

Dynamics of Drift and Microdistribution of Two Mayfly Populations: A Predictive Model

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A model is derived to predict changes in larval microdistribution of *Ephemerella inermis* Eaton and *Baetis tricaudatus* Dodds (Ephemeroptera) that result from drift. Transport by drift was assumed to be a Markov process. Estimates of departure from the substrate, downstream movement, and lateral transport were combined to produce transition matrices from which changes in microdistribution, magnitude of drift, and mean daily downstream displacement of live and dead animals were determined. Predictions from the model were compared with observations made in a river similar in composition to the area modelled. There were marked differences between expected drift of living versus dead animals; estimates for drift of living animals corresponded most closely to values observed in the field. Predicted drift either corresponded to or was less than observed levels. Observed changes in benthic microdistribution were minimal, but the model predicted large-scale relocation of animals toward river margins. Thus, magnitude and spatial pattern of drift could be adequately modelled but benthic distribution could not. Drift is an important redistribution mechanism but animals must have a complementary ability to actively travel towards the river center to maintain constant benthic distribution patterns. Inhibition of movement during floods should produce increased abundance at margins. During stable flow conditions, drift and benthic activity probably act together to produce and maintain microdistributional patterns among vagile organisms. In contrast, drift of invertebrates possessing poor locomotory ability probably reflects larger-scale, permanent displacement events that are a normal aspect of development, or the outcome of aggressive interactions.

On a élaboré un modèle de prédiction des variations de la microdistribution larvaire de *Ephemerella inermis* Eaton et de *Baetis tricaudatus* Dodds (Ephemeroptera) qui résultent de la dérive. On a présumé que le transport par dérive est un processus de Markov. Des estimations de l'émigration du substrat, des déplacements vers l'aval et du transport latéral ont été combinées pour obtenir des matrices de transition qui ont servi à déterminer les variations de la microdistribution, l'importance de la dérive et les déplacements quotidiens moyens d'animaux vivants et morts vers l'aval. Les prédictions tirées du modèle ont été comparées aux observations réalisées dans une rivière semblable à la zone modélisée. Il existait des différences marquées entre la dérive attendue des animaux vivants par rapport aux animaux morts. Les estimations de la dérive des animaux vivants correspondaient plus étroitement aux valeurs observées sur le terrain. La dérive extrapolée était égale ou inférieure aux niveaux observés. Les variations notées dans la microdistribution benthique étaient minimes, mais le modèle prédisait le déplacement à grande échelle des animaux vers les rives. Ainsi, l'amplitude et la répartition spatiale de la dérive peuvent être adéquatement modélisées mais non la répartition benthique. La dérive constitue un important mécanisme de redistribution mais les animaux doivent posséder une capacité complémentaire de déplacement actif vers la partie centrale d'un cours d'eau pour maintenir une répartition benthique constante. La cessation des déplacements au moment de crues devrait entraîner une plus forte abondance au niveau des rives. En présence d'un débit stable, la dérive et l'activité benthique concourent probablement à produire et à maintenir des régimes de microrépartition chez les organismes vagiles. En revanche, la dérive d'invertébrés à faible capacité locomotrice traduit probablement des déplacements permanents à grande échelle qui représentent un aspect normal du développement ou sont le résultat d'interactions agressives.

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Drift is an important aspect of the population dynamics of many lotic invertebrates. It serves to remove individuals from unfavorable microhabitats (Corkum et al. 1977; Walton et al. 1977; Peckarsky 1980; Kohler 1985) and provides animals that may colonize unexploited areas downstream (Ulfstrand et al. 1974; Townsend and Hildrew 1976; Williams and Hynes 1976; Ciborowski and Clifford 1984). Twenty-five years of intensive research on factors inducing departure of animals from the substrate has produced a wealth of data. Virtually every parameter that can be measured within a stream system has been correlated with

the drift of one or more species (Statzner et al. 1984). Yet, the variety of responses seen among both taxa and stream systems has made it difficult to integrate this information to provide a comprehensive interpretation of the phenomenon.

An implicit assumption made regarding drift has been that the force of the current in lotic systems restricts benthic movement of invertebrates to the extent that drift produces a permanent downstream displacement of populations. Accordingly, Müller (1954, 1973, 1974) hypothesized the existence of a colonization cycle. Newly hatched, rapidly growing individuals drift because they are restricted in resources of food

and space. Adults fly upstream to oviposit and complete the cycle. Waters (1965, 1972) observed that drift is not always predominant among early developmental stages. Neither do all species show a preponderance of upstream flight by adults. Consequently, he suggested that drift is a density-dependent phenomenon that removes animals in excess of carrying capacity; drifting animals are lost to the system.

However, neither of these hypotheses can consistently explain why many stream systems apparently support continuously high levels of density-independent drift. A large part of the problem in deriving a comprehensive explanation of the significance of drift has been a failure to adequately integrate the proximal causes of drift episodes with the outcome of the event. Kovalak (1979) proposed that benthic distribution of rheophilic populations was largely maintained by a balance between immigration and emigration through drift mediated by behavioral responses to current velocity. Several investigators have observed that drift can result in seasonal or short-term, small-scale displacement of significant proportions of populations (Ulfstrand 1968; Lehmkuhl and Anderson 1972; Hall et al. 1980; Ciborowski and Clifford 1983).

In this study, I examine the role of daily drift in maintaining the distribution of two mayfly populations among microhabitats in a wide, shallow, relatively homogeneous river. A model is developed to predict fluctuations in transverse distribution of larvae with time, given data on their departure and settling capabilities relative to current velocity. In order to distinguish purely physical influences of water flow from organisms' behavioral responses, all experimental manipulations were conducted with dead individuals concurrently with live animals. Whereas predicted distributions of dead animals would reflect purely mechanical aspects of drift, differences between such distributions and those observed for living animals must be ascribed to individuals' behavioral activity.

A Model Relating Drift to Benthic Microdistribution

Lotic invertebrates may relocate by crawling over or through the substrate, or by drifting. As a working hypothesis, I initially postulate that only the latter mechanism might produce a net change in distribution of animals, i.e. other forms of movement are nondirectional. Drift consists of three events: departure from the substrate, transport in the water column (drift proper), and return to the substrate. Because the actual moment of return to the substrate cannot easily be distinguished from the period of transport, I will refer to these components together as settling.

Current velocity exerts a major influence on benthic microdistribution, departure from the substrate, and settling, both through its direct actions on organisms and indirectly by modifying substrate characteristics or food abundance, to which animals also respond. Consequently, I assume that regions of comparable current velocity will contain equal benthic densities of organisms, each individual exhibiting species-specific departure and settling characteristics.

Entry into the water column may be passive, effected directly by erosion acting upon animals in vulnerable positions on the substrate (Elliott 1967). In such cases, departure tendencies should be greater from regions of high current velocity than from low. Alternatively, some rheophilic organisms may actively desert a microhabitat in which velocity becomes unfavorably reduced (Edington 1965; Minshall and Winger

1968). Other factors such as food abundance (Bohle 1978; Corkum and Clifford 1980; Walton 1980; Kohler 1985) and substrate texture (Corkum et al. 1977; Walton et al. 1977) also modify departure tendencies. These features are frequently correlated with or assume subsidiary importance to current velocity (e.g. Corkum et al. 1977; Horner and Welch 1981).

An animal suspended in the water column can undergo lateral transport as well as downstream movement during the settling event, which may result in a return to the substrate either shoreward or centerward from its point of departure. Degree of lateral displacement depends on time spent in the water column, turbulence, and behavioral actions of the animal during transport (Ciborowski 1983a). The former two factors are directly dependent on current velocity. By simultaneously considering departure from and subsequent settling among all microhabitats, it should be possible to anticipate the role of drift in maintaining microdistribution among habitats.

If a river is longitudinally homogeneous relative to the distance an animal is carried prior to settling, upstream-downstream microhabitat differences will be minimal, and changes in benthic distribution can be considered primarily in terms of organisms' lateral movement. Consider an ideal river, longitudinally partitioned into a discrete number of parallel homogeneous regions (i) of arbitrary width (see Appendix 1.1 for a complete list of symbols). Each has an associated uniform mean current velocity (v_i). Velocity is minimal at river margins and maximal at the center.

Let $B^0 = (b_1^0, b_2^0, b_3^0, \dots, b_i^0)$ be a vector with each b_i^0 the benthic density of animals in region i on a given day (0). Because each region is uniform along its length b_i^0 is constant throughout.

If conditions in the river are constant through time, a fixed proportion of animals will either depart from the substrate and enter the water column ($p(t)_{ii}$) or remain in the substrate ($q(t)_{ii}$) during time interval t at every point along a given region (i). These proportions can be assembled as diagonal matrices, $P(t)$ and $Q(t)$. (It is convenient to consider t as 1 d). Because velocity varies predictably across the river and is a major factor controlling likelihood of departure from the substrate, p_{ii} and q_{ii} can be estimated by considering the position of any particular region relative to a river margin.

