
NOTES

Downstream and Lateral Transport of Nymphs of Two Mayfly Species (Ephemeroptera)

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By releasing live and dead nymphs of two mayfly species, *Baetis tricaudatus* Dodds and *Ephemerella inermis* Eaton, into the water column of a river and catching them downstream in a series of contiguous nets, I estimated settling and lateral dispersal rates. Live animals settled over shorter distances than dead individuals, and became more widely laterally dispersed for any given distance downstream and mean current velocity. Transport of suspended organisms in a river in which mean current velocity increases with increasing distance from shore may produce a skewed cross-river benthic distribution of animals. The degree of skewness will depend on the current velocity gradient and on suspended animals' settling behavior.

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Des nymphes vivantes et mortes de deux espèces d'éphémères, *Baetis tricaudatus* Dodds et *Ephemerella inermis* Eaton, ont été libérées dans l'eau d'une rivière et capturées en aval dans une série de filets contigus, dans le but d'estimer les taux de déposition et de dispersion latérale. Les animaux vivants se sont établis sur le fond après avoir parcouru des distances plus courtes que les sujets morts et, à une distance en aval et une vitesse de courant moyennes données, se sont dispersés latéralement sur une plus grande superficie. Le transport d'organismes en suspension dans un cours d'eau dans lequel la vitesse de courant moyenne augmente en fonction de l'éloignement de la rive peut introduire un biais dans la distribution benthique des animaux d'une rive à l'autre. L'ampleur de ce biais dépendra du gradient de vitesses de courant et du comportement de fixation au fond des animaux en suspension.

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MOST lotic invertebrates occasionally become dislodged from the substrate and transported downstream. The rate of return to the stream bottom depends on the size and shape of each animal (McLay 1970; McKone 1975) as well as current velocity (Elliott 1971). Behavioral actions (swimming motions and thigmotactic responses to contact with the substrate) result in rapid settling rates for certain species (Elliott 1971), especially those frequently appearing in the drift (Ciborowski and Corkum 1980).

Most studies of settling behavior have been concerned with the distance animals are carried downstream; but lateral transport may also be important in determining subsequent benthic

microdistribution. Ulfstrand (1968) postulated that cross-river movements could produce rapid changes in microdistribution of benthic populations. Lehmkuhl and Anderson (1972) reported that animals prone to drift are carried from riffles to backwaters at the stream margin during floods. However, earlier experimental studies have failed to evaluate the degree of lateral dispersal exhibited by animals released into the water column.

My objective was to determine settling rates, downstream movement, and lateral transport of the mayflies *Ephemerella inermis* Eaton and *Baetis tricaudatus* Dodds in the Pembina River, Alberta, Canada. To evaluate the extent to which the organisms are capable of controlling their return to the substrate, I worked with both live and dead animals.

Materials and methods — Experiments were conducted during the last 2 wk of May (spring) and the first 2 wk of October (autumn) 1979, on the Pembina River (53°37'N,

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115°00'W). The river at the study site is wide (about 65 m) and shallow (maximum depth 1.2 m) during normal flow conditions, with a substrate of smooth cobbles embedded in coarse sand. Macrophytes are absent. Ciborowski and Clifford (1983) provided a detailed description of physical characteristics.

The study site was mapped prior to experiments each season. A base line was established along the south river margin. Water depth and mean current velocity (Ott C-1 current meter at $0.6 \times$ depth) were measured at 1-m increments along each of 11 transects, to a distance of at least 12 m from the base line. Linear regression was then used to estimate the relationship between distance from shore and mean current velocity.

Suspended animals were sampled with 12 contiguous drift nets extending from river margin to center. Nets (pore size 0.211 mm) had a mouth opening of 1.0×0.5 m and were 2 m long. Each was anchored with aluminum rods driven into the substrate to filter a column of water 1 m wide and up to 0.5 m deep.

Settling rates were determined for animals along each of five lines established parallel to the base line upstream of the nets, at distances of 2, 4, 6, 8, and 10 m from shore. Five wooden stakes were driven into the substrate along each line to serve as insect release points (Table 1).

Large insects (head widths >0.7 mm in spring, 0.4–0.6 mm in autumn, as determined by later laboratory measurements) were hand-collected and kept in finger bowls containing river water until required. Those designated for dead animal trials were preserved in Kahle's fluid to which was added lignen pink dye (10 drops of saturated solution per 15 mL preservative) and transferred to finger bowls containing river water 30 min before use. *Ephemera inermis* nymphs were too small and cryptic to be used during autumn experiments.

