Hubbard

J. N. Am. Benthol. Soc., 1989, 8(4):322-330

# Distances travelled by drifting mayfly nymphs: factors influencing return to the substrate

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*Abstract.* We determined the distance travelled by drifting nymphs of the mayflies *Baetis* and *Cinygmula* to add to existing knowledge of factors influencing drift distance, and to investigate the influence of drift-exiting behavior upon drift magnitude and periodicity. Individuals were released into the water column of a trough at 0.5-m intervals above the exit point, and numbers remaining in suspension over each release distance were fit to a previously developed model which describes return to the substrate according to a negative exponential function. Drift distance increased with increasing current velocity (range studied: 5–55 cm/s) and with decreasing body size (range studied: ca. 0.1–1 mg dry wt) according to log-linear functions. At higher velocities (35 and 55 cm/s), nymphs of both species drifted much shorter distances alive than dead, indicating active exiting from the drift. Drift distances of live nymphs scarcely differed between day and night, which contradicts the suggestion that greater drift abundances at night are caused by disorientation in darkness and consequently greater drift distances. Furthermore, comparisons using nymphs collected from the drift vs. the benthos, and subsequently fed or starved, also revealed no effect of treatment on drift distance, counter to expectations if drifting individuals were intrinsically weaker or less healthy than their benthic counterparts. Thus, although behavioral ability to exit the drift clearly exists in a number of invertebrate taxa, neither the occurrence of drift nor its diel periodicity was explainable on the basis of drift exiting behavior.

*Key words:* drift, *Baetis, Cinygmula,* current, body size, Ephemeroptera, settling distance.

The downstream drift of invertebrates in streams has been intensively studied for at least three decades. The magnitude of drift makes it important in dispersal and colonization (Ciborowski 1987, Müller 1973), as well as a major food source for fishes. Nocturnal periodicity is common, its proximate control is light level (Müller 1974), and the adaptive explanation seems to be the minimization of predation risk due to visually feeding fishes (Allan 1978). The distance travelled by suspended invertebrates is perhaps the most elegantly quantified aspect of drift, resting on a simple model of settling to the substrate developed and tested by McLay (1970) and Elliott (1971). However, mechanisms that result in drift entry, and the relative contributions of active vs. passive processes, remain controversial (Brittain and Eikeland 1988).

Herein we investigate the joint effects of body size and current speed on distance travelled by drifting mayflies. In addition, variation in drift distance, which may depend upon ability to exit the drift, potentially contributes to drift magnitude and periodicity. The nocturnal increase of drift usually is assumed (perhaps tacitly) to reflect periodicity in drift entry, but an alternative hypothesis (Hughes 1966, Statzner and Mogel 1985) is that individuals drift farther at night because they are disoriented in the absence of light. Night catches would then be greater because they sample drift originating over a greater distance upstream. It has also been suggested that individuals in the drift may be genetically inferior to those in the benthos (Minshall and Petersen 1985), or weakened by infections (Wilzbach et al. 1988). If so, individuals experimentally introduced into the drift from the benthos might have greater ability to regain the substrate than individuals naturally occurring in the drift.

We therefore investigated drift distance at several current speeds for a range of sizes of two species of Ephemeroptera, *Baetis* (Baetidae) and *Cinygmula* (Heptageniidae), obtained from mountain streams in Gunnison County, Colorado. In addition to examining factors that influence distance travelled in the drift, we explored the possibility that mayfly larvae could behaviorally control their time in suspension.

## Methods

### *Measurement of drift distance*

Drift distance was determined in a trough 6.5 m in length constructed from plastic rain gutter. Coarse sand was affixed to inner surfaces with non-toxic, brown spray paint. Stream water, filtered through a 200-μm net, was supplied by gravity feed into a header box from which a spigot controlled current velocity. A collimator made from soda straws reduced turbulence, and louvers at the downstream end of the trough maintained a constant depth throughout. A 200-μm catch net filtered the entire outflow for capture of drifting animals. The trough had a maximum depth and width of 10 cm and 12 cm, respectively, and water depth was 7 cm. Current velocity (V) was set at 5, 15, 35 and 55 cm/s, measured at mid-depth with a Marsh-McBirney current meter. Velocity was nearly uniform throughout the length of the trough, based on measurements at 0.5 m intervals, and always varied <10% from the stated value.

