

Paul L. Douglas · Graham E. Forrester · Scott D. Cooper

Effects of trout on the diel periodicity of drifting in baetid mayflies

Received: 21 June 1993 / Accepted: 5 February 1994

Abstract Some benthic invertebrates in streams make frequent, short journeys downstream in the water column (=drifting). In most streams there are larger numbers of invertebrates in the drift at night than during the day. We tested the hypothesis that nocturnal drifting is a response to avoid predation from fish that feed in the water column during the day. We surveyed diel patterns of drifting by nymphs of the mayfly *Baetis coelestis* in several streams containing ($n=5$) and lacking ($n=7$) populations of rainbow trout, *Oncorhynchus mykiss*. Drifting was more nocturnal in the presence of trout (85% of daily drift occurred at night) than in their absence (50% of daily drift occurred at night). This shift in periodicity is due to reduced daytime drifting in streams with trout, because at a given nighttime drift density, the daytime drift density of *B. coelestis* was lower in streams occupied by trout than in troutless streams. Large size classes of *B. coelestis* were underrepresented in the daytime drift in trout streams compared to nighttime drift in trout streams, and to both day and night drift in troutless streams. Differences in daytime drift density between streams with and without trout were the result of differences in mayfly drift behaviour among streams because predation rates by trout were too low to significantly reduce densities of drifting *B. coelestis*. We tested for rapid (over 3 days) phenotypic responses to trout presence by adding trout in cages to three of the troutless streams. Nighttime drifting was unaffected by the addition of trout, but daytime drift densities were reduced by 28% below cages containing trout relative to control cages (lacking trout) placed upstream. Drift responses were measured 15 m downstream of the cages suggesting that mayflies detected trout using chemical cues. Overall, these data support the hypothesis that infrequent daytime drifting is an avoidance response to fish that feed in the water column during the day. Avoidance is more pronounced in large individuals and

is, at least partially, a phenotypic response mediated by chemical cues.

Key words Predator avoidance · Diel periodicity · Phenotypic plasticity · Streams

Introduction

Predators have a wide variety of influences on the behaviour of their prey (Edmunds 1974). Many diel patterns in behaviour and activity have been hypothesized to function as predator avoidance behaviours. Evidence supporting the predator avoidance hypothesis is, however, available in relatively few cases (Stein 1979; Sih 1987). Drift dispersal, the downstream transport in the water column of benthic stream invertebrates, shows a distinct diel pattern in many streams worldwide (Waters 1972; Müller 1974). The density of invertebrates in the water column is usually much higher at night than during the day. Drifting primarily at night has been hypothesized to be an avoidance response to predatory fish feeding in the water column. These fish, which hunt by sight, feed most effectively during the day and so are suggested to have caused selection against daytime drifting (Allan 1978).

One way to test the predator avoidance hypothesis is to compare prey behaviour in habitats that naturally vary in predator presence. The predator avoidance hypothesis predicts (1) that prey should be more nocturnal (a greater proportion of daily activity occurs at night) in the presence than in the absence of predators and (2) that this should be due to reduced daytime activity, rather than increased nighttime activity. Two tests of the first prediction have provided support for the predator avoidance hypothesis in streams. Malmqvist (1988) found that drift of the mayfly *Baetis rhodani* was more nocturnal in a Madeiran waterway stocked with trout than in a nearby waterway lacking water-column predators. Flecker (1992) found that the ratio of night:day drift density of several mayfly taxa was higher in six Venezuelan

P. L. Douglas · G. E. Forrester · S. D. Cooper (✉)
Marine Sciences Institute and Department of Biological Sciences,
University of California,

streams containing drift-feeding fishes than in two streams without fish.

We present a comparison of the drift periodicity of the mayfly *B. coelestis* in five temperate streams which contain populations of a predatory trout, *Oncorhynchus mykiss*, and seven similar streams which lacked trout. We tested whether drift was more nocturnal (a greater proportion of daily drift occurred at night) in trout streams than in streams lacking trout. We also tested whether any difference in periodicity between streams with and without trout was due to reduced daytime drifting in trout streams, or increased nighttime drifting.

A third prediction of the predator avoidance hypothesis is that prey types at greater risk from predators should show more pronounced avoidance responses. Rainbow trout, in common with most visually oriented fish that feed on invertebrates, select large over small prey whilst feeding during the day (Irvine and Northcote 1983; Newman and Waters 1984). Increases during ontogeny in the extent to which drift is concentrated in hours of darkness have, therefore, been used as support for the predation risk hypothesis (Allan 1978, 1984; Skinner 1985). We compared the size distributions of drifting *B. coelestis* in streams with and without trout to test the prediction that changes in drift periodicity in streams with trout (i.e. more nocturnal drift or reduced daytime drift) should be more strongly expressed in large mayflies.

Behaviours that evolved because they result in the avoidance of predation may be regulated by cues produced by predators, so that prey adjust their behaviour according to short-term changes in predator density (=phenotypic plasticity). Alternatively, they may be regulated by other cues that correlate with the degree of predation risk (=fixed, *sensu* Stein 1979). Short-term manipulations of predator density should not result in changes in fixed prey behaviours. Distinguishing between these alternatives is of interest because fixed avoidance responses are hard to identify (Sih 1987), and most studies of predator avoidance deal with plastic responses (Stein 1979; Dill 1987; Lima and Dill 1990).

