Size-dependent drift responses of mayflies to experimental hydrologic variation: active predator avoidance or passive hydrodynamic displacement?

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Summary. Larger nymphs within aquatic insect taxa have been frequently observed to be transported downstream in the stream drift only at night. Others have hypothesized this pattern results primarily from large nymphs' behavioural avoidance of entering drift during daylight, when size-selective, visually-feeding fish predators are most active. This hypothesis assumes that animals can actively control their entry into the drift, which may not be the case under all flow conditions. We experimentally induced streamflow increases and decreases in adjacent riffles in a hydrologically-stable stream during the daytime to examine whether changes in diel patterns of drift abundance and size-distribution of mayflies were consistent with the hypothesis of active avoidance of diurnal drift. We assessed the likelihood of active vs. passive mechanisms of diurnal drift entry and transport for four taxa that differ with respect to body size, morpho-behavioural attributes, microhabitat use, and general propensity to drift. In each of three seasons, diurnal and nocturnal drift samples were collected in three riffles over two diel cycles. Background drift patterns were established on the first day (no flow manipulation). Six h before sunset on the second day, flow was experimentally increased in one riffle, decreased in the second, and not altered in the third (control). Between-day differences in diurnal and nocturnal drift rate and size composition were then compared among the treatment and reference riffles. Responses of two taxa were consistent with active control over drift entry, transport, or both. For *Baetis* spp., drift-prone mayflies typically preyed upon by fish, diurnal drift rates immediately increased following both flow reduction and flow elevation in all seasons, but only small individuals comprised the drift. Drift by large individuals was delayed until nighttime. *Epeorus longimanus* also exhibited significant in-

creases in drift rates following flow reduction and elevation, but responses of this large-bodied species were restricted to nighttime. Drift responses for these two taxa were largely independent of direction of hydrologic change, thus indicating a strong behavioural control over drift. By contrast, numbers and sizes of drifting *Paraleptophlebia heteronea* and *Ephemerella infrequens* depended strongly on direction of flow change. Drift rates for both species generally declined after flow reduction and increased after flow elevation. Moreover, after flow elevation, larger individuals often drifted diurnally, a finding consistent with expectations under a passive hydrodynamic model. These experiments indicate that size-dependent mayfly drift reflects not only presumed risk from visual fish predators, but also functional attributes of species such as morphology, behaviour, and microhabitat affiliation, which influence aspects of drift entry and transport under variable hydrologic conditions.

Many stream invertebrates exhibit a marked diel periodicity in drift (downstream transport), typically with a nocturnal peak in abundance (see reviews in Waters 1972; Brittain and Eikeland 1988). The observation that larger species and size classes within a species often drift at night led Allan (1978) to hypothesize that selective pressure from day-active, visually-cued predatory fish have served as the ultimate cause for size-structured drift patterns. Observations that more and larger individuals commonly drift nocturnally in streams with drift-feeding fishes (e.g., Allan 1978, 1984; Newman and Waters 1984; Skinner 1985; Andersson et al. 1986) but not necessarily in fishless streams (Flecker 1992), have provided support for the predation-risk hypothesis.

A major assumption underlying the notion of diurnal predator avoidance is that an individual can actively control its entry into the water column by resisting me-

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chanical displacement from the substratum by the shearing force of moving water. While behavioural control of drift has been attributed to many species (e.g., Elliott 1971; Ciborowski and Corkum 1980), much debate remains as to whether animals actively enter the water column or are simply passively eroded from the streambed (e.g., see Allan et al. 1986; Wilzbach 1990). An individual's morphology and body size contribute to its hydrodynamic characteristics, which determine the expected drag and lift forces encountered when exposed to shearing flows (Statzner and Holm 1982, 1989). Within a species, larger individuals experience greater erosive forces (Statzner 1988) and are presumably more prone to passive displacement. Thus, as the speed of the current increases, so does the likelihood of mechanical dislodgement, but in some species-specific and size-dependent manner. Also, distance transported (and hence time of potential exposure to predators) generally increases with current, but in a manner dependent on species' morphology and behaviour (e.g., Elliott 1971; Corkum 1978; Ciborowski and Corkum 1980; Wilzbach et al. 1988) and on individual body size (Corkum and Clifford 1980; Campbell 1985; Allan and Feifarek 1989). The interaction between hydrologic factors and species' functional attributes may therefore result in drift patterns that reveal the relative importance of active vs. passive controls on drift and that accordingly address the generality of the predation risk hypothesis.

Differentiation between active and passive drift is not straightforward but should be most pronounced when animals experience a sudden change in current. Rapid, temporal changes in streamflow are characteristic of many lotic ecosystems (e.g., see Poff and Ward 1989) and have been widely reported to lead to dramatic changes in numbers of drifting organisms (see Poff and Ward 1991 and refs. therein). Yet, an unanswered question is whether changes in streamflow modify the typical diel, size-dependent pattern of invertebrate drift. If drift is largely active, then, regardless of whether current increases or decreases, larger individuals should avoid entering the water column during the day (when risk of predation is high). Even under sudden increases in shear stress, active, size-dependent drift avoidance should occur. However, if drift has a substantial passive component, then species' drift responses should reflect the direction of flow change. That is, an increase in streamflow should result in the immediate displacement of more and proportionally larger individuals, which experience greater relative drag and lift. A decline in streamflow, by contrast, should result in fewer individuals of that species entering the drift.