A trial consisted of releasing 50 live and 50 dead animals of each species into the water just above the streambed at a single stake. Animals were released by placing them in a 118 mL jar containing river water, immersing the jar and removing the lid. Drift nets were submersed for 2 min from the time of release. This provided adequate time for animals to be transported from furthest upstream release points to the nets, yet minimized inclusion of detritus and extraneous drifting animals. The contents of each net were separately enumerated in the field.

To estimate numbers of extraneous animals caught during experiments, the nets were used to sample natural drift at 18:00, 24:00, 09:00, and 12:00 on 28–29 May and 7–8 October 1979. Nets were submersed for 2–5 min in

spring and 15–25 min in autumn. Sampling period varied to ensure that nets did not become clogged with detritus at higher current velocities. Net contents were preserved in Kahle's fluid and sorted in the laboratory. The estimated mean number of appropriately sized *B. tricaudatus* and *E. inermis* nymphs caught per 2 min in daytime drift samples in each net was used as a correction factor for settling trials.

Instantaneous settling rates (r) of live and dead animals of each species for each experimental line were determined by linear regression according to the formula

$$(1) \ln(n_x + 1) = \ln(n_0 + 1) - rx$$

(McLay 1970; Elliott 1971) where

n_x = number of individuals caught in all nets (corrected for extraneous animals)

n_0 = number released

x = downstream distance between point of release and the nets.

Mean current velocity (v_y) for each line (y m from shore) was estimated from the regression equations relating velocity to distance from shore. The relationship between r and v was then determined by linear regression, following logarithmic transformation of both variables (Elliott 1971; Ciborowski and Corkum 1980). The results were then retransformed to the form

$$(2) r = \beta_1 v^{-\beta_2}$$

where β_1 and β_2 are regression constants.

To compare overall settling capabilities of animals, settling capacity (SC) and behavioral settling index (BI) were calculated (Ciborowski and Corkum 1980). SC is determined by integrating equation 2 over the range of mean current velocities tested (approximately $10-50 \text{ cm} \cdot \text{s}^{-1}$, Table 1). The relative contribution of behavior (BI) to settling ability is the complement of the ratio of settling capacities of dead to live animals.

Diffusion theory predicts that suspended particles should disperse normally and in proportion to the square root of the distance from their source, along any single axis (Pielou 1969). Turbulence, which is related to current velocity, should contribute an additional diffusion component (Smith 1975). I used multiple regression analysis to estimate how transverse distribution of suspended nymphs varied with downstream distance from the point of release (x) and with mean current velocity (v_y). The dependent variable was the standard deviation (s) of the mean distance from shore of suspended animals caught in nets for each trial. Independent

TABLE 1. Distance from shore (m), mean current velocity ($\text{cm} \cdot \text{s}^{-1}$) and release points (m upstream of nets) at each line used for settling experiments. Current velocities are interpolated from regression equations in Table 2.

Line No.	1	2	3	4	5
Distance from shore	2	4	6	8	10
Current velocity (spring)	13.9	22.2	30.5	38.8	47.2
Current velocity (autumn)	9.0	18.5	28.1	37.6	36.3
Release points	0.5,1,2,3,5,5	1,2,3,5,5,8	1,2,5,8,11	1,2,5,8,11	1,2,5,9,12

TABLE 2. Regression estimates of relationship between mean current velocity (v_y , $\text{cm} \cdot \text{s}^{-1}$) and distance from shore (y , m) at sample site.

Season	Intercept	Slope (SE)	R^2
Spring	5.64	4.151(0.340)	0.77
Autumn	-0.56	4.773(0.285)	0.84

variables were \sqrt{x} , and v_y . These regressions took the form

$$(3) \quad s = \beta_3 + \beta_4\sqrt{x} + \beta_5v_y$$

where β_3 , β_4 , and β_5 are regression constants.

Results and discussion — Mean current velocity was a linear function of distance from the river margin during both seasons (Table 2), although in autumn velocity became constant at distance from shore greater than 8 m (ANOVA, $P > 0.05$).