Evidence that drift periodicity is influenced by light cues (Müller 1974) has led to the suggestion that drifting primarily at night is a fixed avoidance response (Allan 1978; Flecker 1992). Most past studies testing for plastic responses to water-column predators have involved removing fish from small areas in streams where they were present (Williams 1990; Flecker 1992; Forrester 1992, in press). Such experiments cannot distinguish fixed from plastic responses if invertebrates respond to fish using chemical cues, because invertebrates in removal areas may still be receiving cues from areas upstream of the removal. Laboratory studies (Williams and Moore 1985, 1989) and a field experiment where trout were added to fishless streams (Andersen et al. 1993) have, in fact, demonstrated that gammarid amphipods alter their drift activity in response to chemicals from trout. We therefore tested for phenotypically plastic responses to predatory fish by adding trout to streams previously lacking these fish. We caged the trout, and measured drift several

meters downstream of the cages to test for responses to chemical cues released by the trout. A decrease in daytime drifting following the addition of trout would support the hypothesis that nocturnal drift is a plastic response to predatory fish mediated by chemical cues.

Methods

Study areas and study organisms

The 12 streams used for the study were all small second- and third-order coastal streams located in southern Santa Barbara County, California, United States (34° 30' N, 119° 45' W) (Fig. 1). The streams flow through a mixture of natural chaparral, suburban residential areas, and orchards and agricultural fields. All streams were of moderate gradient (2–5%) with substrata composed of boulders, cobbles and gravel. Five of the streams contained self-sustaining populations of rainbow trout (*Oncorhynchus mykiss*), which is native to this area. California roach (*Hesperoleucas symmetricus*) were observed in two of the trout streams (Manzana and Davey Brown) and three-spined sticklebacks (*Gasterosteus aculeatus*) were observed in a third trout stream (Gaviota). The seven other streams lacked trout, or any other fish.

The history of trout presence in the streams and the reasons for their absence in some streams are difficult to establish. The streams with and without trout were interspersed geographically (Fig. 1), and did not differ systematically in most physical, chemical or hydrographic conditions (Table 1). Some of the streams lacking trout, however, tend to be more susceptible to drying during periods of severe drought, which may explain why trout were not present (e.g. Cold Springs, Oso, Rattlesnake, Refugio).

Mayflies of the genus *Baetis* were present in all 12 streams. All of the mature nymphs identified were *Baetis coelestis* (= *Baetis* sp. A in Morigara and McCafferty 1979), suggesting that this was the most common species in the streams, though other rarer species were probably present. *Baetis* nymphs are common grazers of microalgae and fine organic matter in stony bottomed streams. *Baetis* in the study streams are multivoltine, passing through several generations per year. The nymphs are among the most common stream insects in the drift, and are also common prey of trout, making them especially good subjects for testing the predator avoidance hypothesis. Rainbow trout are predominantly diurnal predators, feeding heavily on drifting invertebrates, although nighttime feeding and feeding on benthic organisms sometimes occur (Jenkins et al. 1970; Elliott 1973; Angradi and Griffith

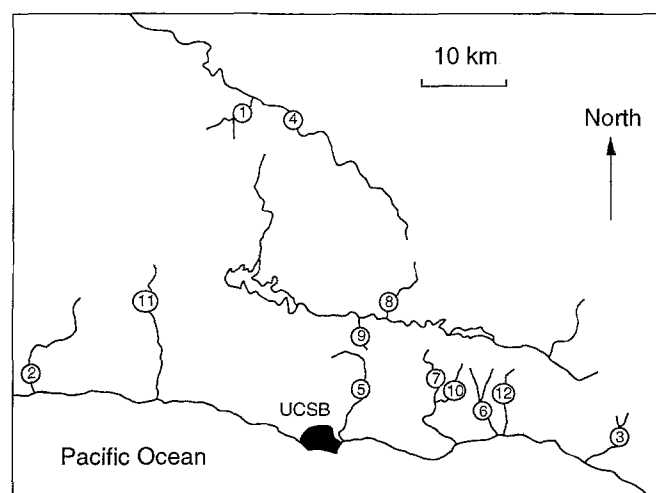


Fig. 1 Map of study sites, showing University of California campus (UCSB). Numbers for streams correspond to those in Table 1

Table 1 Characteristics of study streams

	Trout biomass (g/m ²)	Elevation (m)	Discharge (m ³ /s)	pH	Canopy (%)	Temp. (° C)
Streams containing trout						
1. Davey Brown	5.11	630	0.03	8.2	25	17.0
2. Gaviota	8.46	40	0.09	8.4	5	15.6
3. Gobernador	0.15	100	0.05	8.4	50	20.0
4. Manzana	0.57	550	0.05	8.1	50	17.5
5. San Jose	3.32	300	0.03	8.2	85	15.3
Streams lacking trout						
6. Cold Springs ^a	0	230	0.09	8.3	85	17.1
7. Mission ^a	0	130	0.06	8.3	65	18.1
8. Oso	0	330	0.05	8.2	5	20.4
9. Paradise	0	320	0.01	8.3	20	17.4
10. Rattlesnake ^a	0	280	0.02	8.3	75	18.1
11. Refugio	0	160	0.03	8.1	90	15.5
12. San Ysidro	0	150	0.02	8.4	65	18.3

^aSites for trout addition experiment

1990). *Baetis* nymphs form a significant percentage (mean=29%, n=22) of the trout's daytime diet in the study streams (S.D. Cooper and P.L. Douglas, unpublished data).

