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THE RELATIONSHIP BETWEEN DRIFT AND MICRODISTRIBUTION OF LARVAL EPHEMEROPTERA

by

© JAN J.H. CIBOROWSKI

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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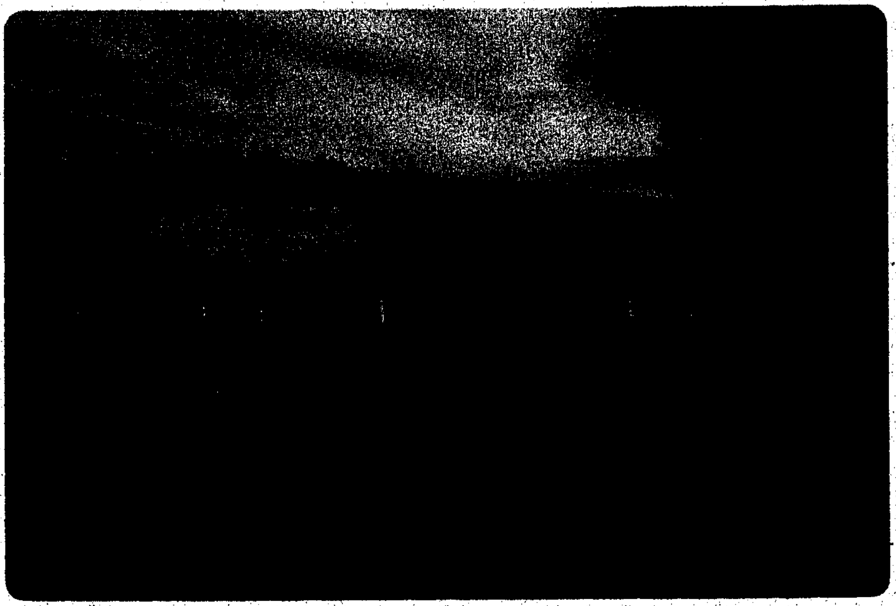

Pembina River sample site with drift nets, and stakes marking insect release points.

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The relationship between drift and microdistribution of larval Ephemeroptera submitted by Jan J.H. Ciborowski in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Abstract

This study evaluates the role of drift in maintaining relative microdistribution of larval populations of two mayfly species in the Pembina River, Alberta, Canada.

Ephemerella inermis Eaton is univoltine. Eggs hatch in August and larvae emerge the following July. *Baetis tricaudatus* Dodds produces three cohorts per year. Emergence periods occur in early June, July and early September. Only one cohort overwinters as larvae.

Early instar *E. inermis* larvae are most abundant near shore but move to deeper water in late autumn. *Baetis tricaudatus* larvae are seldom numerous in nearshore areas. Microdistribution of both species is largely determined by the discharge pattern of the river: flooding results in temporary relocation to nearshore regions.

Drift of both populations is most marked in late spring and summer. Nocturnal drift densities are much greater in slow than in fast water regions.

Laboratory studies indicate that departure from the substrate is density-independent and independent of amount of detritus in the substrate. Nocturnal departure was more pronounced under conditions of low mean current velocity than in faster water. The reverse was true during daylight. Rates of loss of dead animals from the substrate were much lower than departure rates of live organisms.

Settling rates of both live and dead animals were

inversely related to mean current velocity. Live animals had greater settling capacity than did dead organisms. Lateral dispersal of suspended larvae depended on both the downstream distance travelled and on the distance from shore that larvae entered the water column. Live animals became more markedly dispersed laterally than did dead animals.

A model was developed to predict changes in benthic distribution of the two populations that result from drift. Lateral transport of drifting animals was assumed to be a Markov process. Probability estimates of departure, downstream movement and lateral dispersal were combined to produce transition matrices. Temporal changes in microdistribution across the river were then estimated as a Markov chain. Although predicted estimates of drift broadly corresponded with observed levels, predicted and observed benthic distributions were markedly different. I conclude that drift should result in rapid transport of most individuals in each population to stream margins.

I suggest that drift is an important determinant of microdistribution, but observed distributions of larvae are maintained only by the ability of animals to crawl towards the river centre. Active drift of B. tricaudatus and E. inermis larvae may be an adjunct to normal crawling search behaviour. Drift exhibited by relatively sedentary taxa must serve other functions.

Acknowledgements

I thank Dr. Hugh F. Clifford for his support and critical comments on this study, and Dr. Richard C. Routledge for statistical and mathematical advice.

Mrs. G. Hutchinson and my fellow graduate students, Rob Baker, Vytenis Gotceitas, John Richardson, Dan Soluk and Eric Whiting provided technical help, criticisms and good cheer. Mr. Grant Moldenhauer gave invaluable laboratory and field assistance. Mr. Hal Hamilton kindly made available Pembina River flow data.

I also thank Dr. and Mrs. Tom Eustace for their generous hospitality during the field sampling season.

I am most indebted to my wife, Dr. Lynda D. Corkum, whose advice, technical assistance and unfailing encouragement made this study possible.

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List of Symbols

Lower case letters represent scalar quantities. When subscripted they represent elements of vectors or matrices. Upper case letters represent vectors. Underlined upper case letters represent matrices.

Symbol	Description
B^t	Vector of benthic density of animals in transects of model river on day t.
BI	Behavioural index. That portion of settling capacity of individuals due to behaviour.
$\underline{C}^t$	t'th power of transition matrix describing probability of change in benthic position of an animal among transects 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 meters from a point of entry into the water column in a given transect of the model river.
$\underline{I}$, I	Identity matrix, vector.
$\underline{K}$	Matrix representing probability that an animal suspended in the water column in a given transect settles in a given transect of the model river.
L	Numbers of hours of daylight.
M(x)	Vector of proportion of animals suspended in the water column over a unit length of a given transect, x meters downstream of a point of entry into the water column.
N(x)	Vector of number of animals suspended in the water column over a unit length of a given transect, x meters downstream of a point of entry into the water column.
$N_{max}(t)$	Vector of total number of suspended animals that pass a point on a given transect during time interval t.

$\underline{P}(t)$	Diagonal matrix representing proportion of animals that depart from substrate of a given transect during time interval t.
$\underline{Q}(t)$	Diagonal martix representing proportion of animals that remain on substrate of a given transect during time interval t.
R	Vector of instantaneous settling rate of suspended animals in a given transect of model river.
S	Vector of measure of lateral diffusion of suspended animals in a given transect of model river.
SC	Settling capacity of suspended animals. A measure of the ability of suspended animals to return to the substrate over a range of current velocities.
t	Time.
V	Vector of mean current velocity in a given transect of model river.
$\underline{W}$	Matrix representing sums of proportions of animals suspended in water column following departure from a number of points in a given transect.
X	Downstream distance travelled by an animal suspended in the water column in a given transect.
$\underline{\bar{X}}$	Vector of mean daily downstream distance travelled by all animals that depart from the substrate in the model river.
$x_{.50}$	Downstream distance by which one-half of animals suspended in a transect have returned to the substrate.
$\bar{\bar{x}}_N$	Mean daily downstream distance travelled by all animals that depart from substrate in model river.
$\bar{\bar{x}}_B$	Mean daily downstream displacement by drift of a population in the model river.
Y	Vector of distance of midpoint of model river transect from shore.
Z	Vector of mean depth of transects in model river.
β	Regression coefficient.

INTRODUCTION

Intensive research on aspects of invertebrate drift in recent years has done much to elucidate factors influencing downstream transport of benthic animals. Representatives of all species can occasionally be found suspended in the water column. This may be the incidental result of catastrophic changes in the river (catastrophic drift). Alternatively, drift may appear in recurring seasonal or diel cycles, independently of visible modifications in streamflow characteristics. Occurrence of the latter is referred to as behavioural drift and is most prevalent in herbivorous, hemimetabolous aquatic insects, notably Ephemeroptera. The prevailing view of drift attributes these periodicities to an interaction between cyclic nocturnal or seasonal increases in the activity of individuals and the eroding influence of the water current. This causes an accidental dislodgement of animals.

Interpretations of the adaptive significance of the phenomenon differ. Researchers who have studied streams in which the incidence of drift is low relative to benthic densities ascribe little ecological importance to drift. However, in many rivers the number of animals drifting over a portion of substrate during 24 hours frequently exceeds the benthic density. Müller (1954) viewed drift as a means of reducing competition for food or space when high densities of animals occur on the stream bottom.

Individuals that enter the drift then become available to colonize unexploited areas downstream. Drift may thus serve the dual role of regulating and dispersing populations. Müller (1954) felt that some compensating mechanism was required to account for an attrition of populations in upstream areas and proposed a "colonization cycle", wherein emerging adults flew upstream to oviposit and repopulated these reaches.

Waters (1961) observed that drift in highly productive rivers was much greater than in sparsely populated ones, but upstream areas seldom became depopulated by drift. Consequently, he felt upstream flight was not a requisite. Waters postulated the alternative hypothesis that drift in response to competition serves primarily to remove those individuals which the habitat cannot support. Drifting animals are thus indicative of excess production.

Another view holds that drift represents the net response of individuals to the suitability of their respective microhabitats. Early field studies revealed an exponential relationship between total invertebrate drift and stream discharge or the strength of the current (Bailey 1966, Elliott 1967b). However, other workers have found that reduced current can also produce increased drift (Edington 1965, Elliott 1968a, Minshall and Winger 1968, Corkum et al. 1977, Gore 1977). Such evidence suggests that departure from the substrate may be active at times rather than accidental, but more significantly it implies that drift is a controlled response to an environmental gradient. The range of current velocity within which minimal drift occurs may be representative of the zone of preference of a particular population; outside this zone animals tend purposefully to leave their microhabitat.

Similar observations have been made on the influence of other abiotic factors affecting drift, e.g. substrate texture, water temperature and oxygen concentration. The influence of predators (Corkum and Pointing 1979, Corkum and Clifford 1980, Peckarsky 1980b, Walton 1980b) and food availability (Hildebrand 1974, Keller 1976, Bohle 1978, Walton 1978) have also been implicated in modifying the magnitude of drift. Thus, under certain circumstances, benthic organisms may drift in response to many of the biotic and abiotic variables typically used to define aquatic microhabitats.

Figure 1 summarizes the factors that have been shown to influence drift. Pathways are numbered and corresponding references to them are given in Table 1. The tabular summary lists only those studies in which a 'positive' relationship was found or inferred. General descriptive accounts of field studies have not been included.

The relative importance of each of the parameters illustrated in Fig. 1 has yet to be determined for any species, but it is unlikely that all are prominent in governing the drift of a particular population. The complexity of the figure underlines the central problem inherent in a

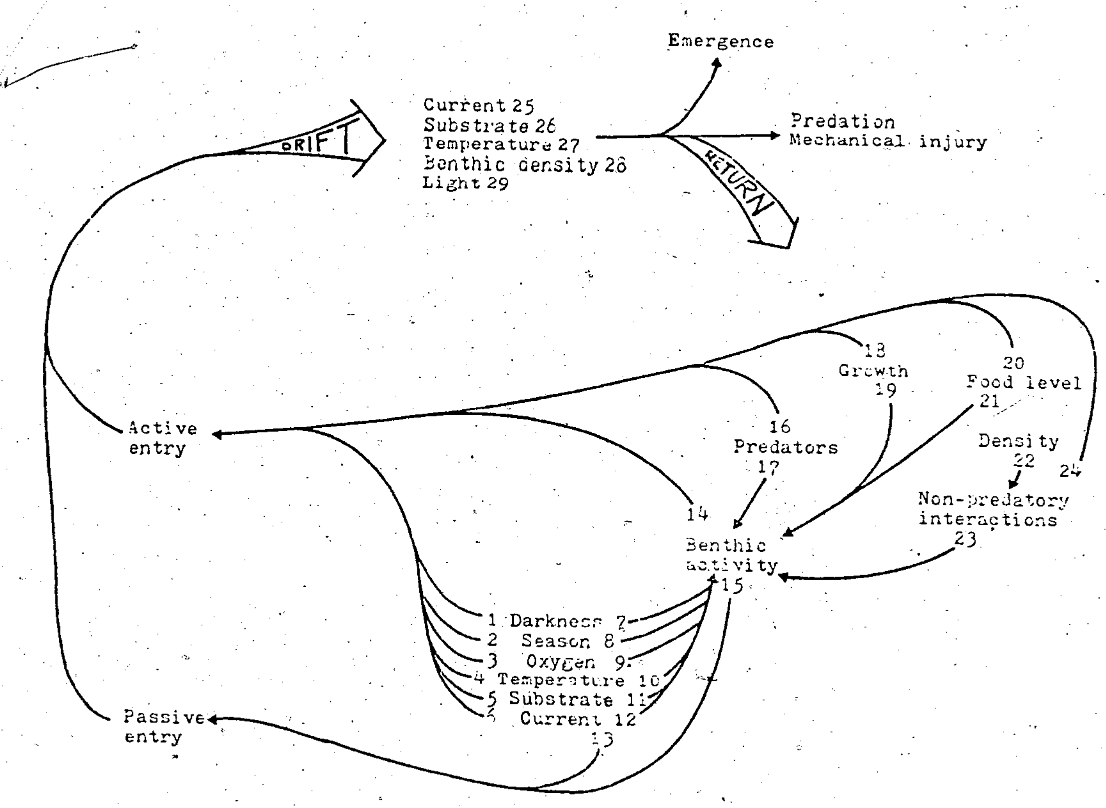


Figure 1. Mechanisms by which animals enter the water column and return to the substrate. Arrows lead from stimuli that induce particular responses. Numbers correspond to references in Table 1 which cite the indicated pathways.

Table 1. Summary of studies on factors that influence departure from substrate or downstream transport of aquatic invertebrates. Numbers heading each column refer to pathways shown in Fig. 1.

1	2	3	4	5
Ciborowski 1979 Corkum et al. 1977 Klyucharitva 1963 Levanidova & Levanidov 1965 Walton 1978 Walton 1980b	Ciborowski 1979 Corkum 1978b Hall et al. 1975 Kroger 1974	Keller 1976 Muller 1974	Muller 1966	Corkum et al. 1977 Corkum and Clifford 1980 Gammon 1970 Klyucharitva 1963 Müller 1974 Walton et al. 1977 Walton 1978 Zimmer 1976

6	7	8	9	10
Colbo and Moorhouse 1979 Corkum et al. 1977 Dickson 1977 Edington 1965 Elliott 1968a,b Gore 1977 Minshall and Winger 1968 Thomas 1969 Waters 1965	Bishop 1969 Bishop and Hynes 1969a Chaston 1969 Chaston 1972 Cloud and Stewart 1974a,b Elliott 1967 a,b Holt and Waters 1967 McLay 1968 Müller 1974 Steine 1972	Bishop and Hynes 1969a Clifford 1972b Corkum 1978b Haydon and Clifford 1974 Larimore 1974 Pearson and Kramer 1972	Kovalak 1976 Kovalak 1979 Hazell 1974 Wiley and Kohler 1980	Bishop and Hynes 1969a Durrett and Pearson 1975 Kovalak 1976 Kovalak 1979 McLay 1970 Madsen 1968 Otto 1976 Pearson and Franklin 1968 Reisen 1976 Wojtalik and Waters 1970

11	12	13	14	15
Ciborowski et al. 1977 Hynes 1973 Wallace et al. 1975	Butz 1973 Ciborowski et al. 1977 Elliott 1967a Haydon and Clifford 1974 Hughes 1970 Kovalak 1976 Kovalak 1979 Pearson and Franklin 1968 Ulfstrand 1968	Anderson and Lehmkuhl 1968 Bailey 1966 Bishop and Hynes 1969 Ciborowski et al. 1977 Clifford 1972a Elliott 1967 a,b Elliott 1969 Haydon and Clifford 1974 Klyucheriva 1963 Kovalak 1979 Logan 1963 Mackay and Kalff 1973 Müller 1954 Pearson and Franklin 1968 Pearson and Kramer 1972 Reisen 1976 Reisen and Prins 1972 Radford and Hartland-Rowe 1971	Corkum 1978a Gallepp 1974 Müller 1963b Müller 1974 Radford and Hartland-Rowe 1971 Wallace et al. 1975 Ulfstrand 1968 Walton 1978 Walton et al. 1977	Bishop 1969 Bishop and Hynes 1969a Butz 1973 Chaston 1968 Chaston 1969 Ciborowski et al. 1977 Cloud and Stewart 1974a,b Dimond 1967 Elliott 1967a,b Hildebrand 1974 Holt and Waters 1967 Keller 1976 McLay 1968 Otto 1976 Pearson and Franklin 1968 Reisen 1976 Reisen and Prins 1972 Steine 1972 Waters 1972 Waters and Hockenstrom 1980 Wiley and Kohler 1980

16	17	18	19	20
Corkum and Clifford 1980 Corkum and Pointing 1979 Peckarsky 1980b	Peckarsky 1980b	Ciborowski 1979 Hall et al. 1980 Klyucharitva 1963 Walton 1980a	Cloud and Stewart 1974b Elliott 1967b Keller 1976 Müller 1974 Reisen and Prins 1972 Waters 1972	Bohle 1978 Keller 1976 Müller 1974 Walton 1978

21	22	23	24	25
Bishop and Hynes 1969a Elliott 1967a,b Gallepp 1974 Hildebrand 1974 Müller 1954 Otto 1976 Wallace et al. 1975	Dimond 1968 McLay 1970 McKone 1975 Pearson and Kramer 1972 Radford and Hartland-Rowe 1971 Steine 1972 Ulfstrand 1968 Waters and Hockenstrom 1980 Walton et al. 1977	McKone 1975 Radford and Hartland-Rowe 1971 Steine 1972 Walton et al. 1977	McLay 1968 Otto 1976 Ulfstrand 1968	Ciborowski and Corkum 1980 Elliott 1971b Keller 1976 Luedke and Brusven 1976 McLay 1970 McKone 1975

26	27	28	29
Elliott 1971b Madsen 1968 Walton 1978	Madsen 1968 McLay 1970	McKone 1975	Luedke and Brusven 1976 Walton 1978

complete understanding of the initiation of drift.

In general, the importance of active entry into the water column has probably been understated in much of the drift literature (Walton 1980a), but whether entry occurs by either active or by passive means, mediated by activity changes, is of limited importance to the outcome of the act. Ulfstrand (1968) stated that, regardless of the means by which animals become suspended in the water column, "the start of drifting movement is by no means accidental." Townsend and Hildrew (1976) observed that the benefits of drift to an individual will accrue regardless of whether entry into the water column is accidental or intentional.

Once in the water column, organisms are carried downstream. A constant proportion return to the bottom for every unit of distance or time travelled (McLay 1970, Elliott 1971a, McKone 1975). Reestablishment may be facilitated by swimming motions made by the animals (McKone 1975). Alternatively, downstream transport of certain animals may be passive (Ulfstrand 1968) and terminated by thigmotactic responses of the individuals upon chance contact with the substrate. A behavioural component of settling results in increased rates of return to the bottom by certain species (Elliott 1971a, Walton 1978, Ciborowski and Corkum 1980). Animals able to stage a rapid return to the substrate tend to be those that frequently show diel drift periodicities (Ciborowski and Corkum 1980).

Current exerts the most important influence on settling rates, although substrate texture, water temperature, benthic density at site of reestablishment, and the presence or absence of light may be modifying factors (references in Table 1).

A fraction of drifting animals are lost as a result of predation by fishes, emergence, and mechanical injury. Mancini et al. (1979) found that removal of drift-feeding fishes from a pool had no influence on the density of invertebrates drifting through it. Consequently, although drifting animals may be an important food source for fish predators, the probability of an individual insect being eaten is low. Laboratory studies suggest that mortality due to mechanical injury is minimal, even at very high water velocities (personal observations). Thus, most individuals that leave the substrate probably return successfully.

Drift often provides the primary source of animals during recolonization of disturbed or denuded stream areas (Waters 1964, Townsend and Hildrew 1976, Williams and Hynes 1976, Sheldon 1977, Gore 1979, Wise and Molles 1979, Shaw and Minshall 1980). When adjacent upstream reaches support high densities of individuals, normal standing stocks of animals can be accumulated on a scoured substrate in as little as 4 days (Waters 1964). Such recolonization must also be a reflection of the turnover of individuals that occurs in all parts of a river by drift and subsequent resettling.

The number of animals on a portion of river bottom necessarily represents the balance between net immigration and emigration as well as births and deaths. Since relatively minor changes in stream discharge can produce large changes in the flow pattern over the bottom and consequently influence both the substrate composition and food resources, it may be expected that animals are adapted to relocate when conditions become unfavourable. Drift could be an important means by which this relocation occurs.

My study was undertaken to evaluate the importance of drift in governing the microdistribution of populations of two mayfly species, Baetis tricaudatus Dodds and Ephemerella inermis Eaton, in the Pembina River, central Alberta, Canada. Both species are numerically abundant in streams throughout western North America and frequently dominate the drift in these streams.

I have presented my research in four chapters. The first establishes the life history, microdistribution and drift characteristics of larvae at a site on the Pembina River near Entwistle, Alberta. Chapter 2 reports the results of laboratory studies which assess the relative importance of current velocity, benthic density of larvae and detritus concentration on departure rates of the organisms. I also studied the effects of current velocity on washing away of dead animals to examine the role that behaviour might play in inducing animals to leave the substrate. Chapter 3 provides information on the transport of larvae in the Pembina River. Live and dead animals were released into the water column. Catches of larvae in a series of downstream nets permitted me to estimate rates of settling and the degree of lateral transport that drifting animals are subject to. In Chapter 4, I derive a mathematical model which incorporates data on larval microdistribution, departure rates, downstream transport, and lateral transport to examine how drift may modify the microdistribution of the two larval populations. Predictions of the relative distribution of larvae after 2 weeks' drift and the number of animals expected in the drift were compared with data collected from the Pembina River.

CHAPTER 1

LIFE HISTORIES, MICRODISTRIBUTION AND DRIFT OF TWO MAYFLY (EPHEMEROPTERA) SPECIES IN THE PEMBINA RIVER, ALBERTA, CANADA.

Introduction

Baetis tricaudatus Dodds and Ephemerella inermis Eaton are among the most widespread and abundant mayfly species in western North America (Johnson 1978, Morihara and McCafferty 1979). Although E. inermis has a simple univoltine life cycle (Hartland-Rowe 1964, Zelt 1970, Hamilton 1979, Barton 1980), its microdistribution may vary with its developmental stage (Minshall and Minshall 1977, Rabeni and Minshall 1977). Corkum and Pointing (1979) reviewed development of B. tricaudatus (as B. vagans McD.) in eastern North America, but the life cycle of western populations is complex and poorly understood (Clifford et al. 1973). Larvae of this species are normally found in fast water (Minshall and Minshall 1977, Rabeni and Minshall 1977, Corkum and Pointing 1979).

Both E. inermis and B. tricaudatus larvae are frequently cited as dominant organisms in stream communities, yet studies on their biology usually treat only their life histories or their microdistribution, seldom both. I investigated whether microdistribution of these two mayflies changes as the larvae develop; and, if so, what mechanisms are responsible for relocation of the animals.

Methods

Study Site

The study was conducted on the Pembina River near the town of Entwistle, central Alberta, Canada (53°37' N., 115°00' W). This fifth order river originates in the Rocky mountains and flows into the Athabasca River. At the study site it drains a watershed area of 4530 km^2, is 65 m wide, and has a maximum depth of 1.2 m during normal flows. Substrate is uniform across the channel, consisting of smooth limestone cobble embedded in coarse sand. The substrate is barren of macrophytes except during extended periods of low discharge, at which time *Cladophora* sp. may become abundant. Current velocity increases evenly from shore to stream centre. Cross-sectional mean velocity is 0.4 $m\ s^{-1}$ during typical summer water levels. Bankside vegetation (*Populus balsamifera* L., *Alnus rugosa* (Du Roi), *Salix* spp., *Picea* spp.) provides the majority of detrital material. The river is ice-covered from November until April. Kellerhals et al. (1972) summarized the hydraulic and geomorphic characteristics of the Pembina River above the study site.

Benthos Collection

Animals were collected with a modified Hess sampler (Waters and Knapp 1961) that enclosed a sample area of 0.1 m^2. Pore size of the netting was 0.380 mm. Benthic samples were taken at 10-15 day intervals during the ice-free period from

May 1978 to March 1980. Collections were made along each of three transects running parallel to the shoreline. Transects on each sampling date were chosen on the basis of water depth; at 10-15 cm, 25-35 cm and 45-55 cm. Except during periods of extremely high or low flow, these corresponded to distances from shore of 3, 7, and 11 m. Current velocity was measured at each transect with a Gurley, Stevens or Ott C-1 current meter except when heavy flood conditions released enough detritus to clog the propeller. Three winter collections were taken through the ice, 25 and 32 m from shore. Water depth beneath the ice was 45 and 55 cm, respectively, in December, but had decreased to 5 and 10 cm by March.

Three Hess samples were taken 1 m apart and pooled at each transect in 1978. In 1979, five separate samples were collected along each transect. The intermediate transect was not sampled in May 1979. All collections were preserved in Kahle's fluid and sorted in the laboratory.

In 1979, all non-animal organic material was removed from the inorganic fraction by elutriation, separated into coarse (≥1.00 mm) and fine (<1.00 mm) portions, air-dried, and weighed to the nearest 0.01 g.

Water temperature was measured with a hand-held thermometer between 1100 and 1130 h on each sampling occasion. Daily discharge data were available from a gauging station maintained by the Water Survey of Canada, 1 km upstream of the sampling site.

Life History

Size distribution of animals on each sampling date was determined by measuring head width at the level of the eyes. In 1978, up to 50 animals per species were measured from each of nearshore and remote transects. Up to 20 animals per sample from all transects were measured in 1979. Where subsampling of collections was necessary for measurements, individuals were visually ranked by size and the appropriate number of organisms selected at regular size increments. Head widths were measured with an ocular micrometer under a dissecting microscope at 40X magnification to the nearest 0.024 mm.

Periods of emergence were estimated by sweeping bank-side vegetation for adults and by noting the presence of mature larvae (those with black wing pads) in benthic samples.

Microdistribution

One-way analysis of variance (ANOVA) was used to test for differences in density of each species between transects on each date in 1979. Where there were significant differences, effects were partitioned using Student-Newman-Keuls tests (Sokal and Rohlf 1969).

Least-squares regression analysis was used to determine the relationship between amounts of organic material and benthic density of each species. Separate regressions were conducted for large (CPOM) and small (FPOM) particle sizes. In addition, the relationship between numbers of all other benthos (AOB) in each sample and the two mayfly species was tested. The regression analyses were performed on the data pooled from all 1979 samples, on samples pooled by date, on samples pooled by transect and on sets of replicates collected along each transect on each date. Pooled coefficients of determination were calculated for each grouping of data by adding together all explained sums of squares for a series of regressions and dividing by the pooled total sums of squares. This provided an estimate of the proportion of the overall variation removed by regressions on the various data groupings.

Drift

Twenty-four hour drift studies were carried out June 5-6, July 5-6 and August 2-3, 1978. Drift was monitored continuously by means of nets with a mouth opening of 9 x 9 cm, and net pore size of 0.320 mm (Clifford 1972a). On each occasion two nets were anchored in the river with steel rods driven into the riverbed; one 4 m from shore in 15-20 cm of water and the other 12 m from shore at a depth of 45-55 cm. Each net was kept 3 cm below the water surface and was emptied at 30-min intervals. Water velocity at the mouth of each net was measured every 6 h. In July [illegible] ust a third net was anchored 3 cm from the substrat [illegible] stakes as the deepwater net.

Net contents were preserved in Kahle's fluid and sorted in the laboratory. Because the amount of water passing through the nets varied with net position and date, drift was expressed as drift density (no. animals m^{-3} water filtered).

Results

Physical Characteristics

Daily discharge and water temperature differed substantially between 1978 and 1979 (Fig. 2). Mean annual daily discharge in 1978 was the second highest since 1956; whereas in 1979 it was the second lowest (Water Survey of Canada, unpubl. data). In 1979, there was relatively little variation in flow apart from the normal run-off peaks of May and June. Four additional major flood peaks occurred in 1978.

The Pembina River remained ice-covered 2 weeks longer in 1979 than in 1978. This delayed the spring warming of the river. However, the frequent flooding in 1978 resulted in lower summer water temperatures than in 1979.

Table 2 summarizes mean current velocity, detrital concentrations and benthic densities of animals other than B tricaudatus and E. inermis along the three transects sampled in 1979. Current velocities varied little throughout the year (a consequence of the sampling design) but FPOM, CPOM and AOB were substantially greater during late summer and early autumn than at other times.

Life History

Ephemerella inermis was univoltine in the Pembina River.

Figure 2. Mean daily discharge (top) and water temperature (bottom) at sample site on Pembina River, 1978 (solid line) and 1979 (broken line).

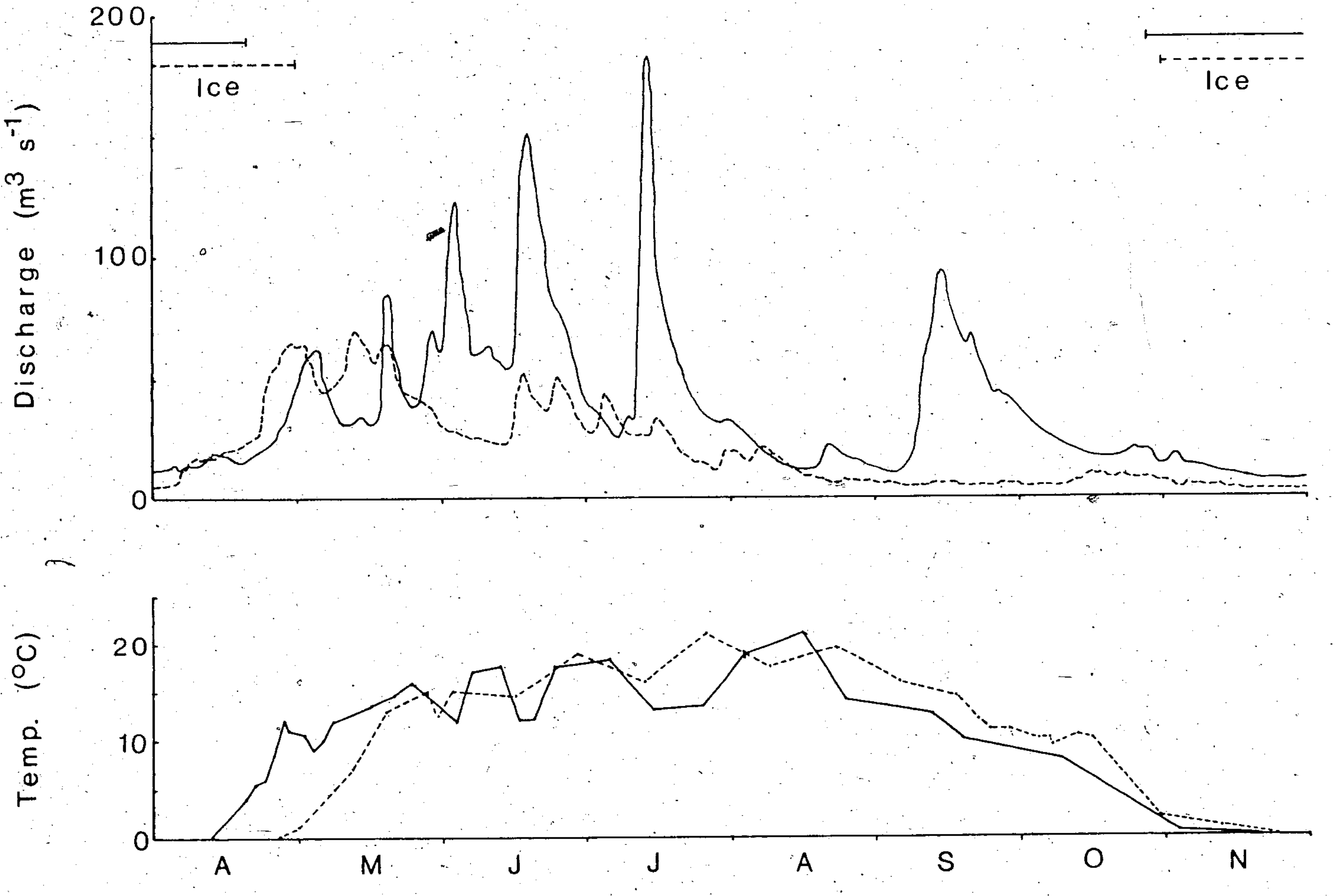

Discharge (m^3 s^{-1})
200
100
0
Ice
Ice
Temp. (^oC)
20
10
0
A
M
J
J
A
S
O
N

Table 2. Means ± 1 standard deviation of current velocities, detrital fractions and density of all other benthos along three transects.

Transect	N	Velocity (cm s^{-1})	N	FPOM (g m^{-2})	CPOM (g m^{-2})	AOB (No. m^{-2})
Nearshore	17	10.7 ± 1.41	70	15.4 ± 10.19	89.2 ± 58.01	9408 ± 10887.4
Intermediate	17	25.3 ± 1.67	60	11.0 ± 11.71	59.1 ± 38.24	9641 ± 7877.0
Remote	17	44.2 ± 3.53	70	6.6 ± 6.40	59.6 ± 61.64	5306 ± 5342.7

Early instar larvae first appeared at the end of July 1979, but not until mid-August 1978 (Fig. 3). Maximum densities of animals were reached in late October 1979 and in early October 1978 (Fig. 4). Growth had ceased by the end of October and did not resume until ice break-up. Mature larvae first appeared at the beginning of June 1978 but were delayed 10 days in 1979. Peak emergence occurred at the end of June, although some larvae persisted in the river until the end of August.

Larvae of *B. tricaudatus* were present throughout the year, although very few remained in the river in June 1979 (Fig. 5). Low water temperatures in early 1979 appeared to delay hatching of eggs in spring more than it delayed emergence of adults. Major periods of emergence were observed at the end of May and August. Lower numbers of individuals also emerged throughout July (Fig. 5). The hatching of young larvae was marked by subsequent peaks of benthic density in June, August and October (Fig. 6).

Microdistribution

During 1978, spring and summer densities of *E. inermis* larvae in slow water near shore were as great as or greater than at either of the more remote transects (Fig. 4). Nearshore densities, however, fell noticeably during the one interflood sampling period. Regions of greatest density were reversed (i.e. greatest along the remote transect) during the same period in 1979. Early instar larvae were

Figure 34. Frequency distribution of head widths of E. *inermis* larvae in 1978 (upper) and 1979 (lower). Solid line above histogram indicates abundant emergence, broken line indicates sporadic emergence.

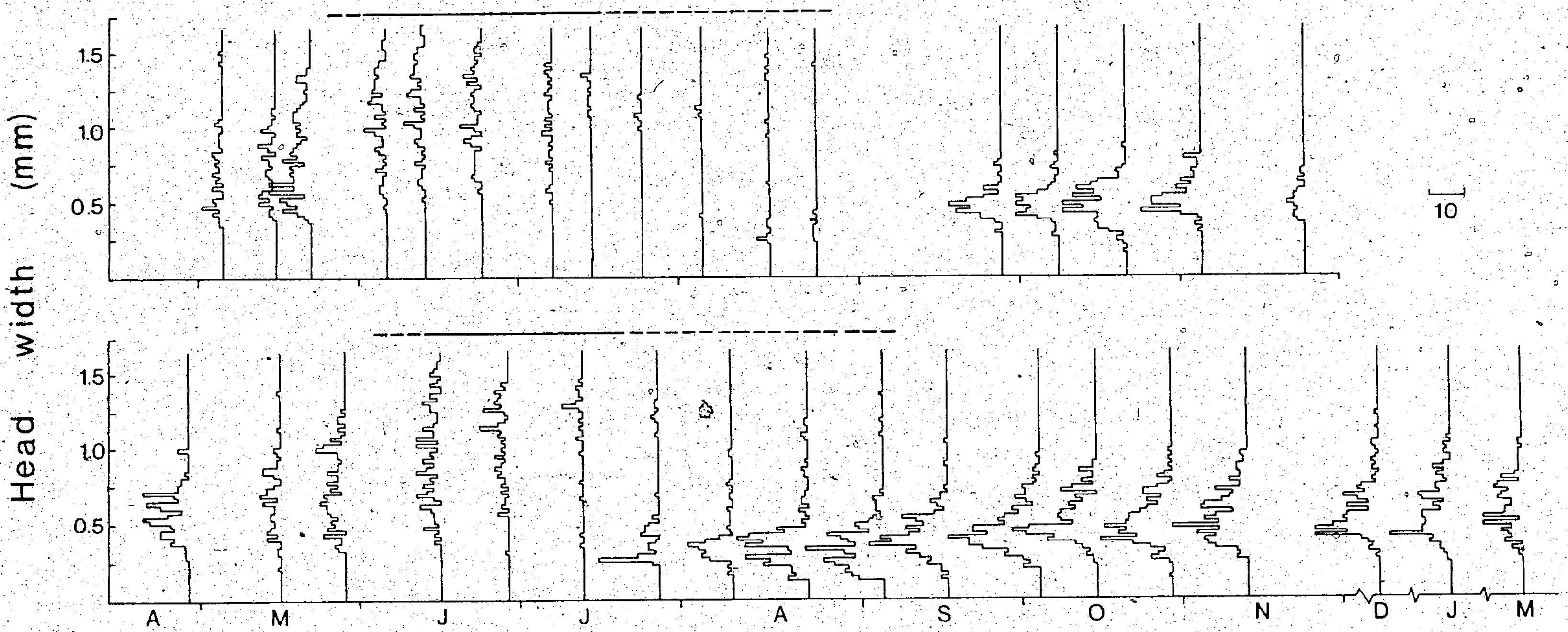

Head width (mm)
1.5
1.0
0.5
1.5
1.0
0.5
10
A
M
J
J
A
S
O
N
D
J
M

Figure 4. Benthic density of *E. inermis* larvae in 1978 (upper) and 1979 (lower; mean ± 1 standard error). Solid line = nearshore, broken line = intermediate, dotted line = remote transect. Vertical bars at top of lower figure connects transects for which mean density did not significantly differ (S-N-K test, $p > 0.05$) on each 1979 sampling date; n, i, and r represent nearshore, intermediate and remote transects, respectively.