Nymphs of *Baetis* and *Cinygmula* were collected, hand-sorted and held (typically <1 hr) in mesh vials in fast-flowing stream water prior to use. They were visually sorted into size categories (small, medium and large *Baetis*, small and large *Cinygmula*); head widths subsequently were determined for 20 individuals per experimental run and converted to dry weights using previously determined regressions. Following the approach of Elliott (1971), we released 20 individuals into the current at progressively greater distances above the end of the trough (i.e., 0, 0.5, 1, 1.5, 2 m, etc.) and recorded numbers in the catch nets. Each treatment was replicated at least three times, and remaining animals were removed before further releases were made. Nymphs were released by slowly submerging a glass vial with a removable base to a standard depth (4 cm). The base of the vial was gently removed, allowing all individuals to be suspended at approximately mid-depth. Individual nymphs were used twice and then discarded. Comparison of distance travelled revealed no differences related to first vs. second use. Hot water was used to kill animals in drift trials using dead nymphs. These trials had a time limit that allowed a continuously drifting individual to reach the drift net, but excluded the possibility of dead animals settling, then becoming resuspended and exiting the trough by multiple drift events. Flashlights with red filters were used for sorting and recovering animals during night trials, but release took place in total darkness.

### *Drift model*

Data were analyzed according to the drift model developed by McLay (1970) and extended by Elliott (1971) and Larkin and McKone (1985). This model relates the numbers ($N_x$) in the drift at some distance (X) downstream from their point of entry to the initial numbers entering the drift ($N_0$) according to a simple exponential decay function

$$N_x = N_0 e^{-RX} \qquad (1)$$

The constant R measures rate of settling to the substrate, and its reciprocal estimates mean distance ($\bar{X}$) travelled by an individual in the drift:

$$\bar{X} = \frac{1}{R} \qquad (2)$$

Data were fitted to the model by linear regression after logarithmic transformation:

$$\log_e(N_x) = \log_e(N_0) - RX \qquad (3)$$

In practice, all values were ($N_x + 1$).

Lastly, the distance traversed by the furthest drifting P% of initial numbers is given by:

$$X_{P\%} = (\log_e 100 - \log_e P)\bar{X} \qquad (4)$$

We chose to use $X_{10\%}$, which can also be interpreted as the distance by which 90% of suspended nymphs regain the substrate.

### *Experimental comparisons*

The principal comparisons of drift distance included live vs. dead animals, day vs. night, effect of current speed and nymphal size, and whether animals were obtained from the drift or the benthos. Day vs. night drift distance was estimated for three size classes of *Baetis* and two size classes of *Cinygmula* at four current speeds.

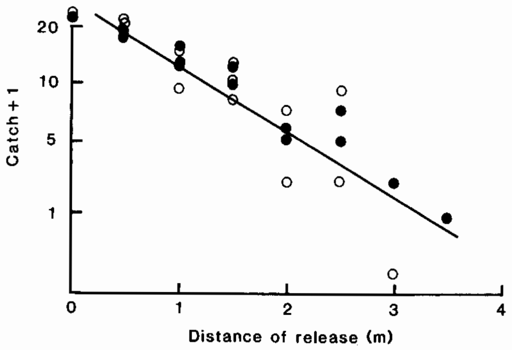

FIG. 1. Drift distance of large *Baetis* at 35 cm/s in experimental troughs, demonstrating exponential decline from the initial release density, of numbers still in the drift as a function of distance travelled.

Drift distance of dead animals also was estimated for each size class and current speed. Drift distance for animals captured from the benthos vs. the drift was compared using large *Baetis* at 35 cm/s. All regressions and analyses of covariance (ANCOVA) were performed using the general linear models procedure of SAS (1982). Homogeneity of variances was tested prior to ANCOVA analysis.