Survey of drift periodicity in streams with and without trout

We sampled drift of *B. coelestis* in each of the streams between 8 April and 30 July 1992. Drift was sampled using a single net (mouth width=1.13 m, mouth height=0.27 m, net length=1 m, mesh size=0.18 mm) which was placed in each stream for one continuous 24-h period. The net sampled from dawn to dusk (=day), was emptied, and then sampled from dusk to dawn (=night). We measured both current velocity (using a Marsh-McBirney current meter) and water depth one-quarter, one-half, and three-quarters of the way across the mouth of the net at the start and finish of each day and night sample. Discharge was calculated as the water depth multiplied by the width of the net and current velocity. Discharge measurements at the beginning and end of a sample were averaged when calculating drift density. Reduction of filtering efficiency due to clogging was slight (mean reduction in discharge through the net during sampling=8%±6% SE). At the end of each day and night sample the contents of the drift net were placed into a pan containing stream water. Subsamples were removed, and counted in smaller pans, until all *B. coelestis* were counted. Samples were then preserved in 70% alcohol.

We used the discharge measurements and counts of *B. coelestis* to calculate a daytime and nighttime drift density (number/m³) of *B. coelestis* for each stream. We also calculated the ratio of nighttime to total (day+night) drift density for each stream as a measure of the extent to which drift was nocturnal. This ratio ranges from 0 (all drift occurs during the day) to 1 (all drift occurs at night). Some of the streams were sampled on two dates (four trout streams and two troutless streams) to test for differences in drift periodicity at different moon phases. No systematic differences were apparent, so average values for each stream were used in analyses. The remaining six streams were sampled on only one date. Effects of trout on the extent to which drift was nocturnal were tested using an independent-samples *t*-test. Prior to this and all subsequent analyses we checked data for assumptions of normality (using normal probability plots of the residuals) and heteroscedasticity (using Bartlett's test and plots of cell means versus residuals). Data were transformed to meet the assumption of the analyses when required.

To test whether differences in drift periodicity between streams with and without trout were size-specific we measured drifting mayflies from all seven of the streams lacking trout and four of the streams containing trout. Preserved mayflies were viewed under a dissecting microscope and the maximum distance across the eyes

was measured using an ocular micrometer. In most cases we measured 50 mayflies from the day sample and 50 from the night sample in each stream; however, fewer mayflies were measured from some streams when fewer than 50 individuals were captured (mean=38.5±3.4 SE).

The predator avoidance hypothesis predicts that daytime and nighttime size distributions should not differ in streams without trout, but that large mayflies should be underrepresented in the daytime drift in trout streams. For each stream, we tested whether the daytime and nighttime size distributions were significantly different using a Kolmogorov-Smirnov test. We then combined the individual test probabilities from the four trout streams to provide an overall test of the hypothesis that day and night size distributions did not differ (using Fisher's method; Sokal and Rohlf 1981). We repeated this procedure for the streams without trout.

To estimate whether any differences in daytime drift rates between streams with and without trout were due to consumption of drifting *B. coelestis* we calculated potential predation rates for the trout in each stream. We estimated the density of trout in each stream by electrofishing (using a Smith-Root model XI-A electrofisher) after drift sampling was completed. Electrofishing commenced at the location of the drift net and continued upstream for at least 100 m (mean=126 m). The width of the stream was measured at intervals to calculate the area shocked. We measured the total length and volume (by water displacement in a graduated cylinder) of each trout captured. Repeated shocking of the same area in previous studies indicated that virtually all trout are captured, or at least seen, on the first pass (S.D. Cooper, unpublished data). Using the relationship between the mass of trout (g) and their volume (ml) (S. Cooper, unpublished data) we estimated trout density in each stream (g/m²) as the total mass of captured trout divided by the area sampled.

Assumptions used when calculating predation rates were deliberately biased to overestimate predation rates. We assumed that the number of *B. coelestis* caught in the net was influenced by trout predation within an arbitrary distance (20 m) upstream from the mouth of a drift net (area influenced=21.6 m²). This is almost certainly an overestimate since most mayflies caught in the net probably originated within 2 m of it (Allan and Feifarek 1989, and references therein). The electrofishing data were used to calculate the biomass of trout occupying this 21.6-m² area in each stream. Using published estimates of food consumption rates of rainbow trout in the field at temperatures similar to those in the study streams (0.46% of wet body weight per 24 h, from Angradi and Griffith 1990) we calculated the total prey consumption rate (mg dry prey wt./h) of trout occupying the 21.6-m² area. We assumed that drifting *B. coelestis* made up 50% by mass of the trout's diets. This is probably an overestimate because *Baetis* made up on average only 29% by number of prey items in the stomachs of trout

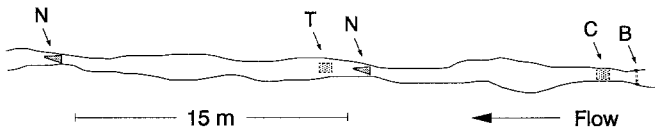


Fig. 2 Diagram of the experimental apparatus for testing effects of trout addition on drift of *Baetis coelestis* in three troutless streams. (T trout addition cage, C control cage, N drift net, B block net)

sampled from three of the study streams ($n=22$) (S.D. Cooper, P.L. Douglas and J. Killian, unpublished data). In addition, *Baetis* weigh less than many other common prey types (Meyer 1989).

To assess the potential for trout to deplete the population of drifting *B. coelestis* we calculated daytime drift rates in terms of biomass. We used a regression equation from Meyer (1989) to predict dry weights of *Baetis* from their head widths. Daytime drift rates in terms of biomass (mg/h) were calculated for each stream as the numeric drift rate (no./h) multiplied by the mean weight of *B. coelestis* in the sample.