In this study, we experimentally induced streamflow increases and decreases in adjacent stream riffles during the daytime to examine whether changes in diel patterns of drift abundance and size-distribution for four mayfly taxa were consistent with the hypothesis of active avoidance of diurnal drift. Experiments were conducted in a hydrologically-stable stream with abundant drift-feeding salmonid predators. The mayfly taxa represented four ephemeropteran families and differed in such important functional attributes as microhabitat affiliation, behav-

iour, morphology, and body size. They also differed in general propensity to drift and hence in degree of presumed risk of predation by drift-feeding fishes.

The primary hypothesis tested for each taxon in each season is as follows: median diurnal and nocturnal sizes of drifting mayfly nymphs are not altered by diurnal decreases or increases in streamflow. We also tested whether numbers drifting were altered by manipulated streamflow. We were primarily interested in comparing drift responses under directional flow changes. For example, an increase in diurnal drift rate and body size after flow elevation, coupled with no change (or a decline) after flow reduction, would strongly suggest a passive drift mechanism. By contrast, no diurnal change (or a decline) in size, coupled with diurnal and nocturnal increases in drift rate, would strongly implicate behavioural control over drift. Field experiments were conducted over three seasons, over which time body sizes and relative abundances of the four taxa changed.

Materials and methods

Study site and mayfly taxa

The study was conducted in the upper Colorado River (2420 m elevation) in Colorado, USA ($\sim 105°\ 55'$ W, $40°\ 07'$ N) over three seasons (Summer: 27–28 August 1985; Autumn: 15–16 November 1985; Spring: 5–6 June 1986). The site was 7 km below a hypolimnetic-release storage impoundment constructed in 1954. The stream's flow regime was completely regulated by predictable, stepwise reservoir releases, occurring annually on May 1, August 1, and September 1. Thus, streamflow was constant for at least two weeks prior to each seasonal experiment (see Poff and Ward 1991 for detailed hydrology). Storm-induced spates did not occur at this site. Channel width was 10–12 m, and mean depth of riffles varied from 25–50 cm, depending on season. The substrata at this site consisted mostly of cobbles and boulders with interspersed gravel and sand.

The four taxa chosen represented the most abundant Ephemeroptera in the drift (Poff and Ward 1991) and in the benthos (N.L. Poff, unpub. data). *Baetis* spp. (Baetidae) (mostly *B. tricaudatus* (Dodds), but also some *B. bicaudatus* (Dodds) and *B. insignificans* (McDunnough)) was the most abundant taxon. Nymphs of this genus are active swimmers (Corkum 1978; Wilzbach et al. 1988), often occur on substratum surfaces exposed to current (Corkum et al. 1977; Rader and Ward 1990; Wilzbach 1990; N.L. Poff unpub. data), and are relatively small (< 3–12 mm body length, Edmunds et al. 1976). *Ephemerella infrequens* (McDunnough) (Ephemerellidae) occurs mostly in sheltered microhabitats (Rader and Ward 1990; N.L. Poff unpub. data) and can be classified as a clinger (Corkum 1978; Wilzbach et al. 1988). Nymphs of this genus are 6–14 mm in length (Edmunds et al. 1976). *Paraleptophlebia heteronea* (McDunnough) (Leptophlebiidae) is intermediate in morphology between baetids and ephemerellids and occurs mostly in sheltered microhabitats (Rader and Ward 1990; N.L. Poff unpub. data). Nymphs of this genus attain lengths of 6.5–10 mm (Edmunds et al. 1976) and can be considered as weak swimmers (Edmunds et al. 1976) and crawlers, having slightly depressed bodies and somewhat dorso-ventrally flattened heads (Corkum 1978). *Epeorus longimanus* (Eaton) (Heptageniidae) is a greatly dorso-ventrally flattened clinger of crawler that occupies sheltered to exposed microhabitats (Rader and Ward 1990; N.L. Poff unpub. data, J.D. Allan, pers. comm.). It hatches, matures and emerges from Spring to mid-Summer. The length of this species (up to 18 mm, Edmunds et al. 1976) and its wide body make this species the largest of the four mayfly taxa. At this location, only *Baetis* possesses more than one generation per year; the other three species are univoltine (Rader and Ward 1989).

Visually-hunting, drift-feeding salmonid predators are abundant at this site. Species present are *Salmo trutta, Oncorhyncus mykiss (= Salmo gairdneri)*, and *Salvelinus fontinalis* (Nehring 1987).

Experimental flow manipulations and drift collections

Three riffles, spaced over a ca. 250 m reach, were selected for the experiments. Each riffle was longitudinally partitioned at midstream with metal sheets (7 m in length) extending from the substatum to above the water surface. For each riffle, one half of the divided stream was designated the experimental channel. The experimental channel furthest upstream served as an unmanipulated control ("reference riffle"). The experimental channel ca. 150 m downstream of the reference riffle was modified by extending fence posts at an angle from the upstream end of the sheet-metal divider to one stream bank. Placement of boards along this wing dam effectively routed water away from the entrance of the experimental channel ("low-flow riffle") and through the remaining half of the whole stream channel. The third riffle (75 m downstream of the low-flow riffle) was also modified with a wing dam that diverted flow from the entire stream channel through the entrance of the experimental channel ("high-flow riffle"). We view the 75 m separating the low-flow and high-flow riffles sufficient to measure independent drift responses, because it exceeds the distance typically drifted by invertebrates over a complete 24 h cycle under non-catastrophic conditions (see Brittain and Eikeland 1988).