Let k_{ij} be the probability that an animal that has entered the drift from region i returns to the substrate (settles) in the original or any other region (j). Because downstream and lateral transport are functions of current velocity, k_{ij} will be constant for each organism in a given homogeneous region. Elements k_{ij} can be assembled into a square probability matrix, K . Matrices $P(t)$, $Q(t)$, and K can then be combined to form a matrix, C , such that each element, c_{ij} , is the probability that any animal presently in the substrate in region i will be located in the substrate in region j on the next day:

$$(1) \quad C = P(t)K + Q(t).$$

That is, the probability of an animal being located in any region j after time t is the probability of departure from the substrate in any region i times the probability of transport from i to j plus the probability that the animal does not drift (i.e. remains in region i). (By including the values of $Q(t)$, one is making animals that do not drift functionally equivalent to those that do drift but do not change regions.) I assume that any individual that does drift does so only once per day. Allowing that each c_{ij} remains constant through time, C is the transition matrix of a Markov chain, and B' , the vector describ-

ing benthic density of animals among regions after t days, is

$$(2) B' = B^0 C'$$

where C' is the t th power of C . This requires the further assumption that location of an individual on any one day depends only on its location the previous day, and not on its location at any time prior to this.

Provided that C has no absorbing states (diagonal elements = 1.0), then, given ample time, an equilibrium will be reached in which the benthic distribution of animals among regions will remain constant. This equilibrium depends only on the structure of C and is independent of B^0 . If, however, one or more absorbing states does exist (i.e. animals that enter a region cannot leave it by drifting), each animal will eventually become restricted to one of these regions.

Prediction of benthic distribution from the model requires the following data: (1) current velocity (v_i) profile of the river under investigation; (2) benthic density (b_i) of animals in regions across the river; (3) likelihood of departure from the substrate in each region ($p(t)_{ii}$); (4) settling abilities and lateral dispersal of animals that depart from the substrate in each region (k_{ij}).

Methods and Analysis

Study Site and Animals

Data were collected from a study site on the south shore of the Pembina River near Entwistle, Alberta, Canada (53°37'N, 115°00'W). The site is wide and shallow (maximum depth 1.2 m) with a spatially uniform substrate of smooth cobbles embedded in coarse sand. It was selected for its evenness of current velocity and depth profiles, both of which increase linearly with increasing distance from the river margin (Ciborowski 1983a). The sample site is approximately 65 m wide during normal flow conditions. However, data on water flow, microdistribution, drift, and settling capabilities of the study animals were collected primarily from within 12 m of the southern riverbank.

Larvae of the mayflies *Baetis tricaudatus* Dodds and *Ephemerella inermis* Eaton were abundant during most of the year. Larvae of both species usually are most numerous in the benthos in regions of faster water, remote from the river margin, although large numbers are common in the drift across the river (Ciborowski and Clifford 1983). Both taxa exhibit strong nocturnal drift periodicities. Dead animals almost never appear in the benthos or as part of the natural drift. Only relatively large larvae could be collected in sufficient numbers for departure and settling experiments (see below). In May 1979, experimental animals had head widths >0.7 mm (both species used). Head widths in October 1979 were 0.4–0.6 mm (*B. tricaudatus* only used).

Model River

Instead of extrapolating data to provide estimates for the entire width of the river, I based my predictions on an hypothetical river with flow characteristics analogous to those of the sampled portions of the Pembina in May and October 1979 (Ciborowski 1983a). The model river was 26 m wide and partitioned into 1-m-wide regions. Depth and mean current velocity between 0 and 12 m from the south margin increased in a manner similar to that estimated for the Pembina River and at twice this rate between 0 and 6 m from the north bank (Fig. 1). The central 8 m were of uniform depth and velocity,

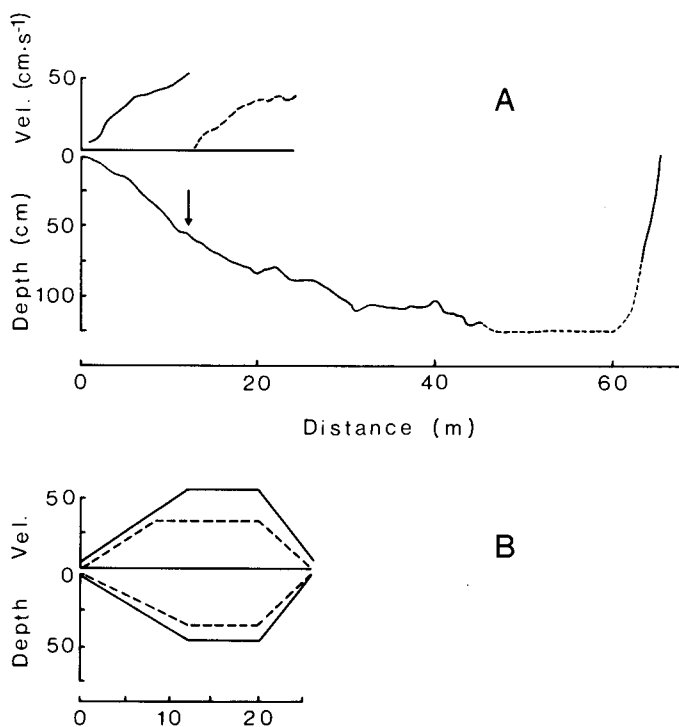


FIG. 1. (A) Depth (below) and current velocity (above) profiles of the Pembina River at the sample site. Left margin of graphs (distance of 0 m) corresponds to position of the south river margin in May. Arrow (below) and broken line (above) represent position of the river shoreline and corresponding current velocity profile in October. (B) Depth (below) and current velocity profile (above) of the model river in May (solid lines) and October (broken lines).

equivalent to values 12 m from the south margin of the Pembina River.

Benthic Distribution

Benthic microdistribution of *E. inermis* and *B. tricaudatus* larvae in the Pembina River was studied at 10- to 15-d intervals throughout 1979 (Ciborowski and Clifford 1983). Five replicate Hess samples (net pore size 0.380 mm) were taken 3 and 11 m from the south margin until mid-June and usually at 3, 7, and 11 m thereafter. Numbers of large animals in each sample within series of replicates on each date were adjusted to reduce sample variances (Sokal and Rohlf 1969) by regressing benthic densities against numbers of all other benthic animals taken in each sample (Ciborowski and Clifford 1983).

Benthic densities in the model river were allocated in relative quantities analogous to those of the Pembina River. I initially determined the relationship between adjusted benthic density of each Pembina River population and distance from the south river margin by linear regression (Table 1). The 12 regions extending from the south side of the model river were assigned densities interpolated directly from these regressions. Densities between 13 and 20 m from the south margin were the same as at the 12-m point. North margin densities were obtained by doubling the slope of the regression equations. "Dead" animals (those that would be affected only by mechanical forces in model runs) were given the same initial benthic distributions as their living counterparts.

Departure from the Substrate

Ciborowski (1983b) studied the influence of benthic density,

TABLE 1. Regression coefficients and coefficients of determination of functions relating benthic distribution (b_i) of animals in each region (i) within 12 m of the south margin of the model river to distance from the south margin (y_i). Equations take the form $b_i = \alpha_0 + \alpha_1 y_i$. Data were obtained from benthic samples collected in the Pembina River.

Species	Date	Intercept α_0	Slope α_1	R^2
<i>E. inermis</i>	15 May	-13.00	7.00	0.86
	28 May	3.25	8.25	0.80
<i>B. tricaudatus</i>	15 May	-13.49	6.72	0.41
	28 May	-23.53	8.50	0.63
	4 Oct.	-16.62	20.01	0.63
	15 Oct.	-115.75	41.30	0.46

detritus concentration, and current velocity on departure of both living and dead individuals from the two populations in laboratory streams. Predatory stoneflies were present in all of these experiments to render observed drift levels more representative of field conditions. Current velocity significantly influenced the departure of the two taxa, but neither benthic density of conspecifics nor amount of detritus affected drift levels. I used regression equations from that study, which related current velocity to departure, to provide estimates of daily departure from regions in the model river. Expected proportions of each population departing from the substrate in each model river region were determined by substituting the appropriate mean current velocity (Fig. 1) into these equations. Where departure was best described as a polynomial function of current velocity, mean departure proportion was estimated by integration. Because the duration of the laboratory experiments was slightly less than 24 h (Ciborowski 1983b), departure proportions were increased to correspond with field photoperiods (16:8 and 12:12 L:D in May and October, respectively (Fig. 2)).