Experimental addition of trout

To test for rapid alterations of drift behaviour in response to the presence of trout we introduced trout into three of the troutless streams (Mission Creek, Rattlesnake Creek and Cold Springs Creek). The experimental setup is shown in Fig. 2. In each stream we selected a roughly 30-m long riffle area. Each riffle was split into two 15-m-long sections. The lower section in each stream was designated for trout addition, and the upper section was used as a control (no trout added). We placed a cage (length=30 cm, width=25 cm, height=15 cm) made of plastic mesh (mesh size=3 mm) at the upstream end of each section and a drift net (mouth width=0.45 m, mouth height=0.30 m, net length=1 m, mesh size=0.33 mm) at the downstream end of each section. The drift nets intercepted all of the stream flow. In addition, a block net (mesh size=0.25 mm) was placed across the upstream end of the control section to ensure that the drift nets in the control and trout addition sections were collecting drift from equal lengths of stream.

The nets sampled drift continuously for 5 days. The first 24 h of drift sampling were done with trout absent from both control and trout addition sections (=before). Then two trout (mean total length=22.5 cm), captured from a nearby stream (Cachuma Creek), were added to each of the downstream cages and sampling was continued for a further 3 days (=during). Finally the trout were removed and sampling continued for a final 24 h (=after). The nets were emptied each day at dawn and dusk to generate nighttime and daytime estimates of drift density. Procedures for measuring discharge and counting *B. coelestis* were identical to those used in the survey of streams with and without trout.

Effects of trout on (1) daytime and (2) nighttime drift were assessed as the percentage difference in drift density between the trout addition and control areas (control–trout addition). Percentage differences in drift were calculated for each time of day, and each stream and date. For each stream, we pooled the measurements on different dates to calculate a mean for the three days during the trout addition (trout present) and a mean for the days before and after the manipulation (trout absent). We tested whether the difference in (1) daytime and (2) nighttime drift between control and addition sites was greater on the days when trout were added than on the days before and after using a paired *t*-test (with streams as replicates, $n=3$).

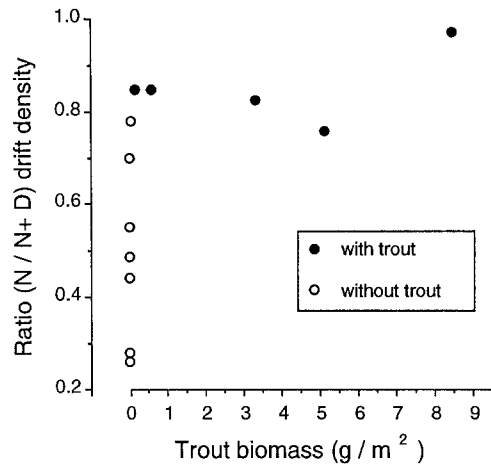


Fig. 3 The proportion of daily drift of *B. coelestis* which occurred at night [night/(night+day) drift density] versus trout biomass in the 12 study streams

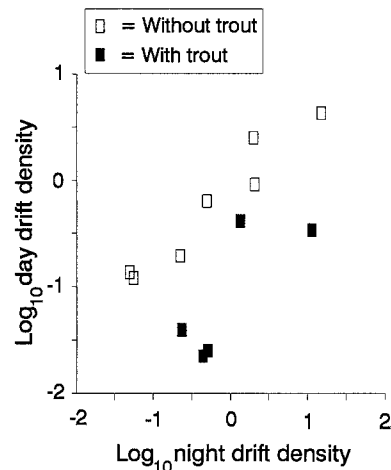


Fig. 4 Nighttime versus daytime drift densities (no. m⁻³) of *B. coelestis* in streams containing rainbow trout and in streams lacking trout

Results

Survey of drift in streams with and without trout

Drift densities

Our results support the first prediction of the predator avoidance hypothesis, that prey should be more nocturnal in the presence of predators than in their absence. Almost all drifting by *B. coelestis* occurred at night in streams containing trout (mean percentage of daily drift occurring at night=85%, $\pm 7.5\%$ SE, $n=5$) (Fig. 3), whereas drift was fairly evenly split between night and day in streams lacking trout (mean percentage of daily drift occurring at night=50%, $\pm 19\%$ SE, $n=7$) (Fig. 3). This shift in periodicity was highly significant (*t*-test on arcsine square root transformed data, $t=3.89$, $df=10$, one-tailed $P=0.0015$). Despite the striking difference in drift peri-

odidity between streams containing versus lacking trout, there was no obvious relationship between trout biomass and the ratio of night to total drift density in streams where trout were present (Fig. 3).

The slope of the relationship between nighttime and daytime drift density was similar for streams with and without trout (ANCOVA, $F_{1,8}=0.004$, $P=0.95$). The elevation of the regression lines was significantly different (ANCOVA, $F_{1,8}=16.1$, $P=0.004$), however, because at a given level of nighttime drift, daytime drift density was lower in the streams containing trout than in the streams lacking these predators (Fig. 4). This provides tentative support for the second prediction of the predator avoidance hypothesis, that prey should reduce daytime activity in habitats occupied by predators.