Drift was collected at the downstream end of each experimental channel over two consecutive diel periods in each season. Two drift nets (45.7 cm wide, 30.5 cm high, 100 cm long) with 425 µm mesh were mounted on steel stakes driven permanently into the substratum for the duration of the study. During each 2-d seasonal sampling period, nets remained in the water for the same amount of time (1 h in Summer and Autumn, 0.5 h in Spring). Drift collections were made at 3-h intervals, seasonally adjusted so that the first sample was taken 6 h before sunset and the third sample was taken 20 min after local sunset (Summer = 20^{00} h, Autumn = 17^{00} h, Spring = 21^{00} h). Diurnal drift rates are generally low and nocturnal drift generally peaks immediately after sunset (see Allan and Russek 1985); therefore, we collected 2 diurnal and 1 nocturnal samples for each day in each riffle per season.

Experimental flow manipulation followed the same procedure in each season. On the first day of each 2-d sampling period, flow was not manipulated in any riffle to establish premanipulation, diel drift pattern. On the second day, the wing dams in the low and high flow riffles were installed 6 h before sunset. In each riffle, depth and velocity readings (at 0.5 depth) were taken at 9 fixed transect locations on both day 1 and day 2 to characterize effectiveness of the flow manipulations (see Poff and Ward 1991 for additional details).

Analytical procedure and statistical analyses

Drift samples were preserved in the field and returned to the laboratory for analysis. All organisms were counted to determine drift rate (no. h^{-1} per net) for each species. Organisms were sized in the laboratory by measuring head capsule width (HCW) with an ocular micrometer at 20x. HCW has been shown to be a significant predictor of live body mass for several mayfly taxa (e.g., Allan 1984). For samples containing < 40 individuals of a taxon, all organisms were measured. For larger samples, a random subsample was taken and at least 40 individuals or ca. 10% of the sample (whichever was larger) were measured. Median HCW was chosen as the measure of central tendency because of the typical skew of size distribution in the samples.

Whole-riffle experimental units were not true, spatial replicates (see Hurlbert 1984), but temporal control data (i.e., pre- and post-manipulation data for all times in all riffles) can be used to allow

meaningful inference of treatment effects (see Stewart-Oaten et al. 1986; Carpenter 1990). In other words, because riffles were similar in all respects except flow manipulation, between-day differences that were observed in the manipulated riffle(s), but not in the unmanipulated reference riffle, could reasonably be attributed to the flow manipulations. We therefore analyzed between-day differences within riffles with standard statistical techniques, but interpretation was conditional on simultaneous non-significant results in the reference riffle.

Separate seasonal analyses were used to examine differences in body size (log-transformed median HCW) for each taxon in each riffle. This approach was chosen due to large seasonal variation among and within taxa in terms of body size and numbers of organisms drifting. Riffle-specific responses were of interest, and a oneway ANOVA (Steel and Torrie 1980) was used to test for differences between four treatment groups: D1 (diurnal day 1, $n=4$), N1 (nocturnal day 1, $n=2$), D2 (diurnal day 2, $n=4$), and N2 (nocturnal day 2, $n=2$). Loss of the first diurnal sample in Summer reduced n from 4 to 2 (and $F_{3,8}$ was accordingly reduced to $F_{3,4}$). The diurnal drift response was of primary interest, but four *a priori* contrasts (Steel and Torrie 1980) were examined: N1 v. D1 (diel pattern under no manipulation); N2 v. D2 (diel pattern following flow manipulation); D2 v. D1 (diurnal difference); N2 v. N1 (nocturnal difference). Some diurnal samples contained < 5 individuals and were excluded from statistical analysis. In these instances, a *t*-test (3 d.f.) was used to compare N2 v. N1.

To examine differences in drift rate among the same four treatment (day × time) groups in each riffle, a oneway ANOVA ($F_{3,4}$ in Summer, $F_{3,8}$ in Autumn and Spring) was performed on log-transformed abundance data. The same four *a priori* contrasts as above were examined.

Results

Current velocity and depth in the experimental riffles were consistently altered by the flow manipulations (Table 1). The magnitudes of change were seasonally variable but generally substantial. In Autumn, low whole-channel discharge conditions precluded further marked reduction of velocity in the low riffle and facilitated relatively large increases in depth and velocity in the high flow riffle (Table 1). The flow fluctuations induced in this study were similar in magnitude to the stepwise discharge releases typical of the regulated Colorado River. Whole channel streamflow had been stable for at least 2 weeks prior to each seasonal flow manipulation, so the fluctuations represented important hydrologic variation, as indicated by the drift responses of the four mayfly taxa.

Drift rates

Drift abundances of the four mayfly taxa varied among seasons and in response to flow manipulation (Table 2). *Baetis* spp. exhibited a consistent diel pattern in drift rate across all seasons, with more individuals (irrespective of size) drifting nocturnally than diurnally. The pattern was weakest in Autumn, when fewer baetids were captured in the drift. No significant ($p > 0.10$) between-day changes in drift rate were found in the reference riffle, indicating that any altered drift rates in the manipulated riffles could be reasonably attributed to the experimental flow fluctuations. Drift rate generally increased both

Table 1. Physical characteristics of three experimental riffles, before (day 1) and after (day 2) streamflow manipulations in each of three seasons

	Reference			Low flow			High flow		
	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn	Spring
Whole-channel									
discharge (m³ s⁻¹)	1.2	0.6	2.1	1.2	0.6	2.1	1.2	0.6	2.1
Mean depth (cm)									
Day 1	35.8	33.3	38.7	30.2	23.5	35.3	37.3	31.0	49.0
Day 2	35.8	33.3	38.7	28.7	23.2	32.0	40.5	37.5	52.8
% Change	0	0	0	−5	−1	−9	+9	+21	+8
Mean current (cm s⁻¹)									
Day 1	36.8	42.9	49.3	33.0	10.1	39.8	49.1	35.4	35.8
Day 2	36.8	42.9	49.3	19.6	9.4	18.8	62.2	62.8	57.4
% Change	0	0	0	−41	−7	−53	+27	+77	+60

