Influence of current velocity, density, and detritus on drift of two mayfly species (Ephemeroptera)

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Drift responses of *Baetis tricaudatus* Dodds and *Ephemerella inermis* Eaton larvae to manipulations of benthic density, sterile detritus, and current velocity were monitored in laboratory streams. The proportion of larvae departing from the substrate was independent of benthic density, amount of detritus, and interactions between these two variables. In spring, departure of larvae of both species was a positive linear function of current velocity during daylight hours. In darkness, departure of *B. tricaudatus* larvae became a negative linear function of current velocity. Nocturnal drift of *E. inermis* larvae was minimal at a mean current velocity of 25 cm·s^{-1} and greater at both higher and lower velocities. None of the factors tested influenced departure of *B. tricaudatus* larvae in autumn experiments. Dead larvae were eroded from the substrate in much smaller proportions than were their live counterparts. This suggests that appearance in the water column of live animals is the direct or indirect consequence of individuals' behaviour. Departure of animals during daytime is largely passive in nature, whereas a substantial proportion of nocturnal drift probably results from active desertion of the substrate.

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Les réactions de dérive des larves de *Baetis tricaudatus* Dodds et d'*Ephemerella inermis* Eaton à des manipulations de densité du benthos et de vitesse du courant ont pu être suivies dans des ruisseaux de laboratoire. La proportion de larves qui quittent le substrat est indépendante de la densité du benthos, de la quantité de détritus ou des interactions entre ces deux variables. Au printemps, le taux d'abandon du substrat chez les deux espèces suit une fonction linéaire positive par rapport à la vitesse du courant durant les heures du jour. À l'obscurité, le taux chez les larves de *B. tricaudatus* suit une fonction linéaire négative. La dérive nocturne des larves d'*E. inermis* est négligeable à une vitesse de courant moyenne de 25 cm·s^{-1}, mais plus importante aux vitesses inférieures et supérieures. Aucun de ces facteurs n'influence la dérive des larves de *B. tricaudatus* en automne. Les larves mortes sont arrachées du substrat dans des proportions plus faibles que les larves vivantes; il semble donc que la présence des animaux vivants dans la colonne d'eau soit une conséquence directe ou indirecte de leur comportement. La dérive durant la journée est en grande partie passive, alors que, durant la nuit, la dérive s'explique probablement par l'abandon volontaire du substrat.

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Introduction

The microdistribution of lotic invertebrates is largely controlled by current velocity, substrate composition, and food availability (Hildrew and Townsend 1976, 1977; Rabeni and Minshall 1977; Williams 1978; Barton 1980; Peckarsky 1980). Drift provides an effective means of removing animals from microhabitats in which one or more of these factors becomes unfavourable (Corkum *et al.* 1977; Walton *et al.* 1977; Corkum and Clifford 1980). Current velocity is of particular importance because it controls the distribution of substrate and food as well as exerting a direct influence on benthic invertebrates.

Other workers have postulated that drift of aquatic invertebrates also reflects intraspecific competition for space (see reviews in Waters 1972; Hildebrand 1974). High benthic densities of animals may increase the frequency of interactions between individuals. This can stimulate benthic activity and result in either a greater probability of accidental dislodgement (Elliott 1967; McLay 1968) or the active desertion of the microhabitat (Walton *et al.* 1977; Hildrew and Townsend 1980). Density-dependent drift (an increase in the *proportion* of animals entering the water column as benthic density increases) occurs when animals are abundant enough to exceed the carrying capacity of the microhabitat. In some rivers, however, physical perturbations (e.g., floods) and predation may maintain population densities below this level, with the result that drift may be density independent at most times (Bishop and Hynes 1969).

This laboratory study was undertaken to examine the relative importance of current velocity, benthic density, and abundance of detritus on drift of two mayfly species, *Ephemerella inermis* Eaton and *Baertis tricaudatus* Dodds when subjected to predation pressure. More

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specifically, I attempted to determine whether (*1*) larvae exhibit density-dependent drift at benthic densities typical of their normal habitat; (*2*) presence of organic material (sterile detritus) modifies the amount of space available to animals in the substrate, and hence departure tendencies; and (*3*) these influences are of greater importance in controlling departure rates of organisms than is current velocity. The response of dead animals to current velocity was also examined to discern to what extent departure is the result of accidental dislodgement of animals.