Size distributions

Kolmogorov-Smirnov tests for each stream indicated that daytime and nighttime size distributions of drifting *B. coelestis* were not significantly different in any of the streams without trout, except Rattlesnake Creek ($P=0.001$) (P for other streams all > 0.14 , mean $P=0.64$). When the test results for individual streams were pooled, the null hypothesis that daytime and nighttime size distributions were similar in troutless streams could not be rejected ($\chi^2=19.8$, $df=14$, $P=>0.25$). In contrast, the probabilities of day and night size distributions being different were consistently low in trout streams (Kolmogorov-Smirnov tests, all $P<0.16$, mean $P=0.085$). Combining the test results for the four trout streams suggests that, overall, size distributions of *B. coelestis* in trout streams differed between day and night ($\chi^2=28.9$, $df=8$, $P=<0.001$).

To assess how size-distributions of *B. coelestis* differed between streams with and without trout we assigned mayflies to one of five equally spaced head-width classes between 0 and 1 mm. We calculated the proportion of mayflies in each size class to generate a relative size frequency distribution for each stream and time of day (Fig. 5). Size distributions under different predation regimes and times of day appear similar, except that large size classes of *B. coelestis* were underrepresented in trout streams during the day.

This pattern is confirmed by inspection of a plot of the difference between day and night in the proportion of *B. coelestis* occupying each size class (Fig. 6). There is little change between day and night in the size distribution of *B. coelestis* drifting in streams without trout. In trout streams, however, the relative frequency of large nymphs (0.4–0.6 mm) was lower during the day than at night, whereas the relative frequency of small nymphs (0.2–0.4 mm) was higher during daylight than after dark (Fig. 6). These results support the third prediction of the predator avoidance hypothesis that large, more vulnerable, nymphs should be more nocturnal than small nymphs.

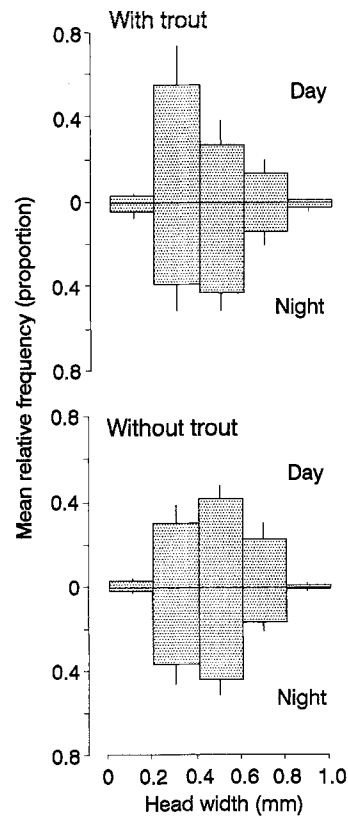


Fig. 5 Size distributions of drifting *B. coelestis* in streams with ($n=4$) and without ($n=7$) rainbow trout during the day and at night. Size distributions were generated for each stream at each time of day. Plotted are mean relative frequencies, with SEs, using streams as replicates

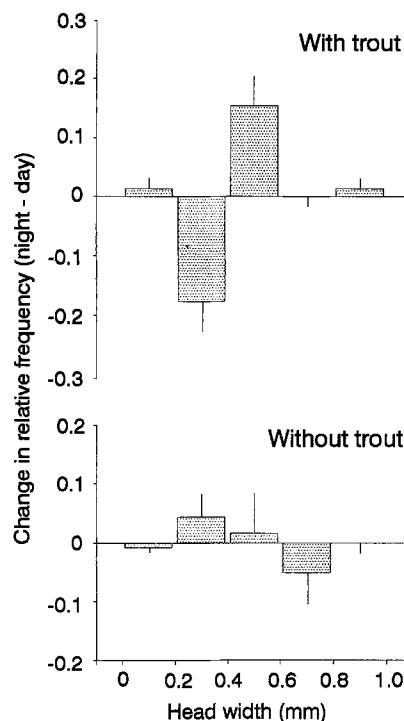


Fig. 6 Differences between day and night in the proportion of drifting *B. coelestis* occupying different size classes. Plotted are means and standard errors using streams as replicates

Rates of predation by trout

Mean daytime drift rates of *B. coelestis* were 1.4 mg per hour (± 1.0 SE, $n=5$) in streams with trout and 5.5 mg per hour (± 2.9 SE, $n=7$) in troutless streams. The mean estimated predation rate on *B. coelestis* by trout occupying the 20 m directly upstream of the drift nets was 0.8 mg per hour (± 0.3 SE, $n=5$). In order to account for the observed difference in drift rate the trout upstream of the drift net would have to consume on average 4.1 mg *B. coelestis* per hour. Our estimates, which were deliberately biased to be overestimates, suggest that direct predation by trout could account for only 17% of the reduction in drift rate in the presence of trout. The difference in drift periodicity between streams with and without trout is not, therefore, due simply to consumption of drifting *B. coelestis* during the day.

Experimental addition of trout

B. coelestis drifting during the night showed no obvious responses following the addition of trout to troutless streams (Fig. 7). The difference in drift density between