Table 2. Drift rates (total numbers h⁻¹) of four mayfly taxa for four pooled diurnal (D) and two pooled nocturnal (N) samples at three seasons. Day 1 is no flow manipulation in all three riffles. Day 2 is flow manipulation in the low flow and high flow riffles, but no flow manipulation in the reference riffle. Oneway ANOVA ($F_{3,8}$ except in Summer at $F_{3,4}$) performed on unpooled, log-transformed abundances followed by *a priori* contrasts: N1 v. D1; N2 v. D2; D2 v. D1; N2 v. N1. Significant changes in drift rate for each contrast are indicated for $p<0.1$ (*), $p<0.05$ (**), and $p<0.01$ (***)

	Baetis spp.		*Paraleptophlebia heteronea*		*Ephemerella infrequens*		*Epeorus longimanus*	
	D	N	D	N	D	N	D	N
Summer								
Reference riffle								
day 1	208 (***)	1368	15 (***)	257	17 (**)	41	0	0
day 2	199 (***)	1671	7 (***)	296	32	38	0	0
Low flow riffle								
day 1	246 (*)	756	8 (***) (**)	50 (*)	30	40	0	0
day 2	306 (**)	1843	2 (***)	89	20	21	0	0
High flow riffle								
day 1	235 (***)	846 (**)	26 (***)	179	28	29 (**)	0	0
day 2	293 (***)	2716	16 (***)	556	38 (**)	71	0	0
Autumn								
Reference riffle								
day 1	31 (***)	187	32 (***)	110	59 (*)	93	0	0
day 2	49 (**)	141	20 (***)	40	34	77	0	0
Low flow riffle								
day 1	15	60	36 (*)	103	42	114	0	0
day 2	37 (**)	97	28	36	82	66	0	0
High flow riffle								
day 1	43 (**)	104 (**)	107 (*)	251	156	167	0	0
day 2	124 (***)	184	244 (**)	468	463	483	0	0
Spring								
Reference riffle								
day 1	196 (***)	513	6 (***)	44	16 (***)	224	7 (***) (*)	41 (*)
day 2	169 (***)	687	2 (***)	40	14 (***)	278	3 (***)	96
Low flow riffle								
day 1	137 (***) (***)	428	3 (***)	23	22 (***) (**)	201 (**)	2 (***)	28 (***)
day 2	655 (***)	769	5 (*)	9	6 (***)	60	12 (***)	633
High flow riffle								
day 1	156 (***) (***)	575 (***)	3 (**)	18 (***)	15 (***)	162	7 (***)	43 (***)
day 2	305 (***)	1463	8 (***)	159	33 (***)	366	9 (***)	327

Table 3. Drift rates (s.e. in parentheses) of four mayfly taxa for separate diurnal samples collected only on day 2 (during flow manipulation) of experiments over two seasons. Sample collection was 6 h (time 1) and 3 h (time 2) before sunset. Summer data not available due to absence of time 1 samples

	Autumn				Spring			
	Low flow		High flow		Low flow		High flow	
Baetis spp.								
time 1	11.0	(4.0)	45.5	(1.5)	127.0	(11.0)	78.0	(27.0)
time 2	7.5	(1.5)	16.5	(4.5)	61.5	(4.5)	74.5	(3.5)
Paraleptophlebia heteronea								
time 1	12.0	(11.0)	111.5	(2.5)	1.5	(1.5)	0.5	(0.5)
time 2	2.0	(0)	10.5	(3.5)	1.0	(1.0)	3.5	(2.5)
Ephemerella infrequens								
time 1	32.5	(26.5)	220.5	(33.5)	1.5	(0.5)	9.5	(6.5)
time 2	8.5	(0.5)	11.0	(1.0)	1.5	(1.5)	7.0	(2.0)
Epeorus longimanus								
time 1	0		0		5.5	(0.5)	2.0	(2.0)
time 2	0		0		0.5	(0.5)	2.5	(0.5)

diurnally and nocturnally following both flow elevation and flow reduction in all seasons. However, significant ($p < 0.01$) daytime increases were observed only in Spring (Table 2). Significant ($p < 0.05$) nocturnal increases occurred in all seasons, but only in response to flow elevation. Diurnal increases in drift were generally more pronounced during the first sample (i.e., 6 h before sunset) than they were during the second sample (3 h before sunset) (Table 3).

Epeorus longimanus exhibited a strong nocturnal peak in drift abundance in Spring, the only season in which it was collected (Table 2). There were very large increases in drift following both flow reduction and flow elevation, but these were delayed until nightfall. A significant between-day nocturnal difference was found in the reference riffle, but it was small relative to the increases in the low flow and high flow riffles.

Ephemerella infrequens was only weakly nocturnal in drift abundance, except in Spring, when a strong nocturnal pattern ($p < 0.01$) occurred in all riffles, both before and after flow manipulation (Table 2). Between-day differences in the reference riffle were small. However, following flow elevation, drift rates generally increased both by day and by night, but significantly so only in Summer ($p < 0.05$). After flow reduction, drift abundances generally declined, but significantly so only in Spring ($p < 0.01$). Diurnal drift responses were seen to occur immediately after flow alteration only in Autumn, when the immediate response to elevated flow was large (Table 3).