## Results

### *Adequacy of the drift model*

The drift distance model provided a reasonable description of data relating drift catches to distance travelled from point of release to the catch net (Fig. 1). Estimated values for $r^2$ for drift distance data fit to equation 3 generally were high, ranging from 0.60 to 0.99, and most were above 0.80. As a further check, for all regressions we tested whether 95% confidence limits on intercept values included $\log_e(21)$. In four out of 58 instances there was significant deviation, approximately the magnitude expected by chance. In each instance the calculated intercept value was too large, suggesting a tendency for the model to generate too steep a settling curve. However, despite large values of $r^2$ and the high predictive value of data fit to equation 3, significant deviations about the regression line occurred in 17 (29%) of the instances, presumably due to random heterogeneity about the regression line (Sokal and Rohlf 1981:483). Fourteen of these were at currents of 5 and 15 cm/s, indicating a poorer fit to the model at low currents. Of the three instances at higher current speeds, two involved dead animals. The amount of heterogeneity in the remaining example, day trials using *Baetis* at 35cm/s, can be evaluated by inspecting Figure 1.

### *Comparison of drift distance in living vs. dead nymphs*

The ability of drifting individuals either to shorten or increase the distance travelled can be assessed most directly by comparing living to dead animals. If they travel identical distances, then exiting from the drift presumably is due to passive settling, whereas any discrepancy in drift distance between live and dead animals presumably reflects behavioral control.

The drift distance model provided an adequate description of settling distance for dead nymphs at 5 and 15 cm/s, where $r^2$ values were $>0.80$. At 35 and 55 cm/s, however, most dead individuals remained in the drift throughout the 6-m length of the trough. Consequently, estimates of $r^2$ generally were $<0.50$ and three of the eight regressions were not significant. However, it was obvious that dead individuals at higher current velocities would be transported considerable distance. Comparison of slopes (ANCOVA) of settling distances of live vs. dead individuals for each combination of species, size class and current velocity revealed significant differences in 17 out of 20 instances. Consequently, mean drift distance generally differed between live and dead animals. However, the direction of the difference depended upon current speed. At slower velocities (5 and 15 cm/s), live animals drifted similar or greater distances than did dead animals (Table 1). At higher velocities (35 and 55 cm/s), however, live animals drifted much shorter distances than did dead nymphs. The ratios of mean distance drifted, dead:live, suggest that this difference is more pronounced in *Baetis* than in *Cinygmula*. However, because the estimates of settling distance for dead animals at higher current velocities are very imprecise, actual values of this ratio must be viewed with caution.

### *Day vs. night drift distances*

Drift distances did not differ between day and night in 13 of the 18 species-size combinations

TABLE 1. The ratio of mean drift distance ($\bar{X}$) for dead nymphs : live nymphs, as a function of species and size (dry wt (mg): mean; one standard error). The symbol (+) shows that the ratio was large, but the estimate for dead nymphs was too imprecise to use. Mean drift distances of live vs. dead nymphs were significantly different by ANCOVA in all but three instances, marked $^{ns}$.

| | Current Velocity (cm/s) | | | |
|---|---|---|---|---|
| | 5 | 15 | 35 | 55 |
| Small *Baetis* | | | | |
| (0.15; 0.022) | 0.50 | 1.05$^{ns}$ | 11.3 | (+) |
| Medium *Baetis* | | | | |
| (0.47; 0.068) | 0.99$^{ns}$ | 0.61 | 64.0 | (+) |
| Large *Baetis* | | | | |
| (0.96; 0.108) | 1.06$^{ns}$ | 0.73 | 92.4 | 8.7 |
| Small *Cingymula* | | | | |
| (0.32; 0.086) | 0.43 | 0.62 | (+) | 7.6 |
| Large *Cinygmula* | | | | |
| (1.04; 0.066) | 0.48 | 0.46 | 2.9 | 1.8 |

(ANCOVA). However, for five comparisons (large *Cinygmula* at 5 and 55 cm/s, medium *Baetis* at 5 cm/s, and large *Baetis* at 35 and 55 cm/s), slopes were found to differ. Of these, estimated night drift distance exceeded the day estimate four times, and the reverse occurred once (large *Cinygmula*, 5 cm/s). Where night drift distance appeared greater, the magnitude ranged from 1.2–1.6 times. There was no apparent tendency for this discrepancy to occur in particular species or size combinations, and we suspect that they are chance events. If drifting mayfly nymphs do indeed travel farther in the dark, the extra distance is small.