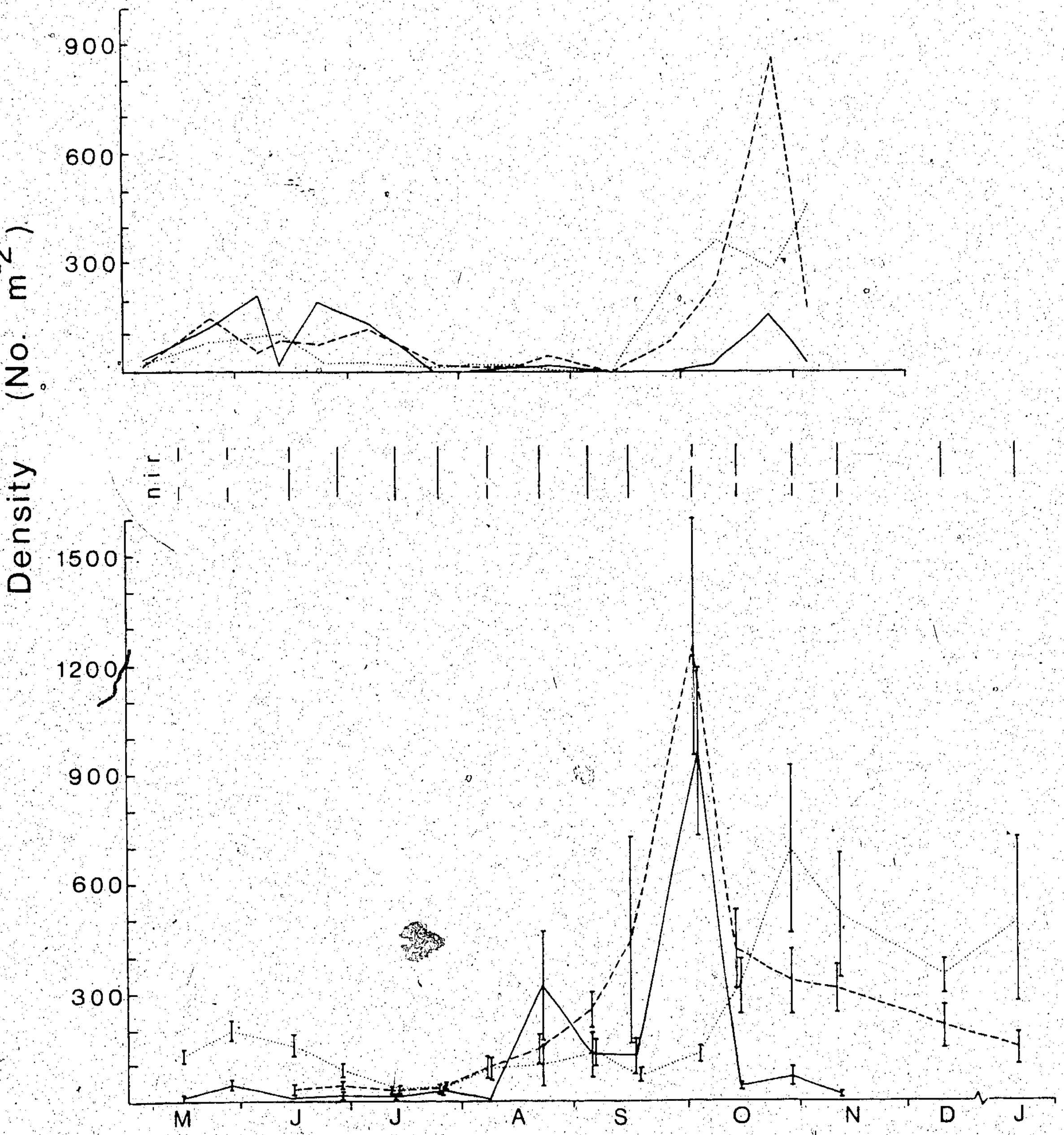

Density (No. m-2)
900
600
300
n
i
r
1500
1200
900
600
300
M
J
J
A
S
O
N
D
J

Figure 5. Frequency distribution of head widths of *B. tricaudatus* larvae in 1978 (upper) and 1979 (lower). Remaining explanation as in Fig. 3.

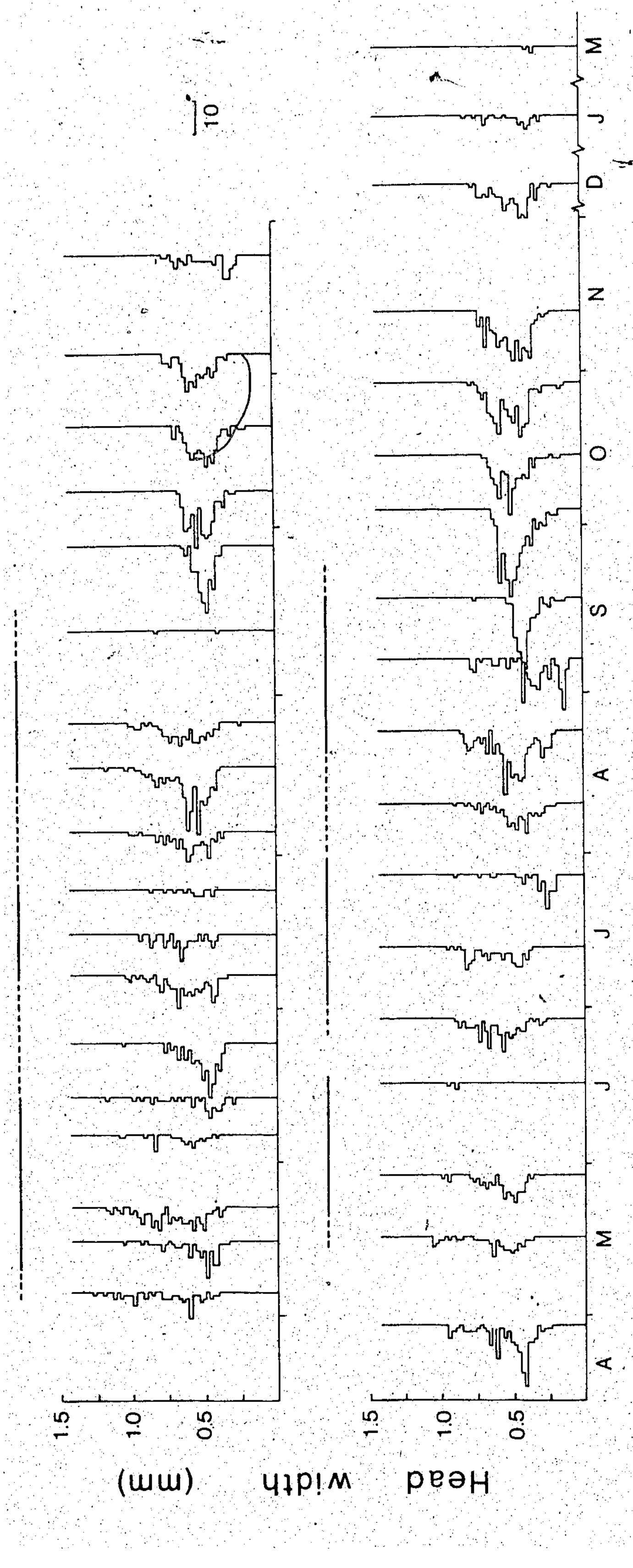
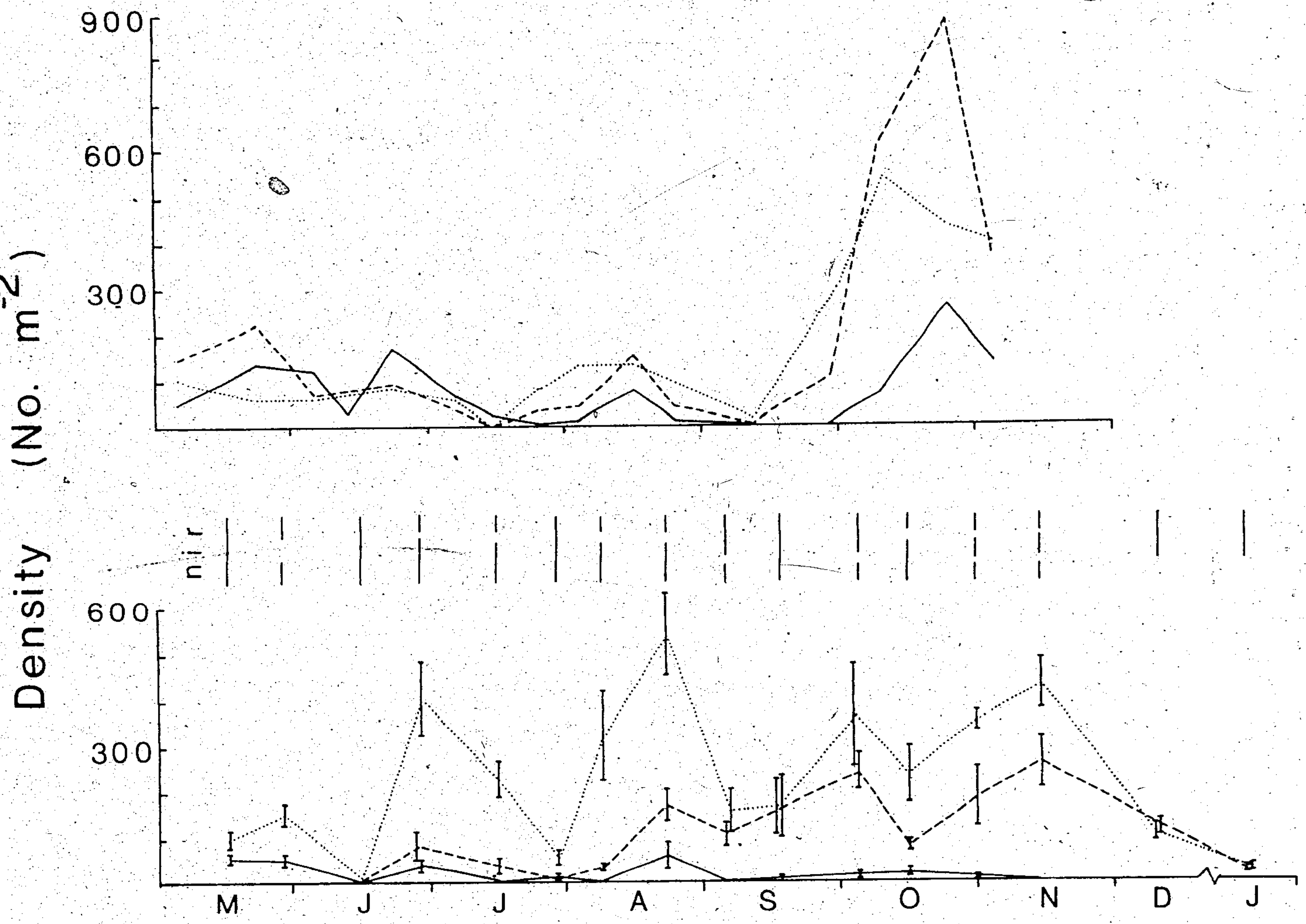

Head width (mm)
1.5
1.0
0.5
1.5
1.0
0.5
A
M
J
J
A
S
O
N
D
J
M
10

Figure 6. Benthic density of *B. tricaudatus* larvae in 1978 (upper) and 1979 (lower; mean ± 1 standard error). Remaining explanation as in Fig. 4.


Density (No. m-2)
900
600
300
n
i
r
600
300
M
J
J
A
S
O
N
D
J

first found at slow-water and intermediate transects and only later at the fast-water transect. Appearance along the remote transect was accompanied by a drop in densities near shore.

Spring and summer distributional patterns of B. tricaudatus larvae were similar to those of E. inermis (Fig. 6). Animals were equally abundant at all transects in 1978, but significantly greater densities were found in fast water along the remote transect during 1979. Densities at the nearshore transect did not exceed those in faster water as was observed for E. inermis in autumn.

Regression analysis of the relationship between the three independent variables (FPOM, CPOM, AOB) and E. inermis/B. tricaudatus abundance removed the greatest amount of variation when transect replicates within each date were separately analysed and then pooled (Table 3). Positive relationships were found between all three variables and density of E. inermis larvae, but only CPOM and AOB removed a significant amount of the variation in B. tricaudatus densities. The relationship between the two detrital fractions and E. inermis abundance was not evident when other groupings of the data were analysed. In contrast, relationships between all three independent variables and B. tricaudatus larvae were negative. The partitioning, by transect, of the two mayfly species into regions of similar current velocity (earlier 1-way ANOVA tests) accounted for 42 and 67 percent of between replicate variation for E. inermis and B. tricaudatus larvae, respectively.

Table 3. Pooled coefficients of determination for regressions of three variables on densities of *B. tricaudatus* and *E. inermis* larvae. * indicates that regressions remove a significant ($p<.01$) amount of variation by ANOVA. Symbols in parentheses indicate whether significant regression coefficients are positive or negative.

Grouping	*B. tricaudatus*			*E. inermis*		
	FPOM	CPOM	AOB	FPOM	CPOM	AOB
Replicate	.21	(+).43*	(+).47*	(+).34*	(+).39*	(+).55*
Transect	.01	(-).07*	(+).14*	.02	.04	(+).53*
Date	(-).46*	(-).22*	(-).18*	.09	(+).22*	(+).41*
All	(-).07*	(-).08*	.00	.01	.00	(+) .41*

Drift

Both *E. inermis* and *B. tricaudatus* larvae showed nocturnal increases in drift, especially in nearshore samples. Although daytime drift density of each species was comparable at both nearshore and remote sites for any particular date, nocturnal drift densities were substantially greater near shore than in deeper water (Fig. 7). Drift densities of *E. inermis* larvae were greater than those of *B. tricaudatus* in June, the only month when benthic densities of the two species were comparable. Drift densities of both species were exceptionally high when compared with values in other field studies (see Armitage 1977).

Ephemerella inermis larvae displayed a single nocturnal peak in drift density in June, whereas *B. tricaudatus* exhibited at least two peaks, the major one occurring just prior to dawn (Fig. 8). Patterns of drift on other dates were similar.

Discussion

In the Pembina River, eggs of *E. inermis* hatch between the end of July and mid-August. Larvae grow rapidly in autumn, complete development the following spring, and emerge at the beginning of July. Similar developmental patterns have been found in Alberta rivers by Zelt (1970), Hamilton (1979) and Barton (1980). Hartland-Rowe (1964) studied the life history of *E. inermis* in a spring-fed foothills stream and found emergence occurring several weeks later.

Baetis tricaudatus was characterised by three peaks of

Figure 7. Drift density of E. *inermis* (upper) and B. *tricaudatus* (lower) larvae in slow and fast water. U and L indicate samples of upper and lower portions of water column. Histograms within each group represent drift density calculated over 8-h intervals; left, 1300-2100 h; centre, 2100-0500 h; right, 0500-1300 h.

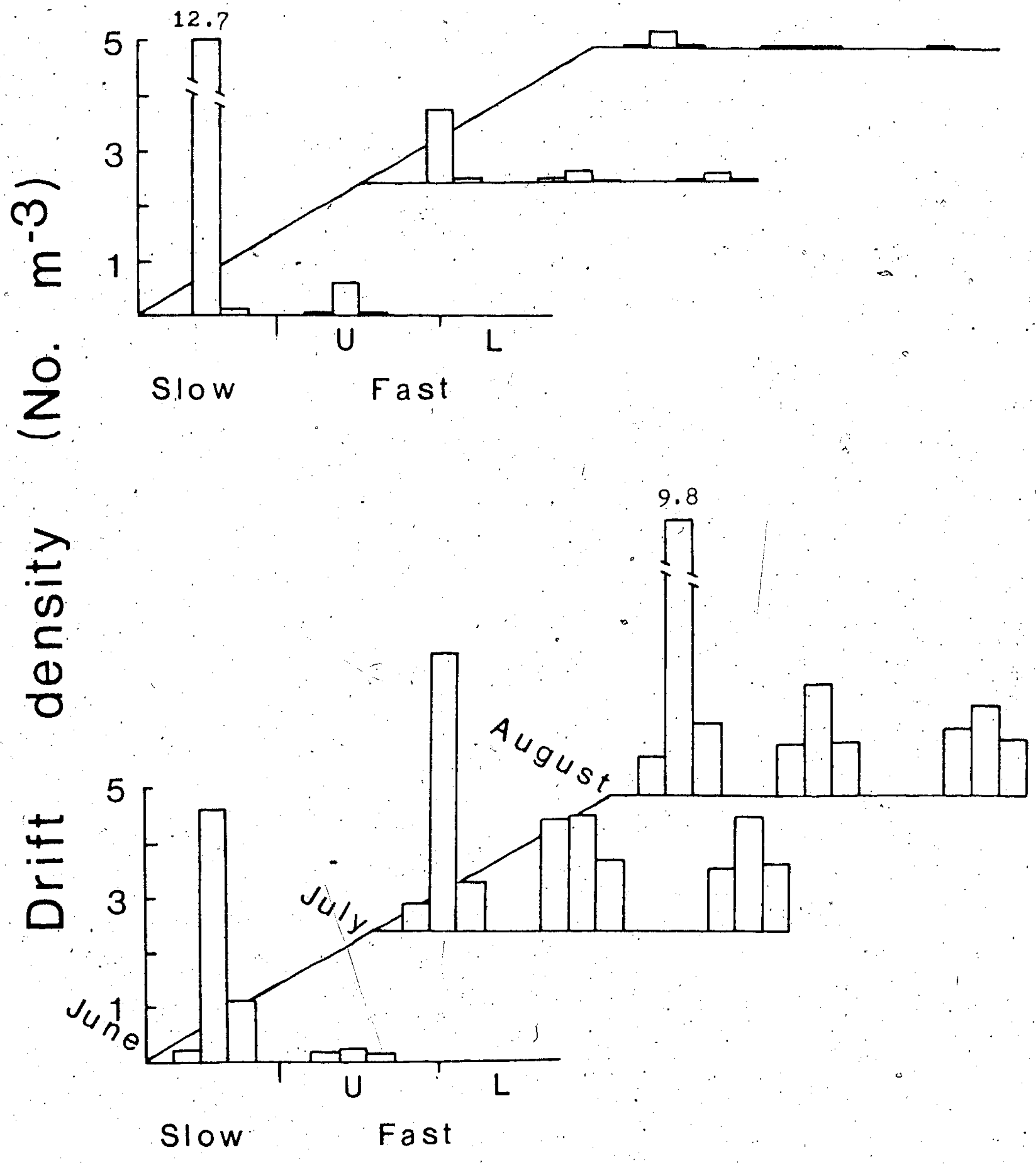
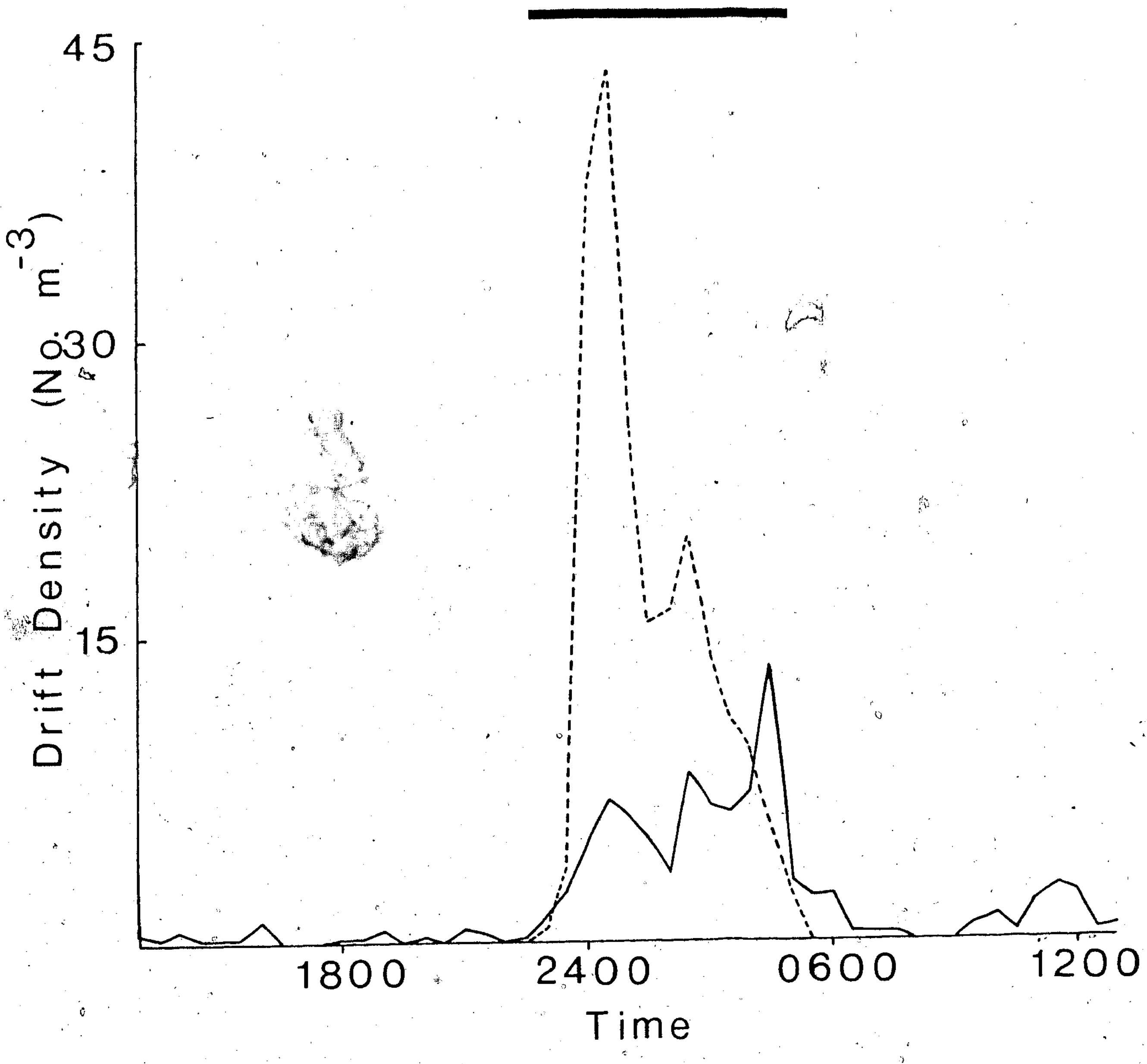

Drift density (No. m-3)
12.7
5
3
1
U
L
Slow
Fast
9.8
August
July
June
5
3
1
U
L
Slow
Fast

Figure 8. Drift density of *E. inermis* (broken line) and *B. tricaudatus* (solid line) larvae in nearshore net, June 5-6 1978. Horizontal bar represents darkness.

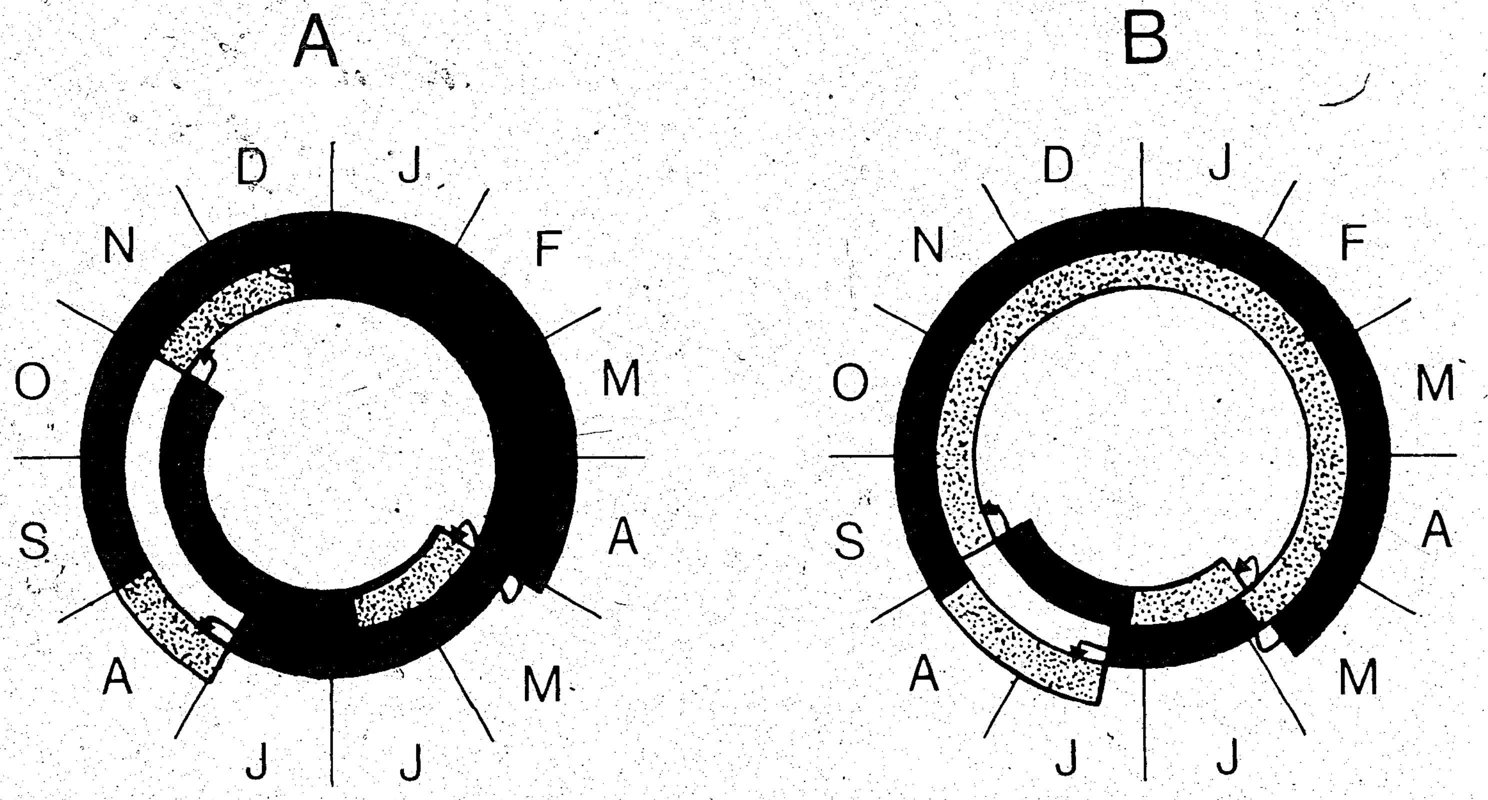

45
30
15
Drift Density (No. m^{-3})
1800
2400
0600
1200
Time

abundance (November, August, late June) followed by two major (May, late August/early September) and a minor (July) period of emergence. This species may be trivoltine in the Pembina River. However, the appearance of young larvae concurrently with adult emergence in spring 1978 and autumn of both years brings this interpretation into question. Murphy (1922) found that B. tricaudatus eggs in a New York stream required 28 days to hatch during May. In the laboratory, eclosion occurred in 11 days.

It is equally possible that the life history pattern of B. tricaudatus is similar to that found by Murphy (1922). Murphy reported that the New York population completed three generations in two years (Fig. 9a). Two of the cohorts, which hatched in autumn, required 9 months to develop from egg to adult, whereas eggs laid in the spring required only 6 months. Clifford et al. (1973) have observed that mayfly species tend more towards summer life cycles in subarctic regions than in more temperate areas. They reported winter dormancy of B. tricaudatus eggs in 3 Alberta streams. It is thus possible that eggs laid in autumn, which would normally hatch in November in more southern localities, overwinter as eggs in the Pembina River (Fig. 9b). Larvae that appear in June grow rapidly to emerge through July. The offspring of this cohort might not hatch until autumn, and then overwinter as larvae. The long winter and rapid warming of water in spring would tend to produce a relatively synchronized emergence of adults once conditions became favourable. Eggs of this winter cohort would

Figure 9. A. Development of _B_. _tricaudatus_ in Ithaca, N.Y. (after Murphy 1922).

B. Possible developmental pattern of _B_. _tricaudatus_ in Pembina River. Stippled areas represent eggs; solid sections represent larvae; arrows denote adult emergence and oviposition.


A
D
J
F
M
A
M
J
J
A
S
O
N
B
D
J
F
M
A
M
J
J
A
S
O
N

then hatch in July to produce another fairly strongly synchronized emergence period in late August/early September.

Neither the trivoltine nor the alternative interpretation of B. tricaudatus life history in the Pembina River is consistent with the egg development times given by Murphy (1922). If B. tricaudatus is trivoltine, then I would estimate that eggs would have to hatch in less than 5-7 days during the summer, whereas the alternative interpretation would require egg development times of approximately 35 days. Controlled studies of egg and larval development will be required before the life history of this species can be properly evaluated.

Several workers have described the life history of B. tricaudatus as bivoltine (Robertson 1967, Clifford 1969, Zelt 1970, Hamilton 1979), but all had examined material collected at 3 to 4-week intervals from qualitative benthic samples. Although their data were not precise enough to permit them to distinguish the rapidly developing summer cohort larvae from the other two, their data are consistent with those from the Pembina River.

Microdistribution of both species reflected the different flow conditions during the 2 years of the study. In 1978, a year of frequent heavy flooding during early summer, animals were equally abundant at all transects. Larvae were much less numerous near shore the following year, when flow conditions were more stable. B. tricaudatus larvae are most commonly found in fast water areas (Minshall and Minshall 1977, Rabeni and Minshall 1977, Corkum and Pointing 1979, Morihara and

McCafferty 1979). However, Lehmkuhl and Anderson (1972) observed that heavy winter flooding in an Oregon stream caused the drifting of B. tricaudatus larvae from riffle areas to backwaters. The return of stable flow in the spring resulted in a movement of animals back to riffles.

Microhabitat preferences of E. inermis were not as distinct as for B. tricaudatus larvae. In 1979, most E. inermis larvae were found in fast water along the remote transect. Yet as the summer progressed, the number of animals in fast water decreased, whereas abundance near the shore remained constant. Thus, the relative proportion of animals in slow water near shore increased through the summer. This microdistributional pattern was maintained despite the much greater nocturnal drift densities observed in the nearshore area. Hall et al. (1980) reported a similar accumulation of larvae of Tricorythodes atratus McD. as a result of drift into pools from riffle areas in the Mississippi River. Nevertheless, it is unclear whether the increased magnitude of drift in the shoreward area reflects immigration of individuals from faster portions of the river, or whether it represents the desertion of the slow-water microhabitat by organisms already there. Bird and Hynes (1981) have also observed greater drift, especially by Baetis spp., occurring at the margin of a stream than in the centre. They attributed this to animals actively leaving the slow-water areas. Other authors have also reported increased drift in response to slow or declining water levels (see reviews in Armitage 1977 and Walton 1980a).

In autumn, E. inermis larvae were concentrated in the slow water areas near shore. Later in the season, however, animals appeared to move towards the river centre. The adaptive significance of this seems clear, since in winter ice on the Pembina River reaches a thickness of 60 cm, and only centre portions of the river maintain a flow of water. Ulfstrand (1968) postulated a similar phenomenon to account for sudden changes of abundance of Ephemerella aurivillii Bgtn. in a north Swedish river.

This movement of larvae is probably accomplished by individuals crawling over or through the substrate rather than by drift. Few species drift abundantly during autumn (Waters 1972, Ciborowski 1979) even though benthic densities of many species are maximal at this time (Hynes 1970). Drift densities of E. inermis larvae in October in the Pembina River are much lower than at the end of May (Chapter 4). Minshall and Minshall (1977) found that E. inermis larvae preferred areas of low current velocity in Mink Creek, Idaho, a stream which apparently does not become ice-covered in winter. Their data suggest that the response to current velocity was weaker in March than in February. Rabeni and Minshall (1977) found E. inermis larvae to have no preference for any current velocity in Mink Creek. They did not report the time of year at which their study was conducted.

There appeared to be no clear-cut associations between abundance of either species and concentrations of organic material or benthic densities of other invertebrates, except within regions of similar current velocity. Neither Minshall and Minshall (1977) nor Rabeni and Minshall (1977) found a direct relationship between detritus accumulations and benthic densities of either *E. inermis* or *B. tricaudatus* larvae. Amount of FPOM was the poorest predictive independent variable for regressions grouped by replicate. Hamilton (1979) reported that this organic fraction made up the greatest volume of gut contents of both *E. inermis* and *B. tricaudatus* larvae in three Alberta rivers. If these species rely on the same food source in the Pembina River, then either FPOM is sufficiently abundant that it is not a factor important in controlling the microdistribution of these animals or the larvae are so active in the substrate that their distribution at the time of collection does not reflect their feeding site.

Corkum et al. (1977) observed that *B. tricaudatus* larvae preferred organic to inorganic substrates in laboratory experiments. This may account for the positive association of both species with the CPOM fraction. Alternatively, the associations of both species with all three independent variables may simply indicate that more habitable areas (interstices) are present within the substrate at some sampling points than at others. Interstices act as traps for detritus and as refuges from the current for all invertebrates (Rabeni and Minshall 1977). The substrate of the Pembina River consists of smooth cobbles embedded in coarse sand. Suitable refuges may therefore be at a premium. Regardless of the relationships between the two mayfly species and the three independent variables, the measurement of either detritus concentrations or density of other benthos provides a means of statistically reducing intersample variability.

Both E. inermis and B. tricaudatus larvae are vagrant species capable of rapid colonization of newly available substrates (Gore 1979, Shaw and Minshall 1980). Thus, their response to the varying physical characteristics of a river or to internally controlled changes in habitat preference is to be expected. The microdistribution of both species appears to depend largely on the constancy of prevailing physical conditions in the Pembina River. In early summer, during periods of stable flow, both species predominate in faster water. Although B. tricaudatus larvae maintain their position in these fast water areas throughout their development, E. inermis larvae may drift to slower water as they reach maturity. Newly hatched larvae of E. inermis are most abundant near shore but travel to deeper and faster water in late autumn. Flood can produce a rapid relocation of individuals of both species, probably by inducing animals to drift. This results in a more even distribution of animals across the river. The distribution of both species within regions of similar current velocity at any given time is associated with areas of high detrital concentrations, especially the coarse fractions. The microdistribution of either species clearly depends upon responses of animals to the interaction of a number of biotic and abiotic factors (Rabeni and Minshall 1977) but the primary controlling factor appears to be the flow regime of the Pembina River.

CHAPTER 2

INFLUENCE OF CURRENT VELOCITY, DENSITY AND DETRITUS ON DEPARTURE FROM THE SUBSTRATE OF TWO MAYFLY SPECIES (EPHEMEROPTERA)

Introduction

The microdistribution of lotic aquatic invertebrates is largely controlled by current velocity (Phillipson 1956, Edington 1965, Madsen 1969, Minshall and Minshall 1977, Rabeni and Minshall 1977), substrate composition (Ulfstrand 1967, Cummins and Lauff 1969, Higler 1975, Hildrew and Townsend 1977, Williams 1978, Barton 1980) and food availability (Egglishaw 1964, Mackay 1969, Hildrew and Townsend 1976, Peckarsky 1980a). 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 major 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 1967a, McLay 1968), or the active desertion of the microhabitat (Walton et al. 1977, Hildrew and Townsend 1980). Density-dependent drift 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 is density-independent at most times (Bishop and Hynes 1969a).

This study was undertaken to examine the relative importance of current velocity, benthic density and abundance of detritus on departure tendencies of _E_. _inermis_ and _B_. _tricaudatus_ larvae. More specifically, I attempted to determine whether: (1) larvae exhibit density-dependent drift at benthic densities typical of the Pembina River; (2) presence of an organic substrate (detritus) modifies the amount of space available to animals in the substrate; (3) these influences are of greater importance in controlling departure rates of organisms than is current velocity. Departure of animals from the substrate was monitored in laboratory streams at various benthic densities under conditions in which the inorganic substrate was augmented with controlled amounts of detritus. Additional experiments were performed to estimate the influence of current velocity on departure. The response of dead animals to current velocity was also examined to discern to what extent departure is the result of accidental physical dislodgement of animals.

Methods

Laboratory Streams

Experiments were conducted in May (spring) and October (autumn) 1979. They were performed in three elliptical, recirculating artificial streams* (channel width 11 cm, water depth 13 cm; Fig. 10). Water in each stream was propelled by a motor-driven paddlewheel. Current velocity was regulated by varying the size of the pulleys that coupled the paddlewheel with the motor. The streams were housed within a controlled-environment room, the temperature being maintained at prevailing Pembina River temperatures (Chapter 1).