Downstream transport — Settling rate was inversely related to current velocity in all series of trials, and live animals exhibited greater settling rates than dead ones (Table 3). In spring, settling rates of *B. tricaudatus* and *E. inermis* nymphs were comparable at low velocities, but *E. inermis* had much lower settling rates at higher mean current velocities than did *B. tricaudatus* nymphs. The different settling rates of live animals were largely due to variations in BI. Although SC due to morphology (i.e. dead animals) was comparable for the two taxa (Table 3), behavior accounted for 0.60–0.64 of total settling capacity for *B. tricaudatus* and only 0.33 of total SC for *E. inermis*. A rapid thigmotactic response to chance contact with the substrate is of primary importance in removing animals of both taxa from the water column (Ulfstrand 1968; Luedke and Brusven 1976; Walton 1978; personal observations), but *Baetis* nymphs are strong swimmers and are better able to control their orientation during transport, especially at higher current velocities (Elliott 1971; McKone 1975). My estimates of BI are somewhat lower than earlier reported determinations for other *Baetis* (0.71–0.82) and *Ephemerella* (0.43–0.62) species (Ciborowski and Corkum 1980).

Lateral transport — Regressions accounted for between 0.49 and 0.79 of total variation in the dependent variable, s (Table 4). All β_4 regression coefficients were significantly greater than zero ($P < 0.01$) and consistently removed more

of the variation in s than did β_5 ; the distance animals were transported downstream was a more important predictive variable than was current velocity. The β_5 coefficients were greater than zero for all analyses except that for *E. inermis* (dead) nymphs.

Relative magnitude of the regression coefficients indicates that dead animals should be less dispersed than live individuals for a given current velocity and distance below a release point. However, because dead animals settle over greater downstream distance than live ones, direct comparison of the coefficients is inappropriate. To provide a better indication of potential lateral dispersal, both between live and dead animals as well as between species, I first determined the estimated distance required for one-half of each sample population to settle ($x_{0.5}$, McLay 1970) where,

$$(4) \quad x_{0.5} = \ln(1/0.50)r^{-1} = 0.6931r^{-1}$$

I calculated values of $x_{0.5}$ for each species, using values of r corresponding to hypothetical releases of animals made 2 and 10 m from shore. In each case r was interpolated from equation 2, using values of v estimated from spring current velocity regressions (Table 2). These estimates represent how far downstream of the release point animals would be at the time one-half had settled (Table 5). Provided that river width does not vary, the mean distance from shore of the 25 animals still suspended will be the same as it was when they were initially released (y), but they will now be normally distributed with a standard deviation given by equation 3. I constructed frequency histograms for the expected transverse distribution of suspended animals by substituting $x_{0.5}$ and v into equation 3 to obtain expected standard deviations (Table 5) and fitting a normal distribution about y .

Dispersal of suspended animals was much greater along the 10 m line than along the 2 m line (Fig. 1). Live *E. inermis* became more widely dispersed than live *B. tricaudatus* nymphs, but dispersal differences between larger (spring) and smaller (autumn) *B. tricaudatus* nymphs were minimal. Even though $x_{0.5}$ was markedly smaller for live than for dead organisms, there were no consistent trends between transverse dispersal of live and dead individuals of the same species. Clearly, the behavioral mechanisms that reduce downstream transport of live animals have the additional effect of substantially increasing transverse movement.

Lateral dispersal may be more important than animals' downstream transport in a wide, shallow river such as the Pembina. Because longitudinal changes in flow structure

TABLE 3. Regression coefficients (β_1 , β_2) and coefficients of determination (R^2) of relationship between instantaneous settling rate (r) and mean current velocity (v) (equations take the form $r = \beta_1v^{-\beta_2}$), and measures of settling ability (SC, BI).

Species	Condition	β_1	β_2 (SE)	R^2	SC	BI
<i>E. inermis</i> (spring)	Live	33.15	1.65(0.187)	0.96	7.41	0.34
	Dead	18.23	1.59(0.600)	0.70	4.84	
<i>B. tricaudatus</i> (spring)	Live	8.01	1.07(0.116)	0.97	10.38	0.64
	Dead	3.43	1.13(0.402)	0.72	3.69	
<i>B. tricaudatus</i> (autumn)	Live	1.46	0.68(0.084)	0.96	6.42	0.63
	Dead	1.12	0.91(0.267)	0.68	2.38	