Paraleptophlebia heteronea always exhibited significant ($p < 0.10$) nocturnal peaks in drift abundance under unmanipulated flow conditions (Table 2). This nocturnal signature persisted under flow elevation but was reduced notably ($p > 0.10$) under reduced flow in Autumn. Following flow elevation, nocturnal drift rate consistently increased, but only significantly so in Spring ($p < 0.01$). Diurnal drift rate changed markedly only in Autumn after elevated flow, and most of this increase occurred immediately after flow manipulation (see Table 3). Fol-

lowing flow reduction, by contrast, drift rates tended to change little, and often in the same direction as the small between-day changes in the reference riffle.

Data were examined in this study in terms of drift rates (no. h^{-1}) rather than drift densities (no. $m^{-3} h^{-1}$), because we were primarily interested in total numbers of animals leaving the experimental riffles in response to directional flow changes (and thus being exposed to predators), regardless of the magnitude of the change in flow. (See Allan 1987 for a discussion on selection of units.) But when viewed in terms of drift densities, the responses of these four mayfly taxa were similar to those reported above for drift rates (see Poff and Ward 1991).

Diel size distributions

Animals collected in the drift were characterized by a wide range of body sizes. For all species, sizes varied both
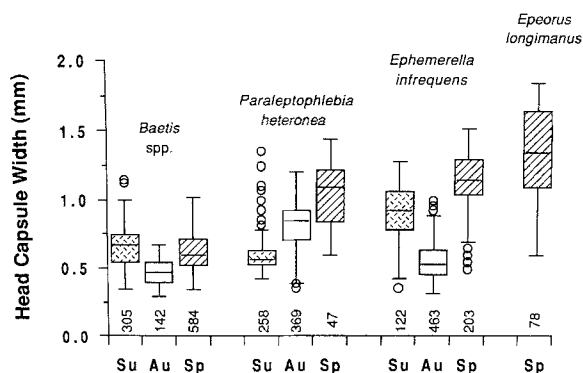

Fig. 1. Size ranges for four mayfly taxa in each of three seasons (Su = Summer, Au = Autumn, Sp = Spring). Samples are pooled diurnal and nocturnal drift collections under unmanipulated flow conditions. Each box encloses 50% of the data with the median marked as a horizontal line. The lines extending from the top and bottom of each box mark the maximum and minimum values, with the exception of extreme outliers, which are indicated by open circles. Numbers beneath boxes indicate number of specimens measured

Table 4. Comparisons of median size of drifting mayflies during daylight and nighttime on each of two sampling day over three seasons. Day 1 is no flow manipulation in all three riffles. Day 2 is flow manipulation in the low flow riffle and the high flow riffle, but no manipulation in the reference riffle. Sampling times are D1 (day 1 diurnal), N1 (day 1 nocturnal), D2 (day 2 diurnal), N2 (day 2 nocturnal). For each taxon by riffle by season combination, a oneway ANOVA was performed, followed by testing for the indicated *a priori* contrasts. Symbol in parenthesis indicates whether median size for first term in contrast is larger (+) or smaller (−) than second term at $p < 0.1$ (*), $p < 0.05$ (**), and $p < 0.01$ (***). Non-significant results are indicated by "ns" and untested comparisons by "O". Where diurnal sample sizes are inadequate for ANOVA, a simple *t*-test was performed for N2 v. N1
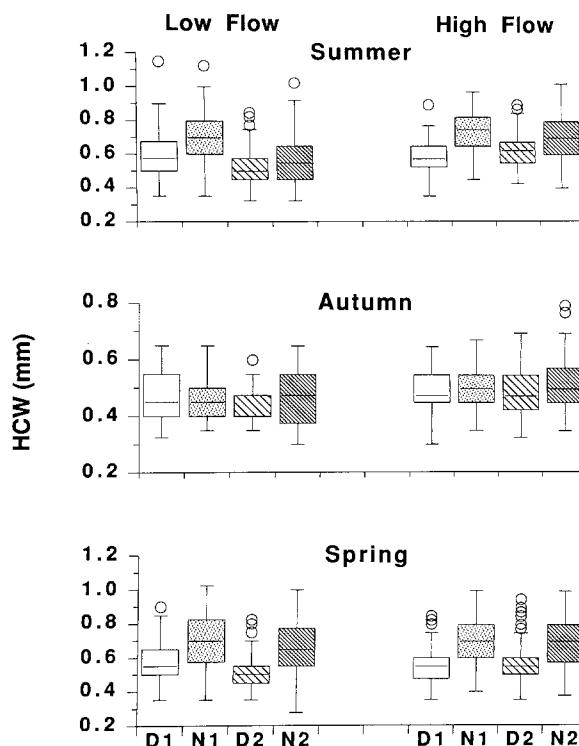
	Baetis spp.			*Paraleptophlebia heteronea*			*Ephemerella infrequens*			*Epeorus longimanus*		
	Ref	Low	High	Ref	Low	High	Ref	Low	High	Ref	Low	High
Summer												
N1 v. D1	***(+)	***(+)	***(+)	O	O	ns	O	ns	ns	O	O	O
N2 v. D2	***(+)	***(+)	** (+)	O	O	**(−)	O	ns	ns	O	O	O
D2 v. D1	ns	** (−)	ns	O	O	**(+)	O	ns	ns	O	O	O
N2 v. N1	ns	** (−)	ns	ns	ns	ns	ns	ns	ns	O	O	O
Autumn												
N1 v. D1	* (+)	ns	ns	**(+)	O	**(+)	**(+)	**(+)	***(+)	O	O	O
N2 v. D2	* (+)	ns	ns	**(+)	O	ns	**(+)	ns	* (+)	O	O	O
D2 v. D1	* (+)	ns	ns	ns	O	* (+)	ns	ns	** (+)	O	O	O
N2 v. N1	ns	ns	ns	ns	ns	ns	ns	ns	ns	O	O	O
Spring												
N1 v. D1	***(+)	***(+)	***(+)	O	O	O	O	O	ns	O	O	O
N2 v. D2	***(+)	***(+)	***(+)	O	O	O	O	O	ns	O	O	O
D2 v. D1	ns	***(−)	ns	O	O	O	O	O	ns	O	O	O
N2 v. N1	ns	ns	ns	ns	O	ns	ns	**(−)	ns	ns	*(+)	ns