Experimental Design

Two series of experiments were conducted in each season. The first series tested the influence of benthic animal density and amount of detritus in the substrate on departure of E. *inermis* and B. *tricaudatus* larvae. A 3 (density) by 4 (detritus) level factorial stratified random design was used, incorporating 3 replicates of each treatment. Levels corresponded to ½X, 1X or 3X maximum recorded abundance in spring 1978 bottom samples. The fourth detritus category was no detritus present (Table 4).

The second series of experiments examined the effect of current velocity on departure of larvae from the substrate. Three replicates were conducted for each of 5 mean current velocities, representing the range of current found in the Pembina River up to a distance of 12 m from shore during non-flood flow conditions. Trials with live animals were all conducted with 3X levels of density and detritus. Treatments were the laboratory equivalents of 17.0, 24.7,

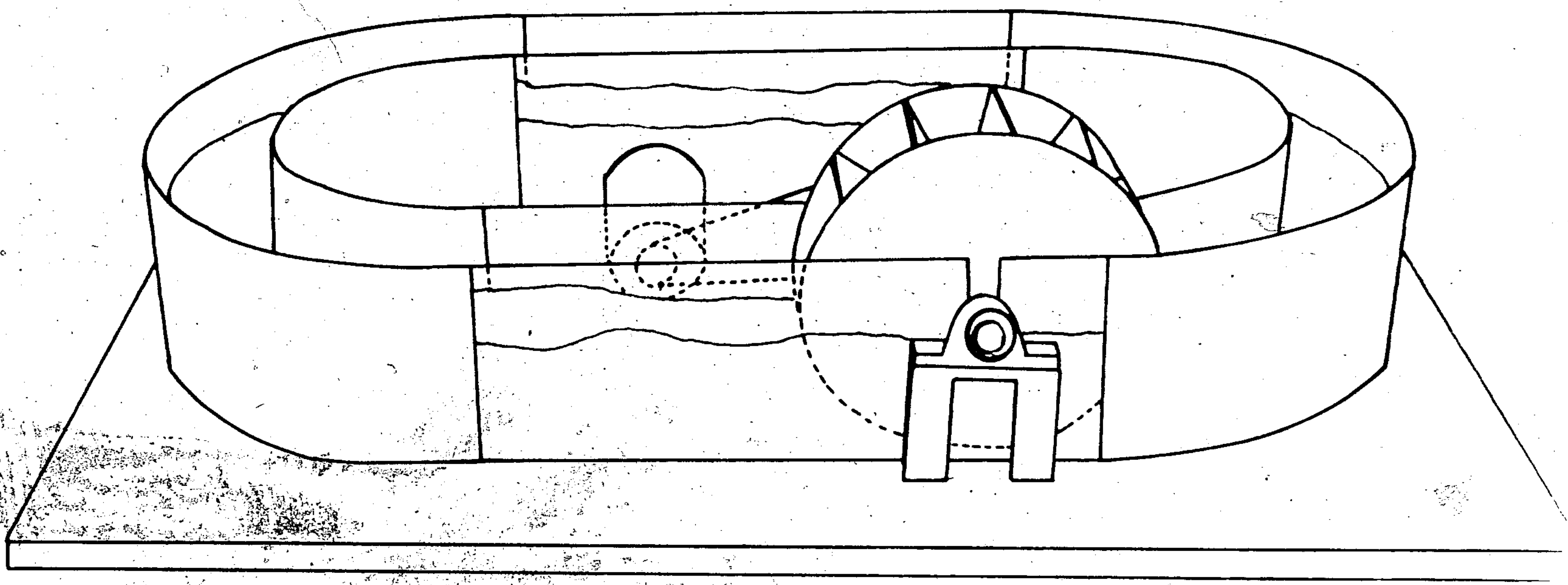


Figure 10. Laboratory stream, showing motor and paddlewheel. Flow is clockwise. Substrate is placed in far straightway.

Table 4. Animals and detritus added to laboratory streams. All confined to an area of 0.066 m^{-2}. Current velocity 31.2 cm s^{-1} unless otherwise specified.

Season	Spring			Autumn		
Treatment Level	½X	1X	3X	½X	1X	3X
E. inermis (No.)	10	20	60	-	-	-
B. tricaudatus (No.)	15	30	90	30	60	180
I. elongatus (No.)	3	3	3	6	6	6
Detritus (g)	1.14	2.28	6.84	1.14	2.28	6.84

31.2, 40.8, and 51.4 cm s^{-1} mean velocity.

Laboratory equivalents to mean velocity in the Pembina River were estimated by taking a series of field current velocity readings with a Gurly current meter. Mean velocity was determined by taking a measurement at 0.6X stream depth. Eight points were selected at increasing distances from shore. Mean current velocity and velocity 5.2 cm above the substrate (equivalent to 0.6X laboratory stream depth) were measured at each point. The relationship between the two measurements was determined by linear regression (Fig. 11).

Preserved animals from earlier experiments were used to determine the effect of current velocity on loss from the substrate of dead organisms. In these trials, 80 E. inermis, 80 B. tricaudatus (spring) and 80 B. tricaudatus (autumn) larvae were used. Baetis tricaudatus larvae were distinguished by size and maturity. Those from spring trials had well-developed wing pads and head widths > 0.7 mm. Larvae from autumn experiments had poorly-developed wing pads and head widths of 0.4 - 0.6 mm. These larvae had been preserved in Kahle's fluid after use in original experiments. They were maintained in dechlorinated tap water for 1 h prior to use.

Several workers have indicated that invertebrate predators influence drift of mayfly larvae (Corkum and Pointing 1979, Corkum and Clifford 1980, Peckarsky 1980b, Walton 1980b). Since predators are ubiquitous in the Pembina River, they were used in all trials except those

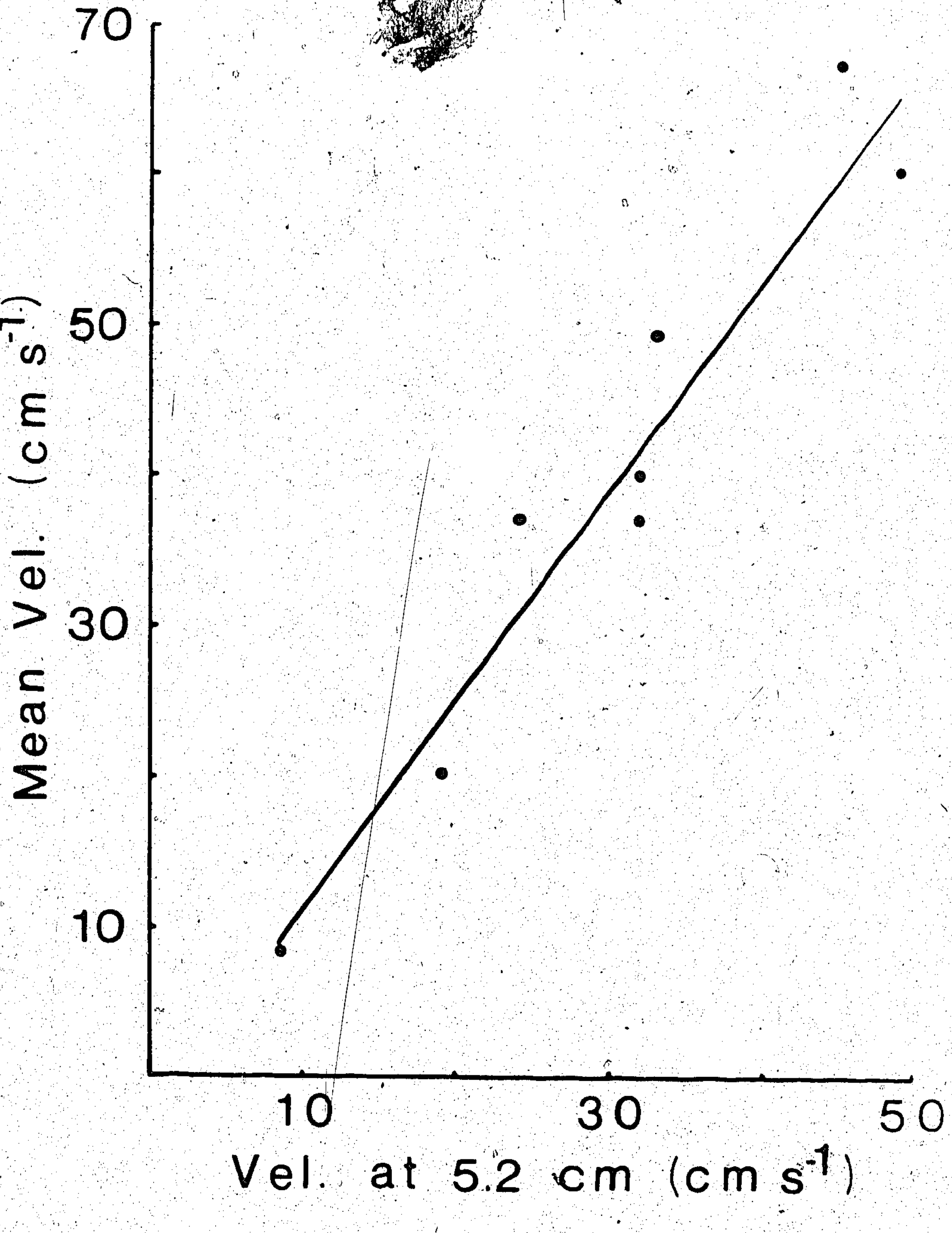


Figure 11. Relationship between current velocity 5.2 cm above substrate (X) and mean current velocity (Y) in Pembina River. Regression equation takes the form $Y = -2.89 + 1.409X$, $R^2 = 0.93$.

concerned with dead animals, to more closely approximate field conditions. Isogenoides elongatus (Hagen) is the dominant predator in the Pembina River and was added to laboratory streams in densities that approximated average abundance of all predators in the field (Table 4).

Larvae of E. inermis were not used in autumn trials, as their small size and cryptic habits made them difficult to collect in sufficient numbers. Experimental densities of B. tricaudatus larvae in autumn were doubled over spring levels to reflect their greater abundance at that time in the field.

Execution of Experiments

Detritus for all experiments was collected from the Pembina River, sorted to remove all animals > 3 mm in length, air-dried and weighed. Particles ranged in size from 0.420 mm to 3.36 mm. The required amount of detritus for each trial was reconstituted in distilled water for 24 h prior to use. This provided only minimal time for bacterial and fungal growth to occur. Animals were hand-collected from the river and maintained in aerated water in enamelled trays until required.

Detritus was placed in two adjacent 11 x 30 cm trays set in a dry laboratory stream and covered with scrubbed substrate from the Pembina River. Predators were then introduced. The stream was filled with refrigerated dechlorinated tap water, with the paddlehweel running, and left for 1 hour. The appropriate number of mayfly larvae was then poured into the stream. 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 at 30-minute intervals for the next 4 hours. The jars were not subsequently changed until the end of the light period of the experiment (spring, 8 h; autumn, 5 h). The lights were then turned off and the catchment jars changed at 30-minute intervals for the duration of the experiment (spring, 8 h; autumn 10 h).

At the conclusion of each experiment, trays containing substrate, detritus, predators and all remaining mayflies were removed. The streams were drained and dried prior to the beginning of the next trial.

Results

The proportion of animals leaving the substrate during light and dark, respectively, was determined by dividing the number of animals caught in drift nets during relevent portions of each experiment by the number present at the beginning of that period. Installment of drift nets produced a noticeable amount of disturbance and resulted in high initial departure rates. For this reason, the first 3 h of each trial were not considered in the analyses. 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 1-way analysis of variance.

Curvilinear regression analysis was used to estimate the relationship between 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.

High initial departure rates of both live and dead insects were characteristic of all trials. In all cases, departure stabilized within 3 h and remained fairly constant for the duration of the light period (Fig. 12). With the onset of darkness, departure of live animals increased substantially. B. tricaudatus larvae showed a more pronounced nocturnal response in spring than in autumn trials. Departure of live animals was consistently greater than erosion of dead insects. The total proportions of B. tricaudatus larvae leaving the substrate, exclusive of the initial portion of experiments, were 0.77 and 0.61 in spring and autumn, respectively. By contrast, only 0.08 and 0.07 of the dead animals were washed away. The proportions of E. inermis larvae leaving the substrate were 0.88 (live) and

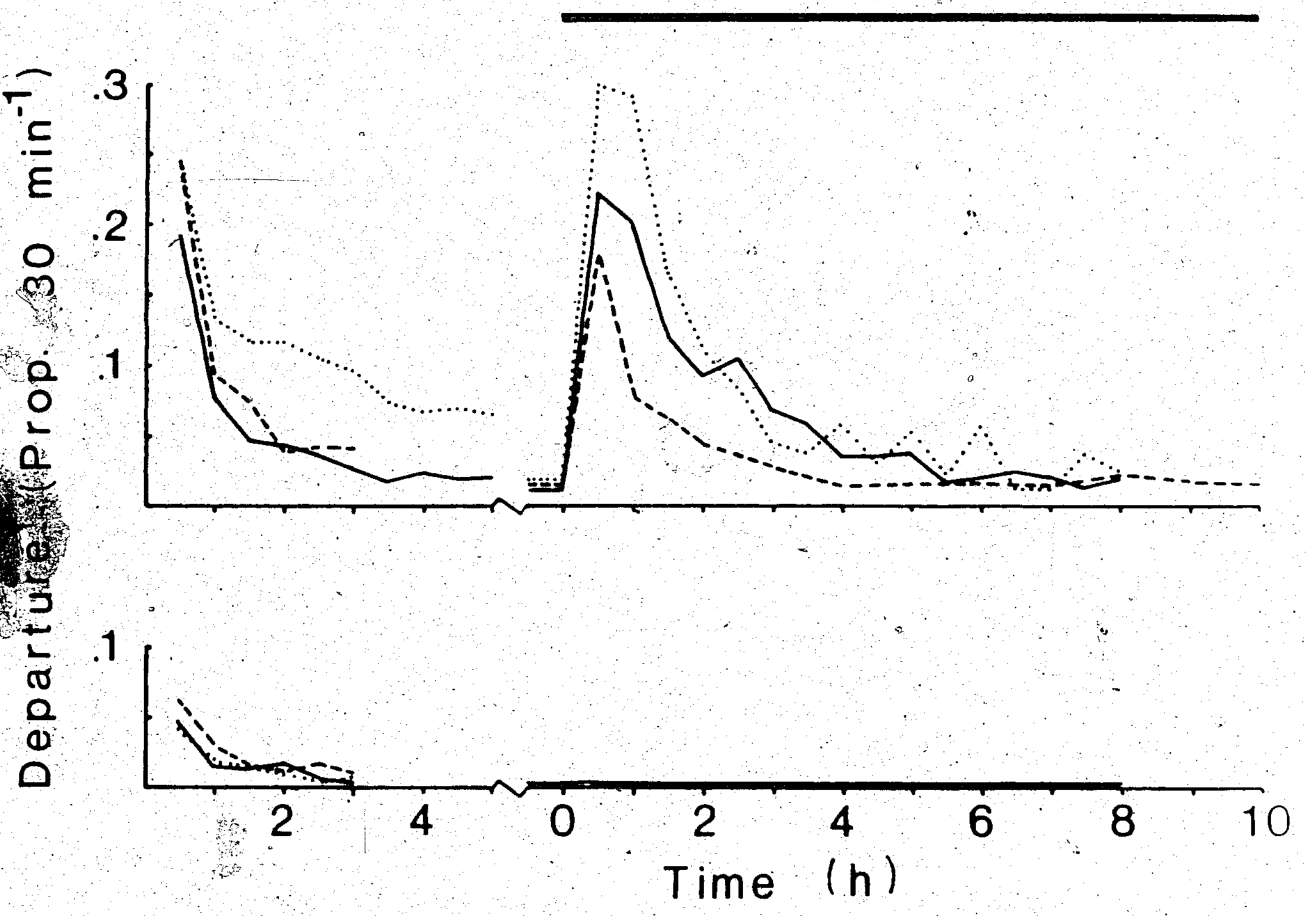


Figure 12. Proportion of live (upper) and dead (lower) animals departing from substrate during density-detritus trials. Solid line, *B. tricaudatus* (spring); dotted line, *E. inermis* (spring); broken line, *B. tricaudatus* (autumn). Bar above figure represents darkness.

0.06 (dead).

Of the 24 regressions performed to test for density dependence (Table 5), only one produced a regression coefficient significantly different from zero ($p < 0.05$). I interpret this single value as 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 in darkness (Fig. 13 and 14). Analysis of covariance indicated that there was no significant heterogeneity of regression coefficients ($p > 0.05$, Table 6), therefore, the interaction of detritus and benthic density did not influence departure rates. There was no significant influence of amount of detritus on the tendency for animals to leave the substrate ($p > 0.05$, Table 7; Fig. 15).

In spring, departure of both *B. tricaudatus* and *E. inermis* larvae was a positive linear function of current velocity (Fig. 16) but only during light portions of the experiments. During darkness, the proportion of B. *tricaudatus* larvae leaving the substrate was inversely related to current velocity. Departure of *E. inermis* larvae was minimal at a current velocity of 25 cm 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 8). Departure of *B. tricaudatus* larvae in autumn was independent of current velocity.

Dead animals of all three types were eroded from the substrate in much lower proportions than were their live

Table 5. Significance of relationship between benthic density and arcsine square root of proportions of animals departing from substrate at various levels of detritus. * indicates $p < 0.05$.

Detritus Level		0X		½X		1X		3X	
	Source	d.f.	S.S.	d.f.	S.S.	d.f.	S.S.	d.f.	S.S.
		LIGHT							
E. inermis (May)	Reg.	1	767.9	1	152.0	1	1124.4	1	479.0
	Error	6	2580.2	6	279.9	7	3841.8	7	1306.3
B. tricaudatus (May)	Reg.	1	616.6	1	49.1	1	5.7	1	145.7
	Error	7	1431.7	7	897.2	7	684.5	7	1175.8
B. tricaudatus (Oct.)	Reg.	1	28.0	1	16.9	1	3.0	1	4.1
	Error	7	360.5	7	697.4	7	302.8	7	514.4
		DARK							
E. inermis (May)	Reg.	1	2355.9	1	1094.2	1	2133.3*	1	5.2
	Error	6	4295.8	6	2285.8	5	1091.7	7	838.7
B. tricaudatus (May)	Reg.	1	69.3	1	62.1	1	7.6	1	175.7
	Error	7	1324.4	7	757.1	7	2135.7	6	460.2
B. tricaudatus (Oct.)	Reg.	1	12.3	1	97.5	1	3.6	1	275.6
	Error	7	1177.7	7	3310.8	7	1164.2	7	460.3

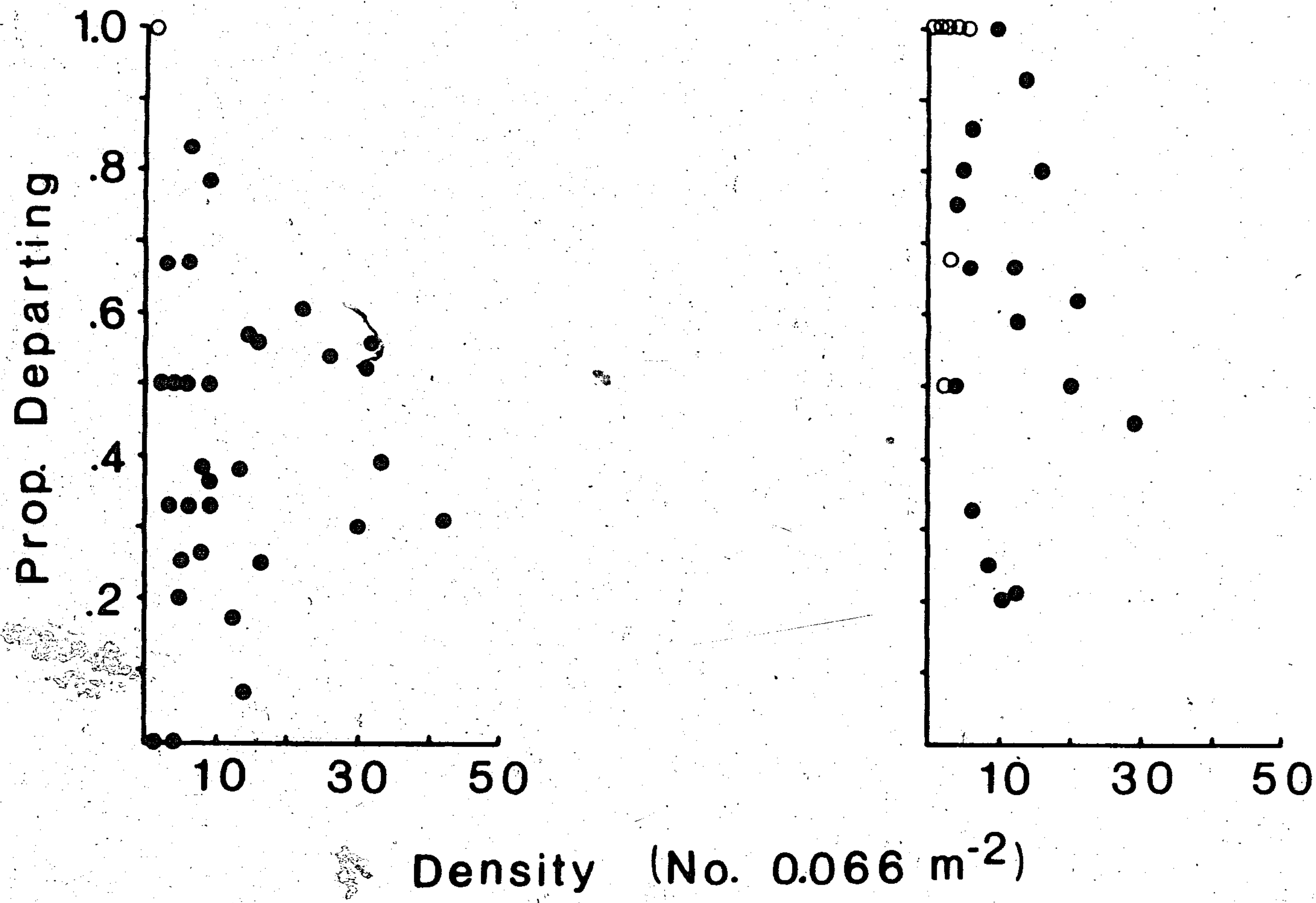


Figure 13. Proportion of E. inermis larvae departing from substrate as a function of benthic density during light (left) and dark (right) portions of experiments. Open points represent two observations.

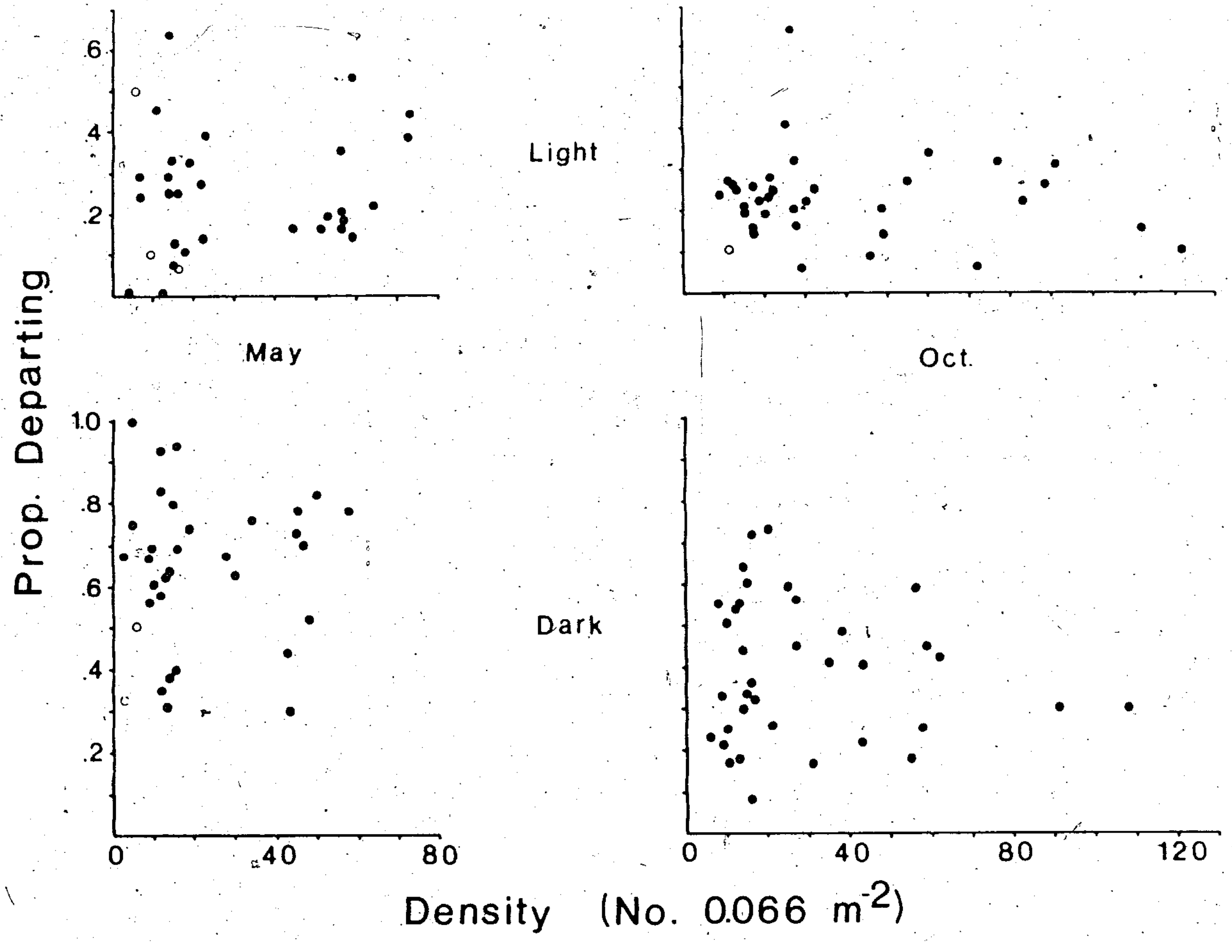


Figure 14. Proportion of *B. tricaudatus* larvae departing from substrate as a function of benthic density during light (upper) and dark (lower) portions of spring (left) and autumn (right) experiments. Open points represent two observations.

Table 6. Tests for homogeneity of regression coefficients among detritus levels. Coefficients describe relationship between benthic density and arcsine square root of proportion of animals departing from substrate. $p > 0.05$ in all cases.

	Source	LIGHT		DARK	
		d.f.	S.S.	d.f.	S.S.
E. inermis (May)	Slopes	3	1788.5	3	1760.2
	Error	26	8008.1	24	8512.0
B. tricaudatus (May)	Slopes	3	425.0	3	261.0
	Error	28	4189.1	27	4695.4
B. tricaudatus (Oct.)	Slopes	3	34.0	3	389.2
	Error	28	1875.1	28	6113.0

Table 7. Analyses of variance testing influence of amount of detritus on arcsine square root of proportion of animals departing from substrate. $p > 0.05$ in all cases.

		LIGHT		DARK	
	Source	d.f.	S.S.	d.f.	S.S.
E. inermis (May)	Detritus	3	1408.5	3	1806.2
	Error	30	10531.4	28	14100.6
B. tricaudatus (May)	Detritus	3	725.3	3	572.5
	Error	32	5006.8	31	5010.1
B. tricaudatus (Oct.)	Detritus	3	254.9	3	268.3
	Error	32	1927.2	32	6502.1

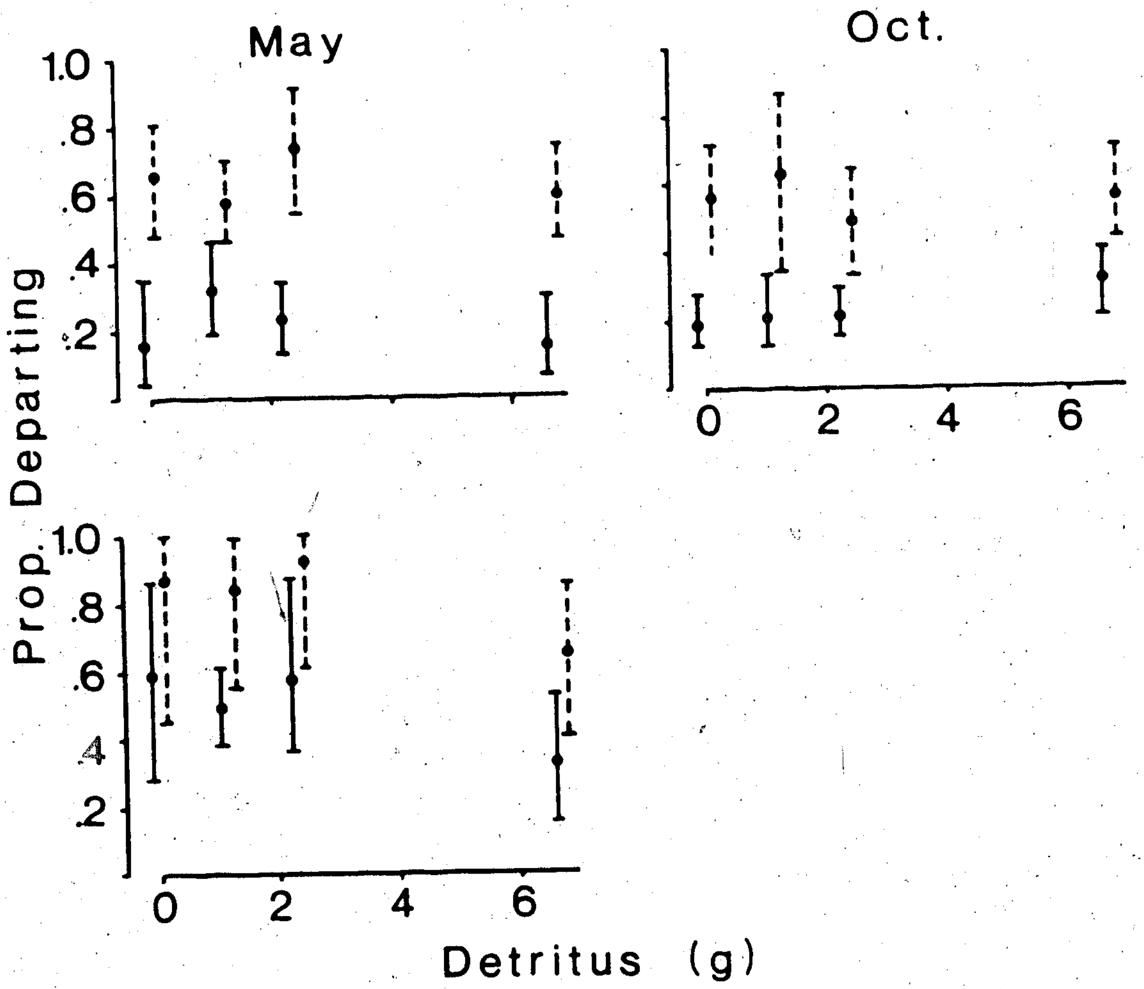


Figure 15. Mean proportion and 95 percent C.I. of B. tricaudatus (upper) and E. inermis (lower) larvae departing from substrate as a function of detritus concentration in spring (left) and autumn (right) experiments. Solid intervals represent light portion of trials, broken intervals represent dark portion.

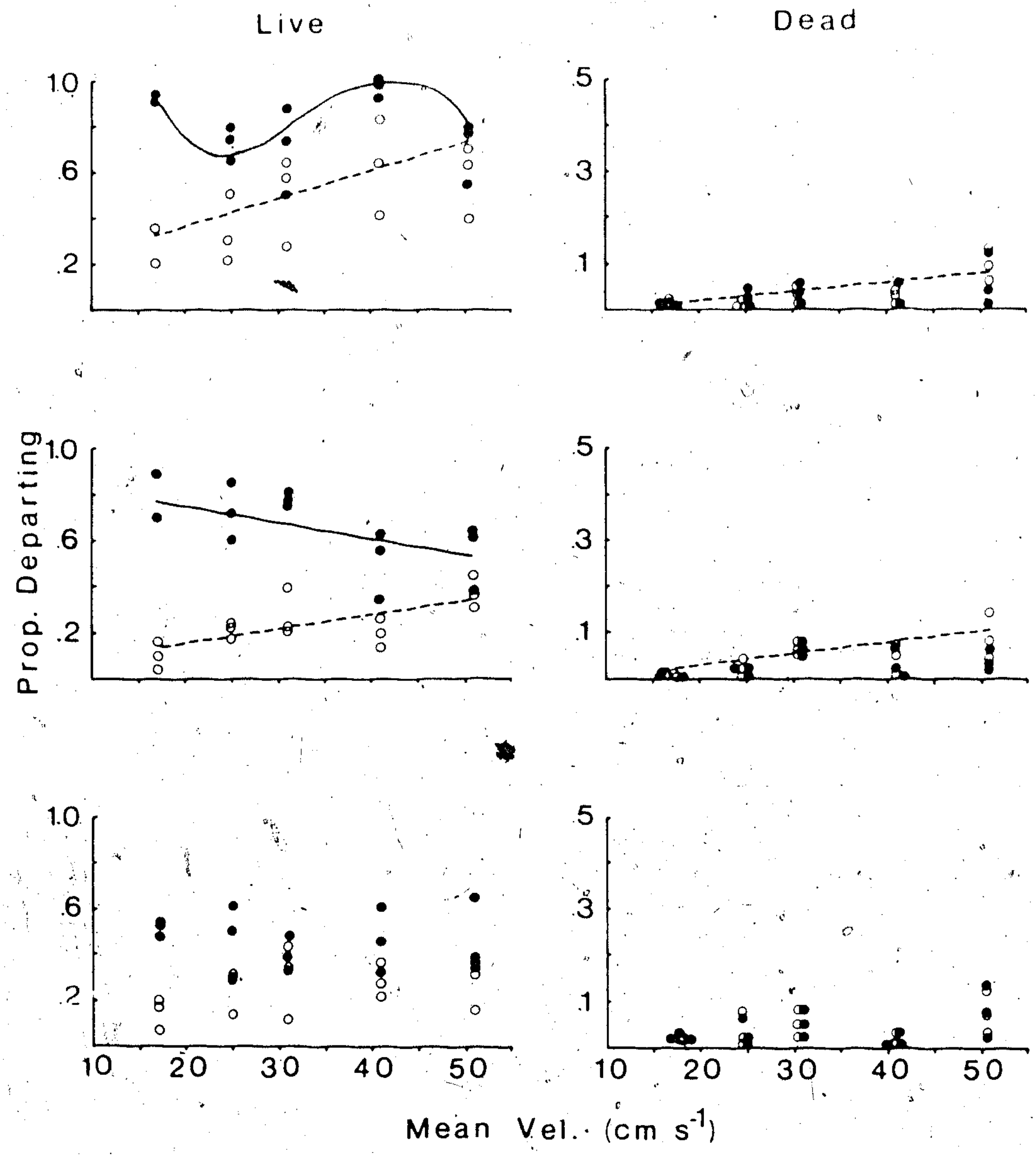


Figure 16. Proportion of live (left) and dead (right) larvae departing from substrate as a function of mean current velocity. Top, *E. inermis* (spring); centre, *B. tricaudatus* (spring); bottom, *B. tricaudatus* (autumn). Open points and broken lines represent light portion of experiments. Solid points and lines represent dark portion.

Table 8. Best estimate polynomial regression coefficients for relationship between current velocity and arcsine square root of proportion of animals departing from substrate. * indicates $p < 0.05$, ** indicates $p < 0.01$ by analysis of variance.

	LIVE					DEAD		
Reg. coeff.	β_0	β_1	β_2	β_3	R^2	β_0	β_1	R^2
LIGHT								
E. inermis (May)	23.74	0.5760			.35*	-3.28	0.4008	.56**
B. tricaudatus (May)	13.69	0.4294			.47**	-3.79	0.4405	.48**
B. tricaudatus (Oct.)	21.84	0.2300			.15	4.91	0.1979	.15
DARK								
E. inermis (May)	346.67	-29.511	0.9484	-0.0094	.64**	6.61	0.0886	.04
B. tricaudatus (May)	73.94	-0.5671			.45**	1.85	0.1987	.12
B. tricaudatus (Oct.)	45.39	-0.0789			.02	6.76	0.0023	.03

counterparts at all current velocities. Positive linear relationships were found between current velocity and departure of larvae of both species from spring experiments, but only during light periods (Table 8). 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, Walton 1978, Gyselman 1980). Interactions between individuals at sub-saturation densities may produce short-distance displacement of animals but seldom result in drift (Corkum 1978a, Wiley and Kohler 1981). Although laboratory densities of animals considerably exceeded benthic abundance of animals in the field (Chapter 1), 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.

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 effect is to be expected.

Aquatic invertebrates deprived of an adequate food supply usually exhibit a density-independent increase in departure rate (Hildebrand 1974, Keller 1976, Bohle 1978). The lack of any departure response to detritus concentration in my experiments may indicate that relatively sterile detritus does not constitute an attractive source of nutrients to E. *inermis* or 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 a 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 if they were 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 transport 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 insects (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 observed (see Walton 1980a). Corkum et al. (1977) found that B. tricaudatus larvae were much more prone to leave substrates in slow water than in fast water under both light and dark conditions. The departure of dead animals in the dark was independent of current velocity, presumably because most animals that lodged in the most exposed areas in high current velocity trials were quickly washed away early in those experiments.