TABLE 4. Regression coefficients (β_3 , β_4 , β_5) of relationship between standard deviation of mean distance from shore of suspended animals (s), distance downstream from point of release (x), and mean current velocity (v). Equations take the form $s = \beta_3 + \beta_4\sqrt{x} + \beta_5v$. Asterisks indicate regression coefficient significantly greater than zero by ANOVA; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	Condition	β_3	β_4 (SE)	β_5 (SE)	R^2
<i>E. inermis</i> (spring)	Live	-1.023	0.600(0.209)**	0.0296(0.0114)**	0.58
	Dead	0.031	0.234(0.068)**	0.0016(0.0036)	0.55
<i>B. tricaudatus</i> (spring)	Live	-0.560	0.659(0.105)***	0.0103(0.0057)*	0.80
	Dead	0.140	0.104(0.025)***	0.0029(0.0014)*	0.56
<i>B. tricaudatus</i> (autumn)	Live	-0.548	0.377(0.111)**	0.0151(0.0073)*	0.48
	Dead	-0.253	0.234(0.056)***	0.0078(0.0041)*	0.60

TABLE 5. Estimates of instantaneous settling rates (r), distance traveled before one-half of animals settle ($x_{0.5}$), and standard deviation (s) of mean distance from shore of suspended animals at $x_{0.5}$.

Species	Condition	Release distance (y)					
		2 m ($v_y = 13.9$)			10 m ($v_y = 47.2$)		
		r	$x_{0.5}$	s	r	$x_{0.5}$	s
<i>E. inermis</i> (spring)	Live	0.431	1.61	0.150	0.057	12.07	2.459
	Dead	0.278	2.50	0.423	0.040	17.44	1.084
<i>B. tricaudatus</i> (spring)	Live	0.479	1.45	0.377	0.130	5.35	1.450
	Dead	0.175	3.95	0.387	0.044	15.74	0.689
<i>B. tricaudatus</i> (autumn)	Live	0.244	2.84	0.297	0.106	6.53	1.128
	Dead	0.102	6.79	0.465	0.034	20.65	1.179

occur over distances much in excess of the downstream distance an animal is likely to drift, it is improbable that an individual will be carried from, e.g. a riffle into a pool. In contrast, except at the river center, current velocity changes rapidly across the river. Consequently, settling animals will more likely experience a change in the primary physical factor controlling microhabitat (current velocity) as the result of lateral dispersal than because of downstream movement.

The instantaneous distribution of suspended nymphs is not by itself an accurate measure of the eventual transverse distribution of nymphs in the substrate. As individuals become increasingly widely laterally dispersed, they come under the influence of increasingly different current velocities. Those insects carried laterally to slower water, near shore, will have greater settling rates than those carried away from the shore, where water is faster (equation 1). Thus, although the instantaneous distribution of suspended animals may be normal, the distribution curve of insects that actually do settle at any distance (x) downstream of a release point should be skewed towards the river center, and mean distance from shore should be less than that of the release point (y). The skewness and reduction in mean distance from shore will be governed by how quickly mean current velocity increases with distance from shore (Table 2), and by the rate at which instantaneous settling rate decreases with increasing mean current velocity (equation 1). The latter is largely determined by the behavioral characteristics of the animals. Other physical characteristics of the riverbed such as roughness or presence of macrophytes, which may modify turbulence and settling rate (Elliott 1971), should also influence degree of lateral transport to some extent. Nevertheless, because the exponent of

equation 2 is always negative, any animal entering the water column has a greater probability of returning to the substrate closer to shore than of becoming reestablished farther from shore.

If all animals in a population were equally likely to drift, regardless of their initial position in the river, one would expect this population to become concentrated along the river margins, given ample time. However, both *B. tricaudatus* and *E. inermis* nymphs are more prone to enter the drift when in slow water regions than when located in fast water (Ciborowski 1983). This may normally counteract the net effect of lateral transport of suspended animals. Indeed, in the Pembina River, both taxa predominate in fast water away from shore during non-flood conditions (Ciborowski and Clifford 1983). When the river floods, however, animals do become more numerous along the margins. Flooding produces higher current velocities (hence greater downstream and lateral transport) as well as tending to increase the rate of erosion of animals from the substrate through scouring. Lehmkühl and Anderson (1972) also reported that flooding carried *B. tricaudatus* nymphs to stream margins.

