the predator was closer (Scrimgeour et al. 1997). These authors hypothesised that this was because larger nymphs had greater acceleration and could afford to wait until the predator was closer.

The size-related response to predator cues observed in this study indicates that *Baetis* undergoes considerable ontogenetic change in its behaviour, probably corresponding to its vulnerability to fish predation. Ontogenetic changes in prey behaviour in response to the presence of predators are common (e.g. Mittelbach 1981; Stamps 1983; Holomuzki and Short 1990; Culp and Scrimgeour 1993) but usually involve prey at a vulnerable stage in development responding to predators and not responding at another invulnerable stage. An interesting result of this study is that *Baetis* shows completely opposite responses at two developmental stages.

Why respond to a predation threat upstream?

Since trout and most visually feeding fish feed facing upstream, prey animals are vulnerable to downstream predators. Therefore, why would a mayfly respond to a predation threat from upstream? We believe the answer lies in understanding the spatial and temporal scales of trout movement in streams. First, although trout hold focal positions, they make regular forays from those positions. For example, one study showed that brown

trout had a mean home range of 15 m^2 (Bachman 1984). Thus, a fish that is < 3.5 m upstream of a mayfly could easily be a similar distance downstream in a short time. Second, although trout are territorial, they tend to aggregate in areas providing suitable cover and critical feeding velocities (Bachman 1984; Fausch 1984; Hughes 1992a, b). Thus, an upstream predator cue could be a reliable indicator that fish are nearby downstream. Finally, in turbulent stream habitats, we doubt that *Baetis* use gradients of chemical cues to determine the specific location of a predator (but see Dahl et al. 1998). Alternatively, we suggest that *Baetis* is responding generally to an increase in the concentration of chemical cues in a section of river rather than to a specific "point-source" of odour.

The extent of the spatial and temporal effect of fish chemical cues on stream communities is largely unknown. *Gammarus* has been shown to habituate to chemicals after 3 days (Williams and Moore 1985), but we have observed the effect on *Baetis* to last for up to 3 weeks (Peckarsky and McIntosh 1998). More data are needed to determine how long these predator chemicals last in the environment and how far downstream they can be detected.

Potential contradictions in the literature are solved

Previous work in our experimental system indicated that the presence of chemical cues from trout resulted in decreased drift of *B. bicaudatus* at night in stream channels (McIntosh and Peckarsky 1996; Peckarsky and McIntosh 1998). However, other studies have reported increased nocturnal drift of *Baetis* mayflies in stream reaches with higher densities of trout than in reaches with low trout densities or no trout (Williams 1990; Douglas et al. 1994; Forrester 1994). For example, a field experiment (Forrester 1994) using fences to manipulate trout numbers indicated that drift of several genera of mayflies, including *Baetis* (species name not stated), increased where trout densities were higher. These contradictory findings may be reconciled by the fact that McIntosh and Peckarsky (1996) and Peckarsky and McIntosh (1998) used large *Baetis* (mean HCW all > 0.84 mm), but the *Baetis* in Forrester's (1994) study were predominately small (mean HCW < 0.65 mm). We suspect that examination of size-specific responses by *Baetis* to trout cues in other systems will explain differences in observed responses.

Implications for detecting the effects of predators on prey abundance

In many respects, this study has produced more questions than answers. Why do small and large *Baetis* behave differently? Do the behavioural changes take place on the substratum or in the water column? What is the chemical cue involved? Over what spatial scale are the cues effective? Nevertheless, the fact that mayfly nymphs

do respond to variations in the concentration of predator odour in a natural setting has important implications for how we view predator-prey interactions in streams. Empirical studies (Cooper et al. 1990; Lancaster et al. 1991), models of stream invertebrate prey movement (Sih and Wooster 1994; Englund 1997), and meta-analyses (Cooper et al. 1990; Wooster and Sih 1995) all indicate that the movement of stream prey is important in determining the effects of predators on local and regional prey abundance. Predator-induced reductions in prey emigration decrease apparent impacts of predators on prey densities, whereas predator-induced emigration should increase the observed impact of predators on prey density. The rapid, size-specific, and spatially explicit nature of the changes in prey movement observed in response to changes in fish odour concentration in this study suggest that models explaining the complex patterns of predator effects on the distribution of prey in natural streams must consider prey size and the spatial scale of interactions between predators and prey. Our data should be useful for modelling the influence of fish spatial distributions on prey populations in streams. Thus, this test of predator-induced changes in prey movement in a natural setting helps resolve the influence of predators not only on prey abundance, but also potentially on spatial and temporal patterns in prey dispersion (e.g. Cooper et al. 1997; Crowl et al. 1997).

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