The model permits animals to drift only once during a 24-h period. Let $p(L)_{ii}$ and $p(D)_{ii}$ be the proportions of animals departing from region i during day (L) and night (D), respectively. The proportions that remain on the substrate are

$$q(L)_{ii} = 1 - p(L)_{ii}$$

$$q(D)_{ii} = 1 - p(D)_{ii}$$

Assuming that the "drift day" begins at dusk, the proportions that depart or remain during 24 h are

$$(3) \quad p(24)_{ii} = P(D)_{ii} + q(D)_{ii} p(L)_{ii}$$

$$(4) \quad q(24)_{ii} = 1 - p(24)_{ii}$$

Settling

Settling animals, whether living or dead, return to the substrate according to a negative exponential function (McLay 1970; Elliott 1971a; Larkin and McKone 1985). The proportion that settles (f_i) over unit length of any region i depends on the instantaneous settling rate r_i . If $m(x)$ is the proportion of animals suspended in the water column over unit length in region i , x metres downstream of the point of entry into the water column ($m(0)_i = p_i$), then

$$(5) \quad m(x)_i = p_i e^{-rx}$$

Consequently, the proportion that settles over a unit of downstream distance is

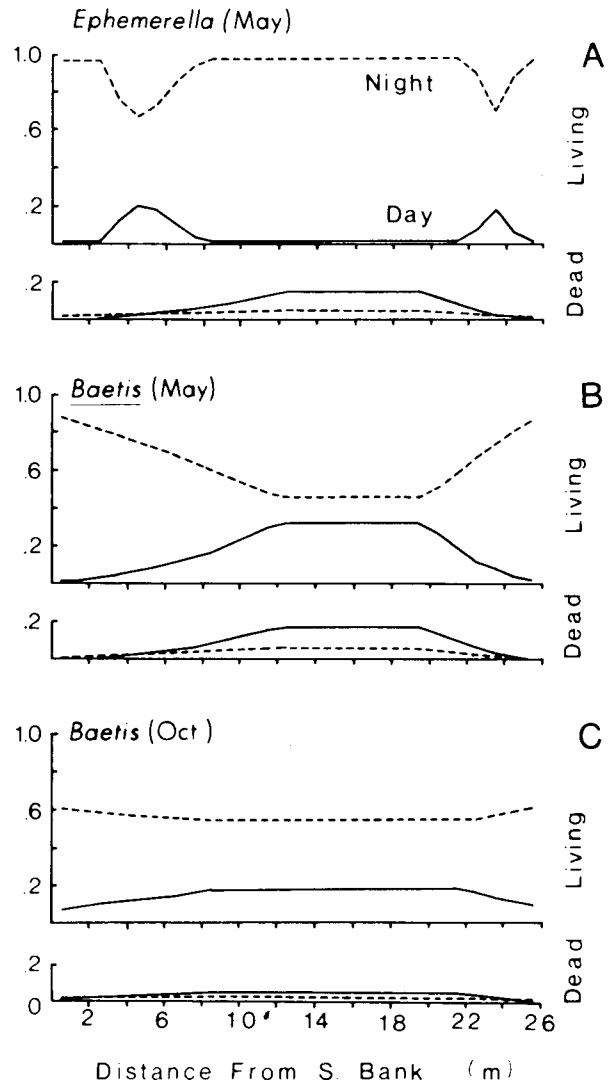


FIG. 2. Proportion of animals that depart from substrate in the model river during day (solid lines) and night (broken lines) based on laboratory studies relating departure to current velocity. (A) *Ephemera inermis* (May). Nonlinearities in nocturnal drift density pattern reflect a polynomial response to velocity. Daytime nonlinearities are an artifact of the model restriction that animals drift only once per 24 h. (B) *Baetis tricaudatus* (May); (C) *B. tricaudatus* (October). Figures above represent departure of living individuals; figures below represent departure of dead animals.

$$(6) \quad f(x)_i = m(x-1)_i - m(x-1)_i e^{-r} \\ = m(x-1)_i (1 - e^{-r})$$

Settling rate is itself a power function of current velocity (v) (Elliott 1971a; Ciborowski and Corkum 1980). However, because current velocity in the model river is a linear function of distance from shore (y) except at the river center (Fig. 1), settling rate can also be expressed as

$$(7) \quad r_i = \beta_1 y^{-\beta_2}$$

where β_1 and β_2 are regression constants specific to the animal population considered.

The lateral distribution of suspended animals about their point of introduction into the water column is normal, with mean given by the initial distance from shore (y_i) and the standard deviation as s_i (Ciborowski 1983a). The standard

TABLE 2. Regression coefficients and coefficients of determination of functions estimating instantaneous settling rate (r) and measures of lateral dispersal (s_i) of suspended animals originating from each region (i ; $i \leq 12$) of the river. Equations take the form $r = \beta_1 y_i^2$ and $s_i = \beta_3 + \beta_4 \sqrt{x} + \beta_5 y_i$, where y_i = distance of a region from the south river margin and x = downstream distance of an animal from its point of departure from the substrate. Data were obtained from field experiments conducted in the Pembina River.

Regression coefficient	Settling			Lateral dispersal			
	β_1	β_2	R^2	β_3	β_4	β_5	R^2
Living							
<i>E. inermis</i> (May)	1.837	-1.526	0.93	-0.767	0.570	0.117	0.56
<i>B. tricaudatus</i> (May)	1.231	-0.983	0.94	-0.526	0.589	0.059	0.79
<i>B. tricaudatus</i> (Oct.)	0.504	-0.642	0.98	-0.547	0.388	0.064	0.49
Dead							
<i>E. inermis</i> (May)	1.206	-1.620	0.88	-0.045	0.243	0.015	0.59
<i>B. tricaudatus</i> (May)	0.387	-0.798	0.72	0.144	0.096	0.015	0.56
<i>B. tricaudatus</i> (Oct.)	0.247	-0.805	0.62	-0.272	0.243	0.035	0.60

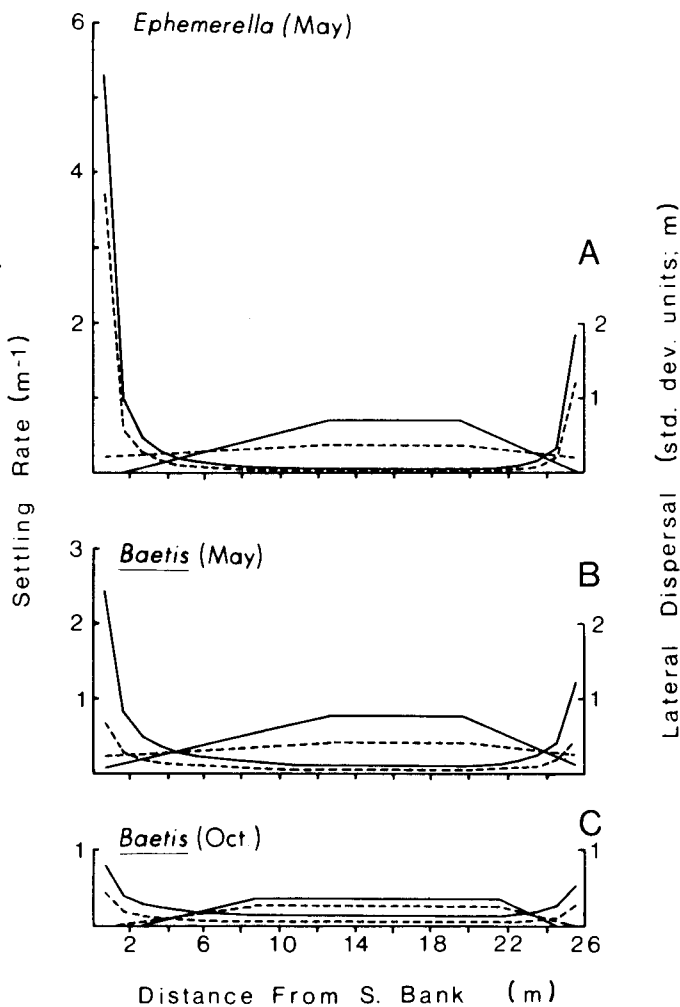


FIG. 3. Instantaneous settling rates, r (concave curves, left axes), and measures of lateral dispersal, s (convex curves, right axes), ascribed to living (solid lines) and dead (broken lines) larvae suspended in the model river. Values were interpolated from release-recapture experiments conducted in the Pembina River. (A) *Ephemerella inermis* (May); (B) *B. tricaudatus* (May); (C) *B. tricaudatus* (October).

deviation is dependent on both the square root of downstream distance travelled ($x^{0.5}$) and mean current velocity (v). The linear relationship between v and y permits s to be expressed as

$$(8) \quad s_i = \beta_3 + \beta_4 x^{0.5} + \beta_5 y_i$$

where β_3 , β_4 , and β_5 are population-specific regression constants (Ciborowski 1983a).

I reanalyzed data collected on settling rates and lateral dispersal of suspended live and dead *E. inermis* and *B. tricaudatus* larvae in the Pembina River in May and October 1979 (Ciborowski 1983a) to express r and s as functions of distance from shore (Table 2). I then estimated r and s in each season for each region of the 12 m from the south shore of the model river by substituting the distance from shore of the midpoint of each region into the regression equations. Estimates for regions 0-6 m from the north margin were determined by substituting twice the midpoint distance into regression equations. Values for the eight central regions were calculated by setting $y = 12$ (Fig. 3). Equations 7 and 8 were used to generate two matrices, K and W (Appendix 1.2). Matrix K , elements of which represent probabilities of transport from region i to region j , was used in equation 1. Matrix W , elements of which represent the sum of proportions of animals departing from region i that would be carried past a line stretching across region j , was used to predict expected numbers of animals that would be caught in drift nets placed across the model river (see below). Matrices K and W were estimated for both living and dead *E. inermis* and *B. tricaudatus* larvae.