Drift results in a continuous redistribution of animals among lotic microhabitats (Townsend and Hildrew 1976). The microdistribution of populations prone to drift possibly represents the dynamic equilibrium achieved by a balance between departure and settling tendencies of the animals. Prediction of the benthic distribution of nymphs from the drift would require determination of the joint probabilities of departure from the substrate, downstream movement and lateral transport of animals in each microhabitat. However, consideration of the influence of these parameters on micro-

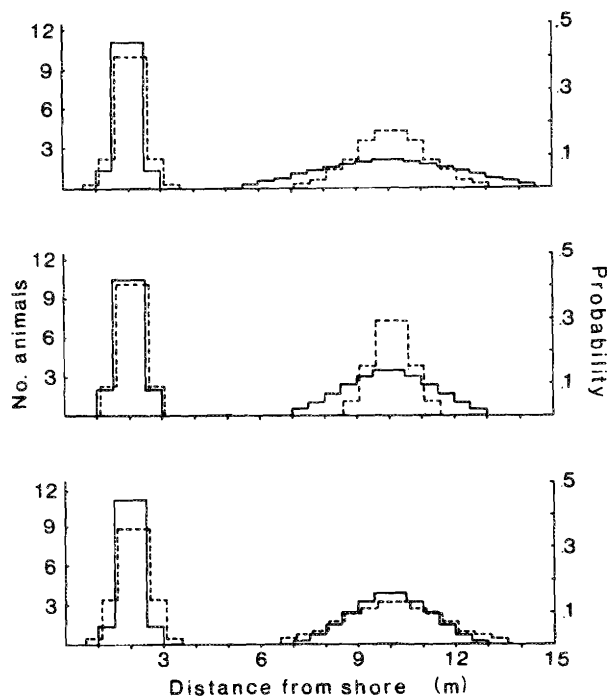


FIG. 1. Hypothetical frequency distribution of suspended animals released 2 and 10 m from shore at the point downstream by which one-half have settled. Left vertical scale indicates animals remaining from an initial release of 50. Right vertical scale represents probability of a suspended animal being a distance from shore indicated by horizontal scale. Top, *E. inermis* (spring); center, *B. tricaudatus* (spring); bottom, *B. tricaudatus* (autumn). Solid lines represent live animals; broken lines represent dead animals.

distribution may provide important insights into the population dynamics of these species.

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CIBOROWSKI, J. J. H. 1983. Influence of current velocity, density and detritus on drift of two mayfly species (Ephemeroptera). *Can. J. Zool.* 61: 119–125.

CIBOROWSKI, J. J. H., AND H. F. CLIFFORD. 1983. Life histories, microdistribution and drift of two mayfly (Ephemeroptera) species in the Pembina River, Alberta, Canada. *Holarct. Ecol.* 6: 3–10.

CIBOROWSKI, J. J. H., AND L. D. CORKUM. 1980. Importance of behavior to the re-establishment of drifting Ephemeroptera, p. 321–330. *In* J. F. Flannagan and K. E. Marshall [ed.] *Advances in Ephemeroptera biology*. Plenum, New York, NY.

ELLIOTT, J. M. 1971. The distances travelled by drifting invertebrates in a Lake District stream. *Oecologia* 6: 350–379.

LEHMKUHL, D. M., AND N. H. ANDERSON. 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. *Ecology* 53: 661–667.

LUEDKE, R. J., AND M. A. BRUSVEN. 1976. Effects of sand sedimentation on colonization of stream insects. *J. Fish. Res. Board Can.* 33: 1881–1886.

MCKONE, W. D. 1975. Quantitative studies of stream drift with particular reference to the McLay model. Ph.D. thesis, Univ. British Columbia, Vancouver, B.C. 118 p.

MCLAY, C. L. 1970. A theory concerning the distance travelled by animals entering the drift of a stream. *J. Fish. Res. Board Can.* 27: 359–370.

PIELOU, E. C. 1969. *An introduction to mathematical ecology*. Wiley-Interscience, New York, NY. 286 p.

SMITH, I. R. 1975. Turbulence in lakes and rivers. *Freshwat. Biol. Assoc. Sci. Publ.* 25: 79 p.

TOWNSEND, C. R., AND A. G. HILDREW. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *J. Anim. Ecol.* 45: 759–772.

ULFSTRAND, S. 1968. Benthic animal communities in Lapland streams. *Oikos Suppl.* 10: 1–120.

WALTON, O. E., JR. 1978. Substrate attachment by drifting aquatic insect larvae. *Ecology* 59: 1023–1030.