Departure of B. tricaudatus larvae in autumn experiments was reduced in comparison to spring 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. Field data (Chapter 1) indicated that B. tricaudatus larvae were strongly concentrated in fast-water areas in spring, whereas distribution was more even with respect to current velocity in early autumn.

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. Passive behavioural departure 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.

CHAPTER 3

DOWNSTREAM AND LATERAL TRANSPORT OF DRIFTING LARVAE OF TWO MAYFLY (EPHEMEROPTERA) SPECIES IN THE PEMBINA RIVER

Introduction

All lotic aquatic invertebrates occasionally become dislodged from the substrate and transported downstream. The rate at which they return to the stream bottom depends on the size and shape of the animals (McLay 1970, McKone 1975) as well as the current velocity (Elliott 1971a). Behavioural actions result in rapid settling rates for certain species (Elliott 1971a), especially those frequently appearing in the drift (Ciborowski and Corkum 1980).

Most studies of settling behaviour have been concerned with the distance animals are carried downstream; but lateral transport of suspended animals may also be important in determining their subsequent benthic microdistribution. Ulfstrand (1968) postulated that cross-river movements of animals 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, there is no experimental work that evaluates the degree of lateral movement exhibited by animals released into the water column.

I conducted experiments to determine settling rates, downstream movement and lateral transport of the mayflies *Ephemerella inermis* and *Baetis tricaudatus* in the Pembina River. To determine the extent to which the animals are capable of controlling their return to the substrate, I worked with both live and dead animals.

Methods

Experiments were carried out during the last 2 weeks of May (spring) and the first 2 weeks of October (autumn) 1979, at a study site on the Pembina River (Chapter 1). The site was mapped with respect to depth and mean current velocity prior to experiments each season. A base line was established along the river margin. Eleven transects, 3 m apart, were set up at right angles to the base line. I recorded mean current velocity and water depth at 1-m increments along each transect 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 for each season.

Twelve large drift nets were constructed to sample suspended animals. They had a mouth opening of 1.0 x 0.5 m and were 2 m long. Netting was composed of polyester sheer drapery material with a pore size of 0.211 mm. The nets tapered to a round opening (8 cm diameter) into which were sewn jar lids with centres removed. These permitted rapid attachment and removal of catchment containers (236 ml jars with bottoms removed and replaced with netting). Nets were anchored by means of aluminum rods driven into the substrate to sample a column of water 1 m wide and up to 0.5 m deep.

The twelve nets were placed contiguously in the river, mouth upstream, in a row extending at a right angle to the base line. Settling rates were determined for animals at each of 5 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 introduction points for the insects (Frontispiece). Positioning of the stakes varied with the line (Table 9).

Insects were hand-collected from the river and maintained in finger bowls containing river water until required. Those designated for dead animal trials were preserved in Kahle's fluid to which was added lignin pink (a vitalline dye). These insects were transferred to finger bowls containing river water 30 minutes before they were used.

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. Nets were submersed for two minutes from the time of introduction of the animals. This was judged adequate to ensure capture of suspended animals at the slowest current, yet minimized inclusion of suspended detritus and extraneous drifting animals. The contents of each net were placed in separate enamelled trays and all appropriate animals were removed by hand and counted. Only large animals were used in experiments (head widths > 0.7 mm in in spring, 0.4 - 0.6 mm in autumn, as determined

Table 9. Distance from shore (m), mean current velocity (cm s^{-1}) and release points (m) along transects used for settling experiments. Current velocities are estimated from Fig. 17 and 18.

	TRANSECT				
	1	2	3	4	5
Distance from shore	2	4	6	8	10
Current velocity (May)	10.3	21.8	34.2	37.3	46.3
Current velocity (Oct.)	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

by later measurements in the laboratory). *Ephemerella inermis* larvae were not used in autumn experiments because their small size and cryptic habits made them difficult to collect at this time.

To estimate the number of extraneous animals caught during experiments, the nets were used to sample drift at 1800, 2400, 0900 and 1200 h on May 28-29 and October 7-8 1979. Nets were submersed for from 2-5 minutes in spring and from 15-25 minutes in autumn. The shorter submersion period of nets in deepest regions was used to ensure that they would not become clogged with suspended detritus.

Net contents were preserved in Kahle's fluid and sorted in the laboratory. Hea[illegible]dths of *E. inermis* and *B. tricaudatus* larvae were det[illegible]ed with an ocular micrometer under a dissecting microscope at 40X magnification to the nearest 0.024 mm. The estimated mean number of appropriately sized animals caught per 2 minutes in daytime drift samples in each net was used as a correction factor for settling trials.

Results

Current Velocity Profile

Mean current velocity was a linear function of distance from the river margin during both seasons (Fig. 17 and 18). In autumn, however, mean current velocity appeared to become constant at distances from shore greater than 8 m. Analysis

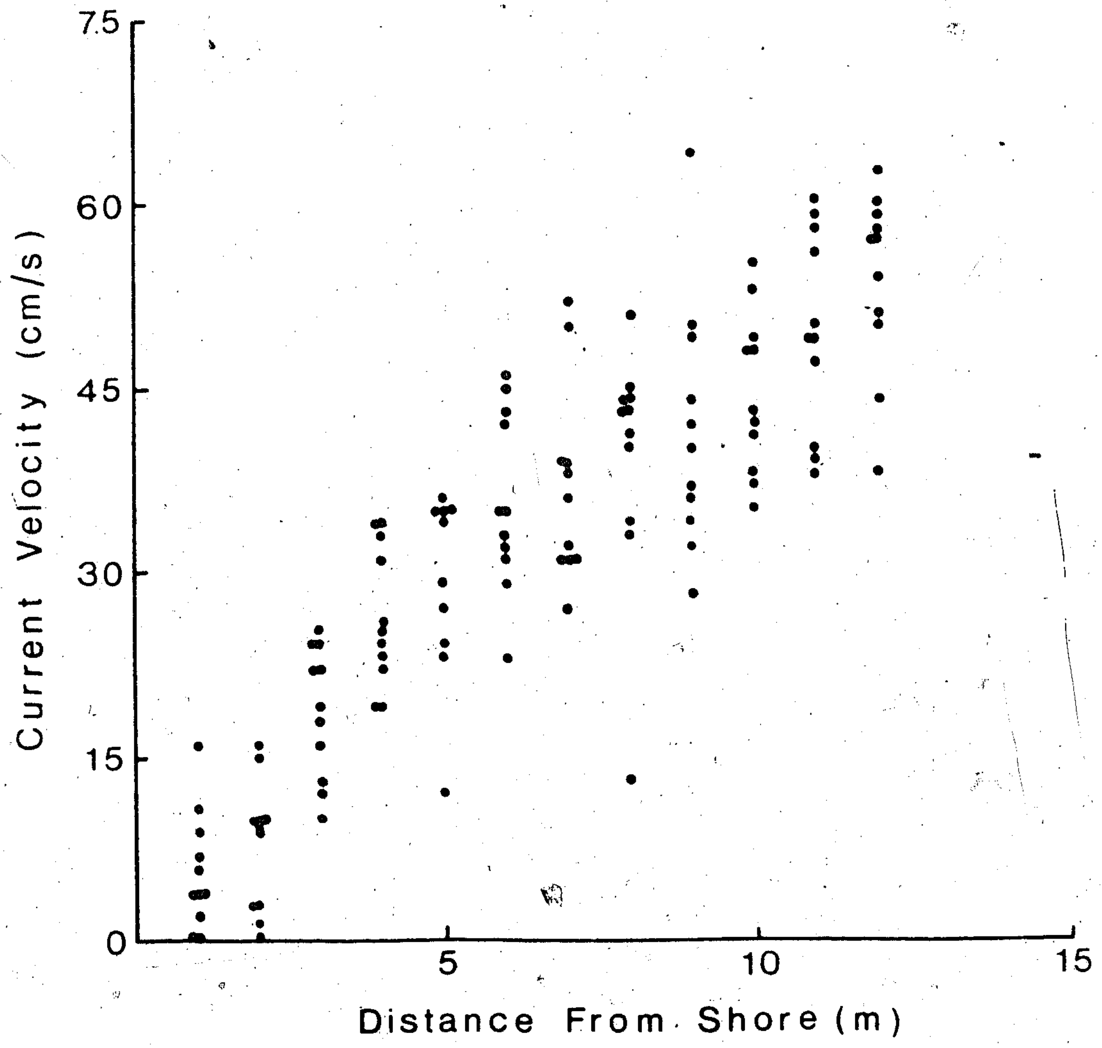


Figure 17. Relationship between mean current velocity and distance from shore in May 1979. Regression equation takes the form v = 5.64 + 4.151y.

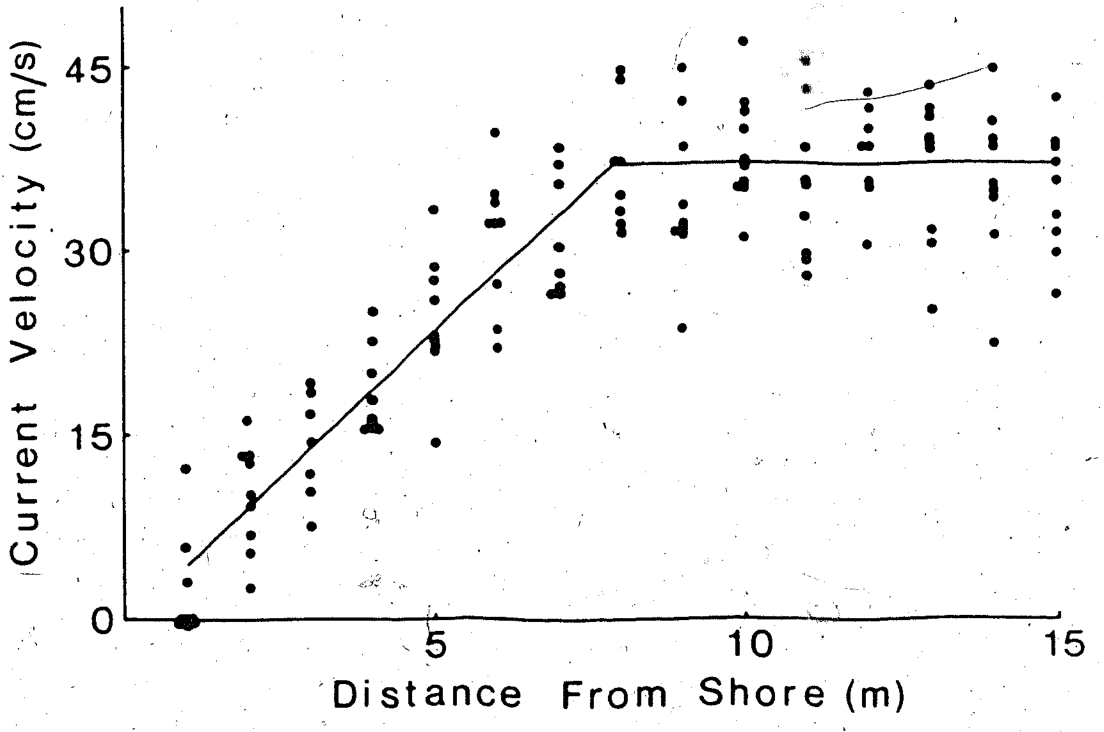


Figure 18. Relationship between mean current velocity and distance from shore in October 1979. Regression equation takes the form $v = -0.56 + 4.773y$ for $y \leqslant 8$ m, and $v = 36.3$ for $y > 8$ m.

of variance of data points eight and more meters from shore indicated no significant increase in current velocity occurred past this point ($p > 0.05$). Linear regression of all data points in spring and of data for the 8 m nearest shore in autumn removed 0.77 and 0.84 of the variation, respectively.

Relationship Between Settling Rate and Mean Current Velocity

Instantaneous settling rates of live and dead animals of each species for each line were determined by the method of McLay (1970). The relationship between number of animals suspended in the water column (n_x) and downstream distance (x) between point of release and the nets is

$$n_x = n_0 e^{-rx} \tag{1}$$

where n_0 is the number of animals released and r is the instantaneous settling rate. A value of r was estimated by linear regression of $\mathrm{Ln}(n_x+1)$, the natural logarithm of the number of animals caught in all nets (corrected for extraneous animals, and adjusted by one to account for zero values), against x for each transect.

Mean current velocity (v_y) for each line (y m from shore) was estimated from Fig. 17 and 18. The relationship between r and v_y was then estimated by regression. Logarithmic transformation of both variables best described the relationship (Fig. 19), giving regression equations of

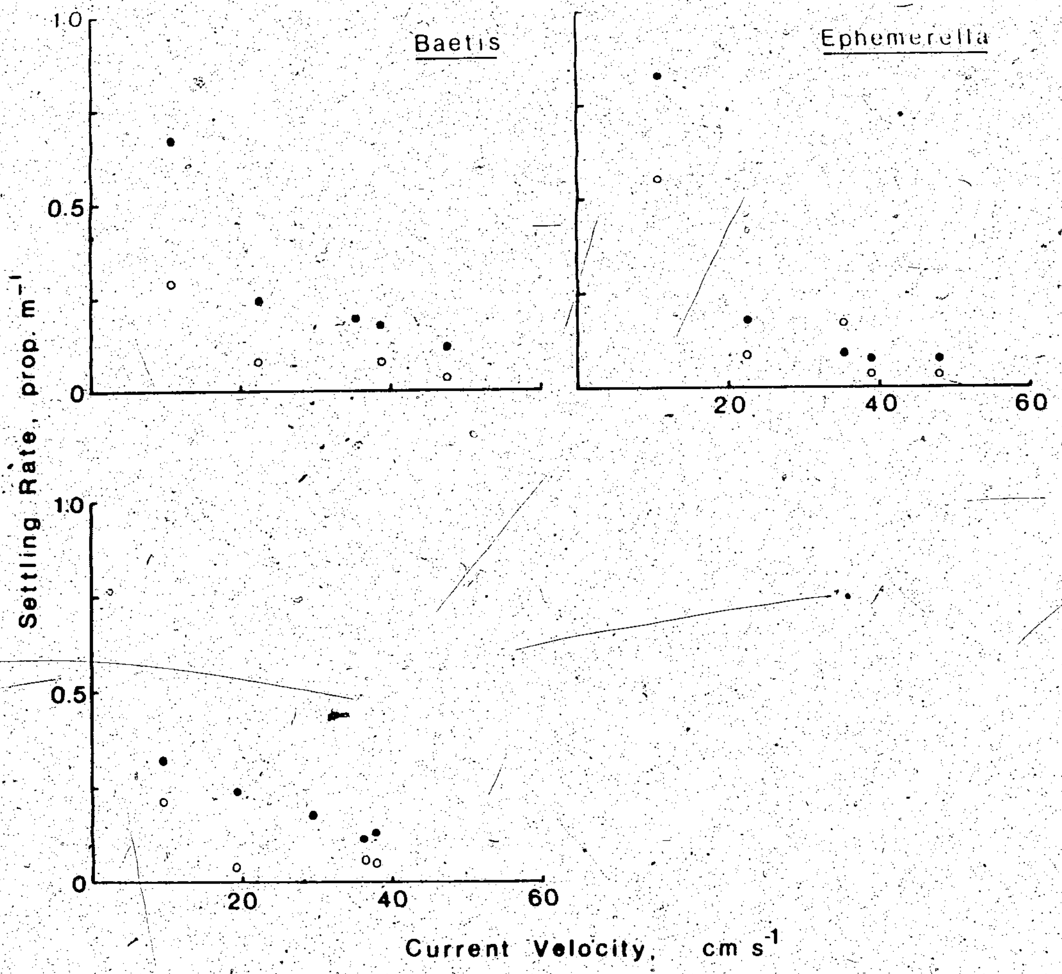


Figure 19. Relationship between instantaneous settling rate and mean current velocity for *B. tricaudatus* (left) and *E. inermis* (right) larvae in May (top) and October (bottom). Solid circles represent trials with live animals; open circles represent trials with dead animals.

the form

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

where β_1 and β_2 are regression constants. Elliott (1971a) and Ciborowski and Corkum (1980) also found this relationship to best fit their data.

Settling Capabilities

To compare the overall settling capabilities of animals, settling capacity (SC) and behavioural settling index (BI) were calculated (Ciborowski and Corkum 1980). Settling capacity is determined by integrating equation 2 over the range of current velocities tested (approximately 10-50 cm s^{-1}, Fig. 19). The relative contribution of behaviour to settling ability of animals (BI) is estimated by taking the complement of the ratio of settling capacities of dead to live animals.

In all series of trials, settling rate was inversely related to current velocity, and live animals exhibited greater settling rates than dead ones (Fig. 19). In spring experiments, settling rates of B. tricaudatus and E. inermis were comparable at low velocities, but E. inermis larvae had much lower settling rates at higher current velocities than did B. tricaudatus larvae. Large B. tricaudatus (spring experiments) had a greater settling capacity than either smaller B. tricaudatus larvae (autumn experiments) or E. inermis larvae (Table 10). Behaviour was of more importance to settling of small than large B.

Table 10. Regression coefficients of relationship between instantaneous settling rate and current velocity, and measures of settling ability of animals.

		β_1	β_2	R^2	SC	BI
E. inermis (May)	Live	33.1502	1.6497	.96	7.4141	.33
	Dead	18.2316	1.5850	.70	4.9428	
B. tricaudatus (May)	Live	8.0154	1.0658	.97	10.5198	.60
	Dead	1.9556	0.9037	.78	4.2496	
B. tricaudatus (Oct.)	Live	1.4054	0.6624	.95	6.5372	.64
	Dead	1.1154	0.9100	.68	2.3765	

tricaudatus larvae; however both had a value of BI greater than that of E. inermis larvae.

Lateral Transport of Suspended Animals

Diffusion theory predicts that suspended particles should disperse normally and in proportion to the square root of the distance from the source of the particles. Turbulence, which is related to current velocity, should contribute an additional diffusion component (Smith 1975). I used multiple regression analysis to determine how the transverse distribution of suspended larvae varied with distance from point of release (x) and with current velocity ($\bar{v}_y$). The dependent variable was the standard deviation (s) of the mean distance from shore of suspended animals caught in nets for each trial. Independent variables were $x^{0.5}$ and $\bar{v}_y$. Values of $\bar{v}_y$ were estimated from Fig. 17 and 18. These regression equations took the form

$$s' = \beta_3 + \beta_4 x^{0.5} + \beta_5 \bar{v}_y \qquad (3)$$

where β_3, β_4, and β_5 are regression coefficients.

Regressions accounted for between 0.49 and 0.79 of the total variation in the dependent variable (Table 11). All β_4 regression coefficients were significantly greater than zero. The β_5 coefficients were greater than zero for all analyses except that for E. inermis (dead) larvae ($p < 0.05$). The β_4 coefficient consistently explained more of the variation in s than did β_5. Thus, the distance animals were transported was a more important predictive variable than was mean current

Table 11. Regression coefficients of relationship between standard deviation of mean distance from shore of suspended animals, distance downstream from point of release (β_4), and current velocity (β_5). β_3 represents intercept. Asterisks indicate that regression coefficient is significantly greater than zero; * $p<.05$, ** $p<.01$, *** $p<.001$.

		β_3	β_4	β_5	R^2
_E_. _inermis_ (May)	Live	-0.714	0.570**	0.0218*	.56
	Dead	-0.038	0.243**	0.0028	.59
_B_. _tricaudatus_ (May)	Live	-0.499	0.589***	0.0110*	.79
	Dead	0.151	0.096***	0.0028*	.56
_B_. _tricaudatus_ (Oct.)	Live	-0.494	0.388*	0.0112*	.49
	Dead	-0.243	0.243***	0.0061*	.60

velocity.

Examination of the regression coefficients in Table 11 indicates that dead animals should be less dispersed than live animals for any given current velocity and distance below a release point. However, because dead animals settle over greater distances than live ones, this is an inappropriate comparison. To provide a better comparison of potential dispersal, both between live and dead animals as well as between species, I determined the distance required for one-half of each sample population to settle ($x_{.50}$). This can be calculated from the formula given by McLay (1970),

$$\begin{aligned} x_{.50} &= \mathrm{Ln}(1/0.50)r^{-1} \\ &= 0.6931r^{-1} \qquad (4). \end{aligned}$$

I determined values of $x_{.50}$ 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 calculated from equation 2, using values of v_y estimated from Fig. 17 (Table 12). The estimates of $x_{.50}$ represent how far downstream of the release point animals would be at the time one-half had settled. The mean distance from shore (y) of the 25 animals still suspended will be the same as it was when they were initially released, but they will now be normally distributed with a standard deviation given by equation 3. I constructed frequency distributions for the expected transverse distribution of suspended animals by substituting $x_{.50}$ and v_y into equation 3 to obtain expected

Table 12. Estimates of instantaneous settling rates (r), distance travelled before one-half of animals settle ($x_{.50}$) and standard deviation (s) of mean distance from shore of suspended animals at $x_{.50}$.

Release distance (y)		2 m (v_y = 13.9)			10 m (v_y = [illegible]2.2)		
		r	$x_{.50}$	s	r	$x_{.50}$	s
E. inermis (May)	Live	0.431	1.61	0.311	0.057	12.07	2.293
	Dead	0.281	2.46	0.383	0.041	17.11	1.110
B. tricaudatus (May)	Live	0.485	1.43	0.358	0.132	5.26	1.372
	Dead	0.181	3.82	0.378	0.060	11.54	0.609
B. tricaudatus (Oct.)	Live	0.245	2.82	0.313	0.109	6.34	1.012
	Dead	0.102	6.82	0.473	0.033	20.73	1.151

standard deviations (Table 12) and fitted a normal distribution about y (Fig. 20).

Dispersal of suspended animals was much greater along the 10 m line than along the 2 m line; but there were no consistent trends between degree of transverse dispersal of live and dead organisms. Live *E. inermis* larvae became more widely dispersed than live *B. tricaudatus* larvae, but dispersal differences between large and small *B. tricaudatus* larvae were minimal.

Discussion

Both *E. inermis* and *B. tricaudatus* larvae have a strong propensity to leave the substrate and become transported by the river current (Chapters 1 and 2). But both have developed behavioural adaptations that minimize the distance they are carried downstream. *Ephemerella* larvae have little control over their orientation during downstream transport. These animals assume a characteristic spread-leg attitude and exhibit periods of undirected swimming activity alternating with periods of passivity. Return to the substrate is largely dictated by their coming into chance contact with the substrate and being able to maintain their position there (Elliott 1971a, McKone 1975, Luedke and Brusven 1976, personal observations). *Baetis* larvae are strong swimmers and are thus better able to control their orientation during transport, especially at higher current velocities.

In some cases these larvae are capable of making a directed return to the substrate (Elliott 1971a, McKone 1975). For both species, a rapid thigmotactic response to contact with the substrate is of primary importance in removing animals from the water column.

The non-directed swimming actions of the larvae have the additional effect of dispersing them transversely in the water column. This is apparent by comparing the regression coefficients of live and dead animals of each species (Table 11). At any given distance downstream of a point of release, live animals will be more widely dispersed than will dead ones. But the greater settling rate of live animals tends to reduce differences in the overall degree of transverse dispersal (Fig. 20).

This lateral transport may be more important than the degree of downstream transport that animals undergo. In a river the size of the Pembina (ca. 65 m wide), longitudinal changes in flow structure occur over distances much in excess of the downstream distance an animal is likely to be transported. Thus, it is improbable that an animal will be carried from, for example, a riffle into a pool section of the river. In contrast, except at the river centre, current velocity changes rapidly across the river. Consequently, animals will be as likely or more likely to experience a change in the primary physical factor controlling microhabitat (current velocity) as the result of lateral transport than because of downstream

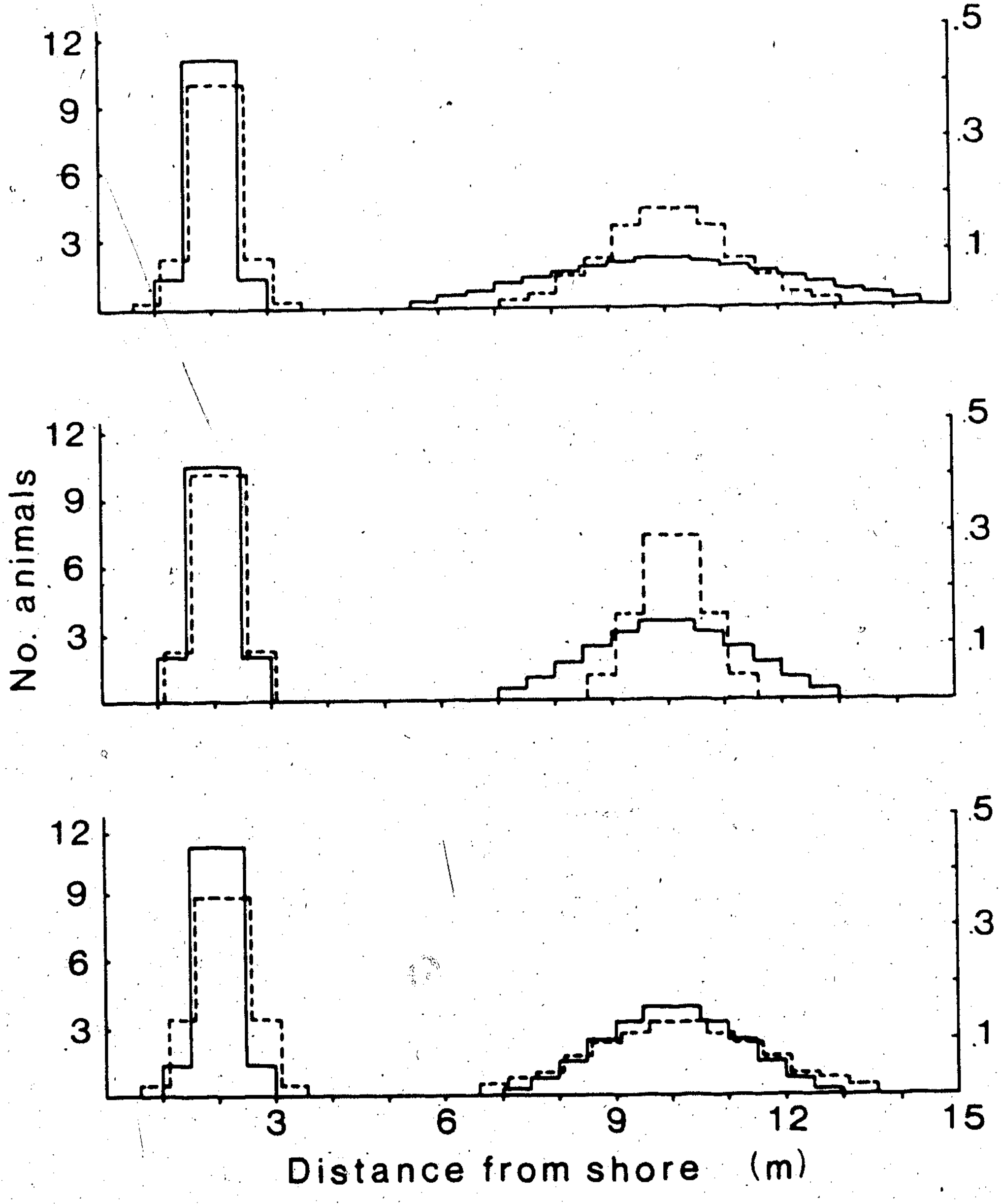


Figure 20. Frequency distribution of suspended animals released 2 and 10 m from shore at the point at which one-half settled. Left vertical axis indicates animals remaining from an initial release of 50. Right vertical axis represents probability of a suspended animal being a given distance from shore. Top, E. inermis (May); centre, B. tricaudatus (May); bottom, B. tricaudatus (Oct.). Solid lines represent live animals; broken lines represent dead animals.

movement.

The instantaneous distribution of suspended larvae is not, by itself, an accurate measure of the eventual distribution of larvae in the substrate. As individuals become increasingly widely laterally dispersed, they come under the influence of increasingly different current velocities. Those insects carried towards shore will have greater settling rates than those carried away from shore. Thus, although the instantaneous distribution of suspended animals may be normal, those individuals carried to slower water will have a greater instantaneous rate of return to the substrate than animals carried to faster water. The distribution curve of insects that actually do settle at any distance (x) below a release point should thus have a mean distance from shore less than that of their release point (y): the curve should be skewed towards the river centre. The skewness of the distribution curve will be determined by how quickly mean current velocity increases as a function of distance from shore. For any given animal entering the water column, there is 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 depart from the substrate, regardless of their 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* larvae are more prone to departure from slow water than from fast water (Chapter 2). This may normally counteract the net effect of lateral transport of suspended animals. Indeed, in the Pembina River, larvae of both species predominate in fast water away from shore during non-flood flow conditions (Chapter 1). When the river floods, however, animals do become more numerous along the margins. Flooding results in both higher current velocities in the river as well as tending to increase the rate of erosion of animals from the substrate. Lehmkuhl and Anderson (1972) also reported that flooding carried _B_. _tricaudatus_ larvae to stream margins.

The microdistribution of populations of animals that are 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 larvae from the drift would require determination of the joint probabilities of departure, downstream movement and lateral transport. Consideration of the influence of these variables on microdistribution may provide important insights into the population dynamics of these species.

CHAPTER 4

INFLUENCE OF DRIFT ON MICRODISTRIBUTION OF TWO MAYFLY SPECIES (EPHEMEROPTERA)

Introduction

Drift is an important aspect of the population dynamics of many lotic invertebrate species. It serves to remove individuals from certain unfavourable microhabitats (Corkum et al. 1977, Walton et al. 1977, Walton 1978, Peckarsky 1980b) and provides an abundant source of animals that colonize unexploited areas downstream (Ulfstrand et al. 1974, Townsend and Hildrew 1976, Williams and Hynes 1976). Many factors can induce animals to depart from the substrate (see Thesis Introduction). The manner in which drifting individuals return to the substrate has also been elaborated (Chapter 3). Several investigators have observed that drift can result in seasonal or short-term displacement of significant proportions of populations (Ulfstrand 1968, Lehmkuhl and Anderson 1972, Hall et al. 1980), but the influence of drift on day-to-day variation in relative distribution of animals has not been examined.

In this chapter, a model is developed that examines the role of daily drift in maintaining the relative distribution of *Ephemerella inermis* and *Baetis tricaudatus* larvae in an ideal river with flow characteristics similar to those of the Pembina River. In the Pembina River, these animals are usually concentrated in fast water (Chapter 1). Nocturnal departure of *B. tricaudatus* larvae is more pronounced from slow water than from fast water areas. Departure of *E. inermis* larvae is minimal at intermediate water velocities (Chapter 2). However, individuals of both populations entering the drift tend to be transported laterally to slower water as well as downstream (Chapter 3). The model developed herein attempts to establish whether the benthic distribution of these populations can be accounted for by simultaneously considering departure and settling capabilities of these animals. The role of behaviour in controlling distribution is also evaluated by comparing predicted changes in distribution of live individuals with those of dead animals, which behave as inert objects.

Methods

Benthic Distribution as a Result of Drift

Aquatic invertebrates can change position in a river either by crawling over or through the substrate or by entering the water column. For the purposes of the model, I will initially assume that the latter mechanism is the only one that results in a net redistribution of animals. Drift is a composite process made up of three events; departure from the substrate, transport in the water column (drift proper), and return to the substrate. It is difficult to separate the actual moment of return to the substrate from the period of transport. Therefore, I will refer to these two components together as settling.

Consider an ideal river composed of a discrete number of parallel homogeneous transects of arbitrary width, running the length of the river. Each transect has an associated known mean current velocity. Current velocity is minimal at river margins and maximal at the centre. A fixed proportion of animals are likely to enter the drift at every point along a given transect each day because departure is a function of current velocity, and current velocity is uniform along the length of each transect. There is also a fixed probability of animals returning to the substrate in the original or any other transect in the river, because settling and lateral transport are also functions of current velocity. If mean current velocity varies predictably across the river, then probabilities of departure and settling can be estimated by considering the position of any particular transect relative to the river margins.

Let $B^0 = (b_1^0, b_2^0, b_3^0, \ldots\ldots b_i^0)$ be a vector where each b_i^0 represents the benthic density of animals in transect i on a given day 0 (symbol conventions are described in List of Symbols). Because each transect is uniform along its length, b_i^0 should be the same for any point along transect i.

Let c_{ij} be the probability that an animal presently in transect i will be located in transect j on the next day. Were it possible to estimate c_{ij} for each transect of the river, one could construct a probability matrix, $\underline{C}$, such that

$$\underline{C} = \begin{pmatrix} c_{11} & \cdots\cdots\cdots & c_{1j} \\ \vdots & & \vdots \\ c_{i1} & \cdots\cdots\cdots & c_{ij} \end{pmatrix}.$$

Assuming that c_{ij} remains constant through time, then $\underline{C}$ is the transition matrix of a Markov chain, and one can expect B^t, the vector describing benthic density of animals among transects after t days to be given by

$$B^t = B^0\underline{C}^t \qquad (5)$$

where $\underline{C}^t$ is the t'th power of transition matrix $\underline{C}$. Matrix $\underline{C}$ represents the probabilities of animals in one transect being located in others after one day. The model requires the assumption that the benthic distribution of an animal on any given day depends only on its location on the prior day, and not on its location at any time previous to this.

Because not all animals depart from the substrate every day, let $\underline{P}(t)$ be a diagonal matrix where each diagonal element $p(t)_{ii}$ represents the proportion of animals that depart from the substrate during time interval t. Thus, $\underline{Q}(t)$ is the proportion of animals that will remain on the substrate,

$$\underline{Q}(t) = \underline{I} - \underline{P}(t) \qquad (6)$$

where $\underline{I}$ is the identity matrix.

Let $\underline{K}$ be a square probability matrix in which each element k_{ij} represents the probability that an animal in transect i that has left the substrate settles in transect j.

$$\underline{K} = \begin{pmatrix} k_{11} & \cdots & k_{1j} \\ \vdots & & \vdots \\ k_{i1} & \cdots & k_{ij} \end{pmatrix}$$

Then the transition matrix, $\underline{C}$, can be determined by

$$\underline{C} = \underline{P}(t)\underline{K} + \underline{Q}(t) \qquad (7).$$

That is, the probability of animals being located in any transect j after time t is the probability of departure from the substrate in any transect i, times the probability of transport from transect i to transect j, plus the probability that an animal in transect j remains there. I assume that any animal that does drift, does not drift more than once per day.

The Model River

In Chapters 1 and 3, I examined the benthic distribution, drift and settling capabilities of live and dead E. *inermis* and B. *tricaudatus* larvae in the Pembina River. This river is approximately 65 m wide during normal flow conditions, but my data have been collected primarily from a region within 12 m of the south riverbank. Within this area, both mean current velocity and depth are linear functions of distance from shore (Chapter 3). Instead of extrapolating this information to provide estimates of flow pattern over the entire width of the Pembina River, I elected to base predictions on a hypothetical river with flow characteristics analogous to those of the sampled portions of the Pembina River. The model river is 26 m wide and is arbitrarily partitioned into 1-m wide transects. Depth and current velocity between 0 and 12 m from the south bank of the model river increase in a manner identical to that estimated for the Pembina River. Depth and current velocity increase at twice this rate between 0 and 6 m from the north bank of the model river. The central eight meters of the model river are of uniform depth and current velocity and are equivalent to values 12 m from the south river margin. Figure 21 illustrates flow characteristics and depth profile of the Pembina and model rivers in May and October 1979.

Departure of Animals From the Substrate

In Chapter 2, regression analysis was used to estimate the relationship between departure rates of live and dead *E. inermis* and *B tricaudatus* larvae and mean current velocity. Estimates of departure from each transect of the model river, during day and at night, were determined by substituting the mean current velocity of each transect into these regression equations. Where departure was a polynomial function of current velocity; mean departure rates were estimated by integration. Because the duration of laboratory experiments was different than field photoperiods, departure rates were corrected to a 16:8 L:D photoperiod in May and to a 12:12 L:D photoperiod in October.