Observed and Predicted Changes in Distribution

All settling and departure estimates were based on results of experiments conducted in May and October 1979. Benthic field samples that most closely corresponded with these periods were collected 15 and 28 May and 4 and 15 October. Consequently, predictions of relative changes in benthic density in the model river were made for 13- and 11-d intervals, respectively, using equation 2. Initial distributions (B^0) corresponded to distributions on 15 May and 4 October, respectively. Expected distributions (B^{13} and B^{11}) were then comparable with observed distributions on 28 May and 15 October, respectively.

Observed and Predicted Drift

Observed drift

Drift was monitored in the Pembina River 28-29 May and 7-8 October 1979 with twelve 1-m-wide contiguous nets (mesh pore size 0.211 mm) extending from the south margin (Ciborowski 1983a). Samples of up to 30-min duration (timed

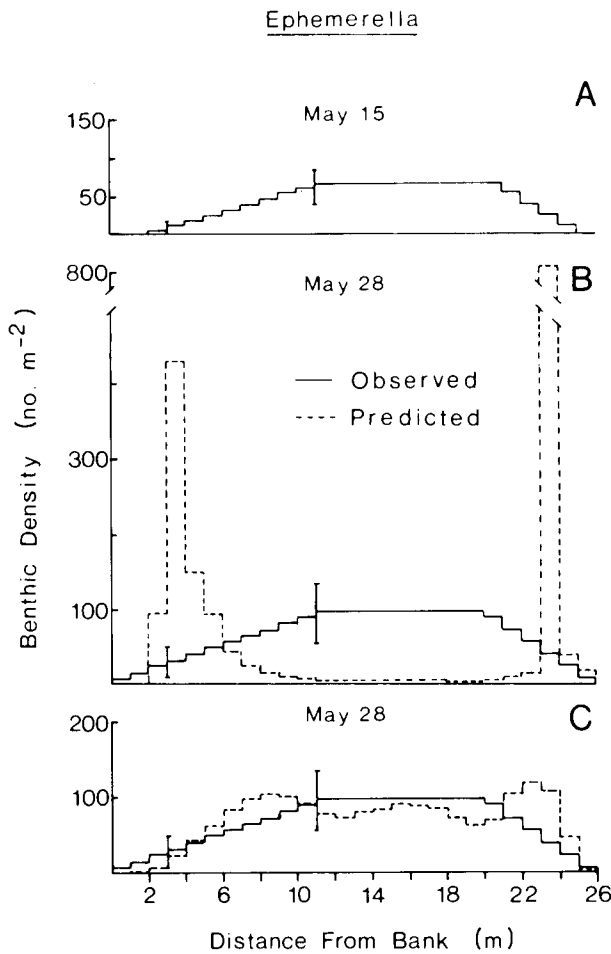


FIG. 4. Observed (solid lines) and predicted (broken lines) distribution of *E. inermis* larvae in the model river. Vertical lines represent 95% C.I. of densities of living larvae observed in the Pembina River 3 and 11 m from the south river margin. (A) 15 May; (B) 28 May (observed and predicted for living animals); (C) 28 May (observed for living animals, predicted for dead animals).

to the nearest minute) were taken at 09:00, 12:00, 18:00, and 24:00. Duration of each sample varied with date and with position of a net in the river. Nets in more central regions accumulated detritus more rapidly and so were submersed for shorter periods than were more shoreward nets. All larvae caught were measured and drift was expressed as drift density (number of large animals (see "Study Site and Animals") per cubic metre of water filtered).

Drift of the two taxa is aperiodic during daylight hours but not at night (Ciborowski and Clifford 1983). Maximum drift of *E. inermis* occurs near midnight whereas *B. tricaudatus* larvae exhibit at least two nocturnal peaks. Average daytime drift density of each population was determined by dividing the total number of large animals caught in the three daytime samples by the total volume of water filtered by each net. Midnight drift levels of *E. inermis* and *B. tricaudatus* in the Pembina River are 3.4 and 1.3 times values determined over the entire night (see Ciborowski and Clifford 1983). Accordingly, average observed nocturnal drift density was obtained by dividing numbers caught in the 24:00 sample by the volume of water filtered at that time and correcting by these conversion factors.

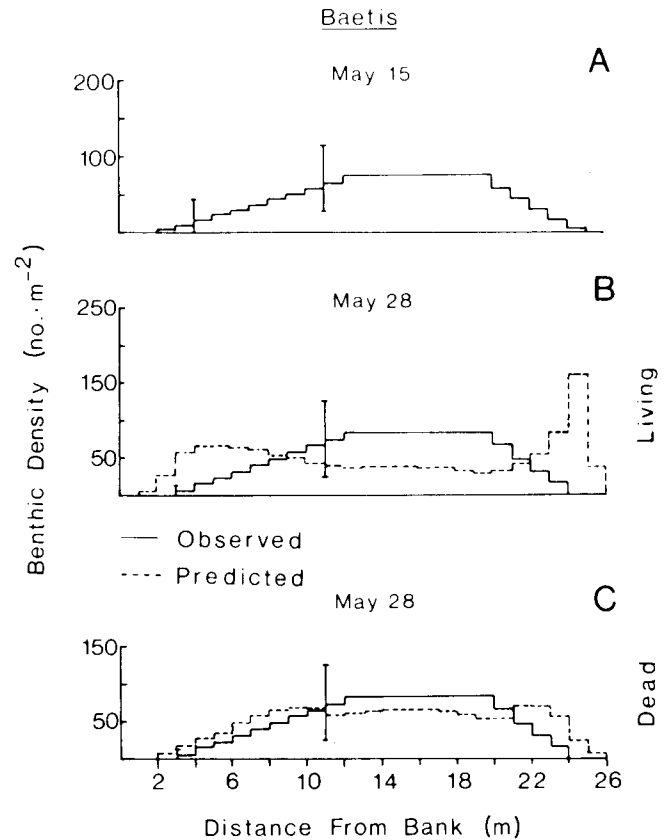


FIG. 5. Observed (solid lines) and predicted (broken lines) distribution of *B. tricaudatus* larvae in the model river. Vertical lines represent 95% C.I. of densities of living larvae observed in the Pembina River 3 and 11 m from the south river margin. (A) 15 May; (B) 28 May (observed and predicted for living animals); (C) 28 May (observed for living animals, predicted for dead animals).

Predicted drift

Expected drift densities of living and dead larvae during day and night were determined using benthic distributions observed on 28 May and 4 October (Appendix 1.3). Total numbers entering the drift were estimated by multiplying the benthic density (b_i^0) by the likelihood of departure from the substrate (p_{ij}) and weighting these values by sums of proportions of individuals contributed from various upstream regions (w_{ij}).

Downstream Distance Travelled

Daily mean downstream distance travelled by living and dead animals during the first day's drift was determined for each season (Appendix 1.4). Separate estimates were generated to describe mean downstream displacement of only those animals that drifted (\bar{x}_N) and of the entire benthic population (\bar{x}_B).

Results

Benthic Distribution

Although actual benthic distributions of animals changed little over the time intervals examined, the model predicted large-scale transport of live animals towards the shore (Fig. 4-6). In all cases, predicted benthic densities of living animals fell outside the 95% confidence intervals of observed densities

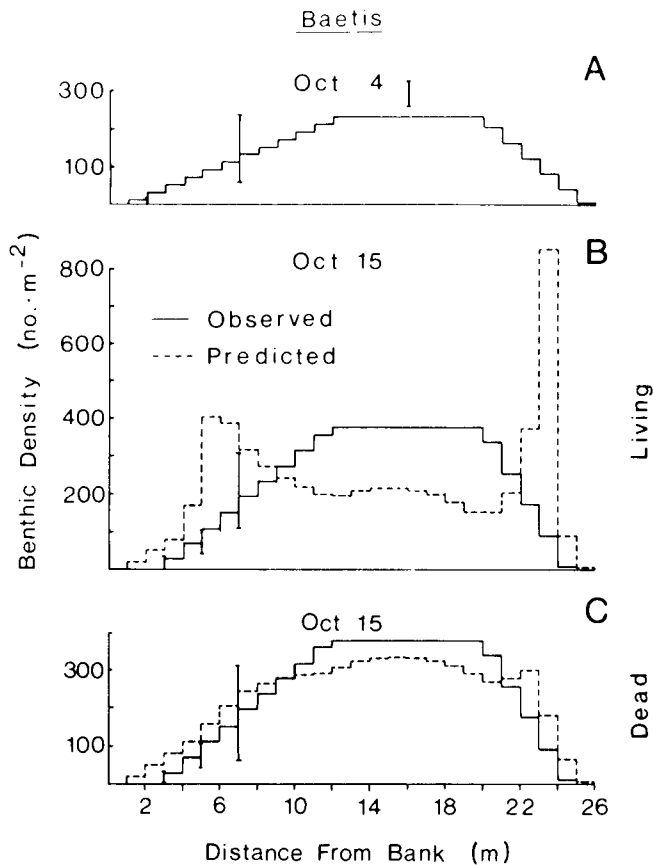


FIG. 6. Observed (solid lines) and predicted (broken lines) distribution of *B. tricaudatus* larvae in the model river. Vertical lines represent 95% C.I. of densities of living larvae observed in the Pembina River at various distances from the south river margin. (A) 4 October; (B) 15 October (observed and predicted for living animals); (C) 15 October (observed for living animals, predicted for dead animals).

at the 3-, 7-, and 11-m distances from shore. Model estimates also suggested that densities should become greater adjacent to the steeper north shore than the south shore.