### *Influence of current velocity and body size on drift distance*

As expected, drift distance increased with increasing current velocity for all species and size combinations. This is illustrated for two size classes of *Baetis* in Figure 2. A power function satisfactorily describes the relationship between R and V, and $X_{P\%}$ and V, as reported by Elliott (1971):

$$R = aV^{-b} \quad (5)$$

$$X_{P\%} = aV^{b} \quad (6)$$

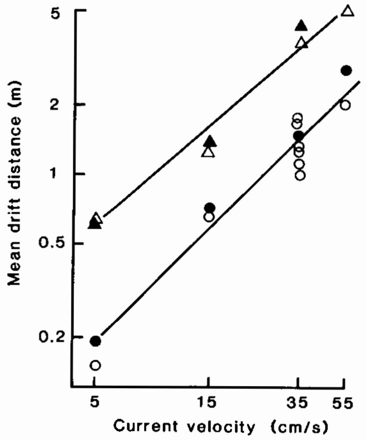

FIG. 2. Mean drift distance ($\bar{X}$, m) as a function of current velocity for two size classes of *Baetis*. Circles = large, triangles = small *Baetis*; open symbols = day, solid symbols = night.

The constants a and b were fitted by log-log regression and are reported in Table 2. Variation in current velocity explained ≥86% of the variation in settling distance. At each current velocity, drift distance varied inversely with body size. The dependence of $X_{10\%}$ on estimated dry wt was broadly similar for all species and size combinations (Fig. 3). An ANCOVA analysis (dependent variable: $X_{10\%}$) was performed for each species, and both current and dry wt were found to be highly significant. Lack of a significant interaction term indicated homogeneity of slopes for *Cinygmula* (>0.2), but not for *Baetis* (<0.02).

From inspection of Figure 3 and ANCOVA tables, drift distance is increased more by a rise in current velocity than by a reduction in body size. Standard partial regression coefficients show that variation in current velocity has a 2 (*Baetis*) to 2.5 (*Cinygmula*) times greater influence on drift distance ($X_{10\%}$), in comparison to variation in dry wt, when both terms are expressed in units of standard deviations (Table 3).

### *Drift distance as a function of drift vs. benthic origin*

The distance drifted by *Baetis* in day trials at 35 cm/s did not appear to depend on either origin (drift vs. benthos), or food treatment (starved vs. fed). Two trials, one in early August

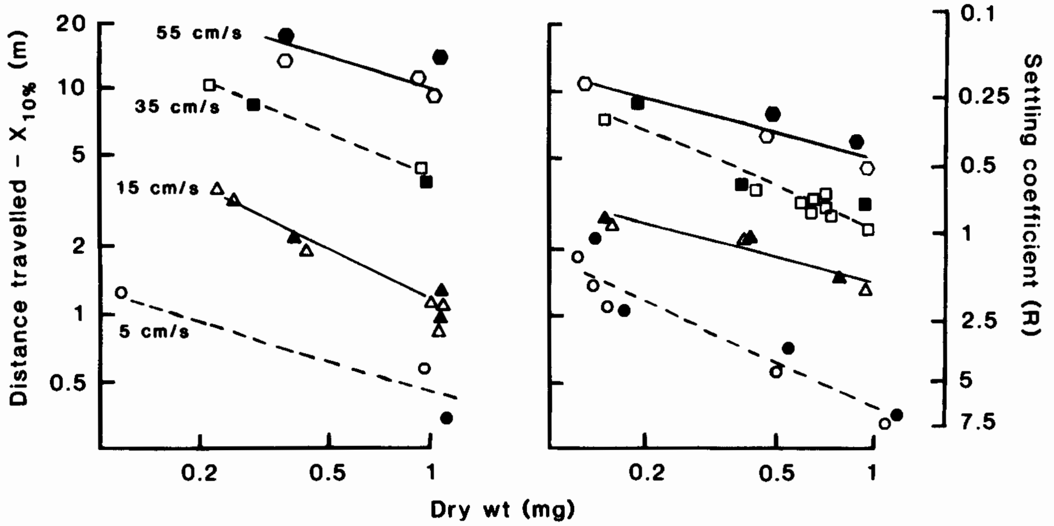

FIG. 3. Distance travelled by farthest drifting 10% of nymphs ($X_{10\%}$) of *Cinygmula* (left panel) and *Baetis* (right panel) as a function of individual size and current velocity. Open symbols = day; solid symbols = night.