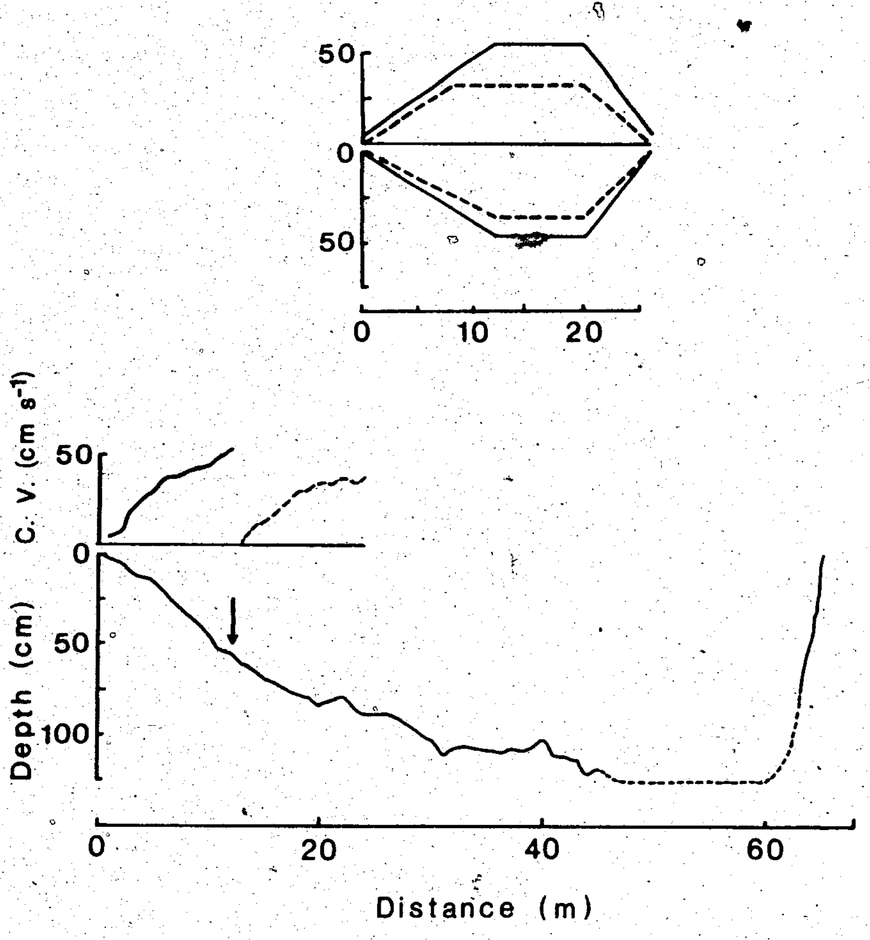


Figure 21. Lower, depth (below) and current velocity (above) profiles of Pembina River at sample site. Arrow (below) and dashed line (above) represent position of river margin in October and corresponding current velocity profile. Upper, depth (below) and current velocity profile (above) of model river in May (solid lines) and October (broken lines). Left margin of graphs corresponds to south river margin.

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 transect i during day and night, respectively. The proportion of animals in transect i that remain on the substrate is

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

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

The proportions that depart or remain during 24 hours are given by

$$p(24)_{ii} = p(D)_{ii} + q(D)_{ii}p(L)_{ii} \quad (8)$$

$$q(24)_{ii} = 1 - p(24)_{ii} \quad (9).$$

Estimates of proportions of live and dead animals that depart from transects of the model river are presented in Fig. 22.

Settling of Animals

The proportion of animals that settle (f_i) over a unit length of any transect i is a function of settling rate, r, and downstream distance, x. Let $m(x)_i$ be the proportion of animals suspended in the water column over a unit length in transect i, x meters downstream of the point of entry into the water column. When x = 0, $m(x)_i = p_{ii}$. The proportion of animals suspended x meters downstream of the entry point is given by

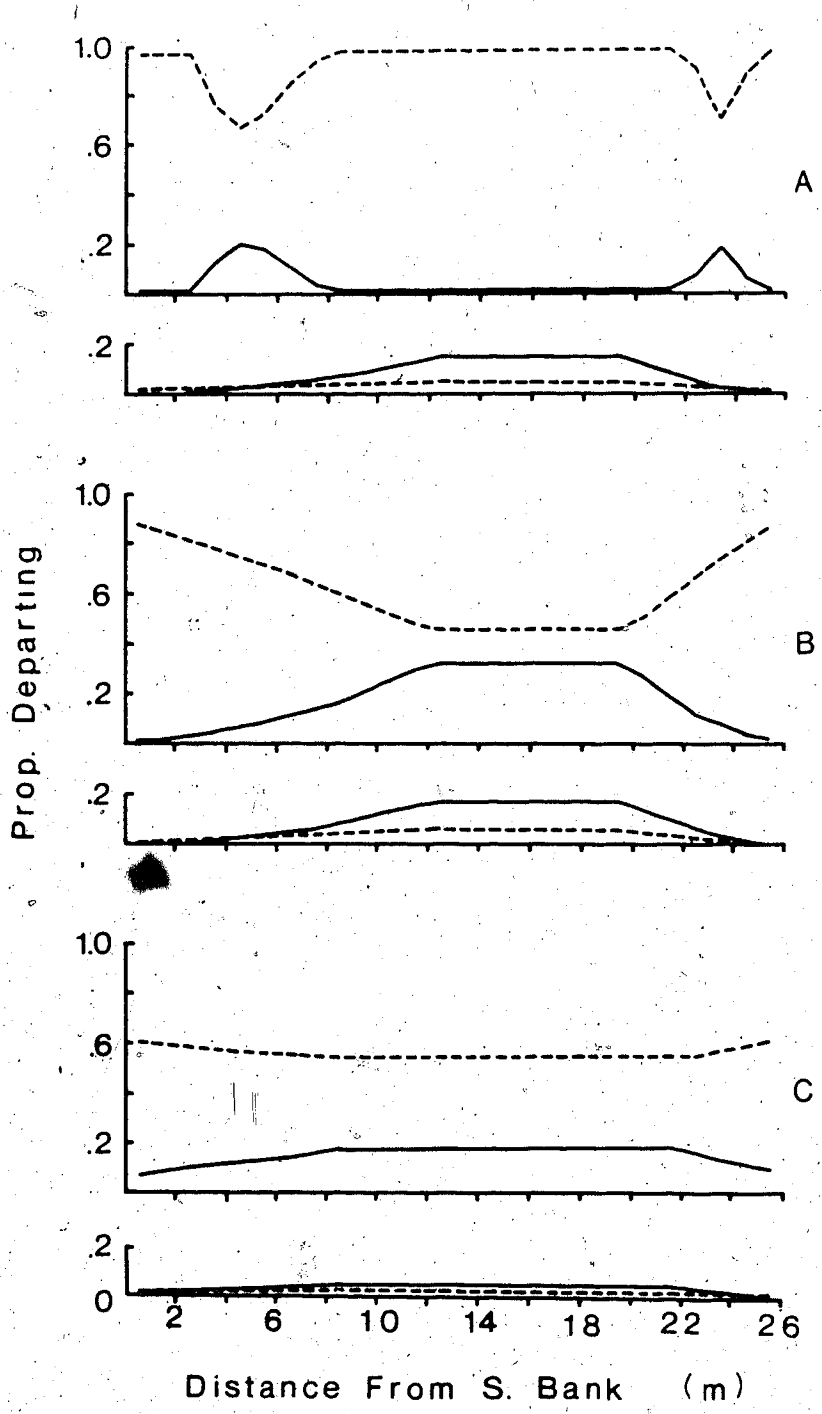


Figure 22. Proportion of animals that depart from substrate in model river during light (solid lines) and darkness (broken lines). A, _E_. _inermis_ (May); B, _B_. _tricaudatus_ (May); C, _B_. _tricaudatus_ (October). Figures above represent departure of live individuals; figures below represent departure of dead animals.

$$m(x)_i = m(0)_i e^{-r_i x} \tag{10}$$

(see Chapter 3). Therefore, the proportion that settle over a unit of downstream distance is given by

$$\begin{aligned} f(x_i) &= m(x-1)_i - m(x-1)_i e^{-r_i} \\ &= m(x-1)_i (1 - e^{-r_i}) \end{aligned} \tag{11}$$

Settling rate is itself a power function of current velocity (v) such that for any transect i,

$$r_i = \beta_1 v_i^{-\beta_2} \tag{12}$$

where β_1 and β_2 are regression constants (see Chapter 3). However, current velocity is a linear function of distance from shore (y) except at the river centre (see Fig. 21). Thus, for any y_i,

$$r_i = \beta_1' y_i^{-\beta_2'} \tag{13}$$

where β_1' and β_2' are regression constants.

The lateral distribution of suspended animals about their point of introduction into the water column (y_i) is normal with the mean given by distance from shore (y_i), and standard deviation s_i (Chapter 3). The standard deviation is dependent on both downstream distance travelled (x) and current velocity (v) such that for animals suspended in any transect i,

$$s_i = \beta_3 + \beta_4 x^{0.5} + \beta_5 v_i \tag{14}$$

where β_3, β_4 and β_5 are regression constants. But because current velocity is a linear function of distance from shore,

$$s_i = \beta_3' + \beta_4' x^{0.5} + \beta_5' y_i \qquad (15).$$

Data on settling rates and lateral dispersal of suspended live and dead E. inermis and B. tricaudatus larvae (Chapter 3) were reanalysed to express r and s as functions of distance from shore (Table 13). An estimate of r_i and s_i for each transect i of the 12 m from the south shore of the model river was determined by substituting the distance from shore of the midpoint of each transect into the regression equations. Estimates for each transect between 0 and 6 m from the north shore were determined by substituting twice the midpoint distance into the regression equations. Values for the eight central transects were calculated by setting $y_i = 12$ and substituting into the equations (Fig. 23).

Probabilities of transport of animals from one transect to all others were generated according to an APL computer program (Appendix 1). The program was designed to determine proportions of animals settling at increasing 1-m steps downstream of the given point of entry, y_i, into the water column. The proportion of animals not settling 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

Table 13. Regression coefficients and coefficients of determination of functions estimating instantaneous settling rate and measures of lateral dispersal of suspended animals in model river.

	SETTLING			LATERAL DISPERSAL			
Reg. Coeff.	β_1'	β_2'	R^2	β_3'	β_4'	β_5'	R^2
			LIVE				
E. inermis (May)	1.837	-1.526	0.93	-0.767	0.570	0.117	0.56
B. tricaudatus (May)	1.231	-0.983	0.94	-0.526	0.589	0.059	0.79
B. tricaudatus (Oct.)	0.504	-0.642	0.98	-0.547	0.388	0.064	0.49
			DEAD				
E. inermis (May)	1.206	-1.620	0.88	-0.045	0.243	0.015	0.59
B. tricaudatus (May)	0.387	-0.798	0.72	0.144	0.096	0.015	0.56
B. tricaudatus (Oct.)	0.247	-0.805	0.62	-0.272	0.243	0.035	0.60

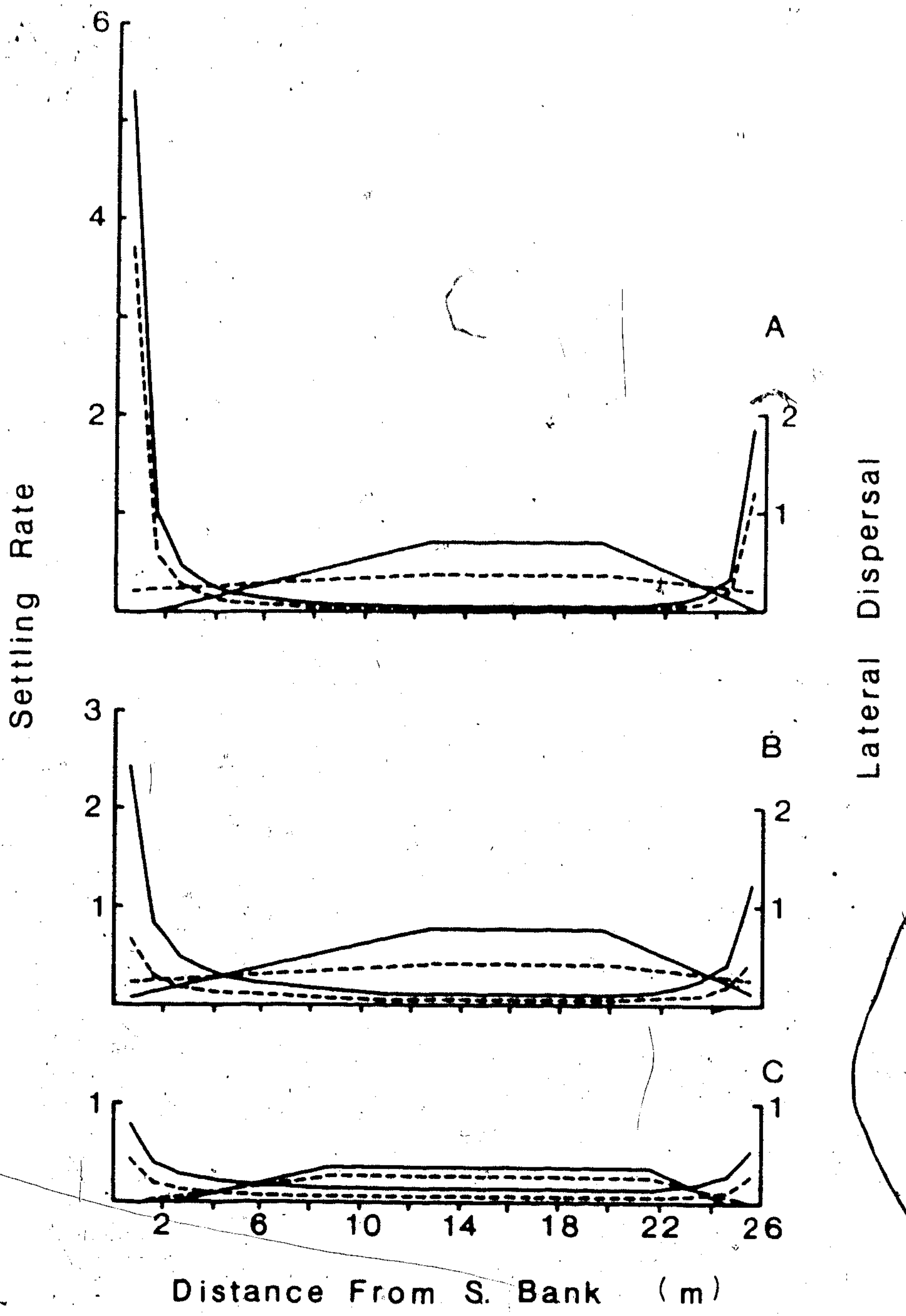


Figure 23. Instantaneous settling rate (concave curves, left axes) and measures of lateral dispersal (convex curves, right axes) of live (solid lines) and dead (broken lines) larvae suspended in model river. A, _E_. _inermis_ (May); B, _B_. _tricaudatus_ (May); C, _B_. _tricaudatus_ (October).

settled exceeded 0.999. The remainder was added to the transect from which animals originated. Summing the proportions of animals suspended at the end of each step provided an estimate (w_{ij}) of the expected contribution of animals originating in transect i, to the drift at other transects, j. Each run of the program produced a vector $K_i = (k_1, k_2, k_3, \ldots\ldots k_{26})$ with each k_j the probability of an animal originating in transect i settling in transect j, and a vector $W_i = (w_1, w_2, w_3, \ldots\ldots w_{26})$, with each w_j the sum of proportions of animals originally suspended in transect i that became part of the drift in transect j. Matrices $\underline{K}$ and $\underline{W}$ were then defined as

$$\underline{K} = \begin{pmatrix} K_1 \\ K_2 \\ K_3 \\ \vdots \\ K_{26} \end{pmatrix} \qquad \underline{W} = \begin{pmatrix} W_1 \\ W_2 \\ W_3 \\ \vdots \\ W_{26} \end{pmatrix} .$$

Matrix $\underline{K}$ was used in equation 7. Matrix $\underline{W}$ was used in determining estimates of numbers of animals that would be caught in drift nets placed across the model river (see below). $\underline{K}$ and $\underline{W}$ were estimated for both live and dead *E. inermis* and *B. tricaudatus* larvae. Matrices are tabulated in Appendix 2.

Benthic Distribution of Animals in the Model River

Data on benthic microdistribution of E. *inermis* and B. *tricaudatus* larvae in the Pembina River were collected throughout the ice-free period in 1979 (Chapter 1). Five replicate Hess samples were taken at 10-15 day intervals at distances of 3 and 11 m from the south bank until mid-June, and at 3, 7, and 11 m from the south bank thereafter until November.

Benthic densities in the model river were based on field benthic densities of only large E. *inermis* and B. *tricaudatus* larvae from May and October (Chapter 2). Numbers of large animals in each sample within series of replicates on each date were adjusted by regressing benthic densities against numbers of all other animals taken in each sample (Chapter 1) to reduce sample variances (Sokal and Rohlf 1969).

The relationship between adjusted benthic density of each population and distance from the south river margin on each date was determined by piecewise linear regression. Benthic densities of animals in the model river were then estimated from these regression equations (Table 14). Densities between 13 and 20 m from the south shore were the same as at the 12 m point. Benthic densities from 0 to 6 m from the north bank were obtained by doubling the slope of the regression equations.

Table 14. Regression coefficients and coefficients of determination of functions describing benthic distribution of animals in model river.

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

Comparison of Observed and Predicted Changes in Benthic Distribution

All settling and departure estimates were based on the results of experiments conducted with large animals collected in May or October 1979. Benthic samples that most closely corresponded with these periods were taken on May 15 and 28, and October 4 and 15, 1979.

Predictions of relative changes in benthic density in the model river were made for 13 and 11 day intervals, respectively, to correspond to the time elapsed between samples taken in the Pembina River. Predictions were made using equation 5. For May trials, the initial distribution of animals (B^0) was the vector of benthic densities estimated from May 15 benthic samples. Initial distribution (B^0) for October trials was that estimated from October 4 samples. Dead populations were given the same initial distributions as their live counterparts.

Comparison of Observed and Predicted Drift of Animals

Observed Drift-- Drift of animals in the Pembina River was studied on May 28-29 and October 7-8, 1979 (Chapter 3). Large drift nets filtered all animals from 12 1-m wide transects extending from the south river bank. Samples were taken at 0900, 1200, 1800 and 2400 h. All E. inermis and B. tricaudatus larvae were measured and only large individuals were used in subsequent analyses. Drift was expressed as drift density (number of animals m^{-3} water filtered).

Drift of E. inermis and B. tricaudatus larvae is aperiodic during daylight hours but not at night (see Fig. 8, Chapter 1). Maximum drift of E. inermis larvae occurs near midnight. Baetis tricaudatus larvae exhibit at least two nocturnal peaks of drift, the major one occurring just prior to dawn. Average daytime drift density of each population in each transect was determined by dividing the total number of animals caught in the three daytime sampling periods by the total volume of water filtered by each net. Average nocturnal drift was estimated by dividing the number of animals caught in each net at 2400 h by the volume of water filtered at that time and multiplying these values by the difference between drift at 2400 h and average nocturnal drift in Fig. 8.

Predicted Drift-- The total numbers of animals expected to depart from one m^2 of substrate in transect i of the model river during day (L) and at night (D) are given by

$$n(L)_i = b_i p(L)_{ii} \qquad (16)$$

$$n(D)_i = b_i p(D)_{ii} \qquad (17)$$

where b_i is the benthic density of animals in transect i and p_{ii} is the proportion that depart from the substrate. Since matrix W represents the sum of proportions of animals departing from transect i that would be carried over a point in transect j, the total number of animals that should be caught in drift nets placed across the transects during day ($N_{max}(L)$) and night ($N_{max}(D)$) would be

$$N_{max}(L) = N(L)\underline{W} \qquad (18)$$

$$N_{max}(D) = N(D)\underline{W} \qquad (19).$$

However, the concentration of animals in the water above each m^2 of each transect also depends on the depth of water (z_i) in each transect i. Thus, the concentration of drifting animals in each transect is given by

$$n'_{max}(L)_i = n_{max}(L)_i/z_i \qquad (20)$$

$$n'_{max}(D)_i = n_{max}(L)_i/z_i \qquad (21).$$

Volumes of water passing points in each transect of the model river were estimated using current velocity and depth estimates from Fig. 21 and assuming photoperiods of 16:8 L:D in May and 12:12 L:D in October. Predicted drift density during day and at night was determined by dividing the total diluted number of animals (N'_{max}) predicted to drift past a point during day and at night by the estimated volume of water passing each point. Expected drift density of live and dead _B. tricaudatus_ larvae was determined using benthic distributions estimated on May 28 and October 4. Expected drift of live and dead _E. inermis_ larvae was determined by using estimated benthic distributions on May 28.

Mean Daily Downstream Distance Travelled by Animals

The sum of proportions of animals that drift past a point in a river is the product of the proportion departing from the substrate and the mean distance travelled (Elliott 1971a). Thus,

$$w = m(0)\bar{x} \qquad (22).$$

When m(0) = 1, as assumed in the settling computer program, this equation reduces to

$$\bar{x} = w \qquad (23).$$

Since W is the matrix of the sums of proportions of suspended animals that are transported from any transect i to each transect j, the mean downstream distance travelled by animals that depart from any transect i ($\bar{x}_i$) is the i'th row total of W, i.e.

$$\bar{x}_i = w_{i1} + w_{i2} + w_{i3} + \ldots\ldots + w_{i26} \qquad (24)$$

and $\bar{X} = (\bar{x}_1, \bar{x}_2, \bar{x}_3, \ldots\ldots \bar{x}_{26})$.

The mean distance travelled by all animals in the population that drift during one day ($\bar{\bar{x}}_N$) is

$$\bar{\bar{x}}_N = \frac{N(24)\bar{X}}{N(24)I} \qquad (25)$$

where N(24) is the vector of the number of animals that depart from the substrate over 24 hours and I is the identity vector.

The mean downstream displacement of the entire population as a result of drift is

$$\bar{\bar{x}}_B = \frac{N(24)\bar{X}}{B^0 I} \qquad (26)$$

where B^0 is the vector of benthic density of animals across the model river on day 0. It is important to note, however, that because $n(24)_i = b_i p(24)_{ii}$, both $\bar{\bar{x}}_N$ and $\bar{\bar{x}}_B$ are dependent on the benthic distribution of animals.

Downstream distances travelled by drifting animals and displacement of populations were calculated for live and dead E. inermis and B. tricaudatus larvae, based on estimates of observed benthic distributions on May 28 and October 4 1979.

Results

Benthic Distribution

The observed benthic distribution of animals changed minimally over the time intervals examined in May and October. In contrast, the model predicted large-scale transport of individuals of all populations towards shore (Fig. 24,25,26). In all cases, predicted densities of animals fell outside the 95 percent confidence intervals of observed densities of organisms. The model also indicated that densities of animals should become greater adjacent to the north bank than the south bank of the model river.

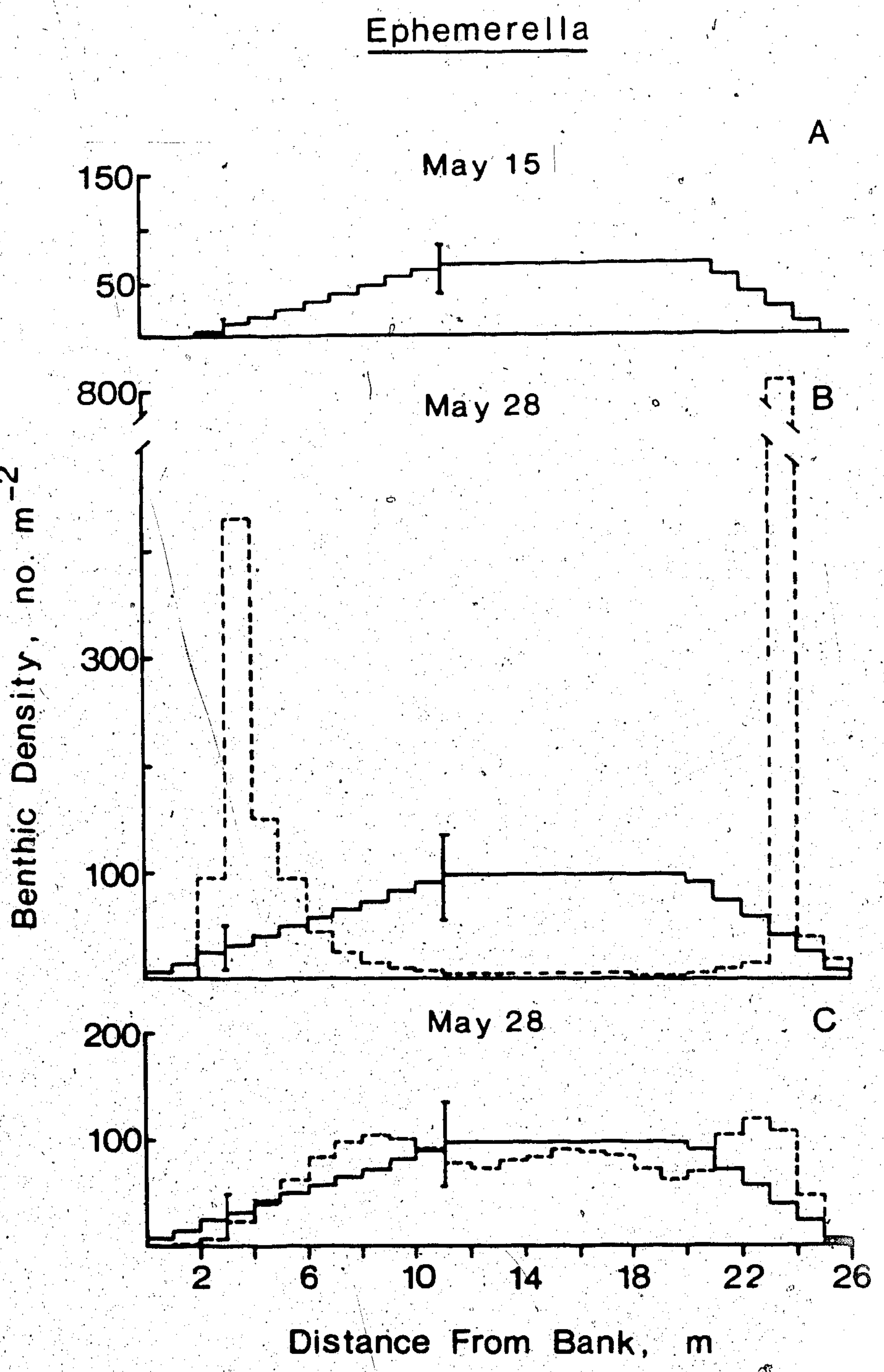


Figure 24. Observed (solid lines) and predicted (broken) lines) distribution of *E. inermis* larvae in the model river. Vertical lines represent 95 percent C.I. of observed densities of larvae. A, May 15 1979; B, May 28 1979 (live animals); C, May 28 1979 (dead animals).

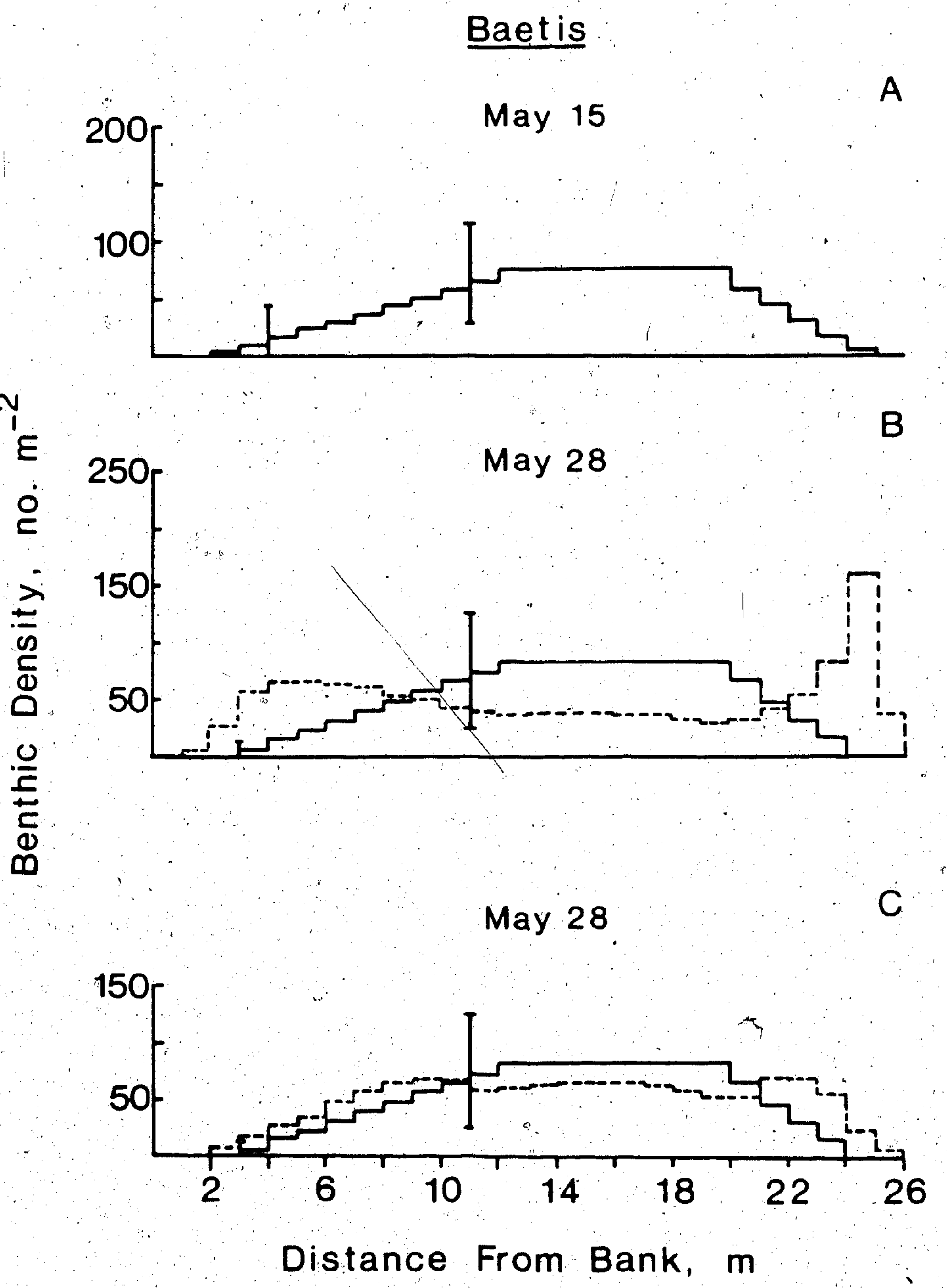


Figure 25. Observed (solid lines) and predicted (broken lines) distribution of B. *tricaudatus* larvae in model river. Remaining explanation as in Fig. 24.

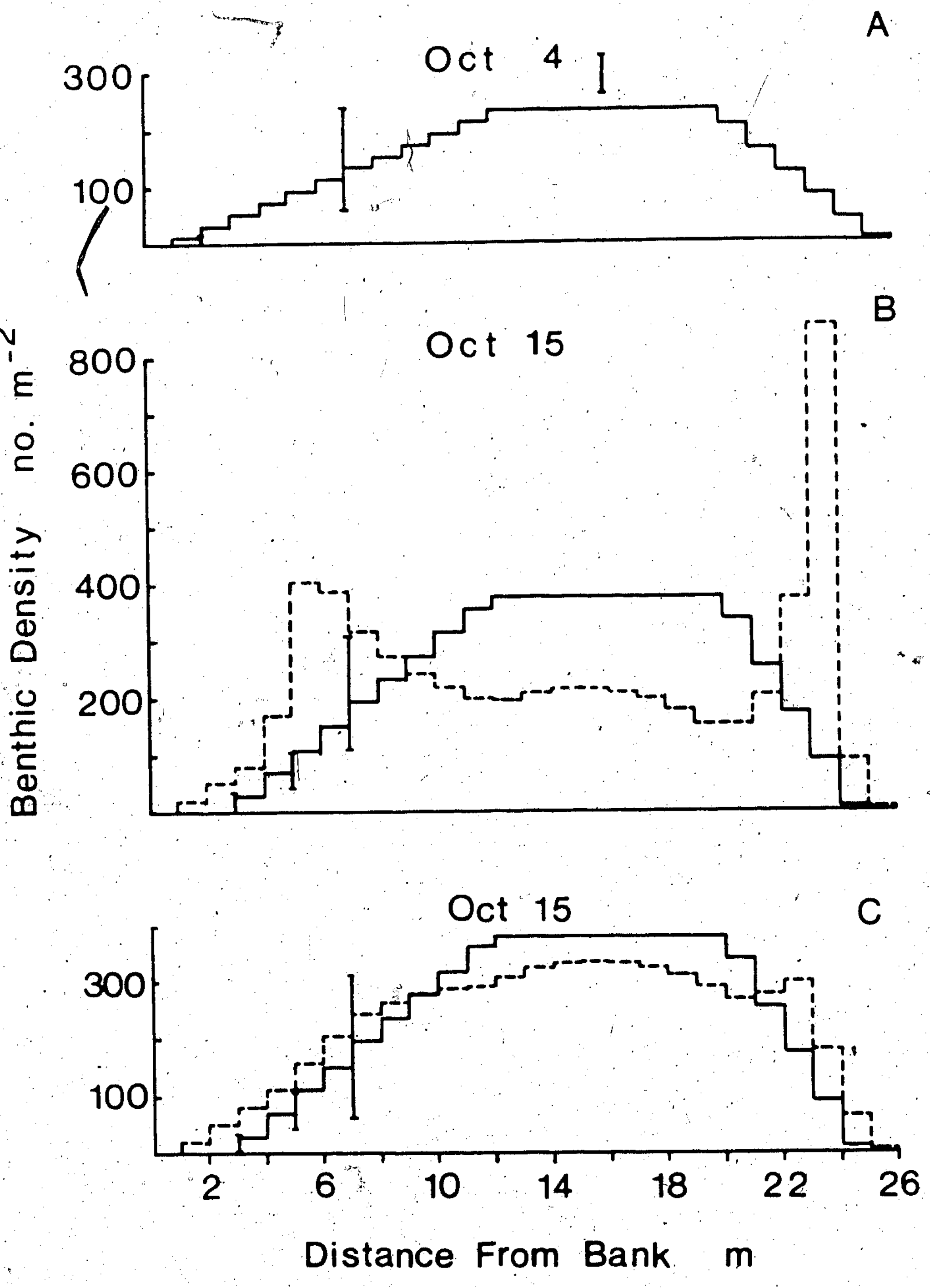


Figure 26. Observed and predicted distribution of B tricaudatus larvae in model river. A, October 4 1979; B, October 15 1979 (live animals); C, October 15 1979 (dead animals). Remaining explanation as in Fig. 24.

Changes in distribution predicted for live animals were more pronounced than for dead populations of the same species. A greater degree of lateral redistribution was evident in May than in October populations of *B. tricaudatus* larvae. In May, changes in benthic distribution of the *E. inermis* population were more noticeable than changes in distribution of the *B. tricaudatus* population.

Drift Density

Predicted drift densities of populations of dead animals were generally much lower than predicted drift densities of corresponding live populations.

Observed drift densities of *E. inermis* larvae were much greater in May than in October (Fig. 27). In May, predicted drift densities of live animals corresponded closely to values observed in the Pembina River both during day and at night.

Observed nocturnal drift densities of *B. tricaudatus* larvae were slightly greater in May than in October (Fig. 28). The reverse was true for daytime drift density values. The model markedly underestimated May drift densities of live *B. tricaudatus* larvae. October predictions of drift density were too high during daytime and too low at night. All predictions of drift densities of dead animals were underestimates of drift density of live animals in the Pembina River.

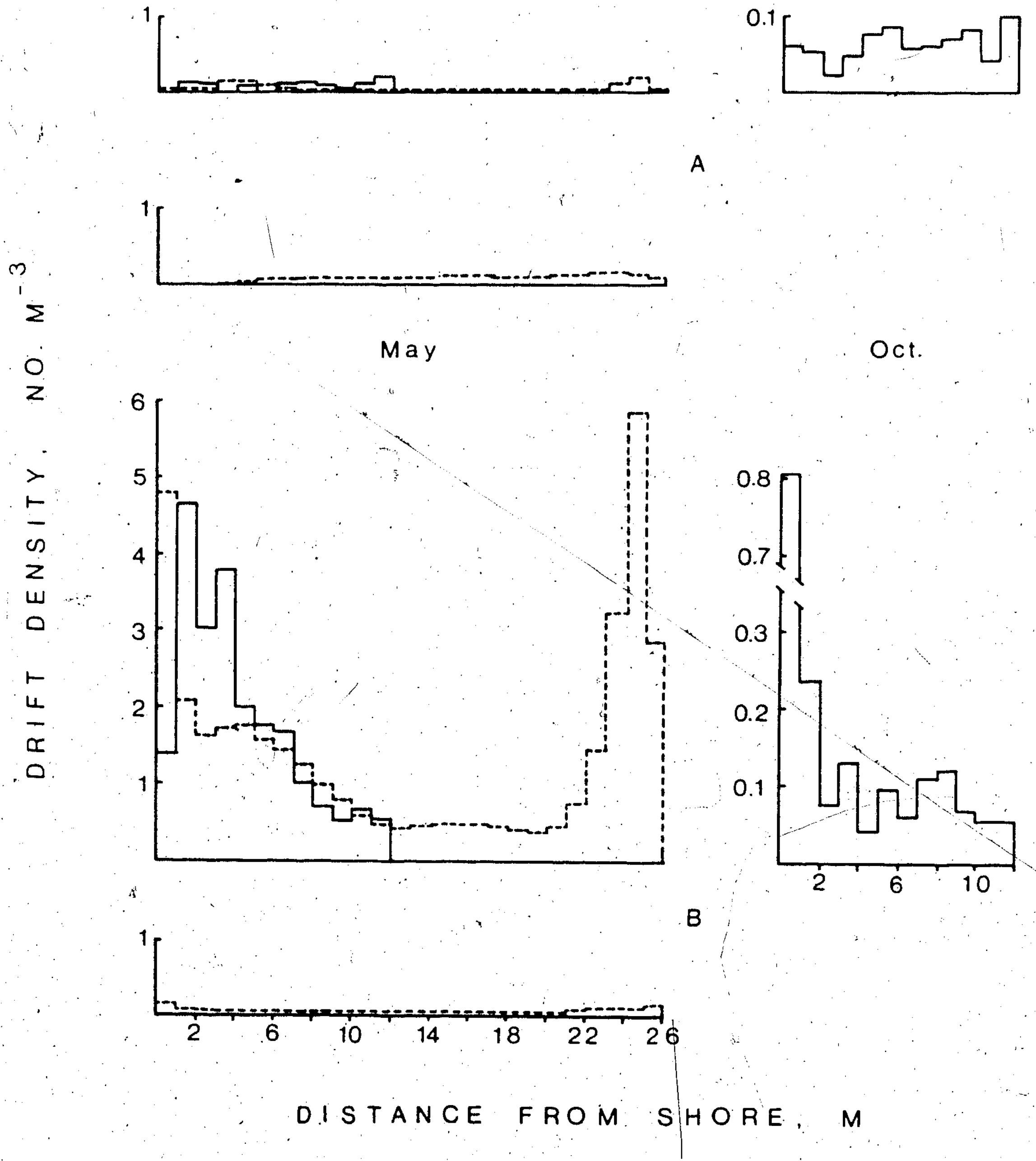


Figure 27. Observed (solid lines) and predicted (broken lines) drift density of *E. inermis* larvae in Pembina and model rivers, respectively, in May (left) and October (right). A, daytime drift density (live animals above, dead animals below); B, nighttime drift density (live animals above, dead animals below). Note that scales of vertical axes differ.