within a season and across seasons (Fig. 1). For the univoltine species, the largest average sizes occurred prior to emergence in Spring, which was also the season of greatest spread of sizes across all groups combined.

Significantly larger ($p < 0.01$) *Baetis* spp. drifted nocturnally vs. diurnally in Summer and Spring in all riffles (Table 4, N1 v. D1 contrast), and this pattern was maintained following both flow elevation and flow reduction (N2 v. D2 contrast). In Autumn, a weaker ($p < 0.10$) diel pattern was found in the reference riffle on both days. After flow elevation in all seasons, median sizes of individuals drifting either diurnally or nocturnally were not altered (Table 4), despite generally increased drift rates (cf. Table 2). However, after flow reduction, the median sizes of diurnally drifting individuals declined significantly in Summer ($p < 0.05$) and Spring ($p < 0.01$) (Table 4). Nocturnally-drifting individuals were also smaller ($p < 0.05$) in Summer after flow reduction. In the reference riffle, between-day differences were observed only in Autumn, when larger individuals ($p < 0.10$) drifted diurnally on the second day, a pattern that was not observed in either experimental riffle. Figure 2 summarizes the between-day patterns in size-distribution for *Baetis* spp. across all seasons and illustrates that smaller individuals consistently tended to drift following reduced flow, whereas no size-dependent responses were associated with increased flow.

E. longimanus individuals were too rare in the diurnal drift to examine diel size distributions. However, larger nymphs ($p < 0.10$) were collected nocturnally following flow reduction but not flow elevation (Table 4).

E. infrequens showed a diel size-distribution pattern

Fig. 2. Size distribution of *Baetis* spp. for two experimental riffles in each of three seasons. Each plot represents pooled samples for day 1 (no manipulation) and day 2 (flow manipulation) to show the range and distribution of the data. Sampling times are D1 (day 1 diurnal), N1 (day 1 nocturnal), D2 (day 2 diurnal), and N2 (day 2 nocturnal). Sample sizes ranged from 58–176 (Summer), 19–90 (Autumn), and 118–289 (Spring). Symbol interpretation same as in Fig. 1
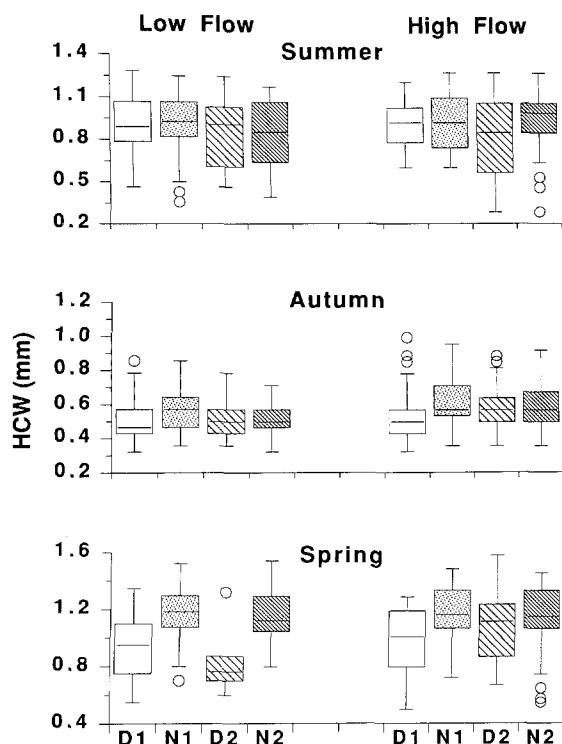
Fig. 3. Size distribution of *Ephemerella infrequens* for two experimental riffles in each of three seasons. Each plot represents pooled samples for day 1 (no manipulation) and day 2 (flow manipulation) to show the range and distribution the data. Sampling times are D1 (day 1 diurnal), N1 (day 1 nocturnal), D2 (day 2 diurnal), and N2 (day 2 nocturnal). Sample sizes ranged from 20–65 (summer), 40–280 (autumn), and 6–140 (spring). Symbol interpretation same as in Fig. 1

under unmanipulated flow conditions only in Autumn, when significantly larger individuals ($p < 0.05$) drifted at night (Table 4). Size-dependent responses of this species were generally related to direction of flow change. Following flow elevation in Autumn, larger individuals drifted diurnally ($p < 0.05$), altering the apparent diel size pattern. Following flow reduction, however, the diel pattern was lost as larger individuals were not found in the nocturnal drift. Similarly, in Spring, significantly smaller individuals ($p < 0.05$) comprised the nocturnal drift after flow reduction, suggesting larger nymphs did not drift. Figure 3 summarizes the seasonal size-dependent drift response of *E. infrequens* and shows the tendencies for smaller nymphs to drift after reduced flow and for larger nymphs to drift after elevated flow, a pattern markedly different than that observed for *Baetis* (cf. Fig. 2).