and a second in early September, gave similar results. A three-way ANCOVA (origin, food treatment, trial) revealed parallel slopes for all eight regressions and no significant differences associated with drift vs. benthic origin or fed vs. starved. However, a significant difference was detected between the two trials, reflecting a small discrepancy in average intercept values.

## Discussion

### *Physical transport in the drift*

The model of drift first proposed by McLay (1970) has proven to be a reasonable description of the return of drifting invertebrates to the substrate, thus allowing quantification of distance travelled. Elliott (1971) demonstrated for

TABLE 2. Relationships between R (settling coefficient) and V (water velocity) fit by log-log regression to the equation $R = aV^{-b}$ for each species and size combination, and for distance travelled by $X_{10\%}$ of the population fit to $X_{P\%} = aV^{b}$. The standard errors of slope estimates ($SE_b$), coefficients of determination ($r^2$) and sample size ($n$) are as shown.

| | a | b | $SE_b$ | $r^2$ | $n$ |
|---|---|---|---|---|---|
| R and V | | | | | |
| Small *Baetis* | 3.78 | −0.731 | 0.106 | 0.86 | 10 |
| Medium *Baetis* | 9.39 | −0.840 | 0.074 | 0.96 | 8 |
| Large *Baetis* | 29.05 | −1.049 | 0.062 | 0.95 | 16 |
| Small *Cinygmula* | 11.50 | −1.090 | 0.144 | 0.89 | 9 |
| Large *Cinygmula* | 45.68 | −1.306 | 0.125 | 0.92 | 12 |
| $X_{10\%}$ and V | | | | | |
| Small *Baetis* | 0.378 | 0.827 | 0.104 | 0.89 | 10 |
| Medium *Baetis* | 0.153 | 0.946 | 0.064 | 0.97 | 8 |
| Large *Baetis* | 0.063 | 1.087 | 0.055 | 0.97 | 16 |
| Small *Cinygmula* | 0.139 | 1.156 | 0.129 | 0.92 | 9 |
| Large *Cinygmula* | 0.034 | 1.371 | 0.123 | 0.92 | 12 |

a number of taxa that drift distance increased with increasing current velocity according to a power curve (eqs. 5, 6), and that taxa varied markedly in the slope of this relationship. Our results accord with these general conclusions, but there are noticeable discrepancies between our estimates and those reported by other investigators. For all current velocities, large *Baetis* in our troughs travelled about 40%, and medium *Baetis* about 70%, of the distance estimated by Elliott (1971) for *Baetis rhodani* (size unspecified but presumably similar to our larger individuals). However, the dependence of mean distance travelled on current velocity was similar in both studies. Elliott conducted his experiments in a small stream (Wilfin Beck) where modal depth typically was ca. 20 cm, and released animals just above the bottom. In our studies, individuals were released ca. 4 cm above the bottom into a water column of 7 cm depth. Since the depth of release did not differ markedly between the two studies, the greater distance travelled in Elliott's study presumably is due to greater turbulence in a natural stream, and a correspondingly greater potential for animals to be dispersed throughout a deeper water column. Larkin and McKone (1985) measured drift distance in an artificial spawning channel <30 cm deep by disturbing the substrate by foot to induce drift, and obtained a very steep function relating mean distance travelled to current velocity. Their function for *Baetis* predicts values much lower than ours or Elliott's at low velocities, and gives much higher drift distances at velocities >40 cm/s. The reason for this difference is uncertain, but the greater water depth in Larkin and McKone's study may be a factor.