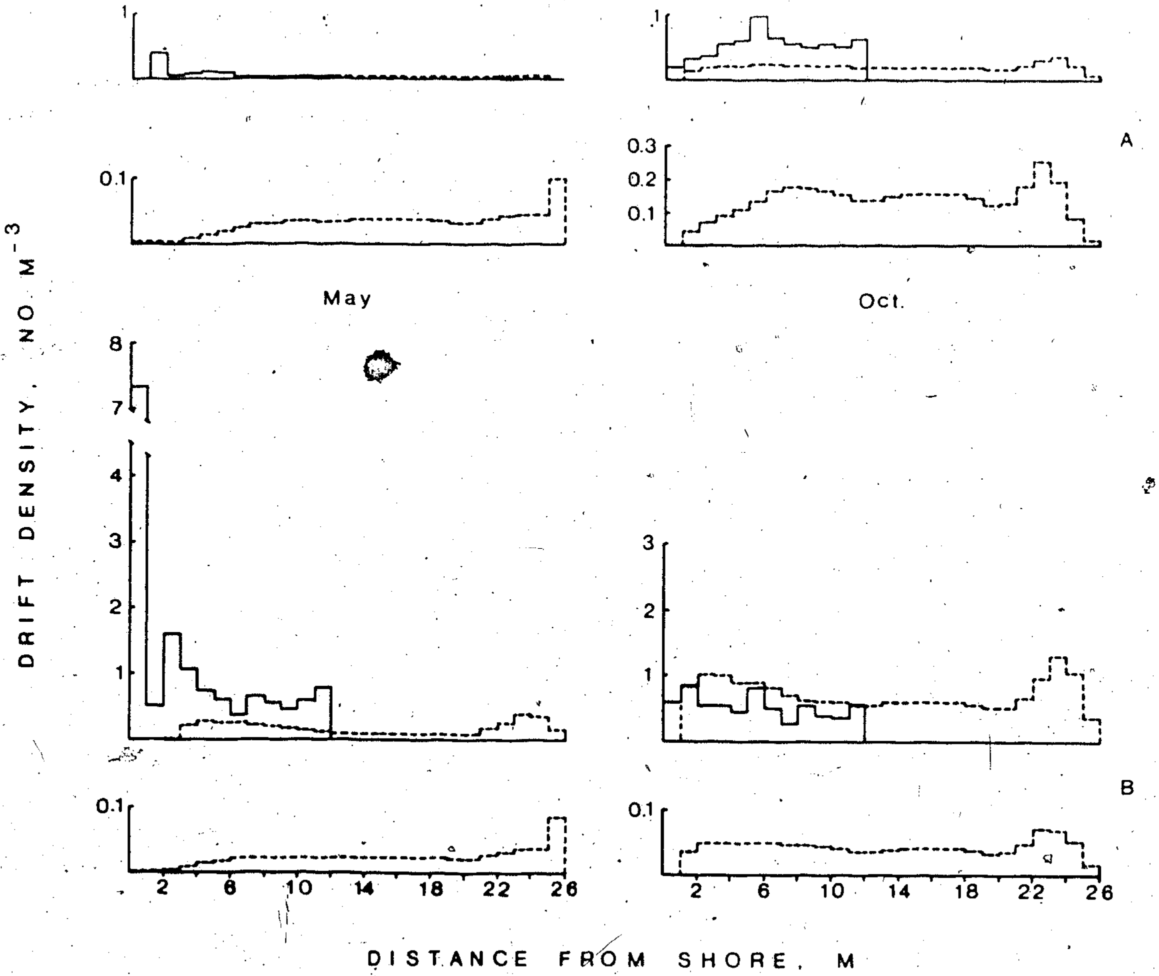


Figure 28. Observed and predicted drift density of B. *tricaudatus* larvae in Pembina and model rivers. Remaining explanation as in Fig. 27.

Distance Drifted Downstream

Dead individuals of both species that departed from the substrate were transported at least twice as far downstream as their live counterparts (Table 15). However, because live animals had higher departure rates, the daily downstream displacement of entire populations was greater for live than for dead animals. Downstream displacement of the _E_. _inermis_ population was over twice as great as for the _B_. _tricaudatus_ population. Displacement of _B_. _tricaudatus_ populations (live animals) were almost identical in May and October.

Discussion

Results of the model runs indicate that drift is responsible for transport of large numbers of animals from the river centre to near-shore regions as well as downstream. This effect was observed for both populations, and was most noticeable in live animals. Test runs of the model using theoretical data (Appendix 3) indicate that animals will become concentrated at stream margins whenever lateral dispersal values at shoreward transects are close to zero, regardless of individuals' departure and settling capabilities. My estimates of lateral dispersal for live animals in both populations included at least one such value. Thus, the model suggests that, given enough time, drift should result in all _E_. _inermis_ and _B_. _tricaudatus_ larvae eventually

Table 15. Predicted mean downstream distance travelled by animals that drift ($\bar{\bar{x}}_N$) and net downstream displacement of populations ($\bar{\bar{x}}_B$) in model river.

Species	Condition	$\bar{\bar{x}}_N$	$\bar{\bar{x}}_B$
E. inermis (May)	Live	15.10	14.89
	Dead	37.29	5.59
B. tricaudatus (May)	Live	8.25	6.44
	Dead	17.70	3.24
B. tricaudatus (Oct.)	Live	8.99	6.43
	Dead	26.00	1.76

becoming located in and remaining in those transects closest to river margins. Estimates of change in distribution of dead organisms were less pronounced, primarily because dead animals were less prone to depart from the substrate. Reduced departure rates tend to slow the rate of change in distribution, even when settling rates of suspended animals are low (Appendix 3).

Differences in the rate of change in distribution among populations of live animals were also largely due to differences in daily departure rate. It appears that behavioural mechanisms that result in reduced departure rates from fast-water areas are inadequate to compensate for the increased degree of lateral transport associated with behavioural mechanisms that facilitate a rapid return to the substrate. Indeed, the influence of behaviour results in more pronounced lateral displacement of animals than would occur if individuals departed and settled in a completely passive manner.

Examination of predicted downstream displacement estimates shows a similar situation. Even though dead animals that became suspended in the water column were transported greater distances downstream than their live counterparts, higher departure rates of live animals resulted in greater net downstream displacement of populations.

Because there was such a large discrepancy between observed and predicted changes of distribution, it is tempting to suggest that the results are an artifact of my estimates of departure, settling or lateral transport. Yet, model estimates of the magnitude and spacial pattern of drift, which were based on the same data, were surprisingly close to drift observed in the Pembina River. Although I had expected the model to overestimate amount of drift because derived departure rates of live animals were almost certainly overestimated (see Chapter 2), the most pronounced deviations were underestimates. It is possible that overestimates in departure rate were compensated for by equally erroneous overestimates of settling rate. All determinations of settling rate were made during daylight hours (Chapter 3), whereas most drift occurred at night, especially in May. Luedke and Brusven (1976) and Walton (1978) found that drifting animals tended to have lower settling rates at night than during the day. However, their experiments were carried out in very shallow laboratory streams (depth less than 6 cm); thus, their observations may not be applicable to all portions of a river. Elliott (1971a) found no differences between daytime and nocturnal settling rates of animals released into the water column of a small English stream.

An alternative explanation is that some animals engage in multiple drift episodes. In such an event, the model would underestimate drift because my estimates of departure assumed that animals drifted not more than once every 24 hours. It should be noted, however, that any true underestimate of the number of animals transported in the water column, or of the downstream distance they are carried, would produce a corresponding underestimate of the amount of lateral redistribution of the population. For this reason, I feel that the predicted changes in distribution are representative of the direction, if not the exact magnitude, of the transportive effects of drift on the distribution of E. inermis and B. tricaudatus populations.

Because there is such a large discrepancy between observed and predicted benthic distribution of larvae, it is clear that drift alone cannot account for the microdistribution of these populations in the Pembina River. The benthos must undergo some form of compensatory benthic movement that counteracts the transportive effects of drift. Although there is no experimental e[illegible]ence that aquatic invertebrates are capable of directed lateral movements in rivers, indirect information from several sources lends credence to the possibility. Seasonal onshore-offshore movements of mayfly populations in lentic habitats have been reported by Gibbs (1973, 1979), Corkum (1982) and Brittain (personal communication). Cheatum (1934) and Horst and Costa (1975) suggested that similar seasonal movements occurred in pulmonate gastropods.

Seasonal changes in benthic distribution of Ephemeroptera in lotic habitats have been reported by Ide (1935), Harker (1953a), Macan (1957), Ulfstrand (1968), Edmunds et al. (1976) and Hall et al. (1980). In addition, Neave (1930), Haydon and Clifford (1974), Keller (1976), and Olsson and Söderström (1978) have observed substantial seasonal upstream movements of mayfly larvae in running waters; on the order of hundreds of meters over one or two weeks.

There is less evidence of short-term lateral movement in lotic systems. Elliott (1971b) found that daily movements of animals towards the centre of a stream were more pronounced than movements towards margins. In contrast, Bird and Hynes (1981) reported that benthic movements of lotic invertebrates in an Ontario stream were random.

Seasonal data on benthic distribution of E. inermis larvae in the Pembina River (Chapter 1) suggest that benthic movements may indeed carry large numbers of individuals towards the river centre at certain times. Maximum abundance of larvae occurs near shore during late summer, but by the time ice forms in autumn, densities have become greatest in regions remote from shore. Because drift of this population is very reduced in autumn, this change in microdistribution can only occur by benthic movement.

There is no simple way to estimate what degree of lateral movement would be necessary to compensate for the effect of drift on distribution indicated by the model, because there is no unique set of probabilities of movement between transects that will exactly counteract the changes in benthic position of animals dictated by the model's transition matrices. However, I used an iterative method to provide a general idea of the minimal degree of movement towards the stream centre necessary to balance the loss of insects from the eight central transects of the model river after the first day's drift. My assumptions were that animals either remained in their present transect or moved towards the stream centre. The mean distance moved was assumed greatest for animals in transects adjacent to river margins (where current velocity was minimal) and to decrease linearly to 0.1 m in transects 12 and 21 (those transects adjacent to the eight central transects). No net lateral movement should occur at the river centre.

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

$$B^{0\prime} = B^1\underline{C}' \qquad (27).$$

The elements of $B^{0\prime}$ corresponding to densities in the eight central transects of the model river were then summed. The function describing benthic movement towards the river centre was judged adequate to compensate for lateral transport by drift if the sum determined above was greater than or equal to 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 calculated and evaluated.

The maximum mean distance that would have to be moved by dead animals at the river margin to compensate for lateral transport by drift was estimated at between 0.3 and 1.0 m per day (Table 16). Live B. tricaudatus larvae would have to move a maximum mean distance of 2-3 m away from the river margin, depending on the season. Ephemerella inermis larvae at the riverbanks would have to travel 6.6 meters. Movements of this magnitude are probably well within the capabilities of these larvae, provided they are able to orient in a direction that will carry them towards the river centre.

Elliott (1971b) estimated that Baetis rhodani (Pictet) and Ephemerella ignita (Poda) larvae moved modal distances of 6.25 and 4.75 m upstream per day in a trough placed within a stream. Although Elliott (1971b) also observed that

Table 16. Functions describing estimated minimum mean lateral distance that must be travelled to compensate for lateral transport by drift in model river.

Species	Condition	Intercept	Slope
E. inermis (May)	Live	6.7	-0.57
	Dead	1.0	-0.08
B. tricaudatus (May)	Live	2.9	-0.24
	Dead	0.7	-0.05
B. tricaudatus (Oct.)	Live	2.1	-0.17
	Dead	0.3	-0.02

lateral movements were not as pronounced as were upstream movements, he found more animals crawled towards the stream centre than towards shore, even though the shoreward-facing nets were situated very close to the river margin. It is certainly possible that orthokinetic responses to low current velocity could result in accumulation of crawling rheophilic animals in faster water. Many studies have indicated lotic invertebrates becoming substantially more active when subjected to reduced current velocities (Edington 1965, Elliott 1968a,b). Animals in fast water tend to become oriented in an upstream-facing direction (Neave 1930) so that little lateral change in position should occur in these regions.

If, in the absence of contrary evidence, preferred microhabitats are defined as those regions in which animals are most abundant during stable flow conditions, then drift does not by itself result in the maintenance of populations within preferred habitats. There is little change in benthic distribution of _B_. _tricaudatus_ larvae during periods of normal summer discharge. _Ephemerella inermis_ larvae become proportionately more numerous near shore in midsummer (Chapter 1), possibly because benthic movements in this population do not completely compensate for drift. Thus, the preferred microhabitat of these populations does not appear to change dramatically during the summer.

Nevertheless, departure rates of larvae, even in regions of maximum abundance, are remarkably high.

Laboratory experiments suggest this is unlikely the result of density-dependent interactions. Departure from the fast-water habitat may be largely the result of predator activity (Corkum and Pointing 1979, Corkum and Clifford 1980, Peckarsky 1980b, Walton 1980b) or local depletion of certain food resources such as diatoms (Hildebrand 1974, Keller 1976, Bohle 1978), or both. Drifting animals are probably incapable of continuously monitoring the substrate over which they pass, since the moment of return to the substrate is largely random and dependent on chance contact with the substrate (Chapter 3). Thus, animals that settle in unfavourable regions must search over the substrate to find other favourable areas. Relatively unidirectional movements (i.e. towards the river centre) may be a more efficient means of finding these microhabitats than random searching (Pyke 1978), especially if they tend to run parallel to the river margins.

The proposed system of drift and lateral countermovement would be particularly efficient in minimizing downstream displacement of animals during extended periods of flooding. During normal discharge conditions, mean downstream transport of all live _E_. _inermis_ and _B_. _tricaudatus_ larvae that drift are approximately 15 and 8 m, respectively. Net downstream displacement of _B_. _tricaudatus_ populations is substantially less, although that of _E_. _inermis_ is not. Upstream benthic movements may partially (Bishop and Hynes 1969b, Hultin et al. 1969, Elliott 1971b, Keller 1976, Bird and Hynes 1981) or completely (Lehmann 1967, Marchant and Hynes 1981) compensate for this. During periods of flooding, however, current velocity at all points in the river increases proportionately to the increase in discharge. Both the change (Bütz 1973, Ciborowski et al. 1977) and the absolute increase in current velocity (Madsen 1968, Anderson and Lehmkuhl 1968) result in increased ("catastrophic") drift and inhibit upstream movement (Elliott 1971b). Besides being more prone to dislodgement, animals will require greater distances to settle. The increased incidence of drift will result in a greater net transport of individuals towards the river margins as well as increased downstream travel. Thus, subsequent erosion of animals from their points of return to the substrate will produce relatively smaller downstream displacement. As long as the erosional influence of the flood inhibits countermovements, each dislodgement will result in further transport closer to shore together with a reduction in the downstream distance travelled. The net effect on populations would be to produce greater abundance of individuals near shore and reduced numbers at the stream centre. Such changes in distribution occur for both populations during floods in the Pembina River. Lehmkuhl and Anderson (1972) observed similar effects in an Oregon stream during flood events.

Subsequent declines in discharge would again permit access to the river centre, and benthic movements would result in rapid return of individuals to "preferred" regions.

Drift and benthic movement are both integral parts of such a redistribution system. For this reason, one would expect only those organisms capable of free-ranging benthic movement to exhibit a high propensity to drift. Indeed, relatively sedentary taxa such as Chironomidae and cyclorrhaphan Diptera do not, as a rule, consistently drift in as great proportions as do more active animals such as Ephemeroptera and amphipods (Waters 1972, Adamus and Gaufin 1976).

The drift model implies another ecologically important aspect of drift: the very high turnover of individuals that must occur throughout the river. If 50 percent of the animals depart from a region each day, the average residence time of an individual is 2 days. Benthic movements of animals may produce either a return of some animals or a loss of others. Townsend and Hildrew (1976) reported a daily turnover rate of 3.6 percent for the entire fauna of a small stream, but as high as 43 percent for active taxa prone to drift. Sheldon (1977) calculated daily turnover of Baetis (mostly B. bicaudatus Dodds) larvae at approximately 20 percent. This compares favourably with an estimate made by Elliott (1971a) of the daily proportion of Baetis rhodani that drifted within a riffle in a small English stream. Complete recolonization of denuded substrates by drift-active species in two weeks or less has been reported by a number of authors (Waters 1964, Ulfstrand et al. 1974, Khalaf and Tachet 1977, Gore 1979, Wise and Molles 1979, Shaw and Minshall 1980), and are indicative of daily turnover rates of at least 20 percent (see Sheldon 1977). Clearly, such high turnover rates indicate that individuals are capable of taking rapid advantage of any favourable microhabitat that becomes available.

Although the model's predictions of the influence of drift on distribution of animals pertain primarily to a large river, the dynamics of transport and countermovement should also be applicable to smaller streams. However, a major difficulty in direct application of the model to smaller systems is that mean current velocity is spacially more variable in smaller streams. Pools and riffles reflect changes in lateral current velocity profile over relatively short longitudinal distances; meanders in the stream result in changes in the relative position of the thalweg; and minor obstructions such as boulders and logs can profoundly interrupt the pattern of flow. The result is that microhabitats available in small streams will tend to take on a mosaic pattern quite different from the relatively homogeneous arrangement on which the model was based. Any animals transported directly downstream in the water column of a small stream would be exposed to a number of different flow conditions. The instantaneous settling rate would still be a function of current velocity, but could vary considerably during the course of the drift episode. Estimates of departure from the substrate would become equally complicated as would lateral dispersal determinations.

Determination of departure and settling probabilities would require detailed mapping of the entire study area and estimation of changes in distribution for each point in the reach rather than for parallel transects. Furthermore, an individual with benthic movement capabilities similar to those postulated for animals in the Pembina River would encounter a much greater variety of microhabitats during one crawling episode than would its counterpart in a large river. Consequently, one might expect drift to be of relatively less importance to populations in small streams than in larger rivers. Populations from large and from small lotic systems could possibly develop different behavioural tendencies to drift or to undertake benthic movements. A study to test for such differences would have to be carefully controlled to screen out confounding influences such as variations in age structure of the populations, as well as differences in the physical and biotic structure of the two systems.

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 appears to be maintained in spite of, rather than because of, the high propensity of animals to drift. Because drift provides access largely to slower portions of the river, benthic movement is a necessary co-requisite to provide individuals access to all regions of the lotic system.

Internally or externally mediated changes in the tendency of individuals either to drift or to engage in benthic lateral movements should result in an alteration of regions of population concentration within the river. An individual that can rapidly change position in the river minimizes downstream displacement during catastrophic events while at the same time maximizing probabilities of encountering randomly located resource-rich areas. This is clearly a strategy suited to opportunistic species.

THESIS DISCUSSION

This study was undertaken to evaluate the role of drift in controlling larval microdistribution of two mayfly populations in an Alberta river. I feel that there is strong evidence that drift is a major determinant of regions of greatest abundance.

Baetis tricaudatus and Ephemerella inermis larvae both exhibit substantial levels of drift in the Pembina River, yet distributions of these animals vary little during periods of stable flow. Laboratory experiments suggest that the tendency to drift is more strongly controlled by mean current velocity than by concentrations of detritus in the substrate or benthic density of conspecifics. Live larvae are more prone to appear in the water column than are dead animals, suggesting that behaviour is important in initiating drift.

Live drifting larvae rapidly return to the substrate but tend to become more strongly dispersed laterally than do dead larvae. Because settling rates of both live and dead animals are inversely related to current velocity, lateral transport during drift results in animals being most likely to return to the substrate in slow water near shore.

Although live animals are more prone to depart from regions of slow current than from faster water, this is insufficient to counteract the effect of net transport towards shore during drift. This finding can only be reconciled with field observations on benthic distribution by concluding that either the total proportion of larvae that drift in the Pembina River is very small, or that lateral transport during drift is compensated for by benthic movements of the animals towards river centre. I feel the latter explanation is more plausible because:

1) the amount of drift normally occurring in the Pembina River broadly corresponds with or exceeds the levels I would predict as a result of laboratory and field experiments;
2) flooding, which would be expected to induce increased levels of drift and to impede animals' benthic movements, produces a decrease in benthic densities at the river centre and an increase at the margins;
3) the only major shift in population microdistribution observed in the field during periods of stable flow consisted of an increase in abundance at stream centre concurrently with a decrease at the margins, at a time when drift of animals within all regions was negligible.

Drifting animals with poor swimming abilities (i.e. capabilities equivalent to those of dead organisms (see Elliott 1971a)) are transported relatively long distances downstream, but shoreward lateral transport is minimized. In contrast, animals that are capable of rapid return to the substrate (e.g. B. tricaudatus and E. inermis larvae) minimize downstream displacement but are more susceptible to transport towards stream margins. Thus, rheophilic animals that drift, whether rapid settlers or not, can be transported to regions of unfavourable current velocity. This is clearly of greater importance to animals with poor locomotory abilities, which could not leave such regions except by further drift. Consequently, one might expect drift to be less prevalent among relatively sedentary organisms than among individuals with well-developed crawling abilities.

Drift and Population Regulation

The prevailing view of the ecological significance of drift is that it serves as a means of population regulation. Müller (1954, 1973, 1974) and Waters (1961, 1965, 1972) both suggest that appearance of high numbers of organisms in the drift results from competition for food and/or space in the substrate. Müller proposes that an important auxilliary function of drift is dispersal of individuals to downstream reaches (distributional drift), which requires compensatory upstream movement of adults prior to oviposition. In contrast, Waters feels that drifting organisms simply represent excess production and that most individuals that drift could be lost from the system. Both authors view drift as primarily a density-dependent phenomenon, but have not elaborated on the nature of competition that might induce individuals to depart from the substrate.

There is evidence that both interference and exploitive competition occur in stream systems and can result in drift.

Several recent studies have described aggressive interactions among space-dependent tube-dwelling or filter feeding organisms. Hart (1982) and McAuliffe (1982) have found that Hydroptilidae (Trichoptera) larvae actively exclude other organisms from the immediate vicinity of their cases. Wiley and Kohler (1981) and Harding and Colbo (1981) reported similar interactions between black fly larvae. Glass and Bovbjerg (1969) and Hildrew and Townsend (1980) presented evidence of aggressive behaviour between net-spinning caddisfly larvae. These interactions occasionally result in departure into the water column (Wiley and Kohler 1981) either as the result of active swimming movements or because increased activity results in erosion of individuals (Hildrew and Townsend 1980).

Steine (1972) and Gyselman (1980) noted that mean size of drifting Ephemeroptera was smaller than that of the benthic population and suggested this resulted from competitive interactions. However, the few observations that have been made on behavioural interactions between mayflies indicate that intraspecific encounters produce short distance crawling movements but not drift (Corkum 1976, 1978a, Wiley and Kohler 1981). Thus, interference competition may or may not be a determinant of the magnitude of drift of mayfly populations.

My experiments on the influence of benthic density on departure rates of E. inermis and B. tricaudatus larvae suggest that interference competition is relatively unimportant in these populations, at least in relation to the influence of current velocity on drift. These findings are consistent with those of other controlled studies on the relationship between drift and benthic density (Hildebrand 1974, Keller 1976, Bohle 1978, Corkum 1978a).

In general, holometabolous insects, which in many cases have poor benthic locomotory abilities and rely on relatively restricted feeding sites, may be more prone to drift as a consequence of intraspecific interactions than hemimetabolous insects or crustaceans, which are capable of free-ranging foraging behaviour.

Drifting holometabolous insects have poor settling ability and generally behave similarly to dead animals (Elliott 1971a). Recurrent drift of these organisms will result in significant downstream displacement. If settling occurs in an unfavourable region, the only means of removal is by further drift, which, in the long run, is counterproductive. In this sense, drift of these organisms is consistent with Waters' hypothesis.

Although drift of highly motile animals may not be a primary response to intraspecific interactions, exploitive competition could produce increased levels of departure from the substrate. Drift often increases when high quality food (e.g. periphyton) is in limited supply

(Hildebrand 1974, Keller 1976, Bohle 1978). Hart (1981) suggested that grazing pressure of the caddisfly Dicosmoecus gilvipes Hagen is severe enough to make food a limiting resource for these animals. In such cases, drift could regulate microhabitat densities even though it is not a proximal response to the presence of other individuals. The frequency with which this occurs in lotic systems is unknown. Bishop and Hynes (1969a) suggested that physical perturbations of the river and predation may maintain densities of animals below levels at which food may become limiting.

Drift of E. inermis and B. tricaudatus larvae was unrelated to detrital concentration in my laboratory studies, even though field population densities were correlated with detritus levels. Although I did not test for a relationship between periphyton abundance and drift, any such relationship should not grossly affect the results of the drift model. Nocturnal drift of both populations was related to mean current velocity; maximal departure occurred at lowest velocities. Because periphyton abundance in rivers tends to be greater at higher current velocities (see Horner and Welch 1981), any drift response to periphyton should parallel responses to current.

Drift and Foraging

Both the distributional drift and excess production hypotheses consider drift as a population phenomenon and associate drift with permanent removal of larvae from the immediate microhabitat (Gyselman 1980). This may be valid for sedentary organisms, but my data suggest that drifting larvae are not transported long distances, and the animals may be able to maintain their position in the substrate through benthic movements. If motile organisms are capable of such compensatory benthic movement, it is unclear why they should drift. Drift is an energy efficient means of transport as compared to crawling; but if an animal drifts, it must subsequently expend an equivalent amount of energy to return to its original or to a comparable position in the river. A rheophilic animal would benefit by exhibiting an orthokinetic response to current velocity whether or not it regularly engaged in drift.

Benthic movement is also a more efficient means of foraging over the substrate than is drift, since a crawling animal can continuously sample substrate conditions, whereas a drifting animal can probably only monitor the point at which it settles. Clearly, drift can only be advantageous to those animals capable of crawling when benthic movement either becomes energetically too costly or involves a greater risk of predation than does drift.

There is strong evidence that crawling animals will drift when in the vicinity of invertebrate predators (Corkum and Pointing 1979, Corkum and Clifford 1980, Peckarsky 1980b, Walton 1980b), yet _E_. _inermis_ and _B_. _tricaudatus_ larvae frequently drift even when predators are not present.

One means of examining the advantage of drift is to initially consider an active benthic animal that would not normally engage in drift behaviour. Such an organism should remain within any microhabitat that offers a current velocity within its zone of preference and an adequate food supply, and should drift only if encountered by a predator. A change in current regime or food availibility will require movement to a new microhabitat. Presumably, this movement will occur at night to minimize exposure to visually-feeding predators (Allan 1978, Corkum and Clifford 1980). The force of the current will tend to orient the animal upstream so that most movements will carry it against the current (Neave 1930) and possibly into faster flowing regions, towards the river centre. Movement should continue until the animal encounters a new microhabitat with adequate resources. The animal may be unsuccessful in its search for a number of reasons:

1) favourable regions may be in short supply;
2) the dimensions of the microhabitat may exceed the animal's moving abilities;
3) there may be a time limit to the duration of crawling movement, dictated either by the animal's energy reserves or by the length of the night;
4) the animal may reach the upstream edge of the habitat (the head of a riffle or the margin of a large stone).

A crawling animal that has been unsuccessful in finding a suitable microhabitat must either remain at its endpoint (cases 1, 2 and 3) or perhaps retrace its path (case 4). Both possibilities entail an inefficient use of time or energy, or both. Alternatively, the organism might drift. There may be only a small probability of settling within a favourable area, but drifting would require a minimum further expenditure of energy and will provide another opportunity for the animal to terminate its search within a suitable microhabitat. Whether the final resting position of the animal subsequent to drifting is upstream or downstream, and centreward or shoreward, of its position prior to searching will depend on the distance previously moved over the substrate, the settling ability of the animal and on the current velocity at the point from which drift occurs.

Many authors have noted a correlation between benthic activity and drift (Chaston 1968, Elliott 1968b, Bishop 1969, Waters 1972, Plosky and Brown 1980, Hildrew and Townsend 1980) and have postulated that drift represents dislodgement of active animals. However, Corkum (1978b) suggested that even though both benthic activity and drift are maximal at night, nocturnal peaks in the two behaviours do not generally correspond; thus, drift and benthic activity should possibly be regarded as independent phenomena.

If drift does represent an independent behaviour that follows unsuccessful benthic searching, one would expect nocturnal drift maxima to lag behind peaks of benthic activity. The few studies that compare drift and benthic activity periodicities suggest that drift peaks are equally likely to precede as to follow periods of greatest activity (Chaston 1968, Elliott 1968b). Thus, although the view of drift as an adjunct to foraging behaviour suggests a mechanism for the initial evolution of active transport in the water column, its temporal relationship with benthic movement does not appear to have been maintained.

Future Work

My interpretation of the influence of drift on distribution of mayflies (and other motile taxa) relies heavily on the assumption that these organisms are capable of substantial upstream and lateral benthic movement. Clearly, this must be adequately tested before the model is accepted as viable.

Monitoring of benthic movement of aquatic invertebrates is difficult because the organisms are small, cryptic, and predominantly night-active. The flowing-water medium itself hinders direct observation. Workers who have attempted to study benthic movements by means of traps placed within rivers (Bishop and Hynes 1969b, Elliott 1971b, Bird and Hynes 1981) have found the movements to be of smaller magnitude than drift. However, a shortcoming of these traps is that animals crawling into them are also able to crawl or drift out. More efficient trap design would alleviate this problem but would still only produce data on numbers of animals moving, not on distances travelled by individuals.

Other authors have attempted to use mark-recapture techniques to study movements (Harker 1953b, Brusven 1970, Gallepp and Hasler 1975, Hart and Resh 1980), but such methods are limited by the potential effects of handling, the large size of populations, and an inability to establish whether final position has been achieved through benthic movement, drift or some combination of the two.

The use of artificial streams to monitor movements of individual animals can provide some estimates of movements (Elliott 1968b, Corkum 1976), but if animals do indeed move to the extent suggested by the drift model, then most laboratory streams would be too small to permit individuals unrestrained movement.

Perhaps the simplest and most conclusive test of the model and its assumptions would be to impede drift or benthic movement in the field and to measure whether predicted changes in distribution actually occur. Benthic movement would seem to be more easily restricted than would drift. This might be accomplished by partitioning a sample site longitudinally with slats embedded in the substrate to restrict lateral benthic movement, but still permit lateral access to each region by drift.

My model predicts that such a partitioning should produce an increase in densities near shore and a decrease at the centre, provided the partitions are long enough to prevent animals from crawling around the ends. This would not necessarily establish whether or not longitudinal displacement of populations occurs, but it would be a measure of the influence of lateral movement and transport on maintenance of distribution. By conducting the experiment at sites with differing lateral slopes, one could also test the premise that increases in density near shore should be more marked where depth and current velocity increase rapidly with distance from the margin than where there is a more gradual change in these features.

My study suggests that E. inermis and B. tricaudatus larvae in the Pembina River are not static organisms, but have the potential for wide-ranging and rapid movement throughout the lotic system. The voluminous literature on drift of other taxa indicates that this is probably not an isolated case. My data also show that, although current velocity is important in defining the microhabitat of these organisms, it is ultimately their behavioural responses to the current which determine the relative distribution of populations in the river. This clearly underlines the need for aquatic biologists to become more aware of the behavioural capabilities of the organisms they are studying to better understand population dynamics of lotic taxa.

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APPENDIX 1

APL PROGRAM TO DETERMINE MATRICES OF SETTLING PROBABILITY AND SUMS OF PROPORTIONS DRIFTING

```
  [0] Q←MMATRIX B;I;INSERT
  [1] T←Q←SUSPENDED←(26 26)⍴0
  [2] M←((⍳12)-0.5),(8⍴12),(11 9 7 5 3 1)
  [3] I←B[1]
  [4] 'GENERAL SETTLING RATE INTERCEPT AND EXPONENT:'
  [5] INT1←⎕
  [6] R←INT1[1]×M*INT1[2]
  [7] 'DISPERSION PARAMETERS:'
  [8] T←GENPROB ⎕
  [9] (⍕'      ')
 [10] (⍕'      ')
 [11] (⍕'RELEASE POINT  '),(⍕I)
 [12] INSERT←NRNORM
 [13] Q[I;]←26↑INSERT
 [14] SUSPENDED[I;]←¯26↑INSERT
 [15] SUSPENDED[I;I]←4 ROUND(SUSPENDED[I;I]+(1-(*(R[I]×¯1)))÷R[I])
 [16] I←I+1
 [17] →(I≤B[2])/9
 [18] Q←EVEN 4 ROUND Q
```

FUNCTION: Calculates probability matrices K and W, either for entire model river or for one or more adjacent transects specified by user.

INPUT: Extrinsic: Right argument, a two element vector representing the first and last transects for which information is desired.

Intrinsic: Terminal will prompt for,

i) a two element vector representing intercept and exponent values that relate instantaneous settling rate (r) to distance from river margin (y). These correspond to β_1' and β_2' (Chapter 4).

ii) a three element vector representing coefficients that relate measure of lateral diffusion (s) to distance from river margin (y). These correspond to β_3', β_4' and β_5' (Chapter 4).

OUTPUT: Extrinsic: A 26x26 element matrix corresponding to K. Rows for which information was not desired will contain only zeros.

Intrinsic: A 26x26 element matrix corresponding to W. Rows (transects) for which information was not desired will contain only zeros. Stored as global variable SUSPENDED.

REQUIRED SUBROUTINES: GENPROB, SD, PROB, NRNORM, ROUND, EVEN

```
[0] T←GENPROB A;I;X
[1] T←(26 26)ρ0
[2] I←1
[3] X←SD A
[4] T[;I]←PROB((I-0.5),X[I])
[5] I←I+1
[6] →(I≤26)/3
```

FUNCTION: Generates a 26x26 element matrix, each column of which represents a normal probability distribution with mean dictated by the position of the column in the matrix and standard deviation externally specified.

INPUT: Extrinsic: Right argument, a 3-element vector, entries of which represent coefficients that relate lateral diffusion measure (s) to distance from margin of model river (y). These correspond to β'_3, β'_4 and β'_5 (Chapter 4).

Intrinsic: None.

OUTPUT: Extrinsic: A 26x26 element matrix. Each column j is a normal probability distribution, N(j-0.5,s) with entries (i,j) the probability of occurrence of a value ranging between j-1 and j.

Intrinsic: None.

REQUIRED SUBROUTINES: SD, PROB

```
[0] T←SD A;NET
[1] T←26ρ0
[2] NET←1
[3] T[NET]←A[1]+A[2]+A[3]×M[NET]
[4] NET←NET+1
[5] →(NET≤26)/3
```

FUNCTION: Calculates estimates of s for each transect of model river.

INPUT: Extrinsic: Right argument, a 3-element vector, entries of which represent β_3', β_4' and β_5'.

Intrinsic: None.

OUTPUT: Extrinsic: A 26-element vector. Each element represents an estimate of s for the corresponding transect of model river a distance of 1 m downstream of a point of entry into water column.

Intrinsic: None.

REQUIRED SUBROUTINES: None.

```
   [0] L←PROB B;C;V;A;F;W
   [1] L←26⍴0
   [2] →((B[2]≤0),B[2]>0)/3,5
   [3] L[(B[1]+0.5)]←1
   [4] →0
   [5] C← 0.196854 0.115194 0.000344 0.019527
   [6] V←⍳26-1
   [7] A←((V,V[⍴V]+1)-B[1])÷B[2]
   [8] V←⍳0
   [9] F←A[1+⍴V]
  [10] W←1-0.5×(1++/C×(|F)*⍳4)*¯4
  [11] V←V,((F<0),F≥0)/(1-W),W
  [12] L[1]←V[1]
  [13] →((⍴V)=1)/15
  [14] L[⍴V]←V[⍴V]-V[(⍴V)-1]
  [15] →((⍴V)<26)/9
  [16] L[26]←L[26]+(1-V[26])
```

FUNCTION: Generates a probability distribution bounded by values 0 and 26, from a specified mean and standard deviation.

INPUT: Extrinsic: Right argument, a two element vector specifying mean and standard deviation.

Intrinsic: None.

OUTPUT: Extrinsic: A 26-element vector, each element j, of which corresponds to probability of occurrence of a value between j-1 and j according to the specified mean and standard deviation.