Model-generated predictions suggested that living animals exhibit more pronounced lateral distributional changes than would their dead counterparts, due in large part to the higher propensity of the former to depart from the substrate (Fig. 2). Comparison of predictions among populations of living animals indicated that the smaller (October) *B. tricaudatus* larvae were less redistributed than the larger (May) animals (Fig. 5, 6). However, the greatest difference between expected and observed benthic distributions occurred for *E. inermis*. Transition matrices (C) of all populations had at least one absorbing state, corresponding to regions near shorelines. Thus, observed benthic microdistributional differences among populations after 11–13 d of drift reflect variation only in rate of accumulation in regions corresponding to these absorbing states and not necessarily differing final distributions: the model suggests that after infinite time, virtually all animals should be in regions adjacent to river margins.

Drift Density

Predicted drift densities of populations of dead animals were substantially lower than predicted drift densities of corresponding living populations except in midstream.

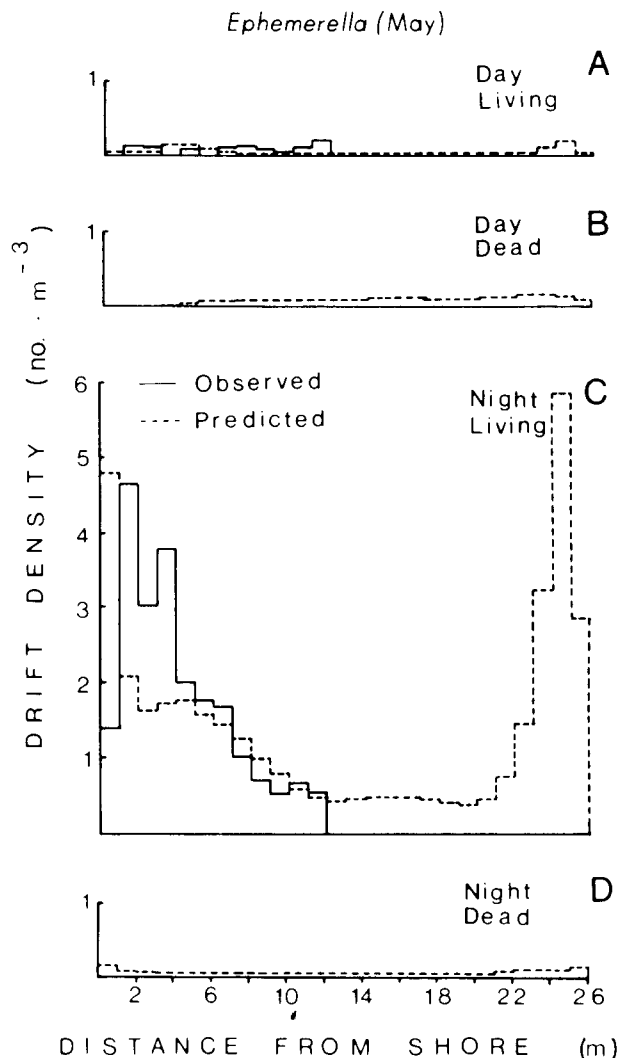


FIG. 7. Observed (solid lines) and predicted (broken lines) drift density of *E. inermis* larvae in May. Observed values are those recorded for living animals in regions within 12 m of the south margin of the Pembina River. Predicted values are those generated for the 26 regions of the model river. (A) living animals, observed and predicted, daytime; (B) dead animals, predicted, daytime; (C) living animals, observed and predicted, nighttime; (D) dead animals, predicted, nighttime. Note that scales of vertical axes differ.

Observed drift densities of *E. inermis* were much greater in May than in October (Fig. 7, 8). In May, predicted drift densities of living animals grossly corresponded to values observed in the Pembina River both during day and night.

Observed nocturnal drift densities of *B. tricaudatus* larvae were slightly greater in May than in October (Fig. 9, 10). The reverse was true for daytime values. The model markedly underestimated May drift densities of living larvae. October predictions of drift density were higher than observed during daytime and lower than observed at night. All predictions of drift densities of dead animals were below the values observed for living animals in the Pembina River.

Downstream Transport Distance

Of animals predicted to depart from the substrate in the model river, dead individuals of both species were carried at least twice as far downstream as their living counterparts

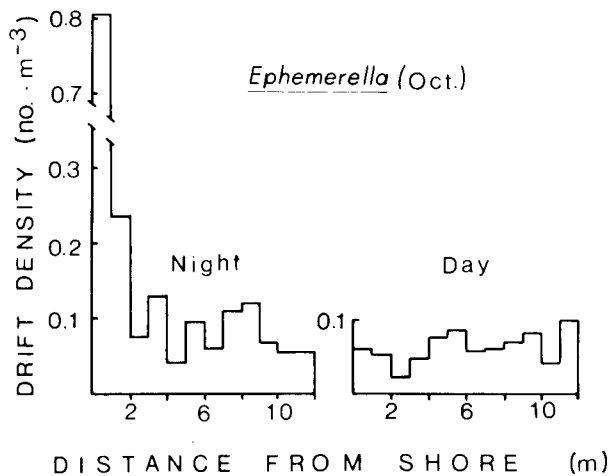


FIG. 8. Observed drift density of *E. inermis* larvae in the Pembina River in October (A) during night and (B) during day.

TABLE 3. Predicted daily mean downstream drift (\bar{x}_N) and net downstream displacement of populations (\bar{x}_B) in the model river.

Species	Condition	\bar{x}_N	\bar{x}_B
<i>E. inermis</i> (May)	Living	15.10	14.98
	Dead	37.29	5.59
<i>B. tricaudatus</i> (May)	Living	8.25	6.44
	Dead	17.70	3.24
<i>B. tricaudatus</i> (Oct.)	Living	8.99	6.43
	Dead	26.00	1.76

(Table 3). However, because living animals had greater overall departure tendencies (Fig. 2), daily downstream displacement of entire populations was greater for living than for dead animals; the *E. inermis* population was displaced the furthest.

Discussion

Model predictions suggest that drift should transport large numbers of both *E. inermis* and *B. tricaudatus* from the river center to nearshore regions. Sensitivity analyses of model behavior (Ciborowski 1982) indicate that the sign of the relationship between departure tendency and current velocity determines where animals will accumulate, provided that lateral dispersal coefficients are greater than zero at all points in the river. If departure is a positive function of velocity, densities increase near shore; if a negative function, greatest densities are maintained at river center. However, if lateral dispersal values near shore approach zero (i.e. water is too shallow or slow moving to permit later emigration by drift), populations will tend to accumulate and become restricted to marginal areas. In such cases, reduced departure tendencies or increased settling rates at stream center can only retard the rate of change of distribution. My estimates of lateral dispersal for living animals of both populations included at least one value near zero. Thus, if the model is valid, and animals relocate only by departing from the substrate, drift activity should eventually transport and restrict all *E. inermis* and *B. tricaudatus* larvae to river margins. Apparently, behavior that reduces departure within fast-water areas cannot compensate for the lateral transport associated with behavioral actions facilitating return to the substrate (Ciborowski 1983a). Indeed, the drift behavior of living animals results in a more pronounced lateral displace-