P. heteronea numbers in the drift were generally low, thus precluding consistent analysis of diel size patterns. In Autumn, larger nymphs were found to drift at night in the unmanipulated high flow riffle (Table 4). After flow elevation in Summer and Autumn, a significant increase ($p < 0.05$) in the median size of diurnally drifting individuals occurred, effectively altering the diel size distribution observed under unmanipulated conditions. No size-related responses to reduced flow could be determined; however, in general, size-related patterns following flow reduction were similar to those of *E. infrequens*.

Discussion

Drift responses of *Baetis* spp. and *Epeorus longimanus* to changes in streamflow were consistent with the active entry hypothesis, while responses of *Paraleptophlebia heteronea* and *Ephemerella infrequens* were often inconsistent with this hypothesis. *Baetis* spp., widely reported as a dominant drift component (e.g., Waters 1972) and a major element of salmonid diets (e.g., Allan 1981), were always abundant in the drift, yet their diel size distribution remained unchanged by diurnal hydrologic manipulations. This result suggests active drift entry and thus satifies the assumption of Allan's (1978, 1984) predation-risk hypothesis. For example, large individuals continued to drift nocturnally, even when diurnal drift rates increased following flow manipulations. Also, after experimental flow reductions, the median size of *Baetis* spp. actually declined, even though diurnal drift rates increased. Furthermore, this group showed its most pronounced diel size distribution pattern in Summer and Spring, when the average body size of drifting animals was greatest (see Fig. 1), as suggested by Allan (1984). The drift response of *E. longimanus* was also consistent with active drift entry, in that this large-bodied species was tenaciously nocturnal, even following diurnal flow increase and decrease.

For *E. infrequens* and *P. heteronea,* changes in diel drift rate and size distribution generally reflected direction of streamflow change, suggesting both that these species were prone to passive displacement by current and that different sized nymphs within these species were differentially responsive to increased v. decreased current. Although these two species showed strong nocturnal peaks in Spring (when body sizes were largest), larger nymphs drifted diurnally following flow elevation in Autumn (both species) and Summer (*P. heteronea* only), in contradiction to the hypothesis of active entry and the expectation under the predation-risk hypothesis. These results indicate that mayfly drift during flow fluctuations reflects not only differences among species in presumed susceptibility to predation, but also differences in species' functional attributes and body size that influence susceptibility to purely hydrologic factors associated with changing current.

Differences among mayfly species in morphology, behaviour, and habitat association have been used to construct a functional classification for drift (Corkum 1978; Wilzbach et al. 1988), which can be used to interpret responses of species in this study to directional streamflow fluctuations. Morphology and locomotory mode for these taxa vary from small, fusiform swimmer (*Baetis* spp.) to slightly dorso-ventrally flattened crawler *(P. heteronea)* to round-bodied clinger *(E. infrequens)* to greatly dorso-ventrally flattened, large clinger or crawler *(E. longimanus)*. In the regulated Colorado River, *Baetis* spp. and *E. longimanus* tend to occupy the more exposed microhabitats, while *E. infrequens* and *P. heteronea* occupy more sheltered locations (Rader and Ward 1990; N.L. Poff, unpub. data).

Other experimental work has shown that drift entry varies with current among congeners of the species exam-

ined in this study. For example, baetids are less likely to drift under high velocity than are species of either *Paraleptophlebia* (Corkum et al. 1977) or *Ephemerella* (Ciborowski 1983). Ephemerellids, in particular, may be easily displaced at relatively low velocities (< 10 cm s^{-1}, Butz 1973) or by sudden increases in current (Ciborowski et al. 1977). Similarly, distance transported varies with current among congeneric species. Ciborowski and Corkum (1980) demonstrated that mayfly species most behaviourally adept at exiting from the drift were also the ones most likely to occur in the drift (i.e., *Baetis vagans* > *Ephemerella subvaria* > *Paraleptophlebia mollis*). A similar high degree of behavioural control by *Baetis* has been observed by others (e.g., Elliott 1971; Campbell 1985; Allan and Feifarek 1989), but smaller individuals take longer to settle or exit the drift (Corkum and Clifford 1980; Malmqvist and Sjöström 1987; Allan and Feifarek 1989). However, the relationship between current velocity and transport is not always straightforward. At low velocities, individuals may actively prolong drift distance, as has been observed for baetids (Campbell 1985), and at least suggested for heptageniids (Allan and Feifarek 1989).

Given these species differences, our results strongly suggest that *Baetis* spp. exerted great behavioural control over its diurnal drift despite hydrologic variation. After flow reduction, small baetids apparently departed immediately (i.e., before sunset), while large individuals awaited darkness. This pattern is consistent with differential susceptibility to salmonid predators (e.g., Allan 1978, 1981; Ringler 1979). After sudden increases in current velocity, no increase in median size occurred, despite the increased drift rates.

The size-related responses of *Baetis* spp. to increased flow are inconsistent with a purely passive hydrodynamic model in which larger individuals, experiencing greater shear stress relative to small individuals (Statzner 1988; Statzner and Holm 1982, 1989), would be expected to be differentially eroded from the substratum. Large and small baetids tend to occupy exposed microhabitats in the regulated Colorado River during the daytime, and the exposed habitats would be expected to experience the same *average* change in near-bed flow following discharge manipulation. Despite this, large individuals did not increase disproportionately in the diurnal drift. A problem with a size-dependent passive hydrodynamic model is that size-dependent compensatory attributes (e.g., muscle mass) may also exist to counteract the erosive potential of proportionately greater shear stresses. Detailed experimental work will be required to address this question, because the existing empirical evidence on size-dependent displacement in baetids is equivocal and contradictory at best. For example, Ciborowski (1983) found that drift entry for large (but not small) *B. tricaudatus* was greater at increased current during the daytime, but a study by Corkum et al. (1977) found drift for large *B. vagans* to *decline* with increasing current during the daytime. Furthermore, in both these studies, at night large individuals were consistently less likely to drift under higher velocites, strongly implicating behavioural control over drift.