Materials and methods

Experimental animals and detritus

Ephemerella inermis and *B. tricaudatus* larvae were collected from a sample site on the Pembina River near Entwistle, Alta (53°37′ N, 115°00′ W). Physical characteristics of the river and life history and microdistribution of these populations have been described in detail by Ciborowski and Clifford (1983). Both populations are most abundant in fast-water areas, overwinter as larvae, and are dominant components of the drift.

Larvae were collected for experiments in May (spring) and October (autumn) 1979. Animals collected in spring and autumn differed in size and maturity. The former had well-developed wing pads and head widths greater than 0.7 mm, and the latter had poorly developed wing pads and head widths of 0.4–0.6 mm. Larvae of *E. inermis* were not used in October experiments, as their small size and cryptic habits made them difficult to collect in sufficient numbers.

Isogenoides elongatus (Hagen) (Plecoptera: Perlodidae) is a major predator of mayflies in the Pembina River and will readily attack the experimental animals in laboratory streams (Corkum and Clifford 1980). These animals were used in all experimental treatments except those concerned with dead mayfly larvae, in numbers that approximated average density of all invertebrate predators at the sample site (J. J. H. Ciborowski, unpublished data).

Detritus for all experiments was collected from the Pembina River, sorted to remove all large animals (greater than 3 mm in length), air-dried, and stored until required. Particles ranged in size from 0.420 to 3.36 mm. This size range was abundant at the study site and could be retained in laboratory stream substrates at the fastest current velocities. The required amount of detritus (measured as dry weight) was reconstituted in distilled water for 24 h prior to use. This provided only minimal time for bacterial and fungal growth to occur.

Laboratory streams

Experiments were conducted in three elliptical, paddle-wheel-driven, recirculating artificial streams (channel width, 11 cm; water depth, 13 cm) housed in a controlled environment room. The temperature was maintained at prevailing Pembina River temperatures (Ciborowski and Clifford 1983).

Current velocity was regulated by varying the size of pulleys that coupled the paddlewheel to the motor. Varying current velocity independently of water depth can produce markedly different effects at the substrate than may normally occur in a natural stream, where mean velocity and depth are usually correlated. Consequently, laboratory equivalents to mean current velocity at the sample site were determined to make results more comparable with a field situation.

Laboratory stream equivalents to mean velocity in the Pembina River were estimated by taking a series of field current velocity readings with a Gurley current meter. Mean velocity was determined by taking a measurement at 0.6× river depth. Eight points were selected at increasing distances from shore. Mean current velocity ($\bar{V}$) and velocity 5.2 cm above the substrate ($V_{5.2}$, equivalent to 0.6× laboratory stream depth) were measured at each point. The relationship between the two variables was estimated as

$$[1] \quad \bar{V} = -2.91 + 1.41V_{5.2}$$

by linear regression ($R^2 = 0.93$). Laboratory equivalents of field velocities were then calculated by substituting direct measurements of mean current velocity in laboratory streams ($V_{5.2}$) into the regression equation.

Substrate consisted of scrubbed inorganic material from the Pembina River, ranging in size from coarse sand to small cobbles. Relative composition was adjusted to match natural composition at the sample site (average particle size, 27 mm; heterogeneity, 2.41 (Williams 1980)).

Density–detritus experiments

Experiments to test the influence of benthic animal density and amount of detritus on departure from the substrate were conducted in both May and October. A 3 (density) by 4 (detritus) level factorial stratified random design was used, with three replicates of each treatment. Levels corresponded to ½×, 1×, or 3× maximum recorded abundance in samples collected from the Pembina River in spring 1978 (Ciborowski and Clifford 1983; Table 1). Experiental densities of *B. tricaudatus* and *I. elongatus* added in October were doubled over May levels to reflect their greater abundance in the field at that time. Mean current velocity for all treatments was laboratory stream equivalent of 31.2 $\mathrm{cm \cdot s^{-1}}$.

Current velocity experiments

Experiments to examine the effect of current velocity on departure ran concurrently with density–detritus trials. Three replicates were conducted for each of five mean current velocities, representing the range of current found in the Pembina River up to a distance of 12 m from shore during nonflood conditions (Ciborowski 1982). Trials with live animals were all conducted with 3× levels of density and detritus, with predators present at the same densities as in density–detritus trials. Treatments were the laboratory stream equivalent of 17.0, 24.7, 31.2, 40.8, and 51.4 $\mathrm{cm \cdot s^{-1}}$.