Intrinsic: None.

REQUIRED SUBROUTINES: None.

```
[0] BOTTOM←NRNORM;INTRO;DIST;SPREAD;NREM;REM;BOTTOM;NET;SETTLING;DRI
[1] DIST←0
[2] DRIFT←SPREAD←NREM←REM←BOTTOM←26⍴0
[3] REM[I]←1
[4] DIST←DIST+1
[5] NREM←REM×(*(R×¯1))
[6] BOTTOM←BOTTOM+(REM-NREM)
[7] SPREAD←T+.×NREM
[8] DRIFT←DRIFT+SPREAD
[9] REM←SPREAD
[10] SPREAD←26⍴0
[11] →((+/REM)≥0.001)/4
[12] BOTTOM←4 ROUND BOTTOM,DRIFT
[13] (⍕'DISTANCE TRAVELLED BY .001:  '),(⍕DIST)
[14] (⍕'DISTRIBUTION OF SETTLED ANIMALS:  '),(⍕26↑BOTTOM)
[15] (⍕'TOTAL PROP. SETTLED:   '),(⍕+/26↑BOTTOM)
[16] (⍕'TOTAL PROP. NOT SETTLED:  '),(⍕(+/REM))
[17] (⍕'REL. PROP. ANIMALS CAUGHT IN A DRIFT NET:  '),(⍕(4 ROUND DRIF
```

FUNCTION: Calculates probability vectors K_i (probability that an animal initially suspended in transect i eventually settles in transect j) and W_i (sums of proportions of animals originally in transect i that will drift past a point on transect j before settling). Also determines downstream distance by which 0.999 of animals have returned to the substrate.

INPUT: Extrinsic: None.

Intrinsic: Requires global variables R (vector of instantaneous settling rates of animals in each transect; generated by MMATRIX) and T (matrix of normal probabilities generated by GENPROB).

OUTPUT: Extrinsic: A 52-element vector. The first 26 elements represent values of K_i. The last 26 elements represent values of W_i.

Intrinsic: Prints out transect number, downstream distance by which 0.999 of animals have settled, total proportion of animals that have and have not settled at termination, and vectors K_i and W_i.

REQUIRED SUBROUTINES: ROUND

```
[0] A←EVEN X;R;V;I
[1] A←X
[2] R←+/X
[3] V←1-R
[4] I←1
[5] A[I;I]←A[I;I]+V[I]
[6] I←I+1
[7] →(I≤(ρV))/5
```

FUNCTION: Adjusts diagonal elements of a square matrix such that row totals are 1.00.

INPUT: Extrinsic: Right argument, matrix to be adjusted.

Intrinsic: None.

OUTPUT: Extrinsic: Adjusted matrix.

Intrinsic: None.

REQUIRED SUBROUTINES: None.

```
[0]  T←A ROUND B
[1]  T←(10*(-1×A))×⌊0.5+(B×10*A)
```

FUNCTION: Rounds numbers to a given number of places right of the decimal.

INPUT: Extrinsic: Left argument, number of places to right of decimal desired. Right argument, value(s) to be rounded.

Intrinsic: None.

OUTPUT: Extrinsic: Rounded value(s).

Intrinsic: None.

REQUIRED SUBROUTINES: None.

APPENDIX 2

MATRICES DESCRIBING SETTLING PROBABILITIES AND SUMS OF PROPORTIONS OF DRIFTING *B. TRICAUDATUS* AND *E. INERMIS* LARVAE IN MODEL RIVER

Each page lists elements of two matrices. Entries in upper matrix describe the probability that an animal that departs from substrate in any given transect (row) settles in any transect (column). Entries in lower matrix describe sums of proportions of all animals that depart from a given transect (row) that would pass a point on a given transect (column).

```
1      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      1      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      1      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0.2264 0.9495 0.0167 0.0024 0.0006 0.0002 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0.006  0.1991 0.6667 0.0894 0.0233 0.0082 0.0034 0.0016 0.0008 0.0005 0.0003 0.0002 0.0002 0.0001 0.0001 0.0001 0      0      0      0      0      0      0      0
0      0      0.0024 0.0761 0.256  0.4598 0.1199 0.0426 0.018  0.0086 0.0045 0.0025 0.0017 0.0013 0.001  0.0008 0.0006 0.0004 0.0003 0.0002 0.0002 0.0002 0.0003 0.0004 0.0002 0
0      0      0.0012 0.0409 0.1339 0.228  0.3514 0.1236 0.0523 0.025  0.0131 0.0074 0.0049 0.0038 0.0029 0.0023 0.0018 0.0014 0.001  0.0008 0.0007 0.0008 0.0009 0.0011 0.0008 0
0      0      0.0008 0.0254 0.0832 0.1418 0.1984 0.2824 0.1155 0.0553 0.029  0.0165 0.011  0.0083 0.0065 0.0051 0.004  0.0031 0.0023 0.0017 0.0015 0.0016 0.0021 0.0025 0.0017 0
0      0      0.0005 0.0176 0.0576 0.0983 0.1353 0.1707 0.2313 0.1025 0.0545 0.031  0.0206 [illegible] 0.0123 0.0096 0.0075 0.0057 0.0043 0.0033 0.0029 0.0032 0.0039 0.005  0.0033 0
0      0      0.0004 0.0131 0.0428 0.073  0.1027 0.1283 0.1446 0.1908 0.0893 0.0519 0.0344 [illegible] 0.0205 0.0161 0.0125 0.0096 0.0073 0.0055 0.0049 0.0055 0.0055 [illegible] 0.0055 0
0      0      0.0003 0.0101 0.0332 0.0556 0.0795 0.0993 0.114  0.1204 0.1565 0.0773 0.053  0.0402 0.0315 0.0247 0.0192 0.0148 0.0112 0.0064 0.0075 0.0066 0.0102 0.0123 0.0085 0.0001
0      0      0.0002 0.008  0.0263 0.0448 0.063  0.0786 0.0902 0.0976 0.0991 0.1338 0.0733 0.0561 0.0454 0.0356 0.0277 0.0213 0.0161 0.0121 0.0108 0.0123 0.0147 0.0155 0.0124 0.0001
0      0      0.0002 0.0064 0.0208 0.0355 0.0499 0.0623 0.0715 0.0774 0.0812 0.083  0.125  0.0762 0.0622 0.0487 0.0379 0.0291 0.022  0.0165 0.0148 0.0169 0.0201 0.0253 0.017  0.0001
0      0      0.0002 0.005  0.0164 0.028  0.0394 0.0492 0.0564 0.061  0.0641 0.0681 0.0777 0.1269 0.0792 0.0644 0.0501 0.0385 0.0291 0.0216 0.0196 0.0223 0.0266 0.0335 0.0224 0.0002
0      0      0.0001 0.0039 0.0129 0.022  0.031  0.0387 0.0444 0.048  0.0504 0.0536 0.0635 0.0793 0.1294 0.0805 0.065  0.0499 0.0377 0.0263 0.0254 0.0283 0.0344 0.0414 0.0291 0.0002
0      0      0.0001 0.0031 0.0101 0.0173 0.0243 0.0303 0.0348 0.0376 0.0395 0.042  0.0497 0.0645 0.0805 0.1298 0.0804 0.0641 0.0484 0.0353 0.0376 0.0371 0.0442 0.0557 0.0373 0.0003
0      0      0.0001 0.0024 0.0079 0.0134 0.0189 0.0236 0.0271 0.0293 0.0307 0.0327 0.0387 0.0501 0.065  0.0894 0.1288 0.0787 0.0618 0.0463 0.0415 0.0473 0.7553 0.071  0.0476 0.0003
0      0      0.0001 0.0018 0.006  0.0103 0.0145 0.0181 0.0208 0.0225 0.0236 0.0251 0.0297 0.0365 0.0499 0.0641 0.0788 0.1267 0.0754 0.0589 0.0528 0.05   0.0715 0.0931 0.0604 0.0004
0      0      0      0.0014 0.0045 0.0078 0.0109 0.0137 0.0157 0.017  0.0178 0.0189 0.0224 0.029  0.0376 0.0463 0.0516 0.0752 0.122  0.0716 0.0559 0.0751 0.0935 0.1141 0.0765 0.0005
0      0      0      0.001  0.0033 0.0056 0.0079 0.0099 0.0114 0.0123 0.013  0.0138 0.0163 0.0211 0.0274 0.0351 0.0448 0.0569 0.0694 0.1168 0.081  0.0952 0.1147 0.1445 0.0959 0.0007
0      0      0      0.0007 0.0022 0.0038 0.0053 0.0067 0.0077 0.0083 0.0087 0.0093 0.011  0.0142 0.0185 0.0237 0.0302 0.0387 0.0491 0.0636 0.1338 0.1171 0.1438 0.1815 0.1217 0.0008
0      0      0      0.0004 0.0013 0.0022 0.0031 0.0039 0.0045 0.0049 0.0051 0.0054 0.0065 0.0084 0.0108 0.0139 0.0178 0.0225 0.0287 0.0367 0.0583 0.1923 0.1794 0.2281 0.1523 0.0009
0      0      0      0.0002 0.0006 0.001  0.0014 0.0018 0.0021 0.0022 0.0024 0.0025 0.003  0.0039 0.005  0.0064 0.0082 0.0104 0.0133 0.0179 0.0322 0.0852 0.2939 0.364  0.2014 0.001
0      0      0      0      0.0001 0.0002 0.0003 0.0004 0.0005 0.0006 0.0005 0.0006 0.0008 0.001  0.0013 0.0017 0.0022 0.0028 0.0036 0.0048 0.0095 0.0219 0.0785 0.5465 0.2209 0.0011
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0.0002 0.001  0.397  0.0019
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      1

0.1929 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      1.2242 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      2.5402 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0.0777 3.8598 0.1104 0.0192 0.0061 0.0024 0.0011 0.0005 0.0003 0.0002 0.0001 0.0001 0      0      0      0      0      0      0      0      0      0      0      0
0      0      0.0155 0.8259 3.846  0.7006 0.2324 0.1011 0.0509 0.0283 0.0169 0.0108 0.0075 0.0055 0.0042 0.0032 [illegible] [illegible] 0.0013 0.0009 0.0007 0.0005 0.0004 0.0003 0.0001 0
0      0      0.0065 0.3261 1.513  3.532  1.1949 0.5224 0.2651 0.1487 0.0903 0.0587 0.0413 0.0313 0.0244 0.0189 [illegible] 0.0111 0.0083 0.0062 0.0048 0.004  0.0032 0.0024 0.0008 0
0      0      0.0034 0.1717 0.7913 1.7877 3.4416 1.5168 0.7708 0.4338 0.2637 0.1718 0.1215 0.0923 0.0722 0.0565 0.0438 0.0336 0.0253 0.0189 0.0148 0.0124 0.0102 0.0079 0.0025 0
0      0      0.0021 0.1067 0.4916 1.1118 1.9767 3.4111 1.7032 0.9516 0.5847 0.3812 0.2598 0.2054 0.1609 0.126  0.0979 0.0752 0.0557 0.0425 0.0334 0.0282 0.0231 0.0179 0.006  0
0      0      0.0015 0.0739 0.3407 0.7704 1.3778 2.0948 3.3608 1.7872 1.098  0.7148 0.5063 0.3855 0.3022 0.2369 0.1842 0.1415 0.1068 0.0902 0.0531 0.0532 0.0438 0.034  0.0114 0
0      0      0.0011 0.0549 0.2532 0.5724 1.0229 1.5746 2.1321 3.272  1.7995 1.1979 0.8454 0.5842 0.5052 0.3961 0.3081 0.2368 0.1788 0.1343 0.1053 0.0893 0.0735 0.0571 0.0192 0
0      0      0.0008 0.0426 0.1961 0.4435 0.7925 1.2186 1.6812 2.0932 3.1521 1.7843 1.3039 0.9884 0.7754 0.6091 0.4731 0.3637 0.2747 0.2053 0.1623 0.1372 0.113  0.0879 0.0295 0.0001
0      0      0.0007 0.0337 0.1553 0.3511 0.6275 0.9648 1.3298 1.6959 1.9983 3.0425 1.8046 1.4298 1.1173 0.8759 0.6817 0.524  0.3959 0.2973 0.234  0.1978 0.153  0.1265 0.0425 0.0001
0      0      0.0005 0.0267 0.1231 0.2783 0.4975 0.7649 1.0541 1.3446 1.5376 1.9173 3.0253 1.8758 1.5309 1.1987 0.9323 0.7169 0.5416 0.4268 0.320  0.2706 0.2231 0.1735 0.0583 0.0001
0      0      0.0004 0.0211 0.0971 0.2196 0.3924 0.6034 0.8316 1.0604 1.2916 1.5731 1.9111 3.0833 1.9476 1.5646 1.2316 0.9464 0.7152 0.5372 0.4234 0.3576 0.2947 0.2292 0.077  0.0002
0      0      0.0003 0.0168 0.0764 0.1728 0.3085 0.475  0.5547 0.8349 1.0152 1.2368 1.5625 1.9508 3.1332 1.9813 1.5992 1.226  0.9274 0.6957 0.5491 0.4609 0.3522 0.2972 0.0999 0.0002
0      0      0.0003 0.013  0.0599 0.1354 0.242  0.3722 0.5131 0.6543 0.7955 0.9608 1.223  1.5869 1.981  3.1487 1.9731 1.5776 1.1904 0.8927 0.7045 0.5932 0.4774 0.3818 0.1252 0.0003
0      0      0.0002 0.0101 0.0465 0.1053 0.1833 0.2896 0.3992 0.5091 0.6199 0.7541 0.9513 1.2333 1.599  1.9781 3.1269 1.9371 1.5137 1.1398 0.8079 0.7585 0.6251 0.4864 0.1635 0.0004
0      0      0.0002 0.0077 0.0358 0.0809 0.1447 0.2226 0.3069 0.3915 0.4766 0.5798 0.7316 0.9479 1.2281 1.5779 1.9376 3.0544 1.8552 1.449  1.1405 0.9629 0.7936 0.6175 0.2076 0.0005
0      0      0.0001 0.0058 0.0269 0.0609 0.109  0.1676 0.2312 0.2949 0.3591 0.4369 0.5514 [illegible] 0.9251 1.1878 1.5161 1.8507 2.9542 1.7612 1.4464 1.2202 1.0047 0.7815 0.2578 0.0005
0      0      0.0001 0.0042 0.0195 0.0442 0.0792 0.1218 0.1681 0.2145 0.2612 0.3178 0.4012 [illegible] 0.6732 0.864  1.102  1.4001 1.7060 7.63   1.7567 1.543  1.2722 0.9597 0.3327 0.0008
0      0      0.0001 0.0028 0.0131 0.0297 0.0533 0.082  0.1132 0.1445 0.176  0.2143 0.2705 [illegible] 0.4542 0.5829 0.7431 0.9423 1.2084 1.5537 2.8462 1.9761 1.5958 1.2433 0.4181 0.001
0      0      0      0.0016 0.0076 0.0174 0.0311 0.048  0.0663 0.0847 0.1033 0.1258 0.158[illegible] [illegible] 0.2662 0.3476 0.437  0.5542 0.7063 0.9531 1.4885 3.0373 1.5562 1.5672 0.5732 0.0011
0      0      0      0.0007 0.0034 0.0079 0.0142 0.0219 0.0304 0.0387 0.0475 0.058  0.0733 0.0952 0.1235 0.1596 0.2024 0.2569 0.3277 0.4414 0.6567 1.3565 3.1039 1.9624 0.6916 0.0012
0      0      0      0.0002 0.0008 0.0019 0.0034 0.0054 0.0076 [illegible] 0.0122 0.015  0.0191 0.0249 0.0325 0.0419 0.0537 0.0684 0.0775 0.1181 0.156  [illegible] 0.271  [illegible] 1.1221 0.0013
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0001 0.0001 0.0003 0.0006 0.0015 0.0049 0.2678 0.0022
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0.6459
```

E. *inermis* (live animals). Data for May 1979.

FINE PRINT

```
0.9395  0.0001  0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0
0.0131  0.9751  0.0114  0.0004  0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0
0.0026  0.0472  0.0195  [illegible] 0.0033  0.0004  0.0001  0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0
0.0001  0.0051  [illegible] [illegible] [illegible] 0.0108  0.0022  0.0025  0.0001  0       0       0       0       0       0       0       0       0       0       0       0       0       0       0
0       0.0029  0.0177  0.1475  0.6551  0.1044  0.0222  0.006   0.002   0.0007  0.0003  0.0001  0.0001  0       0       0       0       0       0       0       0       0       0       0
0       0.0002  0.0047  0.0229  0.184   0.5914  0.1261  0.0348  0.0116  0.0045  0.0019  0.0009  0.0005  0.0003  0.0001  0.0001  0       0       0       0       0       0       0       0
0       0.0001  0.0015  0.0134  0.0633  0.2029  0.5022  0.1361  0.0463  0.016   0.0078  0.0036  0.002   0.0012  0.0007  0.0004  0.0002  0.0001  0       0       0       0       0       0
0       0       0.0007  0.0056  0.0264  0.0645  0.2078  0.4255  0.1476  0.0555  0.0241  0.0114  0.0062  0.0039  0.0023  0.0014  0.0009  0.0005  0.0001  0.0001  0.0001  0       0       0
0       0       0.0003  0.0027  0.0122  0.0406  0.0908  0.2036  0.3657  0.1419  0.0619  0.0291  0.016   0.0099  0.0061  0.0037  0.0023  0.0014  0.0003  0.0003  0.0002  0.0001  0       0
0       0       0.0002  0.0014  0.0069  0.0217  0.0533  0.1089  0.1947  0.3371  0.1376  0.0649  0.0357  0.0221  0.0137  0.0094  0.0052  0.0032  0.0008  0.0006  0.0004  0.0002  0.0001  0
0       0       0.0001  0.0008  0.0039  0.0125  0.0308  0.063   0.1126  0.1625  0.2766  0.1298  0.0714  0.0442  0.0274  0.0169  0.0104  0.0064  0.0016  0.0013  0.0009  0.0005  0.0002  0
0       0       0.0001  0.0005  0.0024  0.0076  0.0185  0.0363  0.0685  0.1111  0.1675  0.24    0.1314  0.0814  0.0504  0.0312  0.0193  0.0118  0.0029  0.0024  0.0017  0.0009  0.0003  0
0       0       0       0.0003  0.0015  0.0047  0.0116  0.0238  0.0425  0.0699  0.1039  0.1479  0.2272  0.1399  0.0867  0.0537  0.0332  0.0204  0.0051  0.0041  0.0029  0.0015  0.0005  0
0       0       0       0.0002  0.0009  0.0029  0.0072  0.0147  0.0263  0.0427  0.0643  0.0917  0.14    0.2323  0.1432  0.0867  0.0548  0.0337  0.0084  0.0069  0.0049  0.0027  0.0008  0.0001
0       0       0       0.0001  0.0006  0.0018  0.0045  0.0091  0.0163  0.0264  0.0399  0.0569  0.0867  0.1432  0.2343  0.1443  0.0892  0.0549  0.0137  0.0114  0.008   0.0044  0.0013  0.0001
0       0       0       0.0001  0.0003  0.0011  0.0028  0.0056  0.0101  0.0164  0.0247  0.0352  0.0537  0.0887  0.1443  0.2347  0.1444  0.0889  0.0223  0.018   0.0129  0.0071  0.0022  0.0002
0       0       0       0       0.0002  0.0007  0.0017  0.0035  0.0062  0.0101  0.0152  0.0217  0.0332  0.0548  0.0892  0.1444  0.2345  0.1437  0.036   0.0291  0.0209  0.0115  0.0037  0.0003
0       0       0       0       0.0001  0.0004  0.001   0.0021  0.0038  0.0062  0.0094  0.0134  0.0204  0.0337  0.0549  0.0889  0.1437  0.2333  0.0581  0.0471  0.0337  0.0186  0.0057  0.0005
0       0       0       0       0.0001  0.0003  0.0006  0.0013  0.0023  0.0038  0.0057  0.0081  0.0124  0.0205  0.0334  0.0542  0.0875  0.1413  0.0937  0.075   0.0544  0.03    0.0092  0.0008
0       0       0       0       0       0.0001  0.0004  0.0008  0.0014  0.0022  0.0033  0.0048  0.0073  0.0121  0.0196  0.0321  0.0518  0.0837  0.1512  0.1225  0.0878  0.0484  0.0149  0.0013
0       0       0       0       0       0.0001  0.0002  0.0004  0.0007  0.0012  0.0018  0.0026  0.004   0.0066  0.0107  0.0174  0.0282  0.0455  0.245   0.1977  0.1416  [illegible] 0.0239  0.0021
0       0       0       0       0       0       0.0001  0.0002  0.0003  0.0005  0.0008  0.0012  0.0018  0.003   0.0049  0.008   0.0129  0.0203  0.1122  0.3323  0.2275  [illegible] 0.04    0.0035
0       0       0       0       0       0       0       0.0001  0.0001  0.0002  0.0003  0.0004  0.0006  0.001   0.0017  0.0027  0.0045  0.0072  0.0392  0.115   0.4563  0.2526  0.0771  0.0057
0       0       0       0       0       0       0       0       0       0       0       0.0001  0.0001  0.0002  0.0003  0.0005  0.0009  0.0015  0.0087  0.0245  0.097   0.5453  0.1969  0.0171
0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0.0001  0.0005  0.0017  0.007   0.0479  0.6674  0.0752
0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0.0001  0.0025  0.997
```

```
0.2553  0.0003  0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0
0.0134  1.8427  0.0481  0.0026  0.0002  0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0
0.0007  0.1016  3.6776  0.265   0.0334  0.0057  0.0011  0.0002  0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0
0.0001  0.0109  0.4266  5.4538  0.7232  0.1478  0.039   0.012   0.0041  0.0014  0.0005  0.0002  0.0001  0       0       0       0       0       0       0       0       0       0       0       0       0
0       0.002   0.0741  1.0071  6.3185  1.4243  0.3925  0.1343  0.053   0.023   0.0105  0.005   0.0025  0.0012  0.0006  0.0003  0.0001  0       0       0       0       0       0       0       0       0
0       0.0005  [illegible] 0.2659  1.6394  8.0158  2.2345  0.7738  0.2153  0.1447  0.0722  0.038   0.0212  0.0123  0.0059  0.0038  0.0021  0.0011  0.0005  0.0003  0.0001  0.0001  0       0       0       0
0       0.0002  0.0057  0.0919  0.6325  2.7678  8.6144  3.0669  1.2557  0.5823  0.2959  0.1599  0.0928  0.0552  0.0338  0.0201  0.0118  0.0068  0.0033  0.0021  0.0011  0.0005  0.0003  0.0001  0       0
0       0.0001  0.002   0.0381  0.2625  1.1531  3.6826  9.4055  3.8628  1.795   0.9151  0.4983  0.2922  0.1797  0.1101  0.0671  0.0405  0.0243  0.0144  0.0082  0.0047  0.0027  0.0012  0.0004  0.0001  0
0       0       0.0013  0.0183  0.1256  0.5539  1.769   4.5256  9.8573  4.5905  2.3454  1.2784  0.7519  0.4545  0.2865  0.1763  0.106   0.0657  0.0395  0.023   0.0135  0.0078  0.0037  0.0012  [illegible] 0
0       0       0.0007  0.0098  0.0676  0.296   0.9454  2.4193  5.2747  10.2043 5.2214  2.846   1.677   1.0378  0.6418  0.3953  0.244   0.1494  0.0904  0.0531  0.0317  0.0185  [illegible] [illegible] [illegible] 0
0       0       0.0004  0.0055  0.0391  0.1711  0.5465  1.3955  3.0494  5.9034  10.436  5.6981  3.3568  2.0788  1.287   0.7958  0.4911  0.3015  0.1831  0.1079  0.0648  0.0379  [illegible] [illegible] [illegible] 0
0       0       0.0003  0.0034  0.0238  0.1041  0.3327  0.8514  1.8565  3.5942  6.3552  10.4727 6.174   3.8247  2.369   1.456   0.9055  0.5558  0.3386  0.2     0.1204  [illegible] [illegible] [illegible] [illegible] 0
0       0       0.0002  0.0021  0.0147  0.0645  0.2051  0.5275  1.1505  2.2277  3.9393  6.4921  10.6101 6.5746  4.0733  2.5216  1.5583  0.9589  0.5835  0.3401  0.2079  0.1221  [illegible] [illegible] [illegible] 0.0001
0       0       0.0001  0.0013  0.0091  0.0399  0.1276  0.3266  0.7128  1.3804  2.4412  4.0235  6.5757  10.8573 6.727   4.1554  2.5749  1.585   0.9553  0.5712  0.3444  0.2224  [illegible] [illegible] [illegible] [illegible]
0       0       0.0001  0.0008  0.0056  0.0247  0.079   0.2023  0.4414  0.8549  1.5122  2.4927  4.0743  6.7273  10.9493 6.7801  4.192   2.5812  1.5724  0.9308  0.5514  0.3301  [illegible] [illegible] [illegible] [illegible]
0       0       0       0.0005  0.0035  0.0152  0.0488  0.1251  0.273   0.529   0.9359  1.5431  2.5275  4.1656  6.7801  10.9757 6.7657  4.1791  [illegible] 1.5076  0.9145  [illegible] [illegible] [illegible] [illegible] [illegible]
0       0       0       0.0003  0.0021  0.0094  0.0301  0.0771  0.1605  0.3266  0.5781  0.9534  1.559   2.575   4.1919  6.7861  10.9527 6.7512  4.114   2.4362  1.4705  0.8548  [illegible] [illegible] [illegible] [illegible]
0       0       0       0.0002  0.0013  0.0057  0.0184  0.0472  0.1024  0.2005  0.3553  0.5864  0.9593  1.585   2.5808  4.1797  6.7831  10.6974 6.6406  3.9328  2.3734  1.3965  [illegible] [illegible] [illegible] [illegible]
0       0       0       0.0001  0.0008  0.0035  0.0111  0.0266  0.0627  0.1217  0.2159  0.3565  0.5835  0.9048  1.5717  2.5456  4.1133  6.6402  10.7154 6.2859  3.8301  2.2339  [illegible] [illegible] [illegible] [illegible]
0       0       0       0.0001  0.0005  0.002   0.0065  0.0167  0.0368  0.0716  0.1271  0.2102  0.3446  0.5701  0.9294  1.5261  2.4345  3.9311  6.3442  10.2265 [illegible] [illegible] [illegible] [illegible] [illegible] [illegible]
0       0       0       0       0.0002  0.0011  0.0034  0.0089  0.0196  0.0384  0.0604  0.1135  0.1864  0.3099  0.5044  0.8182  1.3226  2.1363  3.432   5.5735  9.9577  5.6557  2.6203  [illegible] [illegible] [illegible]
0       0       0       0       0.0001  0.0004  0.0015  0.0029  0.0065  0.017   0.0306  0.0511  0.0844  0.1405  0.2302  0.3744  0.6068  0.9816  1.386   2.552   4.5873  [illegible] 4.7295  [illegible] [illegible] [illegible]
0       0       0       0       0       0.0001  0.0004  0.0011  0.0026  0.0053  0.0098  0.0167  0.028   0.0473  0.0783  0.1255  0.2096  0.3407  0.5522  0.8317  1.502   3.4405  9.0563  [illegible] [illegible] [illegible]
0       0       0       0       0       0       0       0.0001  0.0003  0.0007  0.0014  0.0025  0.0045  0.0082  0.0144  0.0245  0.0415  0.0591  0.114   0.1057  [illegible] [illegible] [illegible] [illegible] [illegible] [illegible]
0       0       0       0       0       0       0       0       0       0       0       0       0       0.0001  0.0002  0.0005  0.0012  0.0027  0.0054  0.0115  0.0214  [illegible] [illegible] [illegible] [illegible] [illegible]
0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       0       [illegible] [illegible] [illegible] [illegible]
```

E. inermis (dead animals). Data for May 1979.

```
1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0.0005 0.999 0.0005 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0.0132 0.9746 0.0115 0.0006 0.0001 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0.0109 0.0526 0.8821 0.0475 0.0056 0.001 0.0002 0.0001 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0.0001 0.0082 0.1289 0.7499 0.0896 0.017 0.0043 0.0013 0.0004 0.0002 0.0001 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0.0021 0.0301 0.1731 0.6293 0.1196 0.0305 0.0095 0.0034 0.0013 0.0006 0.0003 0.0001 0.0001 0 0 0 0 0 0 0 0 0 0 0
0 0 0.0007 0.0094 0.0538 0.1919 0.5377 0.1367 0.0427 0.0154 0.0062 0.0027 0.0013 0.0007 0.0004 0.0002 0.0001 0.0001 0 0 0 0 0 0 0 0
0 0 0.0003 0.0035 0.0203 0.0725 0.1963 0.4697 0.1448 0.0523 0.021 0.0092 0.0046 0.0025 0.0014 0.0008 0.0004 0.0002 0.0001 0.0001 0 0 0 0 0 0
0 0 0.0001 0.0015 0.0089 0.0316 0.0856 0.1939 0.4169 0.1469 0.0592 0.026 0.013 0.0072 0.0041 0.0023 0.0013 0.0007 0.0004 0.0002 0.0001 0.0001 0.0001 0 0 0
0 0 0.0001 0.0007 0.0043 0.0154 0.0417 0.0946 0.1678 0.2741 0.1446 0.0637 0.0313 0.0178 0.0101 0.0058 0.0033 0.0018 [illegible] 0.0005 0.0003 0.0002 0.0001 0.0001 0 0
0 0 0 0.0004 0.0023 0.0061 0.0221 0.0501 0.1 0.1791 0.3277 0.1352 0.0701 0.0392 0.0223 0.0127 0.0072 0.0041 0.0023 0.0012 0.0008 0.0005 0.0003 0.0002 0 0
0 0 0 0.0002 0.0013 0.0046 0.0124 0.0282 0.0562 0.1216 0.1672 0.305 0.1298 0.079 0.045 0.0256 0.0146 0.0083 0.0046 0.0025 0.0015 0.0011 0.0007 0.0003 0.0001 0
0 0 0 0.0001 0.0007 0.0026 0.0071 0.0161 0.0321 0.0591 0.0969 0.1526 0.2974 0.1456 0.0842 0.0479 0.0273 0.0155 0.0087 0.0042 0.003 0.0021 0.0013 0.0007 0.0002 0
0 0 0 0.0001 0.0004 0.0015 0.004 0.0092 0.0183 0.0331 0.0532 0.0883 0.1466 0.2954 0.1484 0.0858 0.0499 0.0277 0.0156 0.0087 0.0053 0.0037 0.0024 0.0012 0.0003 0
0 0 0 0 0.0002 0.0009 0.0022 0.0052 0.0104 0.0169 0.0315 0.0503 0.0848 0.1484 0.2972 0.1492 0.0862 0.0489 0.0276 0.0153 0.0094 0.0065 0.0042 0.0021 0.0006 0
0 0 0 0 0.0001 0.0005 0.0013 0.003 0.0059 0.0107 0.0179 0.0286 0.0482 0.0858 0.1492 0.2978 0.1493 0.0861 0.0484 0.027 0.0165 0.0115 0.0073 0.0038 0.001 0
0 0 0 0 0.0001 0.0003 0.0007 0.0017 0.0034 0.0061 0.0102 0.0163 0.0275 0.0488 0.0862 0.1493 0.2973 0.1489 0.0851 0.0473 0.0292 0.0202 0.0129 0.0066 0.0018 0.0001
0 0 0 0 0 0.0001 0.0004 0.0009 0.0019 0.0034 0.0058 0.0092 0.0156 0.0277 0.0489 0.086 0.1489 0.2956 0.1472 0.0831 0.0512 0.0355 0.0227 0.0115 0.0032 0.0001
0 0 0 0 0 0.0001 0.0002 0.0005 0.0011 0.0019 0.0032 0.0052 0.0088 0.0156 0.0275 0.0484 0.0851 0.1472 0.2935 0.1436 0.0899 0.0622 0.0397 0.0204 0.0055 0.0002
0 0 0 0 0 0 0.0001 0.0003 0.0006 0.001 0.0016 0.0028 0.0048 0.0086 0.0151 0.0266 0.0459 0.0871 0.1419 0.2871 0.1552 0.1093 0.0698 0.0359 0.0098 0.0004
0 0 0 0 0 0 0.0001 0.0001 0.0003 0.0005 0.0009 0.0014 0.0024 0.0043 0.0076 0.0133 0.0234 0.0412 0.0721 0.1305 0.312 0.198 0.1216 0.0623 0.0171 0.0005
0 0 0 0 0 0 0 0.0001 0.0001 0.0002 0.0003 0.0006 0.001 0.0018 0.0031 0.0056 0.0098 0.0172 0.0302 0.0551 0.1249 0.3859 0.2194 0.1127 0.0303 0.0011
0 0 0 0 0 0 0 0 0 0.0001 0.0001 0.0002 0.0003 0.0005 0.001 0.0017 0.0031 0.0054 0.0096 0.0175 0.0397 0.1211 0.4961 0.2385 0.0647 0.0024
0 0 0 0 0 0 0 0 0 0 0 0 0 0.0001 0.0001 0.0003 0.0005 0.0009 0.0017 0.0031 0.0072 0.0219 0.0898 0.6867 0.1811 0.0066
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0.0001 0.0002 0.0006 0.0029 0.0225 0.9402 0.0334
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
```

```
0.4715 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0.0006 1.4575 0.0023 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0.0233 2.2636 0.0394 0.0025 0.0003 0.0001 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0.0015 0.1592 2.7622 0.1946 0.0274 0.0058 0.0015 0.0005 0.0002 0.0001 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0.0002 0.0234 0.4274 2.9313 0.4356 0.0958 0.0274 0.0093 0.0035 0.0014 0.0006 0.0003 0.0001 0.0001 0 0 0 0 0 0 0 0 0 0 0
0 0.0001 0.0055 0.0998 0.708 2.9491 0.674 0.1956 0.0681 0.0269 0.0116 0.0054 0.0027 0.0014 0.0007 0.0004 0.0002 0.0001 0 0 0 0 0 0 0 0
0 0 0.0017 0.031 0.2201 0.9332 2.9343 0.876 0.3063 0.1221 0.0537 0.0254 0.013 0.0071 0.0039 0.0021 0.0012 0.0005 0.0003 0.0002 0.0001 0 0 0 0 0
0 0 0.0005 0.0117 0.0831 0.3524 1.1065 2.9211 1.0394 0.4155 0.1834 0.0874 0.0453 0.0251 0.0142 0.0079 0.0044 0.0024 0.0013 0.0007 0.0004 0.0002 0.0001 0 0 0
0 0 0.0003 0.0051 0.0262 0.1535 0.4625 1.2421 2.9121 1.1672 0.5161 0.2455 0.1283 0.0715 0.0406 0.0229 0.0129 0.0072 0.004 0.0022 0.0012 0.0007 0.0003 0.0001 0 0
0 0 0.0001 0.0025 0.0175 0.0747 0.2348 0.6058 1.3477 2.9006 1.2502 0.6039 0.3146 0.1758 0.1001 0.0569 0.0322 0.0182 0.0101 0.0055 0.0031 0.0018 0.0009 0.0003 0.0001 0
0 0 0.0001 0.0013 0.0093 0.0396 0.1244 0.3209 0.7176 1.4231 2.8746 1.3195 0.6918 0.3865 0.2204 0.1254 0.0713 0.0403 0.0226 0.0125 0.007 0.004 0.002 0.0007 0.0001 0
0 0 0 0.0007 0.0052 0.0222 0.0699 0.1804 0.4032 0.807 1.4569 2.826 1.3792 0.7733 0.4441 0.253 0.1439 0.0816 0.0459 0.0254 0.0144 0.0082 [illegible] 0.0016 0.0003 0
0 0 0 0.0004 0.003 0.0127 0.04 0.1032 0.2307 0.4613 0.8445 1.4463 2.8221 1.436 0.8309 0.4729 0.2693 0.1529 0.085 0.0473 0.0271 0.0156 0.0079 0.003 0.0005 0
0 0 0 0.0002 0.0017 0.0072 0.0228 0.0558 0.1314 0.2629 0.4808 0.8369 1.4454 2.8535 1.4634 0.8451 0.4812 0.2733 0.154 0.0856 0.0496 0.028 0.0142 0.0054 0.001 0
0 0 0 0.0001 0.001 0.0041 0.0129 0.0334 0.0749 0.1498 0.2741 0.4765 0.8361 1.4633 2.8631 1.4717 0.8501 0.4823 0.2718 0.1512 0.0659 [illegible] 0.0251 [illegible] [illegible] 0
0 0 0 0.0001 0.0005 0.0023 0.0073 0.019 0.0426 0.0853 0.1562 0.2716 0.4759 0.846 1.4717 2.8732 1.4728 0.8487 0.4777 0.2559 0.1521 0.087 0.0442 0.0159 [illegible] 0.0001
0 0 0 0 0.0003 0.0013 0.0042 0.0108 0.0242 0.0485 0.0888 0.1546 0.271 0.4811 0.8501 1.4728 2.8717 1.4683 0.8234 0.4665 0.2653 0.1529 [illegible] [illegible] [illegible] 0.0001
0 0 0 0 0.0002 0.0007 0.0023 0.0061 0.0137 0.0274 0.0503 0.0877 0.1538 0.2733 0.4822 0.8486 1.4682 2.8626 1.4514 0.8196 0.4634 0.2662 0.1365 0.0522 [illegible] 0.0002
0 0 0 0 0.0001 0.0004 0.0013 0.0034 0.0076 0.0154 0.0282 0.0492 0.0865 0.1539 0.2717 0.4776 0.8395 1.4515 2.8325 1.4163 0.8173 0.4704 0.2354 0.0915 0.0164 0.0003
0 0 0 0 0 0.0002 0.0007 0.0018 0.0041 0.0084 0.0154 0.027 0.0475 0.0845 0.1493 0.2627 0.4611 0.8102 1.399 2.7711 1.4114 0.8764 0.4201 0.1575 0.0298 0.0005
0 0 0 0 0 0.0001 0.0003 0.0009 0.002 0.0041 0.0076 0.0134 0.0236 0.0422 0.0747 0.1316 0.2313 0.406 0.7115 1.2862 2.7726 1.4217 0.732 0.2799 0.0502 0.0009
0 0 0 0 0 0 0.0001 0.0003 0.0008 0.0016 0.0031 0.0054 0.0097 0.0174 0.031 0.0549 0.0967 0.1702 0.3323 0.5435 1.1364 2.8495 1.3153 0.5045 0.0904 0.0016
0 0 0 0 0 0 0 0.0001 0.0002 0.0004 0.0009 0.0016 0.0029 0.0053 0.0095 0.017 0.0303 0.0526 [illegible] 0.1724 0.3613 0.9154 [illegible] 1.0583 [illegible] [illegible]
0 0 0 0 0 0 0 0 0 0 0.0001 0.0007 0.0004 0.0008 0.0015 0.0027 0.0051 0.0092 0.0156 0.0208 0.0631 0.156 0.5411 [illegible] [illegible] [illegible]
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0.0001 0.0001 0.0003 0.0007 0.0018 0.005 [illegible] [illegible] [illegible] [illegible]
0 0 0 0 0 0 0 0   0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0.0011 0.9561
```