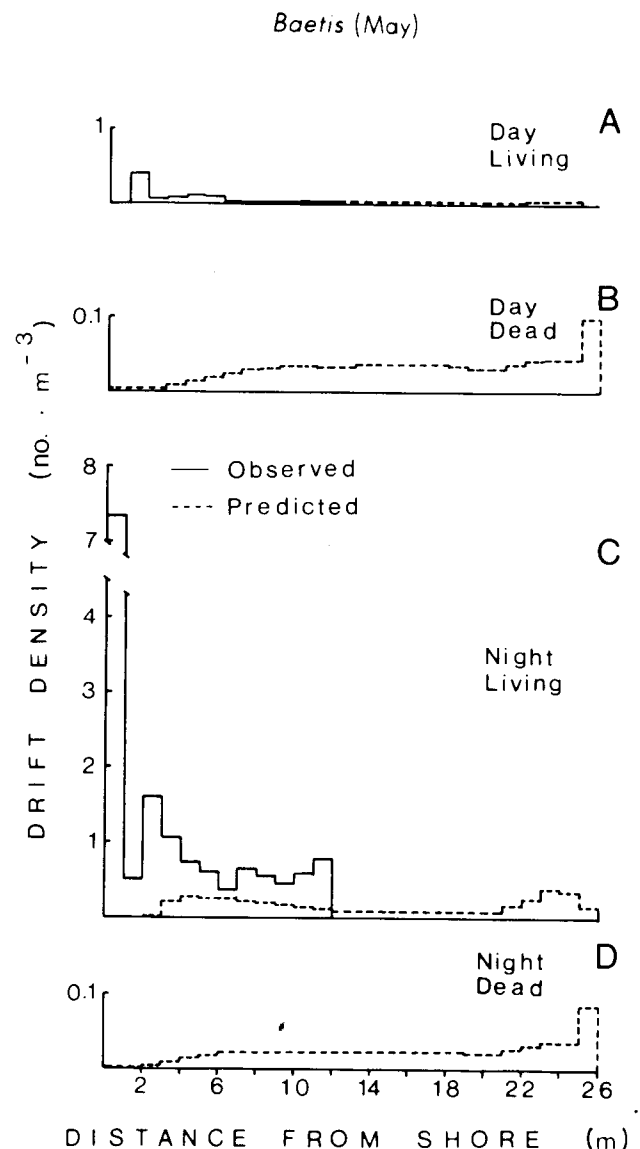


FIG. 9. Observed (solid lines) and predicted (broken lines) drift density of *B. tricaudatus* larvae in May. Observed values are those recorded for living animals in regions within 12 m of the south margin of the Pembina River. Predicted values are those generated for the 26 regions of the model river. (A) living animals, observed and predicted, daytime; (B) dead animals, predicted, daytime; (C) living animals, observed and predicted, nighttime; (D) dead animals, predicted, nighttime. Note that scales of vertical axes differ.

ment than would occur if drift was just a mechanical phenomenon: an erosion and displacement of dead organisms. Note that many other taxa transported in the water column have minimal settling capabilities (Elliott 1971a). Because return to the substrate of such animals (e.g. Chironomidae, Simuliidae, some Trichoptera) is a function of size rather than shape (Ciborowski and Corkum 1980), their expected redistributions resulting from drift could be expressed by the transition matrices for dead animals.

The model clearly fails to predict the standing benthic distribution of animals across the river. This precludes using drift alone to explain microdistribution of these rheophilic populations. Yet, the predicted magnitude and spatial patterns of drift density, which were derived from the same data, were surprisingly similar to those observed in the Pembina River.

Baetis (Oct)

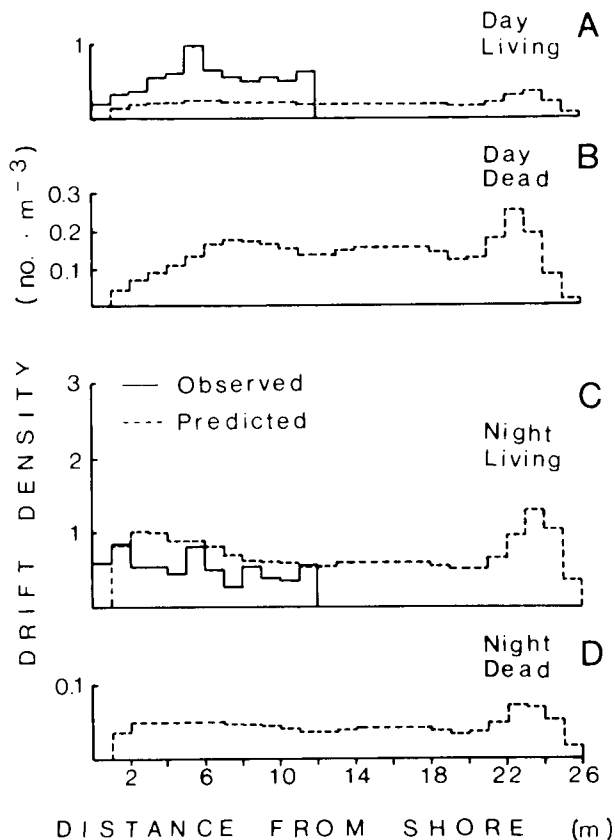


FIG. 10. Observed (solid lines) and predicted (broken lines) drift density of *B. tricaudatus* larvae in October. Observed values are those recorded for living animals in regions within 12 m of the south margin of the Pembina River. Predicted values are those generated for the 26 regions of the model river. (A) living animals, observed and predicted, daytime; (B) dead animals, predicted, daytime; (C) living animals, observed and predicted, nighttime; (D) dead animals, predicted, nighttime. Note that scales of vertical axes differ.

Where marked differences occurred, they were underestimates of observed levels. This could result from a possibly inappropriate assumption that nocturnal settling rates are equivalent to daytime settling rates (Luedtke and Brusven 1976; Walton 1978; but see Elliott 1971a), or because certain individuals engaged in multiple drift episodes. However, any significant underestimate of either numbers of animals transported or of downstream transport distance would produce a corresponding underestimate of lateral redistribution. Consequently, the changes in benthic distribution predicted by the model must describe the direction, if not the exact magnitude, of the effect of drift on microdistribution of the two mayfly populations.

If benthic patterns predicted from drift alone cannot explain benthic microdistribution of *E. inermis* and *B. tricaudatus* larvae in the Pembina River, and the estimates of drift are realistic, then these organisms must undergo some form of compensatory movement that counteracts the effects of drift. The net lateral active movement necessary to balance predicted lateral transport cannot be directly estimated because there is no unique set of probabilities of travel among regions that will exactly counteract the changes in position dictated by the

TABLE 4. Functions describing estimated mean lateral benthic travel distance (g_i) that must be traversed by animals presently in each region (i ; $i \leq 12$) to compensate for previous lateral transport by drift in the model river. Equations take the form $g_i = \gamma_0 + \gamma_1 y_i$ where y_i is distance from the south river margin.

Species	Condition	Intercept		Slope
		γ_0	γ_1	
<i>E. inermis</i> (May)	Living	6.7	-0.57	
	Dead	1.0	-0.08	
<i>B. tricaudatus</i> (May)	Living	2.9	-0.24	
	Dead	0.7	-0.05	
<i>B. tricaudatus</i> (Oct.)	Living	2.1	-0.17	
	Dead	0.3	-0.02	

transition matrices. However, I used an iterative method to generate one estimate of the approximate minimal degree of movement towards stream center necessary to balance loss of insects from the model river's eight central regions after the first day of drift (Appendix 1.5). Maximum daily net distance that would have to be travelled by dead animals starting at the south river margin (intercept of compensating function) would be between 0.3 and 1.0 m (Table 4). Maximum net distances calculated for living *B. tricaudatus* and *E. inermis* larvae were 2-3 and 6.7 m, respectively.

Movements of this magnitude are probably within the capabilities of larvae of these species. Elliott (1971b) estimated that *B. rhodani* (Pictet) and *E. ignita* (Poda) larvae travelled daily modal upstream distances of 6.25 and 4.75 m in a field-situated running water trough. Although lateral movements in his source stream were not as pronounced as those upstream, Elliott (1971b) trapped many more animals crawling towards the center than towards the margins. In contrast, Bird and Hynes (1981) reported random benthic movements of invertebrates in an Ontario river.

Seasonal data on benthic distribution of *E. inermis* larvae in the Pembina River (Ciborowski and Clifford 1983) indicate that benthic movements do carry large numbers of animals, away from margins at certain times. Newly hatched larvae predominate near margins in late summer, but by mid-October, densities have become greatest in regions remote from shore. Because drift is reduced in autumn (Fig. 8), this redistribution can occur only through benthic movement. Seasonal net offshore movements of lentic mayfly populations have been reported by several investigators (Gibbs 1979; Corcum 1984; J. E. Brittain, University of Oslo, pers. comm.).

Changes in benthic microdistribution in the Pembina River during and after flood episodes are also consistent with model implications. *Baetis tricaudatus* and *E. inermis* larvae become more concentrated near shore, and densities further from margins become reduced (Ciborowski and Clifford 1983). Because benthic invertebrate movement is inhibited by high current velocities (Elliott 1971b), increased discharge associated with flooding would both accelerate lateral transport and restrict larvae to relatively slow-water marginal areas. Both effects would result from an increased incidence of (catastrophic) drift due to scouring as well as animals' inability to regain more central regions. Only after water levels recede could animals again return to the more central regions. This microdistributional pattern has also been reported for other mayflies in an Oregon stream (Lehmkuhl and Anderson 1972).