Preserved animals (kept in Kahle's fluid) from earlier experiments were used to determine the effect of the same current velocities on loss from the substrate of dead organisms. In these trials, 80 *E. inermis* (May), 80 *B. tricaudatus* (May), and 80 *B. tricaudatus* (October) larvae were used. Animals were placed in dechlorinated tap water for 1 h prior to use. Substrates in all of these trials were augmented with 3× levels of detritus.

Execution of experiments

Detritus was placed in two adjacent 11 × 30 cm trays set in a dry laboratory stream and covered with 4 kg of substrate. Predators were then introduced. The stream was immediately filled with refrigerated dechlorinated tap water with the

TABLE 1. Animals and detritus added to laboratory streams, all confined to an area of 0.066 m^2 with current velocity at 31.2 $cm \cdot s^{-1}$ unless otherwise specified

Treatment	May			October		
	½×	1×	3×	½×	1×	3×
Ephemerella inermis (no.)	10	20	60	—	—	—
Baetis tricaudatus (no.)	15	30	90	30	60	180
Isogenoides elongatus (no.)	3	3	3	6	6	6
Detritus (g)	1.14	2.28	6.84	1.14	2.28	6.84

paddlewheel running and left for 1 h. The appropriate number of mayfly larvae was then added. All larvae eventually settled on the substrate instead of on bare portions of the stream. Two hours after introduction of the mayfly larvae, a drift net was placed in each stream. A removable catchment jar on each net was replaced immediately and at 30-min intervals thereafter for the next 4 h. The jars were not subsequently changed until the end of the light period of the experiment (May, 8 h; October, 5 h). The lights were then turned off and the catchment jars changed at 30-min intervals for the duration of the experiment (May, 8 h; October, 10 h). Natural photoperiods at the time of experiments were 16 h light : 8 h dark (May) and 12 h light : 12 h dark (October).

Analysis

Magnitude and pattern of departure

Departure of animals during each sample interval was pooled across all experimental treatments. The proportion of animals departing during each 30-min period was determined by dividing the pooled number of animals captured during a period by the pooled number of organisms in the substrate prior to the start of that period.

Density–detritus experiments

The proportion of animals leaving the substrate during light and dark portions of experiments, respectively, was determined by dividing the number of animals caught in drift nets during relevant portions of each trial by the number present at the beginning of that period. All data were transformed by taking the arcsine of square roots of proportions.

The relationship between proportion of animals leaving the substrate and benthic density was tested by linear regression analysis. Separate regression lines were fitted for each level of detritus. Analysis of covariance was then used to test for homogeneity of the regression coefficients. Proportions of animals departing under different detritus treatments were compared by one-way analysis of variance.

Current velocity experiments

Curvilinear regression analysis was used to estimate the relationship between arcsine square root of proportion of animals departing and current velocity. Increasingly higher order polynomials were fitted to the data until no significant improvement in fit ($p > 0.05$) was observed.

Results

Magnitude and pattern of departure

Installation of drift nets disturbed the streams and caused high initial departure rates of both live and dead larvae (Fig. 1). Consequently, the first 3 h of each trial were not considered in later analyses. Departure remained fairly constant for the duration of the light period. With the onset of darkness, departure of live animals increased substantially. *Baetis tricaudatus* larvae showed a more pronounced nocturnal increase in May than in October trials. Departure of live animals was consistently greater than that of dead animals. The total proportions of *B. tricaudatus* larvae leaving the substrate, exclusive of the initial portion of experiments, were 0.77 and 0.61 in May and October, respectively. In contrast, only 0.08 and 0.07 of the dead animals were washed away. The proportions of *E. inermis* leaving the substrate were 0.88 (live) and 0.06 (dead).