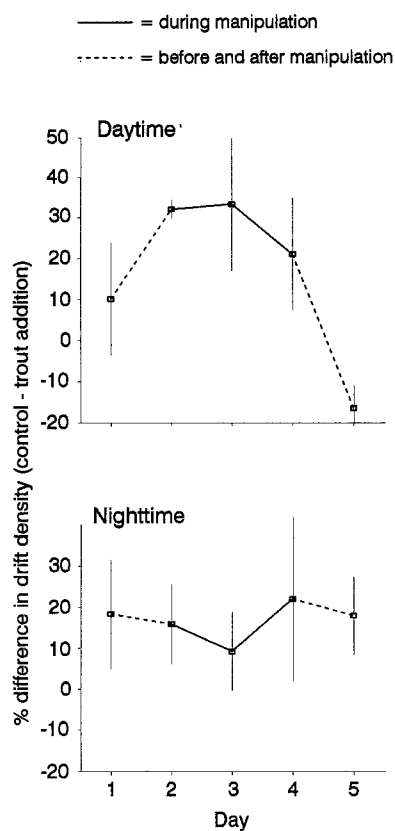


Fig. 7 Responses of *B. coelestis* to the addition of trout in previously troutless streams. Plotted are differences in the drift density of *B. coelestis* between experimental (trout added—located downstream) and control (no trout added—located upstream) areas in each of three streams. Mean differences, with SEs, are plotted for the day before (1), 3 days during (2, 3, 4) and 1 day after (5) trout addition

control and trout addition areas was similar on the days before, during and after the trout were present (paired t -test, $t=0.23$, $df=2$, two-tailed $P=0.84$). In contrast, daytime drift densities were slightly, but consistently, depressed below trout addition cages compared to control cages on the three days when trout were present (mean depression over all 3 days=28%). This depression of daytime drift density was not apparent on the day immediately before the trout were added or the day after they were removed (Fig. 7). The extent to which daytime drift was reduced below trout addition cages differed significantly between days when trout were present to the days before and after the manipulation (paired t -test, $t=4.53$, $df=2$, two-tailed $P=0.045$).

Discussion

Our estimates of potential trout feeding rates allow us to exclude the possibility that differences in drift periodicity between streams were due to consumption by trout of *B. coelestis* drifting during the day. Differences in drift periodicity between the two sets of streams must, therefore, reflect changes in drifting behaviour.

Our results confirmed the first prediction of the predator avoidance hypothesis, because drifting was more nocturnal in streams containing fish that feed visually in the water column than in streams lacking these predators. Two previous studies testing this prediction reported similar results. Malmqvist (1988) found predominantly nocturnal drift of *Baetis rhodani* in a Madeiran waterway occupied by trout, whereas the same mayfly drifted aperiodically in a nearby troutless waterway. This comparison was, however, unreplicated making it difficult to confirm that predator presence caused the difference between the two sites. Flecker (1992) compared the night:day drift ratios of several mayfly taxa in eight neotropical streams in the Venezuelan Andes. Drift-feeding fish were absent from two of the streams at high elevation, but the biomass and species richness of fish progressively increased with decreasing altitude in six other streams. The ratio of night:day drift density of mayflies increased as predator biomass and richness increased. Unfortunately, the gradient of predator density among the streams covaried with a gradient of physical and chemical conditions (e.g. elevation, temperature), which raises the possibility that patterns of drift periodicity were caused by other factors covarying with the predation gradient. The presence and absence of trout in the streams we surveyed covaried to some extent with the stream's susceptibility to drying, again raising the possibility that the patterns we observed were caused by a factor covarying with predator presence. We suggest, as did Flecker (1992), that the differences in physical conditions among the streams are unlikely to affect diel periodicity of drifting. More importantly though, we argue that the chance of there being a spurious correlation between drift periodicity and predator presence in all three

systems is very low. Although the three studies have weaknesses individually, considered together they provide convincing support for the predator avoidance hypothesis.

The predator avoidance hypothesis also predicts that daytime drift should be reduced in the presence of trout, because trout predation should select against daytime drifting rather than for nighttime drifting. Our survey suggested that daytime drift was reduced in streams containing trout because, at a given level of nighttime drift, daytime drift was lower in trout streams than in streams lacking trout. This conclusion is made cautiously, however, because we did not measure benthic densities of *B. coelestis* in the streams, and so cannot be certain that the probability of drifting during the day was different for mayflies under different predation regimes. Large *B. coelestis* apparently reduced their daytime drifting to a greater extent than small *B. coelestis*, providing support for a third prediction of the predator avoidance hypothesis, that larger, more vulnerable nymphs should show stronger avoidance of trout. Overall, therefore, our survey data provide good evidence that drifting primarily at night is an avoidance response to visual predators in the water column.

The second issue we sought to address was whether this avoidance was the result of fixed or phenotypically plastic behaviours. Demonstration of plastic responses is relatively simple because prey should respond rapidly to experimental manipulation of predator presence. For this reason, most studied examples of predator avoidance responses are of this type. Fixed responses are difficult to demonstrate experimentally, because prey do not respond to the short-term manipulation of predator presence (Sih 1987). Surveys documenting differences in prey behaviour under different predation regimes, coupled with lack of plastic responses to predator manipulation, however, constitute reasonable evidence for a fixed avoidance response (Endler 1986).

Most previous studies testing for plastic responses to water column predators have removed predators from small areas in streams occupied by predators (Williams 1990; Flecker 1992; Forrester in press). In some studies, most (Williams 1990; Forrester in press) or all (Flecker 1992) prey taxa showed no change in drift density following predator removal. Unfortunately these experiments do not exclude the possibility that prey were responding phenotypically to chemical cues from fish upstream of the removal areas. Allan (1982) removed trout from a long (1.2 km) stretch of stream thus greatly increasing the chance of removing cues indicating the presence of trout. Trout were, however, not completely eliminated from the manipulated area (25% of the initial biomass remained) so invertebrates could still potentially respond to cues from predators. Flecker (1992) argued that nocturnal peaks of drifting observed in laboratory streams where water-column predators were absent (e.g. Corkum et al. 1977; Ciborowski 1983; Kohler 1985), indicate a fixed diel periodicity of drifting. At least one of these studies was, however, done using stream water mi-

xed with tap water, so chemical cues from fish may have been present (Kohler 1985).