If my hypothesis that frequent participation in drift requires a coincident ability to engage in extensive lateral benthic

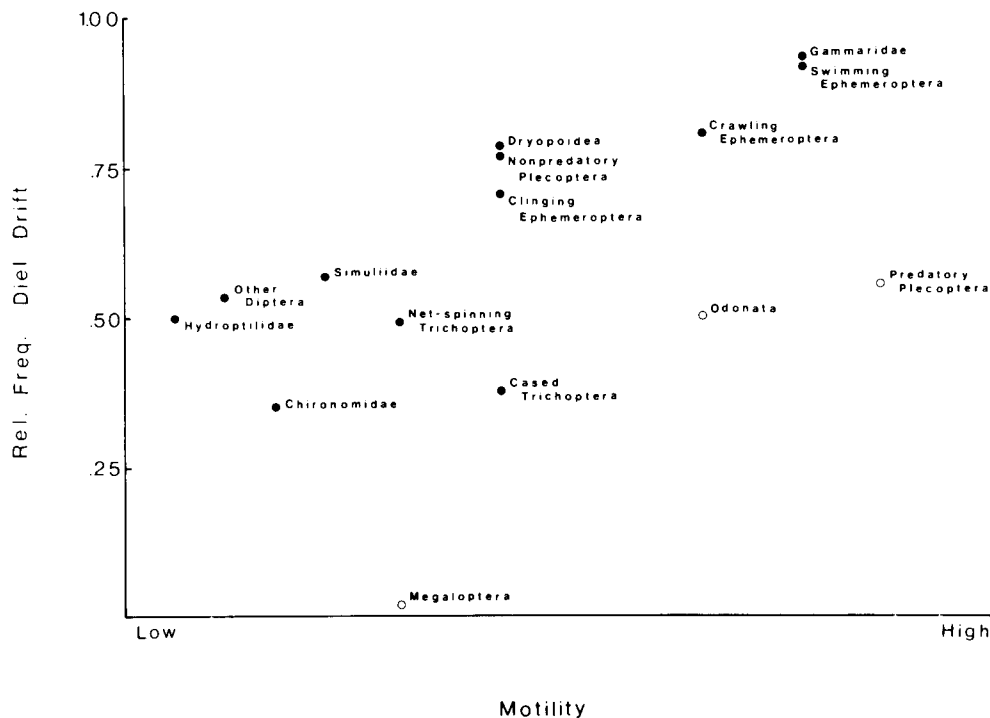


FIG. 11. Relationship between nondrift motility (subjective ranking) and relative frequency of reports of nocturnal periodicity in drift among 15 behavioral/taxonomic groups of lotic invertebrates. Solid circles represent nonpredatory organisms; open circles represent predatory organisms.

movement is valid, one would expect to find less pronounced drift among sessile organisms than among vagile animals. To evaluate this, I subjectively ranked the locomotory ability of 15 behavioral/taxonomic groups of aquatic invertebrates. I then searched the literature for reports of drift periodicity of these groups (Appendix 1.6). My measure of behavioral drift activity was the relative frequency of citations for which diel (night-active) periodicity was observed. Two trends were evident (Fig. 11). Drift periodicity of nonpredatory taxa was more prevalent than that of predatory organisms; and frequency with which diel drift periodicity occurs was positively correlated with benthic locomotory ability (Spearman's rank correlation coefficient = 0.57, $p < 0.05$ (all taxa included), and 0.78, $p < 0.01$ (nonpredatory taxa only)).

Drift has traditionally been viewed as an accidental consequence of foraging and/or competition that permanently removes individuals from their immediate surroundings (Gyselman 1980). This is suggested to result in either colonization of unexploited downstream reaches (Müller 1954, 1973, 1974) or use of the excess production (Waters 1965, 1972) by other trophic levels (drift-feeding predators). Both of these hypotheses have received qualified support. Reports of large-scale drift of early instars of aquatic taxa (Waters 1972; Müller 1974; Colbo and Moorehouse 1979) are consistent with Müller's hypothesis. Although density-dependent drift responses of older animals, which support Water's hypothesis, have been observed in certain circumstances for some taxa (Wiley 1981; Statzner et al. 1984), unequivocal results for free-ranging organisms have seldom been demonstrated. Among vagile Ephemeroptera and nonpredatory Plecoptera, most controlled studies indicate that predator activity (Corkum and Pointing 1979; Corkum and Clifford 1980; Peckarsky 1980; Walton 1980), local food depletion (Hildebrand 1974; Keller 1976; Bohle 1978; Kohler 1985), and current velocity

(Corkum et al. 1977; Ciborowski 1983b) all supersede competitive interactions as factors inducing drift.

It is significant that those taxa for which density-dependent drift has been implied to occur typically rely upon a fixed area of substrate to fulfill spatial or feeding requirements, and are coincidentally aggressive toward intruders (net-spinning caddisflies, Glass and Bobbjerg 1969; Hildrew and Townsend 1980; Mogel et al. 1985; Hydroptilidae, Hart 1983; McAuliffe 1983; Simuliidae, Harding and Colbo 1981; Wiley and Kohler 1981; Chironomidae, Wiley 1981). Furthermore, the morphology of these animals is not conducive to efficient large-scale benthic movement. Although these organisms do occasionally drift in large numbers, they do not exhibit the marked periodicity characteristic of other taxa. In contrast, taxa that do not show density-dependent drift are mobile grazing or leaf shredding animals. Interactions involving these organisms elicit short-scale benthic movement, but not drift (Corkum and Clifford 1980; Wiley and Kohler 1981; Statzner and Mogel 1985). Drift of the study taxa in the Pembina River is so pronounced that loss of these animals would decimate populations within the central riverbed within several days. Consequently, I suggest that drift of such larvae results in only local displacement, and is thus an adjunct to normal benthic activity. The population turnover rates implied by recent colonization studies suggest that this is not a unique phenomenon (Sheldon 1984).

Yet drift cannot serve as a local relocation mechanism independently of active benthic movement. Drifting animals are probably incapable of continuously monitoring the quality of substrate over which they pass, and tend to be carried to less suitable (slow-water) regions. The model indicates that these areas can only be left by active means; this would nullify any possible energetic savings of drift over benthic movement. Presumably, a mobile herbivore should drift only if the alter-

native is mortality (predator attack) or if prior active movement fails to carry it into a suitable microhabitat (adequate food, substrate, or current). Largely unidirectional movement is the most efficient means of locating randomly distributed resources (Pyke 1978), and this should be even more the case where resources are longitudinally stratified (i.e. more abundant in some regions (sensu the model) than others). Kohler (1984, 1985) has recently related directionality and degree of movement of *Baetis* larvae to periphyton levels. Periphyton abundance is frequently positively associated with specific current velocity levels in rivers (Horner and Welch 1981). Rheophilic animals, whether drift prone or not, would benefit from active movement that directs them into faster water. Subsequent lateral transport by drift, however, may act to transport unsuccessful animals to a point (near stream margin) from which further lateral benthic movement would carry them centerward across the entire gradient of available microhabitats. In such instances, drift would have provided an energetically efficient means of sampling at least one new microhabitat (the point of settling) and without necessarily having caused large net downstream or lateral displacement relative to a premovement position. This might be particularly important where the relative position of resources changes through time in concert with daily or seasonal variations in flow pattern or discharge.

Because drift represents a generalized response to many factors, it is not surprising that no single hypothesis can adequately describe its ecological significance among all aquatic taxa. Although the hypotheses of Müller and Waters do pertain to certain organisms at some times, they are not universally applicable. Implications of the drift model regarding dynamics of transport provide some predictive value in anticipating the role of drift among different aquatic groups. High intensity, possibly endogenous seasonal drift of early instars of several aquatic taxa (Baetidae, some Trichoptera, Simuliidae) probably entails permanent downstream transport. Although this may produce significant mortality, it permits successful colonization of unexploited downstream reaches (distributional drift model of Müller (1973)). Among larger rheophilic animals that have poor locomotory ability and depend on being in suitable feeding locations, drift may reflect the outcome of aggressive interactions. Drifting animals of these populations may indeed be lost from the system, since they lack the locomotory capacity to regain more favorable areas. These organisms behave in accordance with Waters' limited production model. I propose that among larger free-ranging taxa, drift is a complement to benthic search behavior, serving to transport and relocate animals from unfavorable regions to either more suitable areas or to a "starting point" from which further search may be initiated.

Note that because the model was developed for a large, spatially stratified system, this latter interpretation of the role of drift may not apply as well to small streams in which microtopography (snags, boulders) may produce a mosaic of microhabitats. Although the dynamics of departure and transport should still pertain as presented here, downstream variability in settling rates and lateral transport could induce quite different microdistributional patterns of larvae. Furthermore, the dimensions of small streams may be such that free-ranging individuals could sample the entire range of microhabitats available solely through relatively short-scale benthic movement. In such an instance, drift may assume subsidiary importance. Incidence of drift (drift density) in smaller systems is

typically substantially less than that observed in the Pembina River (see Armitage 1977). This raises the possibility that the behavioral repertoire governing locomotion of vagile aquatic invertebrates might be regulated among lotic systems to coincide with the spatial arrangement of suitable microhabitats rather than simply to the extensiveness of those microhabitats.