Density–detritus experiments

Of the 24 regressions performed to test for density dependence, only one produced a regression coefficient significantly different from zero (*E. inermis* at 1× detritus in spring; $p < 0.05$). This single value is likely a Type I error. Thus, the proportion of animals departing from the substrate was independent of benthic density for both species, under all levels of detritus, in light and

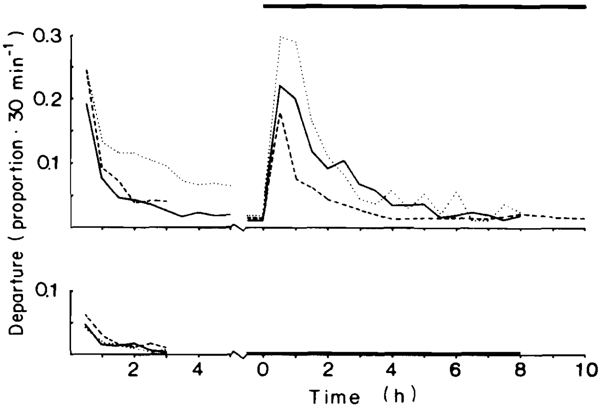

FIG. 1. Pooled proportion of remaining live (upper) and dead (lower) animals departing from substrate each 30 min. —, *B. tricaudatus* (May); ---, *B. tricaudatus* (October); ...., *E. inermis* (May). Bar above figure represents darkness.

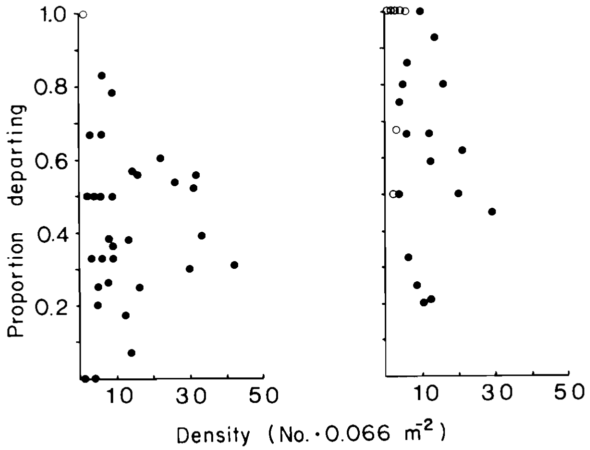

FIG. 2. Proportion of *E. inermis* larvae in substrate that depart as a function of benthic density during light (left) and dark (right) portions of experiments. ●, one trial; ○, two observations. Missing observations are the result of 100% departure during a prior portion of a trial.

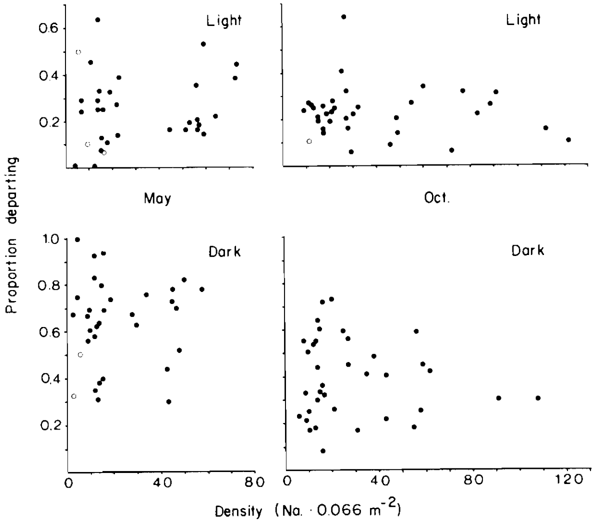

FIG. 3. Proportion of *B. tricaudatus* larvae in substrate that depart as a function of benthic density during light (upper) and dark (lower) portions of May (left) and October (right) experiments. Remaining explanation as in Fig. 2.

in darkness (Figs. 2 and 3). Analysis of covariance indicated that there was no significant heterogeneity of regression coefficients for either species, on either date, in either light condition ($p > 0.05$). Therefore, the interaction of detritus and benthic density had no influence on departure. There was no significant influence of amount of detritus on the tendency for animals to leave the substrate ($p > 0.05$, Fig. 4).