Previous studies have compared the distances travelled by live vs. dead nymphs to assess whether animals actively exit the drift (Elliott 1971, Corkum and Clifford 1980, Campbell 1985, Otto and Sjöström 1986). Elliott recognized three groups of taxa: (1) those in which live animals settle in a shorter distance than their dead counterparts, indicating active exiting of the drift; (2) those in which active exiting occurs only at relatively slow current velocity (<19 cm/s), and (3) those drifting equal distances alive and dead. *Baetis* and *Cinygmula* fall into the first category, as expected from prior work, and this was true for all size classes studied (Table 2). *Cinygmula*, a dorsoventrally flattened member of the Heptageniidae, travelled considerably farther than the fusiform *Baetis*, and Elliott (1971) found a similar difference between the heptageniid *Ecdyonurus venosus* and *B. rhodani.*

TABLE 3. Multiple regression analysis of the combined influence of insect size (mg dry wt) and current velocity (cm/s) on the drift distance of the farthest travelling 10% of the population. Standard partial regression coefficients are used, expressing average change in terms of standard deviation units of all terms.

*Baetis*

$\log(X_{10\%}) = -2.28 - 0.52 \log(\text{dry wt}) + 0.98 \log(V)$

*Cinygmula*

$\log(X_{10\%}) = -3.20 - 0.36 \log(\text{dry wt}) + 0.91 \log(V)$

At current velocities of 5 cm/s, we found either no difference or an apparent tendency for individuals to travel farther alive than dead, implying that drift was actively prolonged. These results are based on relatively few data because of the short distances travelled at low current speeds, suggesting caution in their interpretation. Moreover, for those species most adept at exiting the drift, Elliott (1971) observed shorter drift distances in live than in dead nymphs at 10 and 12 cm/s. Nonetheless, Campbell (1985) observed that live *Baetis* nymphs display several behaviors that reduce their sinking rate relative to dead individuals. Live animals adopted a posture of upraised abdomen and outstretched legs ("parachuting"), swam upwards, and on occasion inserted a leg into the surface film. Campbell found the latter two behaviors to be more common in the smallest nymphs, and we also observed small *Cinygmula* inserting a leg into the surface film at low current velocities. Hence it is plausible that, in slow currents, live mayfly nymphs actively prolong the time suspended, in order to depart from less suitable regions. This view is consistent with reports that reduction of flow causes mayfly nymphs to actively swim up into the water column (Minshall and Winger 1968). However, based on Campbell's laboratory studies, one would expect the effect to be more pronounced in smaller stages; if this is the case, we did not detect it.

Previous studies have reported an inverse relationship between settling time and body size in *Baetis.* A strong inverse correlation between body size and time in suspension in a settling column is apparent for dead *Baetis*, although the relationship is further complicated in live nymphs owing to body posture and upward swimming movements (Campbell 1985). Ciborowski and Corkum (1980) observed that settling rate of dead nymphs varied across a number of taxa in association with head width. Malmqvist and Sjöström (1987) fround an inverse relationship between *Baetis* size and time in suspension (and by inference drift distance) in laboratory streams. Although our results confirm that drift distance decreases as a function of increasing size, it is unlikely that this decrease is due to a difference either in passive sinking rate or in type of behavior exhibited. At 35 and 55 cm/s, live nymphs in all sizes of both *Baetis* and *Cinygmula* actively settled out of the water column, and this must have involved swimming downwards. It seems most plausible that settling takes longer for small individuals (and thus they drift farther than large individuals) because of differences in swimming speed and the number of body lengths that must be travelled.

Drift distance in invertebrates that are capable of actively exiting from the drift clearly depends on both current velocity and body size. A complete assessment of the relative importance of these two factors requires that one consider the full range of both variables, but it is hardly practicable to use nymphs much smaller or current velocities greatly higher than those we employed. Within the range chosen, current had roughly twice as great an effect as dry wt. Nonetheless, the effect of body size is not trivial, and distance travelled at a given velocity differs markedly and significantly over the ontogeny of a species.