An alternative interpretation for our observations of *Baetis* drift may be drawn from size-dependent drift distances. Smaller individuals tend to drift farther than larger individuals (Malmqvist and Sjöström 1987), both at high velocities where regaining the bottom is difficult (e.g., Allan and Feifarek 1989) and at very low velocities where active prolonging of transport can occur (Corkum et al. 1977; Campbell 1985; Allan and Feifarek 1989). Therefore, a similar size spectrum of baetids may have entered the drift, but only small individuals remained in suspension long enough to be captured by the nets. While this cannot be eliminated as a possibility, it is worth emphasizing that passive transport distances for small individuals in the high flow riffle should have greatly increased (see Table 1), but no proportional increase in captured small individuals occurred. However, it is also possible that larger baetids were both differentially eroded into the drift and behaviourally capable of quickly exiting after flow elevation, leading to no net change in observed size distribution. Unfortunately, without knowledge of precise changes in hydraulic conditions for the points of origin of drifting individuals, it is impossible to infer the exact mechanisms that are responsible for the observed size-dependent patterns. We would argue, however, that the active avoidance of entry into the drift (to avoid predators) provides the most parsimonious explanation for *Baetis'* drift pattern, because its size-dependent drift response was seasonally consistent in the face of simultaneous, diametrically-opposed hydrologic disturbances.

E. longimanus was the largest of the four mayfly taxa in this study (Fig. 1). Thus, this species would be expected to exhibit inhibition to diurnal drift under the hypothesis of size-specific predation pressure (cf. Allan 1984), and our data support this. The consistent drift response of *E. longimanus* to hydrologic change, irrespective of direction of flow change, also indicated behavioural control. This species delayed its dramatic increase in drift rate until nightfall, a pattern that has been observed for other heptageniids following flow reductions (e.g., Gore 1977).

Drift responses to streamflow fluctuations by *E. infrequens* and *P. heteronea* varied according to direction of flow change. Species' functional attributes (unfavorable hydrodynamic profiles, poor swimming ability) would suggest an increase in drift rate immediately following flow elevation and a decrease after flow reduction, as was frequently observed (see Tables 2 and 3). Moreover, our observations that larger individuals tended to drift after elevated flow is consistent with the passive hydrodynamic expectation that susceptibility to passive displacement should increase with increasing body size (cf. Statzner and Holm 1982, 1989). These species typically occupy sheltered microhabitats by day (Rader and Ward 1990; N.L. Poff pers. obs.), and thus may not be likely to be eroded. However, Wilzbach (1990) has suggested that turbulent eddy intrusion into "sheltered" habitats can displace resident organisms in turbulent, stony-bottomed streams. In our study, turbulence intensity very likely increased in the high flow riffle following flow manipulation, whereas it would have declined in the

low flow riffle. These arguments strongly *suggest* passive entry of these taxa into the water column. However, because diel patterns in drift rate were often not altered by flow changes and because marked seasonal differences were observed, some behavioural component to drift is indicated, possibly related to nocturnal increases in activity rates and exposure to current (e.g., Elliott 1968). Thus, these observations serve to emphasize the point that both active and passive mechanisms of drift are probably important for these two species, though they are relatively hydrodynamically susceptible to displacement by current, as has been previously suggested (e.g., Corkum et al. 1977; Ciborowski et al. 1977).

Alteration of streamflow has been mentioned as a possible management tool for augmenting food availability for drift-feeding fishes (Minshall and Winger 1968; Elliott 1973). This study provides little optimism for such an approach. Taxa that might be considered appropriate food resources for fish predators by virtue of their abundance (e.g., *Baetis*) or their relatively large biomass (e.g., *E. longimanus*) appeared to exert great behavioral control over entry into the water column, typically by delaying the peak in their drift abundance to a time of reduced predation risk. Where daytime abundances were increased, as with *Baetis* spp., small individuals least preferred by trout comprised the great proportion of the drift. Streamflow increases might effectively increase the size of diurnally drifting *P. heteronea* and *E. infrequens;* however, because the pulse of increased drift was brief (most occurred in first sample; fewer were drifting 3 h after flow manipulation – see Table 3), trout would have to "switch" quickly to take advantage of this ephemeral resource. Moreover, these two species were abundant in the diurnal drift only in Autumn, when they were relatively small (see Fig. 1) and, coincidentally perhaps, when water temperatures reduce feeding activities of salmonids (e.g., Cunjak 1987).

Although precise drift mechanisms governing drift entry and transport cannot be demonstrated from this study, our data suggest that both passive (hydrologic) and active (predation avoidance) mechanisms are involved in mayfly drift. An individual's ability to avoid diurnal drift (and the associated risk of predation) after a sudden change in streamflow is strongly correlated with that species' functional attributes (morphology, behaviour, microhabitat affiliation), which can themselves be used to characterize species differences in drift propensity under more stable hydrologic conditions (e.g., Corkum 1978; Wilzbach et al. 1988). Thus, our findings broadly support the conclusion that both species, functional attributes and the inferred relative risk of predation are strongly correlated and provide a basis for predicting mayfly drift responses to normal hydrologic variability in streams and rivers.

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