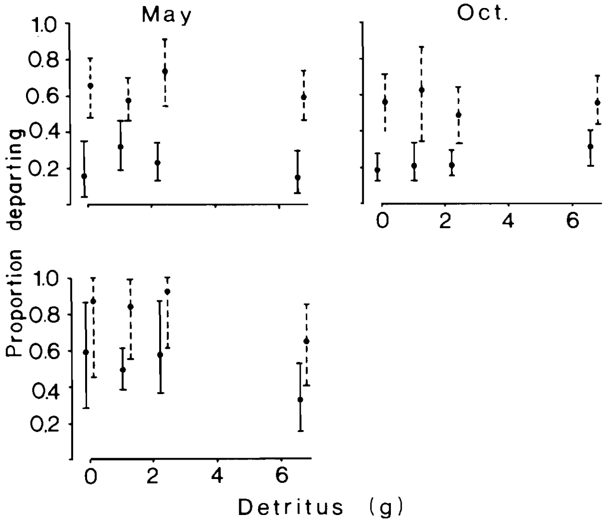

FIG. 4. Mean proportion and 95% confidence intervals of *B. tricaudatus* (upper) and *E. inermis* (lower) larvae departing from substrate as a function of detritus concentration in May (left) and October (right) experiments. Solid intervals represent light portion of trials; broken intervals represent dark portion.

Current velocity experiments

In May, departure of both *B. tricaudatus* and *E. inermis* larvae was a positive linear function of current velocity (Fig. 5) but only during light portions of the experiments. During darkness, the proportion of *B. tricaudatus* larvae leaving the substrate became a negative linear function of current velocity. Departure of *E. inermis* was minimal at a current velocity of $25\,\text{cm}\cdot\text{s}^{-1}$ and greater at both higher and lower velocities. A third-order polynomial provided the best fit to data for *E. inermis* larvae in darkness (Table 2). Departure of *B. tricaudatus* larvae in October was independent of current velocity.

Dead animals of all three types were eroded from the substrate in much lower proportions than were their live counterparts at all current velocities. Positive linear relationships were found between current velocity and departure of larvae of both species from May experiments, but only during light periods (Fig. 5). Departure of dead insects during darkness was independent of current velocity in all cases.

Discussion

Density-dependent drift responses occur when the number of animals present in the substrate exceeds the space available (Waters 1972; Walton *et al.* 1977; Gyselman 1980). Interactions between individuals at subsaturation densities may produce short-distance displacement of animals but seldom result in drift (Corkum

TABLE 2. Best estimate polynomial regression coefficients for relationship between current velocity and arcsine square root of proportion of animals departing from substrate

	Species	Live					Dead		
		β_0	β_1	β_2	β_3	R^2	β_0	β_1	R^2
Light	*E. inermis* (May)	23.74	0.5760			0.35*	−3.28	0.4008	0.56**
	B. tricaudatus (May)	13.69	0.4294			0.47**	−3.79	0.4405	0.48**
	B. tricaudatus (October)	21.84	0.2300			0.15	4.91	0.1979	0.15
Dark	*E. inermis* (May)	346.67	−29.511	0.9484	−0.0094	0.64**	6.61	0.0886	0.04
	B. tricaudatus (May)	73.94	−0.5671			0.45**	1.85	0.1987	0.12
	B. tricaudatus (October)	45.39	−0.0789			0.02	6.76	0.0023	0.03

NOTE: *, $p < 0.05$; **, $p < 0.01$ by analysis of variance.

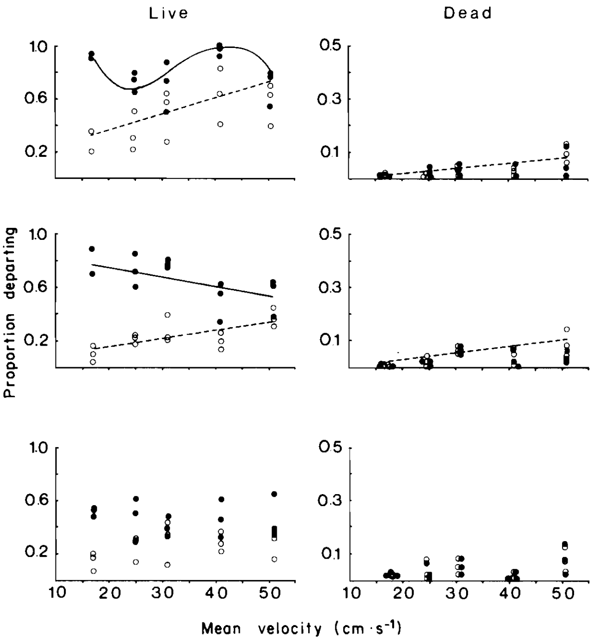

FIG. 5. Proportion of live (left) and dead (right) larvae departing from substrate as a function of current velocity. Top, *E. inermis* (May); centre, *B. tricaudatus* (May); bottom, *B. tricaudatus* (October). ○, ---, light portion of experiments; ●, —, dark portion.