We tested for plastic responses by adding caged trout to troutless streams. Control areas in our troutless streams can be assumed to be uninfluenced by predators, so a lack of response to predator addition, coupled with our survey data, would be good evidence for a fixed avoidance response. We did, however, detect an immediate (within 24 h) reduction in daytime drift density by *B. coelestis* following trout addition. Our observation of reduced daytime drifting in response to trout addition suggests that at least part of the difference in drift periodicity of *B. coelestis* among streams containing versus lacking trout is caused by a phenotypically plastic response to trout presence. Interestingly, the type of plastic response to trout shown by *Baetis* in our experiment was different from responses of *Baetis* and another mayfly (*Paraleptophlebia*) to trout removal in a New Hampshire stream (Forrester in press). Instead of showing lowered daytime drift in the presence of trout, these mayflies increased their rate of nighttime drift in areas containing trout. This suggests that there is variation both within and among taxa in plastic drift responses to water column predators. Similar variation is also apparent in the response of mayflies to other kinds of predators, including stoneflies (Peckarsky 1980; Corkum and Pointing 1979; Walton 1980; Malmqvist and Sjöström 1987; Lancaster 1990) and benthic fish (Kohler and McPeck 1989; Culp et al. 1991).

We suggest that the layout of our experiment (the trout were caged in a small area and the drift nets were 15 m downstream of the cages; Fig. 2) isolated chemical cues as the cause of reduced daytime drifting following trout addition. Mean drift distances of *Baetis* are usually less than 2 m (Allan and Feifarek 1989 and references therein) so it is unlikely that trout influenced the drift net catches by consuming *Baetis*, or that *Baetis* caught in the drift nets were responding to other cues from trout (e.g. visual, hydrodynamic or auditory stimuli). Gammarid amphipods also show reduced drift activity in response to chemical cues from fishes (Williams and Moore 1985, 1989; Andersson et al. 1986; Andersen et al. 1993).

Our detection of a plastic drift response to trout does not exclude the possibility that there is also a fixed component to the difference in drift periodicity between streams with and without trout. Studies in other systems suggest the possibility that avoidance responses to predators may have both fixed and plastic components. For example, intertidal snails from populations varying in the density of a predatory octopus all showed flexible avoidance of the predator (by moving higher up the shore when predators were present), but superimposed on this was a fixed pattern consistent with avoidance; snails from shores dense with predators positioned themselves higher on the shore than snails from shores with few octopodes regardless of predator presence (Fawcett 1984).

Light cues have long been known to influence the timing of activity and drifting in stream insects (Elliott 1965; Müller 1966; Holt and Waters 1967; Bishop 1969;

Haney et al. 1983). These cues are likely to regulate diel drift periodicity when nocturnal drifting is a fixed avoidance response to predators. The diel vertical migrations of zooplankton can be regulated by either light cues, predator cues, or a combination of the two (Leibold 1990; Dawidowicz et al. 1990; O'Bryan 1991; Ringelberg 1991a, b; Neill 1992). Future studies will likely uncover a comparable mixture of regulatory mechanisms for diel drift periodicity.

Acknowledgements This work was supported by NSF grants DEB 9207228 to S.D. Cooper and BSR 9016445 to P.F. Sale and G.E. Forrester. Thanks to W.P. McCafferty for identifying the mayfly nymphs.