In summary, drift of *E. inermis* and *B. tricaudatus* larvae in the Pembina River is of great enough magnitude to produce profound changes in benthic microdistribution of populations over short time intervals. Short-term stability in distribution of these populations appears to be maintained despite the propensity of animals to drift. Because drift provides access largely to slower portions of the river, active movement is a necessary corequisite to permit exploitation of all regions of the lotic system. An individual that can relocate by drifting and continue benthic search may have an increased likelihood of encountering stratified, resource-rich areas. In contrast, benthic organisms with poor locomotory ability may be relegated to unfavorable marginal areas. Internally or externally mediated changes in the tendency of individuals to drift or to engage in active lateral movements should result in an alteration of regions of population concentration.

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Appendix

1.1 List of Symbols

Lowercase letters represent scalar quantities. When subscripted, they represent elements of vectors or matrices. Uppercase letters represent vectors. Boldfaced uppercase letters represent matrices.

Symbol	Description
B^i	Vector of benthic density of animals in regions of model river on day t
C^i	i th power of transition matrix describing probability of change in benthic position of an animal among regions of model river
D	Number of hours of darkness
$F(x)$	Vector of proportion of suspended animals that settle over a unit of downstream distance, x metres from a point of entry into the water column in regions of the model river
I, I	Identity matrix, vector
K	Matrix representing probability that an animal suspended in the water column a given region settles in a given region of the model river
L	Number of hours of daylight

$M(x)$	Vector of proportion of animals suspended in the water column over unit length of regions, x metres downstream of a point of entry into the water column
$N(x)$	Vector of number of animals suspended in the water column over unit length of regions, x metres downstream of a point of entry into the water column
$N_{\max}(t)$	Vector of total number of suspended animals that pass a line transecting regions during time interval t
$P(t)$	Diagonal matrix representing proportion of animals that depart from substrate of regions during time interval t
$Q(t)$	Diagonal matrix representing proportion of animals that remain on substrate of regions during time interval t
R	Vector of instantaneous settling rate of suspended animals in regions of model river
S	Vector of measure of lateral diffusion of suspended animals (standard deviation units) in regions of model river
t	Time
V	Vector of mean current velocity in regions in of model river
W	Matrix representing sums of proportions of animals suspended in the water column following departure from a number of points upstream in regions
x	Downstream distance travelled by an animal suspended in the water column
\bar{X}	Vector of mean daily downstream distance travelled by all animals that depart from the substrate in regions in the model river
\bar{x}_N	Mean daily downstream distance travelled by all animals that depart from substrate in model river
\bar{x}_B	Mean daily downstream displacement by drift of entire population in the model river
Y	Vector of distance of midpoint of model river regions from shore
Z	Vector of mean depth of regions in model river
α	Regression coefficient
β	Regression coefficient

1.2 Calculation of Matrices K and W

Probabilities of transport of animals from one region to all others were estimated using equations 7 and 8 (see also Ciborowski 1982). Proportions of animals settling at increasing 1-m steps downstream of a given entry point, y_i , into the water column were determined from equation 6. The proportion not settling ($m(x)_i$) at each step was partitioned according to a normal probability distribution generated around a mean (y_i) and a standard deviation (s_i). Proportions returning to the substrate at each step were summed until the total fraction that had settled exceeded 0.999. The remainder was added to the region from which animals originated. Summing the proportions of animals suspended in each region at the end of each step ($m(x)_i$) provided an estimate, w_{ij} , of the contribution of animals originating in each region i to the drift at other regions, j . Documentation for and copies of computer programs (written in APL) used to generate these data and other model results are available from the author.

1.3 Estimation of Predicted Drift

The expected total number of animals, n_i , departing from

1 m² of substrate in region i of the model river during day (L) and at night (D) are

$$(9) \quad n_i(L) = b_i p(L)_{ii}$$

$$(10) \quad n_i(D) = b_i p(D)_{ii}$$

where b_i is the benthic density and p_{ii} is the proportion that depart. However, because the concentration of animals in the water column above each square metre of each region also depends on water depth (z_i), the concentration in each region is

$$(11) \quad n'_i(L) = n_i(L)/z_i$$

$$(12) \quad n'_i(D) = n_i(D)/z_i.$$

Since matrix W represents the sum of proportions of animals departing from region i that would be carried across a line in region j , the total expected number of animals caught in drift nets placed across the regions during the day ($N_{\max}(L)$) and at night ($N_{\max}(D)$) would be

$$(13) \quad N_{\max}(L) = N(L)W$$

$$(14) \quad N_{\max}(D) = N(D)W.$$

Predicted drift density in each region was estimated by dividing $N_{\max}(L)$ and $N_{\max}(D)$ by the volumes of water expected to pass through drift nets (determined from Fig. 1) during day and night, respectively.

1.4 Downstream Distance Travelled

The sum of proportions of animals that drift past a line across a river is the product of the proportion departing from substrates upstream and mean distance travelled (Elliott 1971a). Thus,

$$(15) \quad w = m(0)x.$$

When $m(0) = 1.0$, as is the initial condition in estimating values for matrices K and W , this reduces to

$$(16) \quad x = w.$$

Since W is the matrix of sums of proportions of suspended animals transported from any region i to each region j , the mean downstream distance travelled by animals departing from the substrate in any region (\bar{x}_i) is the i th row total of W , i.e.

$$(17) \quad \bar{x}_i = w_{i1} + w_{i2} + \dots + w_{i26}$$

$$\bar{X} = (x_1, x_2 \dots x_{26}).$$

The mean distance travelled by all animals that drift during 1 d (\bar{x}_N) is

$$(18) \quad \bar{x}_N = N(24) \bar{X} / N(24)I$$

where $N(24)$ is the vector of the number of animals that depart from the substrate over 24 h and I is the identity vector (a vector with all elements consisting of ones). Mean daily downstream displacement of the entire population resulting from drift is

$$(19) \quad \bar{x}_B = N(24)\bar{X}/B'I$$

where B' is the vector of benthic density of animals on day t . Note that because $n(24)_i = b_i p(24)_{ii}$, both \bar{x}_N and \bar{x}_B depend on benthic distribution and consequently vary as this changes.

1.5. Interpolated Benthic Distances Moved

To estimate lateral benthic movement necessary to balance drift, I assumed that activity (thus, net distance that would be travelled) was a negative linear function of mean current velocity (hence initial distance from shore) (see Edington 1965; Elliott 1968) and that animals either remained in their present region or moved towards stream center. Net movement was arbitrarily presumed to be nondirectional (zero) in central regions and $0.1 \text{ m}\cdot\text{d}^{-1}$ in regions immediately adjacent to center.

Probability of movement from any particular region to a more central region was assigned according to a Poisson series. The first iterative step involved selecting an arbitrary intercept value for the relationship between initial distance from shore (south margin) and mean net lateral distance moved. The slope necessary to produce mean lateral travel of $0.1 \text{ m}\cdot\text{d}^{-1}$ adjacent to the center was then determined and the mean distance moved by animals within all other regions interpolated from this linear function. Probability of lateral movement by any animal from a given region to each other region was calculated according to the Poisson distribution corresponding to the interpolated mean distance travelled from that region. Probabilities were then assembled as a transition matrix, C' . The inner product of this matrix and the vector describing benthic distribution after 1 d of drift (B^1) was then calculated:

$$(20) \quad B^{0'} = B^1 C'$$

The elements of $B^{0'}$ corresponding to densities in the model river's eight central regions were then summed. The function describing active movement was judged adequate to compensate for lateral transport by drift if the sum above equalled or exceeded the corresponding sum of elements of B^0 . If the

function was inadequate, a new (greater) intercept was selected, a corresponding slope determined, and a new transition matrix derived and evaluated.

1.6. Literature Survey of Diel Periodicity

Citations were taken from field studies that addressed day-night drift variations of at least one taxon (63 papers). A citation consisted of a verbal, tabular, or figured description of one taxon appearing in the drift at one stream site on one date in amounts great enough for periodicity to be potentially discerned. Where drift was repeatedly sampled, multiple citations were admitted for each sample at least 1 mo removed from other collections, to a maximum of 12. If samples were taken throughout a year and only a general statement of pattern was made, I assigned up to four citations (one per season). Where patterns were described for specific developmental stages, periodicity was assessed on the basis of drift of all stages pooled over one date.

Relative frequency was calculated by summing all instances of night-active periodicity for a group and dividing by all citations for that group. Total number of citations and the number of papers on which they were based is as follows: Gammaridae (Amphipoda) 14 (10 papers); Odonata 2 (2); swimming Ephemeroptera 101 (36); crawling Ephemeroptera 77 (24); clinging Ephemeroptera 54 (21); predaceous Plecoptera (Systellognatha) 38 (12); herbivorous Plecoptera (Holognatha) 56 (15); Megaloptera 2 (2); Dryopoidea (Coleoptera) 37 (10); net-spinning Trichoptera 61 (15); Hydroptilidae (Trichoptera) 19 (4); case-building Trichoptera 56 (15); Chironomidae (Diptera) 114 (24); Simuliidae 65 (19); other Diptera 45 (14). A bibliography of papers from which citations were taken is available from the author.