The finding that drift distance depends upon species and size class affects the inferences drawn from drift studies. A higher proportion of small than large nymphs in day drift may indicate different tendencies to enter the drift. However, if these two size classes enter the drift equally but the smaller nymphs drift up to three times as far, as our results predict, drift samples would catch three times as many. This cannot explain the diel change in the size composition of drift reported by Allan (1978), but it could cause small animals to appear to be over-represented to a greater degree than actually is the case, a point also made by Ciborowski and Corkum (1980), Similarly, comparisons of abundance in the drift to the benthos often are viewed as an indication of a species' tendency to enter the drift, yet a species that drifts greater distances will likewise appear more abundant in drift catches. A related point is that seasonal variation in magnitude of drift in association with variation in flow may not be due to changes in drift entry, but instead to greater drift distances at higher velocities (Elliott 1971).

### *Implications of a drift distance analysis for interpreting drift behavior*

The idea that invertebrates may drift farther in darkness than in light because of an inability to orient has been proposed as a possible cause of the diel periodicity of drift (Hughes 1966, Statzner and Mogel 1985). Luedtke and Brusven (1976) found settling rates to be reduced in the dark, which accords with this hypothesis. Elliott (1971) conducted a small number of daytime vs. darkness trials and reported a consistent but non-significant trend in *Gammarus pulex* for greater distances at night. However, several mayfly species showed no difference. The trend for greater drift distances in small *Baetis*, compared with large, was most apparent in night trials by Malmqvist and Sjöström (1987), but inspection of their data suggests little difference between day and night. Our substantial number of comparisons showed drift distance at night to significantly exceed distance during the day in only 4 of 18 comparisons, and in those instances the effect was small. Because numbers drifting at night often exceed numbers drifting during the day by an order or magnitude or more, diel differences in drift distance are of little or no help in explaining diel periodicity.

Our results also bear on the idea that drifting individuals differ from non-drifters within the same population in some intrinsic characteristics. Minshall and Petersen (1985) raised the possibility of genetic differences, and Wilzbach et al. (1988) suggested that pathogenic or parasitic infestations may enhance likelihood of drifting. Our comparison between individuals collected from the drift and those from the benthos showed that both groups were equally capable of exiting the water column at the current velocity used (35 cm/s). This similarity would not be expected if animals in the drift were an intrinsically less robust sub-group. Elliott's (1971) finding that drift distances were similar by night and by day was based on individuals collected from the drift and the benthos, respectively, and so his results also argue against any difference in distance travelled relating to origin of animals.

In conclusion, some taxa of drifting invertebrates clearly are capable of exiting the drift by active behaviors. There is convincing evidence that some taxa markedly reduce distance travelled at higher currents compared to passive settling (Elliott 1971, this study), and some evidence of prolonged drift at lower current speeds (Campbell 1985, this study). Species, current velocity and body size are factors that potentially influence distance travelled, while light level and drift vs. benthic origin do not. Our results also indicate that recent feeding experience has no detectable effect on drift distance, although this is based on only a few comparisons.

We believe that this body of results, while demonstrating an active and behavioral component to exiting the drift, nonetheless also establishes that answers to why drift occurs, and exhibits a diel rhythm, must be sought elsewhere. Differential drift distance appears an inadequate explanation for the common observation that drift abundances are much greater by night than by day. Moreover, although ability to exit the drift is most prevalent in taxa that show strong drift periodicity (Ciborowski and Corkum 1980), we do not concur with Campbell's (1985) view that because animals have the power to exit the water column, drift must therefore be active and voluntary. We agree that it is highly likely that drift entry also is an active behavior in many instances, and several lines of indirect evidence are supportive. Invertebrates have been recorded high in the water column of pools having negligible current (Walton 1980); field observations of substrate surfaces have reported non-concordance in periodicity between drift and the availability of nymphs for erosion into the current (Statzner and Mogel 1985, Allan et al. 1986, Casey 1987); and drift rate has been shown to respond to food availability (Kohler 1985). Further research is needed to establish the relative contributions of active and passive mechanisms to drift entry.

## Acknowledgements

We thank W. Brown, C. Anderson, B. Inouye and M. Smith for assistance with experiments and the Rocky Mountain Biological Laboratory for laboratory facilities. J. H. C. Ciborowski, S. L. Kohler, and anonymous reviewers kindly commented on an earlier draft. Research was supported by a grant from the National Science foundation (BSR-8705210).

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*Received: 18 May 1988*
*Accepted: 22 August 1989*