1978; Wiley and Kohler 1981). Although laboratory densities of animals considerably exceeded benthic abundance of animals in the field (Ciborowski and Clifford 1983), departure of *E. inermis* and *B. tricaudatus* larvae was density independent. Thus, departure of these organisms in the Pembina River is unlikely to be the result of competition for space. These results are consistent with other experimental studies on the relationship between benthic density and drift of mayflies (Hildebrand 1974; Keller 1976; Corkum 1978; Bohle 1978; Walton 1980*a*).

Increasing substrate complexity has been shown to reduce aggressive intraspecific interactions between lotic invertebrates (Glass and Bovbjerg 1969). I had anticipated that should interactions between larvae be responsible for increased departure rates of animals at high densities, the addition of detritus might modify this response. However, since all drift responses were density independent, the lack of a significant density–detritus interaction is to be expected.

Many aquatic invertebrates deprived of an adequate food supply exhibit a density-independent increase in departure rate (Hildebrand 1974; Keller 1976; Bohle 1978). The lack of any departure response to detritus concentrations in my experiments may indicate that relatively sterile detritus does not constitute an attractive source of nutrients to *E. inermis* and *B. tricaudatus* larvae. As such, departure rates in my experiments should be regarded as maximal rather than typical of the field situation.

Behavioural drift refers to those animals that have become suspended in the water column as the result of some change in their internal state (Waters 1972). Behavioural drift may be active, the result of animals releasing themselves from the substrate, or passive, whereby activity or positioning renders individuals especially susceptible to accidental dislodgement. The magnitude of the behavioural component of drift should be evident as the difference between transport of live animals, which are capable of resisting the eroding influence of the current, and dead animals, which are deposited and then eroded from the substrate as inert particles.

The positive linear relationship between current velocity and departure of both live and dead animals during the light portion of experiments suggests that transport is passive at this time. Live animals may have been more prone to erosion than dead ones because they selected exposed areas of substrate rather than lodging in interstices. Corkum *et al.* (1977) reported that *B.*

tricaudatus larvae inhabit all surfaces of substrate particles and are not restricted to the relatively sheltered undersides. Movements of the animals over the substrate may also contribute substantially to the increased frequency of erosion of live animals (Butz 1973) especially at high current velocities.

Nocturnal departure rates of live animals in spring were greatest in trials of low rather than high current velocity. This suggests an added active behavioural response on the part of the organisms during darkness. High incidence of nocturnal drift from areas of reduced current has been commonly reported (see Walton 1980*b*). Corkum *et al.* (1977) found that *B. tricaudatus* larvae were more prone to leave substrates in slow water than fast water under both light and dark conditions. The apparent differences in drift of *E. inermis* and *B. tricaudatus* with respect to current velocity would be even more pronounced if departure rates were expressed as drift density (number of animals per cubic metre of water passing over the substrate) as is commonly done in reporting field levels of drift.

Departure of *B. tricaudatus* larvae in October experiments was reduced in comparison with May trials and was not influenced by current velocity. This may reflect a lower overall level of activity by these animals as well as a broader tolerance for reduced currents. *Baetis tricaudatus* larvae in the Pembina River are strongly concentrated in fast-water areas in spring, but distribution is more even with respect to current velocity in autumn (Ciborowski and Clifford 1983).

The departure of dead animals in the dark was independent of current velocity, presumably because most animals that lodged on the most exposed areas in high current velocity trials were quickly washed away early in those experiments. Walton (1978) observed that dead animals that settled in substrate tended to be washed away almost immediately or to remain in the substrate for the duration of an experiment.

Clearly, the marked difference in departure tendencies between live and dead animals of both species reflects a major behavioural component of their drift. However, of the factors investigated in this study, only current velocity exerted a significant modifying influence. This is also the most important factor influencing microdistribution of these populations in the Pembina River (Ciborowski and Clifford 1983). Passive behavioural departure from the substrate produces an important contribution to the drift during daylight, but it is the active nocturnal component that is indicative of the field distribution of the larvae.

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