References

- Allan JD (1978) Trout predation and the size-composition of stream drift. *Limnol Oceanogr* 23: 1231–1237
- Allan JD (1982) The effects of reduction in trout density on the invertebrate community of a mountain stream. *Ecology* 63: 1444–1455
- Allan JD (1984) The size composition of invertebrate drift in a Rocky Mountain stream. *Oikos* 43: 68–76
- Allan JD, Feifarek BP (1989) Distances travelled by drifting mayfly nymphs: factors influencing return to the substrate. *J N Am Benthol Soc* 8: 322–330
- Andersen TH, Friberg N, Hansen HO, Iversen TM, Jacobsen D, Krogaard L (1993) The effects of introduction of brown trout (*Salmo trutta* L.) on *Gammarus pulex* L. drift and density in two fishless Danish streams. *Arch Hydrobiol* 126: 361–371
- Andersson KG, Brönmark C, Hermann J, Malmqvist B, Otto C, Sjöström P (1986) Presence of sculpins (*Cottus gobio*) reduces drift and activity of *Gammarus pulex* (Amphipoda). *Hydrobiologia* 133: 209–215
- Angradi TR, Griffith JS (1990) Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. *Can J Fish Aquat Sci* 47: 199–209
- Bishop JE (1969) Light control of aquatic insect activity and drift. *Ecology* 50: 371–380
- Ciborowski JJH (1983) The influence of current velocity and substrate on the distribution and drift of two species of mayflies (Ephemeroptera). *Can J Zool* 61: 119–125
- Corkum LD, Pointing PJ (1979) Nymphal development of *Baetis vagans* McDunnough (Ephemeroptera: Baetidae) and drift habits of large nymphs. *Can J Zool* 57: 2348–2354
- Corkum LD, Pointing PJ, Ciborowski JJH (1977) The influence of current velocity and substrate on the distribution and drift of two species of mayflies (Ephemeroptera). *Can J Zool* 55: 1970–1977
- Culp JM, Glozier NE, Scrimgeour GJ (1991) Reduction of predation risk under the cover of darkness: avoidance responses of mayfly larvae to a benthic fish. *Oecologia* 86: 163–169
- Dawidowicz PJ, Pijanowska J, Ciechomski K (1990) Vertical migration of *Chaoborus* larvae is induced by the presence of fish. *Limnol Oceanogr* 35: 1631–1637
- Dill LM (1987) Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Can J Zool* 65: 803–811
- Edmunds M (1974) Defence in animals: a survey of antipredator defences. Longman, Harlow, Essex
- Elliott JM (1965) Daily fluctuations of drift invertebrates in a Dartmoor stream. *Nature* 205: 1127–1129
- Elliott JM (1973) The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. *Oecologia* 12: 329–347
- Endler JA (1986) Natural selection in the wild. Princeton University Press, Princeton
- Fawcett MH (1984) Local and latitudinal variation in predation on an herbivorous marine snail. *Ecology* 65: 1214–1230
- Flecker AS (1992) Fish predation and the evolution of invertebrate drift periodicity: evidence from neotropical streams. *Ecology* 73: 438–448
- Forrester GE (1992) Predator-prey interactions between fish and insects in streams. Ph.D. dissertation, University of New Hampshire
- Forrester GE. Diet patterns of drift by five species of mayfly at different levels of fish predation. *Can J Fish Aquat Sci*, in press
- Haney JF, Beaulieu TR, Berry RP, Mason DP, Miner CR, McLean ES, Price KL, Trout MA, Vinton RA, Weiss SJ (1983) Light intensity and relative light change as factors regulating stream drift. *Arch Hydrobiol* 97: 73–88
- Holt CS, Waters TF (1967) Effect of light intensity on the drift of stream invertebrates. *Ecology* 48: 225–234
- Irvine JR, Northcote TG (1983) Selection by young rainbow trout (*Salmo gairdneri*) in simulated stream environments for live and dead prey of different sizes. *Can J Fish Aquat Sci* 40: 1745–1749
- Jenkins TM Jr, Feldmuth CR, Elliott GV (1970) Feeding of rainbow trout (*Salmo gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. *J Fish Res Bd Can* 27: 2356–2361
- Kohler SL (1985) Identification of stream drift mechanisms: an experimental and observational approach. *Ecology* 66: 1749–1761
- Kohler SL, McPeck MA (1989) Predation risk and the foraging behavior of competing stream insects. *Ecology* 70: 1811–1825
- Lancaster J (1990) Predation and drift of lotic macroinvertebrates during colonization. *Oecologia* 85: 48–56
- Leibold MA (1990) Resources and predators can affect the vertical distributions of zooplankton. *Limnol Oceanogr* 35: 938–944
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68: 619–640
- Malmqvist B (1988) Downstream drift in Madeiran Levadas: tests of hypotheses relating to the influence of predators on the drift of insects. *Aquat Insects* 10: 141–152
- Malmqvist B, Sjöström P (1987) Stream drift as a consequence of disturbance by invertebrate predators. *Oecologia* 74: 396–403
- Meyer E (1989) The relationship between body length parameters and dry mass in running water invertebrates. *Arch Hydrobiol* 117: 191–203
- Moriyara DK, McCafferty WP (1979) The *Baetis* larvae of North America (Ephemeroptera: Baetidae). *Trans Am Entomol Soc* 105: 139–221
- Müller K (1966) Zur Periodik von *Gammarus pulex*. *Oikos* 17: 207–211
- Müller K (1974) Stream drift as a chronobiological phenomenon in running water ecosystems. *Annu Rev Ecol Syst* 5: 309–323
- Neill We (1992) Population variation in the ontogeny of predator-induced vertical migration of copepods. *Nature* 356: 54–59
- Newman RM, Waters TF (1984) Size selective predation on *Gammarus pseudolimnaeus* by trout and sculpins. *Ecology* 65: 1535–1545
- O'Bryan LM (1991) Changes in the horizontal distribution of *Chaoborus punctipennis*: effects of moonlight and fish. Thesis, University of New Hampshire, Durham, New Hampshire, USA
- Peckarsky BL (1980) Predator-prey interactions between stoneflies and mayflies: behavioral observations. *Ecology* 61: 932–943
- Ringelberg J (1991a) A mechanism of predator-mediated induction of diel vertical migration in *Daphnia hyalina*. *J Plankt Res* 13: 83–89
- Ringelberg J (1991b) Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). *J Plankt Res* 13: 17–25

- Sih A (1987) Predators and prey lifestyles: an evolutionary and ecological overview. In: Kerfoot WC, Sih A (eds) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, pp 203–224
- Skinner WD (1985) Night- day drift patterns and the size of larvae of two aquatic insects *Hydrobiologia* 124: 283–285
- Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, New York
- Stein RA (1979) Behavioral responses of prey to fish predators. In: Stroud RH, Clepper H (ed) Predator-prey systems in fisheries management. Sport Fishing Institute, Washington DC pp 343–353
- Walton OE Jr (1980) Invertebrate drift from predator-prey associations. *Ecology* 61: 1486–1497
- Waters TF (1972) The drift of stream insects. *Annu Rev Entomol* 17: 253–272
- Williams DD (1990) A field study of the effects of water temperature, discharge and trout odour on the drift of stream invertebrates. *Arch Hydrobiol* 119: 167–181
- Williams DD, Moore KA (1985) The role of semiochemicals in benthic community relationships of the lotic amphipod *Gammarus pseudolimnaeus*: a laboratory analysis. *Oikos* 44: 280–286
- Williams DD, Moore KA (1989) Environmental complexity and the drifting behaviour of a running water amphipod. *Can J Fish Aquat Sci* 46: 1520–1530