P. tricaudatus (live animals). Data for May 1979.

```
0.9505 0.0134 0.001  0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0.2714 0.8427 0.0515 0.0064 0.001  0.0002 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0.0337 0.1136 0.7694 0.0288 0.0145 0.003  0.0007 0.0002 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0.0018 0.0215 0.1455 0.6853 0.1131 0.024  0.0051 0.0018 0.0008 0.0002 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0.0004 0.0053 0.0355 0.1671 0.612  0.1305 0.0337 0.0101 0.0034 0.0012 0.0005 0.0002 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0
0.0001 0.001  0.0105 0.0493 0.1802 0.5501 0.1421 0.0477 0.0144 0.0053 0.0021 0.0009 0.0004 0.0002 0.0001 0      0      0      0      0      0      0      0      0      0      0
0      0.0005 0.0036 0.0165 0.0615 0.1872 0.4977 0.1494 0.0506 0.0189 0.0076 0.0032 0.0015 0.0008 0.0004 0.0002 0.0001 0      0      0      0      0      0      0      0      0
0      0.0003 0.0014 0.0064 0.0235 0.0716 0.1698 0.4536 0.1335 0.0574 0.0232 0.01   0.0047 0.0024 0.0012 0.0005 0.0003 0.0001 0.0001 0      0      0      0      0      0      0
0      [illegible] 0.0006 0.0027 0.0089 0.03   0.0796 0.1895 0.4165 0.1552 0.0629 0.027  0.0128 0.0065 0.0033 0.0017 0.0008 0.0004 0.0002 0.0001 0.0001 0      0      0      0      0
0      0      0.0003 0.0012 0.0045 0.0136 0.036  0.0859 0.1575 0.3844 0.1552 0.0658 0.0319 0.0162 0.0083 0.0042 0.0021 0.0011 0.0005 0.0003 0.0001 0.0001 0      0      0      0
0      0      0.0001 0.0006 0.0021 0.0065 0.0173 0.0412 0.0901 0.1839 0.3566 0.1529 0.0728 0.0372 0.019  0.0097 0.005  0.0025 0.0013 0.0006 0.0003 0.0002 0.0001 0      0      0
0      0      0.0001 0.0003 0.0011 0.0033 0.0087 0.0207 0.0454 0.0925 0.1783 0.33   0.1552 0.0799 0.0409 0.0209 0.0107 0.0054 0.0028 0.0014 0.0007 0.0004 0.0002 0.0001 0      0
0      0      0      0.0001 0.0005 0.0017 0.0045 0.0106 0.0232 0.0474 0.0913 0.1678 0.3198 0.1526 0.0833 0.0425 0.0212 0.0111 0.0057 0.0028 0.0015 0.0009 0.0005 0.0002 0.0001 0
0      0      0      0.0001 0.0003 0.0009 0.0023 0.0054 0.0119 0.0243 0.0466 0.086  0.1626 0.3229 0.1643 0.0841 0.0431 0.022  0.0112 0.0056 0.003  0.0018 0.0009 0.0004 0.0001 0
0      0      0      0      0.0001 0.0004 0.0012 0.0028 0.0061 0.0124 0.0239 0.044  0.0833 0.1643 0.3233 0.1647 0.0843 0.0431 0.022  0.011  0.006  0.0035 0.0018 0.0009 0.0003 0.0001
0      0      0      0      0.0001 0.0002 0.0006 0.0014 0.0031 0.0063 0.0122 0.0225 0.0427 0.0841 0.1647 0.3242 0.1648 0.0843 0.0429 0.0215 0.0117 0.0065 0.0036 0.0016 0.0005 0.0001
0      0      0      0      0      0.0001 0.0003 0.0007 0.0016 0.0032 0.0063 0.0115 0.0218 0.0431 0.0843 0.1648 0.324  0.1646 0.0838 0.0421 0.0229 0.0124 0.007  0.0032 0.0011 0.0002
0      0      0      0      0      0.0001 0.0001 0.0004 0.0008 0.0016 0.0032 0.0059 0.0111 0.022  0.0431 0.0843 0.1646 0.3235 0.1637 0.0821 0.0446 0.0261 0.0138 [illegible] 0.0021 0.0003
0      0      0      0      0      0      0.0001 0.0002 0.0004 0.0008 0.0016 0.003  0.0057 0.0112 0.0219 0.0429 0.0838 0.1637 0.3217 0.1604 0.0875 0.051  0.0269 0.0121 0.0042 0.0009
0      0      0      0      0      0      0      0.0001 0.0002 0.0004 0.0008 0.0015 0.0028 0.0056 0.011  0.0215 0.042  0.0821 0.1603 0.3151 0.1728 0.0995 0.0526 0.0287 0.0082 0.0017
0      0      0      0      0      0      0      0      0.0001 0.0002 0.0004 0.0007 0.0013 0.0026 0.0051 0.0101 0.0197 0.0386 0.0754 0.1475 0.3357 0.1944 0.1025 0.0463 0.0159 0.0034
0      0      0      0      0      0      0      0      0      0.0001 0.0001 0.0003 0.0005 0.0011 0.0021 0.0041 0.0081 0.0159 0.0312 0.061  0.1384 0.3962 0.2079 [illegible] 0.0323 0.0069
0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0002 0.0003 0.0007 0.0014 0.0027 0.0054 0.0107 0.021  0.0475 0.136  0.4729 0.2173 0.0731 0.0157
0      0      0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0002 0.0003 0.0007 0.0013 0.0027 0.0054 0.0123 0.0751 0.122  0.5757 0.1966 0.0426
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0002 0.0004 0.0008 0.0018 0.0034 0.019  0.0903 0.7265 0.1555
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0.0002 0.0008 0.0043 0.0356 0.9569
```

```
1.7274 0.0758 0.0063 0.0006 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0.1495 3.3959 0.3343 0.0462 0.0088 0.0018 0.0004 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0.0156 0.4549 4.4297 0.6681 0.1321 0.0318 0.0087 0.0026 0.0008 0.0002 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0.0037 0.0681 0.8549 5.0806 1.0271 0.2542 0.0737 0.0239 0.0084 0.0031 0.0012 0.0004 0.0002 0.0001 0      0      0      0      0      0      0      0      0      0      0      0
0.0009 0.0215 0.2089 1.257  5.4922 1.3784 0.4044 0.1348 0.0485 0.0196 0.0081 0.0035 0.0015 0.0007 0.0003 0.0001 0      0      0      0      0      0      0      0      0      0
0.0003 0.0063 0.0616 0.371  1.6362 5.7518 1.7044 0.5714 0.2125 0.0858 0.0359 0.0165 0.0078 0.0037 0.0017 0.0008 0.0004 0.0002 0.0001 0      0      0      0      0      0      0
0.0001 0.0022 0.021  0.1266 0.5564 1.9773 5.9159 1.999  0.7461 0.3034 0.132  0.0604 0.0292 0.0145 0.0071 0.0035 0.0016 0.0008 0.0003 0.0002 0.0001 0      0      0      0      0
0      0.0008 0.008  0.0454 0.2137 0.7567 2.277  6.0198 2.2511 0.9213 0.4026 0.1854 0.0906 0.0459 0.0231 0.0115 0.0057 0.0028 0.0013 0.0006 0.0003 0.0001 0      0      0      0
0      0.0003 0.0034 0.0203 0.0896 0.3174 0.9554 2.5373 6.0853 2.4921 1.0906 0.5035 0.2471 0.1259 0.0639 0.0323 0.0162 0.0081 0.004  0.0019 0.0009 0.0004 0.0002 0.0001 0      0
0      0.0002 0.0015 0.0092 0.0405 0.1436 0.4321 1.1478 2.7621 6.1243 2.6912 1.2438 0.6115 0.3124 0.1595 0.0812 0.0412 0.0208 0.0104 0.0051 0.0025 0.0012 0.0005 0.0002 0      0
0      0.0001 0.0007 0.0044 0.0195 0.069  0.2077 0.5519 1.3282 2.9517 6.1365 2.8451 1.3998 0.716  0.3652 0.1871 0.0953 0.0484 0.0244 0.0121 0.006  0.0029 0.0012 0.0004 0.0001 0
0      0      0.0004 0.0022 0.0098 0.0347 0.1045 0.2776 0.6664 1.4857 3.0923 6.0941 3.005  1.5379 0.7873 0.4028 0.2058 0.1049 0.0531 0.0264 0.013  0.0066 0.0028 0.001  0.0002 0
0      0      0.0002 0.0011 0.005  0.0177 0.0534 0.1421 0.3423 0.761  1.5842 3.1239 6.1043 3.1281 1.6021 0.8202 0.4195 0.2142 0.1082 0.0543 0.027  0.0135 0.0059 0.002  0.0005 0
0      0      0.0001 0.0005 0.0025 0.009  0.0273 0.0727 0.1752 0.3895 0.8113 1.5002 3.1288 6.1671 3.1608 1.6186 0.8286 0.4234 0.2154 0.1078 0.0546 0.0272 0.0119 0.0041 0.0009 0.0001
0      0      0      0.0003 0.0013 0.0046 0.0139 0.0371 0.0895 0.1993 0.4153 0.8195 1.6026 3.1609 6.1838 3.1691 1.6226 0.8297 0.4224 0.2117 0.1077 0.0536 0.0233 0.0081 0.0019 0.0002
0      0      0      0.0001 0.0006 0.0023 0.0071 0.0189 0.0457 0.1019 0.2124 0.4194 0.8206 1.6189 3.1691 6.1875 3.1702 1.6215 0.8259 0.4141 0.211  0.105  0.0457 0.0159 0.0037 0.0004
0      0      0      0.0001 0.0003 0.0012 0.0036 0.0096 0.0232 0.0513 0.1005 0.2144 0.4198 0.8286 1.6225 3.1701 6.1863 3.1662 1.613  0.8091 0.4124 0.2058 0.0894 0.0312 0.0073 0.0007
0      0      0      0      0.0002 0.0006 0.0018 0.0048 0.0118 0.0264 0.0552 0.1093 0.2143 0.4234 0.8296 1.6213 3.1661 6.1778 3.1492 1.5801 0.8057 0.4022 0.1749 0.061  0.0143 0.0014
0      0      0      0      0.0001 0.0003 0.0009 0.0024 0.0059 0.0133 0.0279 0.0554 0.1088 0.2152 0.4221 0.8255 1.6128 3.1491 6.144  3.0848 1.5737 0.7856 0.3418 0.1193 0.026  0.0028
0      0      0      0      0      0.0001 0.0004 0.0012 0.0029 0.0065 0.0138 0.0275 0.0542 0.1075 0.2112 0.4135 0.8024 1.5792 3.0835 6.0123 3.0159 1.5316 0.6675 [illegible] 0.0548 0.0054
0      0      0      0      0      0.0001 0.0002 0.0005 0.0013 0.0029 0.0063 0.0126 0.0251 0.0501 0.0988 0.1939 0.3798 0.7425 1.4508 2.8268 5.99   2.9934 1.303  0.455  0.107  0.0108
0      0      0      0      0      0      0.0001 0.0002 0.0005 0.0011 0.0024 0.005  0.01   0.0203 0.0403 0.0796 0.1565 0.3067 0.6001 1.1744 2.4086 5.012  2.6351 0.9216 0.2166 0.0216
0      0      0      0      0      0      0      0      0.0001 0.0003 0.0007 0.0015 0.0031 0.0065 0.0133 0.0266 0.053  0.1046 0.2057 0.4037 0.8566 2.0945 5.3486 [illegible] 0.4908 0.0488
0      0      0      0      0      0      0      0      0      0      0.0001 0.0003 0.0006 0.0014 0.0029 0.0062 0.0128 0.026  0.037  0.1032 [illegible] 0.5411 1.1489 [illegible] 1.3817 0.1327
0      0      0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0002 0.0006 0.0014 0.0032 0.007  0.0148 0.033  0.0831 0.2411 0.6881 4.7955 0.5462
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0003 0.0009 0.003  0.0104 0.0423 0.2459 2.8123
```

B. *tricaudatus* (dead animals). Data for May 1979.

FINE PRINT

```
1      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      1      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      1      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      1      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      0.0006 0.9989 0.0006 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      0      0.0256 0.9521 0.02   0.0019 0.0003 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      0      0.0031 0.1167 0.727  0.0737 0.0138 0.0037 0.0012 0.0005 0.0002 0.0001 0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      0      0.0007 0.0201 0.1891 0.6176 0.1155 0.0312 0.0104 0.004  0.0018 0.0009 0.0004 0.0002 0.0001 0      0      0      0      0      0      0      0      0
0      0      0      0      0.0002 0.0094 0.0633 0.2055 0.5061 0.1365 0.0457 0.0175 0.0079 0.0039 0.002  0.001  0.0005 0.0002 0.0001 0.0001 0      0      0      0      0      0
0      0      0      0      0.0001 0.0038 0.0256 0.0833 0.2021 0.4343 0.1449 0.0556 0.025  0.0125 0.0064 0.0032 0.0016 0.0008 0.0004 0.0002 0.0001 0.0001 0      0      0      0
0      0      0      0      0      0.0017 0.0117 0.0382 0.0927 0.1937 0.3337 0.1457 0.0655 0.0329 0.0158 0.0086 0.0044 0.0022 0.0011 0.0005 0.0003 0.0002 0.0001 0      0      0
0      0      0      0      0      0.0009 0.0058 0.019  0.0462 0.0966 0.1823 0.3431 0.1503 0.075  0.0389 0.0198 0.0101 0.0051 0.0026 0.0013 0.0007 0.0004 0.0003 0.0001 0      0
0      0      0      0      0      0.0004 0.003  0.0097 0.0236 0.0495 0.0936 0.1662 0.3289 0.1588 0.0814 0.0416 0.0212 0.0108 0.0055 0.0027 0.0015 0.0009 0.0005 0.0002 0      0
0      0      0      0      0      0.0002 0.0015 0.005  0.0121 0.0253 0.0478 0.0852 0.1594 0.3327 0.1615 0.0828 0.0423 0.0216 0.0109 0.0054 0.003  0.0019 0.0011 0.0003 0      0
0      0      0      0      0      0.0001 0.0008 0.0025 0.0052 0.0129 0.0244 0.0436 0.0817 0.1615 0.3341 0.1621 0.0831 0.0424 0.0215 0.0107 0.0059 0.0037 0.0022 0.0006 0      0
0      0      0      0      0      0.0001 0.0004 0.0013 0.0031 0.0066 0.0125 0.0223 0.0418 0.0828 0.1621 0.3344 0.1622 0.083  0.042  0.0209 0.0115 0.0074 0.0044 0.0012 0      0
0      0      0      0      0      0      0.0002 0.0005 0.0016 0.0033 0.0064 0.0114 0.0213 0.0423 0.0831 0.1622 0.3344 0.1519 0.0823 0.041  0.0225 0.0144 0.0087 0.0022 0      0
0      0      0      0      0      0      0.0001 0.0003 0.0008 0.0017 0.0032 0.0058 0.0109 0.0216 0.0424 0.083  0.1519 0.2337 0.1605 0.0801 0.0442 0.0263 0.017  0.0045 0      0
0      0      0      0      0      0      0      0.0002 0.0004 0.0008 0.0016 0.0029 0.0055 0.0108 0.0214 0.042  0.0823 0.1605 0.3311 0.1562 0.0865 0.0553 0.0233 0.0095 0.0001 0
0      0      0      0      0      0      0      0.0001 0.0002 0.0004 0.0008 0.0014 0.0027 0.0054 0.0106 0.0208 0.0407 0.0796 0.1552 0.3223 0.1587 0.1062 0.0653 0.0175 0.0001 0
0      0      0      0      0      0      0      0      0.0001 0.0002 0.0003 0.0006 0.0012 0.0023 0.0047 0.0091 0.0179 0.0352 0.0687 0.1335 0.3495 0.2104 0.1271 0.034  0.0002 0
0      0      0      0      0      0      0      0      0      0.0001 0.0001 0.0002 0.0004 0.0008 0.0015 0.0031 0.006  0.0119 0.0233 0.0469 0.1176 0.4547 0.2627 0.0703 0.0004 0
0      0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0001 0.0002 0.0005 0.001  0.002  0.004  0.0081 0.0205 0.0791 0.6588 0.1645 0.0011 0
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0005 0.0041 0.9894 0.0059 0
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      1      0
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      1

1.527  0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      2.9325 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      3.9661 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      4.8461 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      0.003  5.6282 0.0037 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      0.0001 0.1465 6.0506 0.1427 0.0144 0.0029 0.0008 0.0003 0.0001 0      0      0      0      0      0      0      0      0      0      0      0      0      0
0      0      0      0      0.0179 0.7525 5.5207 0.5715 0.1151 0.033  0.0116 0.0046 0.0021 0.001  0.0005 0.0002 0.0001 0      0      0      0      0      0      0      0      0
0      0      0      0      0.0043 0.1011 1.3455 4.7122 0.955  0.2787 0.0991 0.04   0.0183 0.009  0.0045 0.0022 0.0011 0.0005 0.0002 0.0001 0.0001 0      0      0      0      0
0      0      0      0      0.0014 0.0605 0.4506 1.5933 4.1582 1.2194 0.4344 0.176  0.0809 0.0405 0.0206 0.0104 0.0052 0.0026 0.0013 0.0006 0.0003 0.0002 0.0001 0      0      0
0      0      0      0      0.0006 0.0244 0.1824 0.6453 1.6063 3.8129 1.3751 0.5581 0.2572 0.1292 0.0659 0.0335 0.017  0.0085 0.0043 0.0021 0.001  0.0005 0.0003 0      0      0
0      0      0      0      0.0003 0.0112 0.0836 0.2959 0.7745 1.7312 3.5792 1.4617 0.6743 0.3392 [illegible] 0.0884 0.045  0.0228 0.0115 0.0056 0.0029 0.0015 0.0008 0.0002 0      0
0      0      0      0      0.0001 0.0055 0.0415 0.1473 0.3859 0.6632 1.7309 3.3629 1.5533 0.7825 [illegible] [illegible] 0.1043 0.0531 0.0268 0.0132 0.0069 0.0038 0.0019 0.0004 0      0
0      0      0      0      0.0001 0.0026 0.0212 0.0754 0.1976 0.4421 0.8885 1.6678 3.3271 1.6352 [illegible] [illegible] 0.2188 0.1115 0.0564 0.028  0.0146 0.0092 0.0041 0.0009 0      0
0      0      0      0      0      0.0014 0.0108 0.0384 0.1009 0.226  0.4543 0.8551 1.642  3.3581 [illegible] [illegible] 0.4354 0.222  0.1124 0.0559 0.0292 0.0164 0.0084 0.0016 0      0
0      0      0      0      0      0.0007 0.0055 0.0196 0.0515 0.1154 0.2322 0.4371 0.8417 1.6629 [illegible] [illegible] 0.8555 0.4264 0.2211 0.1099 0.0575 0.0324 0.0167 0.0036 0      0
0      0      0      0      0      0.0004 0.0027 0.0099 0.0262 0.0569 0.1185 0.2234 0.4302 0.8523 [illegible] [illegible] 1.6708 0.8545 0.4331 0.2155 0.1128 0.0637 0.0329 0.0071 0      0
0      0      0      0      0      0.0002 0.0014 0.005  0.0133 0.03   0.0604 0.114  0.2197 0.4354 [illegible] [illegible] 3.3844 1.6675 0.8474 0.4218 0.2205 0.1249 0.0646 0.0141 0.0001 0
0      0      0      0      0      0.0001 0.0007 0.0025 0.0067 0.0152 0.0307 0.056  0.112  0.222  [illegible] [illegible] 1.6675 3.3773 1.6532 0.8251 0.4321 0.2446 0.1267 0.0277 0.0001 0
0      0      0      0      0      0      0.0003 0.0012 0.0033 0.0076 0.0154 0.0292 0.0566 0.1123 [illegible] [illegible] 0.8473 1.6532 3.349  1.6093 0.845  0.4763 0.246  0.0543 0.0002 0
0      0      0      0      0      0      0.0001 0.0006 0.0016 0.0037 0.0075 0.0143 0.0278 0.0553 0.109  0.7139 0.4167 0.8193 1.5579 3.2632 1.649  0.931  0.4653 0.1563 0.0035 0
0      0      0      0      0      0      0.0001 0.0002 0.0007 0.0016 0.0032 0.0062 0.0121 0.0242 0.048  0.0943 0.1949 0.3622 0.7078 1.4262 3.3509 1.6194 0.9452 0.2075 0.0039 0
0      0      0      0      0      0      0      0.0001 0.0002 0.0005 0.001  0.002  0.004  0.008  0.016  0.0216 0.0613 0.1224 0.2396 0.4832 1.1484 3.8604 1.9533 0.4267 0.0119 0
0      0      0      0      0      0      0      0      0      0.0001 0.0001 0.0003 0.0005 0.0013 0.0026 0.0053 0.0135 0.021  0.014  0.0639 0.2    0.6643 5.1195 1.1242 0.2005 0
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0.0001 0.0002 0.0005 0.0011 0.004  [illegible] [illegible] [illegible] 0
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      4.4101 0
0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      0      2.3053
```

B. <u>tricaudatus</u> (live animals). Data for October 1979.

FINE PRINT

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1        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        1        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        1        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        0        1        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        0        0.0016   0.9959   0.0015   0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        0        0        0.0197   0.9624   0.0166   0.0011   0.0002   0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        0        0        0.0018   0.0661   0.8414   0.0584   0.0089   0.0022   0.0007   0.0003   0.0001   0.0001   0        0        0        0        0        0        0        0        0        0        0        0
0        0        0        0        0.0004   0.0179   0.1751   0.6643   0.102    0.025    0.0081   0.0032   0.0015   0.0009   0.0005   0.0003   0.0001   0.0001   0        0        0        0        0        0        0        0
0        0        0        0        0.0001   0.0059   0.0578   0.2194   0.5154   0.1251   0.0413   0.0151   0.0079   0.0044   0.0025   0.0014   0.0008   0.0004   0.0002   0.0001   0.0001   0.0001   0        0        0        0
0        0        0        0        0.0001   0.0025   0.0298   0.0941   0.2206   0.4119   0.1346   0.0527   0.0257   0.0145   0.0081   0.0046   0.0026   0.0014   0.0008   0.0004   0.0003   0.0002   0.0001   0        0        0
0        0        0        0        0        0.0013   0.0124   0.0471   0.1105   0.2058   0.341    0.1332   0.0651   0.0366   0.0206   0.0116   0.0065   0.0036   0.002    0.0011   0.0007   0.0005   0.0003   0.0001   0        0
0        0        0        0        0        0.0007   0.0068   0.0258   0.0606   0.1128   0.186    0.287    0.1398   0.0708   0.0444   0.025    0.0141   0.0079   0.0044   0.0023   0.0015   0.0012   0.0008   0.0001   0        0
0        0        0        0        0        0.0004   0.0039   0.0145   0.0341   0.0636   0.1049   0.1611   0.2704   0.1515   0.0854   0.0481   0.0271   0.0152   0.0084   0.0045   0.0023   0.0021   0.0013   0.0003   0        0
0        0        0        0        0        0.0002   0.0021   0.0082   0.0192   0.0359   0.0592   0.0909   0.1516   0.2768   0.1553   0.0675   0.0493   0.0276   0.0153   0.0082   0.0052   0.0042   0.0028   0.0005   0        0
0        0        0        0        0        0.0001   0.0012   0.0046   0.0108   0.0202   0.0333   0.0512   0.0855   0.1553   0.279    0.1564   0.0681   0.0494   0.0274   0.0147   0.0094   0.0075   0.005    0.0005   0        0
0        0        0        0        0        0.0001   0.0007   0.0026   0.0061   0.0114   0.0188   0.0283   0.0482   0.0875   0.1554   0.2792   0.1565   0.0678   0.0488   0.0252   0.0157   0.0134   0.009    0.0017   0        0
0        0        0        0        0        0        0.0004   0.0014   0.0034   0.0064   0.0106   0.0162   0.0271   0.0493   0.0881   0.1565   0.2793   0.1559   0.0856   0.0464   0.0296   0.0239   0.0159   0.003    0        0
0        0        0        0        0        0        0.0002   0.0008   0.0019   0.0036   0.0059   0.0091   0.0152   0.0276   0.0494   0.0878   0.1559   0.278    0.1535   0.0824   0.0525   0.0424   0.0283   0.0054   0        0
0        0        0        0        0        0        0.0001   0.0004   0.001    0.002    0.0033   0.005    0.0084   0.0153   0.0274   0.0498   0.0566   0.1535   0.2738   0.1461   0.0933   0.0751   0.0502   0.0096   0.0001   0
0        0        0        0        0        0        0.0001   0.0002   0.0005   0.001    0.0017   0.0027   0.0045   0.0082   0.0147   0.0261   0.0464   0.0823   0.145    0.2606   0.1654   0.1333   0.0891   0.0171   0.0001   0
0        0        0        0        0        0        0        0.0001   0.0002   0.0005   0.0006   0.0013   0.0021   0.0038   0.0065   0.0123   0.0219   0.0385   0.069    0.1226   0.2949   0.2362   0.158    0.0303   0.0002   0
0        0        0        0        0        0        0        0        0.0001   0.0001   0.0003   0.0004   0.0007   0.0013   0.0022   0.0042   0.0074   0.0132   0.0235   0.0417   0.1      0.4487   0.2988   0.0574   0.0004   0
0        0        0        0        0        0        0        0        0        0        0        0        0.0001   0.0002   0.0003   0.0006   0.001    0.0018   0.0032   0.0058   0.014    0.0627   0.753    0.1463   0.001    0
0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0.0001   0.0004   0.0049   0.9851   0.0065   0
0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        1        0
0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        1
```

```
1.7596   0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        6.0277   0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        8.8964   0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        0.0002   11.5325  0.0304   0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        0        0.0183   13.977   0.0248   0.0005   0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        0        0.0004   0.2777   15.7805  0.3106   0.0238   0.0039   0.001    0.0003   0.0001   0.0001   0        0        0        0        0        0        0        0        0        0        0        0        0
0        0        0        0        0.0249   1.4156   15.7237  1.2249   0.2065   0.0546   0.019    0.0078   0.0038   0.002    0.0011   0.0006   0.0003   0.0001   0.0001   0        0        0        0        0        0        0
0        0        0        0        0.0051   0.2946   3.2817   13.8364  2.3597   0.6307   0.2226   0.0932   0.0456   0.0259   0.0143   0.0076   0.0043   0.0023   0.0012   0.0006   0.0003   0.0002   0.0001   0        0        0
0        0        0        0        0.0017   0.0972   1.0838   4.5991   11.8786  3.1858   1.1281   0.4743   0.239    0.1341   0.0751   0.0419   0.0233   0.0128   0.0059   0.0036   0.0021   0.0013   0.0006   0.0001   0        0
0        0        0        0        0.0007   0.0416   0.4645   1.9726   5.1335   10.3591  3.6774   1.548    0.7817   0.4398   0.2473   0.1389   0.0777   0.0432   0.0237   0.0126   0.0073   0.0049   0.0025   0.0002   0        0
0        0        0        0        0.0004   0.0208   0.2324   0.988    2.557    5.1968   9.2711   3.9109   1.9761   1.1129   0.627    0.3528   0.1981   0.1109   0.0612   0.0326   0.0192   0.013    [illegible] 0.0009   0        0
0        0        0        0        0.0002   0.0113   0.1271   0.5411   1.401    2.846    5.0838   8.3685   4.2459   2.3923   1.3465   0.7596   0.4272   0.2393   0.1325   0.0708   0.042    0.0295   [illegible] [illegible] 0        0
0        0        0        0        0.0001   0.0064   0.0715   0.3048   0.7898   1.6061   2.8574   4.7323   8.1598   4.6022   2.5949   1.4623   0.823    0.4614   0.2550   0.137    0.0814   0.0556   0.0201   0.0043   0        0
0        0        0        0        0.0001   0.0036   0.0402   0.1716   0.445    0.9054   1.6169   2.5689   4.6035   8.3603   4.7159   2.6582   1.4965   0.8395   0.4658   0.2497   0.1485   0.1018   0.0557   [illegible] 0        0
0        0        0        0        0        0.002    0.0225   0.0964   0.2505   0.5101   0.9113   1.5047   2.5959   4.716    8.4235   4.7499   2.6747   1.5008   0.8331   0.463    0.266    0.1825   0.0956   0.0145   0.0001   0
0        0        0        0        0        0.0011   0.0125   0.054    0.1408   0.2871   0.5133   0.8478   1.463    2.6583   4.7499   8.4398   4.7542   2.6582   1.4913   0.7948   0.4733   0.3261   0.1778   0.026    0.0001   0
0        0        0        0        0        0.0006   0.0069   0.0302   0.0789   0.1612   0.2685   0.4759   0.8234   1.4965   2.6746   4.7541   8.4333   4.7348   2.6295   1.4108   0.8405   0.5776   0.3164   0.0465   0.0002   0
0        0        0        0        0        0.0003   0.0038   0.0167   0.0439   0.09     0.1615   0.2672   0.4616   0.8394   1.5006   2.668    4.7347   8.3941   4.6635   [illegible] 1.4912   1.0252   0.5621   0.0828   0.0004   0
0        0        0        0        0        0.0002   0.002    0.0091   0.0241   0.0496   0.0692   0.1479   0.2558   0.4655   0.8328   1.4612   2.6291   4.6633   8.2665   4.4374   2.6445   1.8165   0.9978   0.1471   0.0007   0
0        0        0        0        0        0.0001   0.001    0.0047   0.0127   0.0263   0.0474   0.0789   0.1367   0.2491   0.446    0.7938   1.4097   2.501    4.4354   7.665    4.6888   3.2247   1.7001   0.2612   0.0012   0
0        0        0        0        0        0        0.0004   0.0021   0.0057   0.012    0.022    0.0368   0.064    0.117    0.2099   0.3743   0.6654   1.1814   2.095    3.7226   6.3115   5.7163   3.1333   0.4634   0.0021   0
0        0        0        0        0        0        0.0001   0.0006   0.0017   0.0038   0.0071   0.012    0.0212   0.039    0.0705   0.1263   0.7253   0.401    0.7174   1.2662   2.9341   10.8036  5.4354   1.6765   0.0338   0
0        0        0        0        0        0        0        0        0.0002   0.0004   0.0008   0.0014   0.0026   0.0049   0.0092   0.0159   0.0305   0.0551   0.0967   0.1754   0.2363   [illegible] 15.1033  7.0342   0.101    0
0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0.0001   0.0002   0.0003   0.0006   0.0011   0.0025   [illegible] [illegible] [illegible] 0.1674   0
0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        10.2366  0
0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        0        4.445
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B. *tricaudatus* (dead animals). Data for October 1979.

FINE PRINT

APPENDIX 3

TEST RUNS OF DRIFT MODEL USING THEORETICAL DATA

Methods

Behaviour of the model was tested by conducting runs in which each component was varied singly while holding other components constant. The model has three major variables, each of which are direct functions of current velocity, thus indirect functions of distance from shore. Settling rate is negatively related and lateral dispersal (diffusion) is positively related to distance from shore. Departure can vary positively, negatively or independently of distance from shore.

Individual values of functions for each transect were determined using the distance from shore of the midpoint of each transect. Benthic densities of animals used in all test runs approximated the benthic distribution of the two mayfly populations studied in the Pembina River. Animals were most abundant at the river centre (100 individuals m^{-2}). Abundance declined linearly to densities of four animals m^{-2} in the transects adjacent to river margins. All test runs estimated distributions of animals after 15 days.

Departure (p)

Rate of Departure-- Equal proportions of animals departed from all transects. Departure levels were set at one of 0.2, 0.4, 0.6, 0.8 or 1.0 per 24 hours. Settling rate (r) and lateral diffusion (s) were constant at all transects with values of 0.200 and 0.300 respectively.

Departure as a Function of Distance from Shore-- Departure rates were made either positive or negative linear functions of distance from shore. Minimum value was assigned as 0.04. Maxima in separate trials were 0.20, 0.40, 0.60, 0.80 or 1.00. Settling and diffusion values were constant as indicated above.

Settling Rate

Settling rate normally varies inversely with current velocity, hence distance from shore (y). Equations used to calculate values of r for the model river were

$$r = \beta_1' y^{\beta_2'} \qquad \text{(south margin, } y<12\text{)}$$

$$r = \beta_1' (12)^{\beta_2'} \qquad \text{(river centre, } y>12\text{)}$$

$$r = \beta_1' (2y)^{\beta_2'} \qquad \text{(north margin, } y< 6\text{)}.$$

Varying the Intercept (β_1')-- The intercept of the above functions is a measure of animals' ability to settle at all transects across the river. When β_1' is large, animals settle over short downstream distances. As β_1' decreases, animals settle at increasingly greater distances downstream from their point of entry into the water column. Intercept values (β_1') were set at either 0.50, 0.75, 1.00, 1.25, 1.75 or 2.00. The exponent (β_2') was assigned a value of -1.00 for all trials. Lateral diffusion (s) was constant, with a value of 0.300 for all transects. Departure rates were either positive (range 0.04 - 1.00), negative (range 0.04 - 1.00) or independent (0.50) functions of distance from shore.

Varying the Exponent (β'_2)-- The exponent of the above functions is a measure of the rate of change of settling rate (r) across the river. When the exponent has a large negative value, animals at the river centre travel much greater distances downstream before returning to the substrate than do animals at the margins. When the exponent has a small negative value, the differences in downstream distance travelled from different portions of the river are minimized. Exponent values (β'_2) were set at either -0.600, -0.800, -1.00, -1.200, -1.400 or -1.600. The intercept (β'_1) was assigned a value of 1.00 for all trials. Lateral diffusion values (s) were constant across the river, with a value of 0.300. Departure rates were adjusted as indicated above.

Lateral Diffusion (s)

Lateral diffusion rate (s) varies with both the distance that suspended animals have been transported downstream (x) and current velocity, hence distance from shore (y)

$$s = \beta'_3 + \beta'_4 x^{0.5} + \beta'_5 y \quad .$$

Because the model determines values of s at 1-m downstream intervals, the above equation reduces to

$$\begin{aligned} s &= \beta'_3 + \beta'_4 (1)^{0.5} + \beta'_5 y \\ &= (\beta'_3 + \beta'_4) + \beta'_5 y \quad . \end{aligned}$$

The series of equations used to determine values of s for all transects in the model river was

$$s = (\beta_3' + \beta_4') + \beta_5'y \qquad \text{(south margin, } y<12)$$

$$s = (\beta_3' + \beta_4') + \beta_5'(12) \qquad \text{(river centre, } y>12)$$

$$s = (\beta_3' + \beta_4') + \beta_5'(2y) \qquad \text{(north margin, } y< 6).$$

Varying the Intercept ($\beta_3' + \beta_4'$)-- The intercept of these functions is a measure of the animals' tendency to become laterally dispersed at all transects. When the intercept is large, animals become widely dispersed. As the intercept approaches zero, all animals are transported directly downstream, and there is no lateral transport. Intercept values ($\beta_3' + \beta_4'$) were set at either 0.100, 0.200, 0.300, 0.400, 0.800 or 1.000. The slope (β_5') was set at zero. Settling rate was constant, with a value of 0.200 for all transects. Departure rates were either positive (range 0.04 - 1.00), negative (range 0.04 - 1.00) or independent (0.50) functions of distance from shore.

Varying the Slope (β_5')-- The slope of the lateral diffusion function is a measure of the rate of change of lateral dispersal across the river. When the slope (β_5') is large, animals at the river centre become more widely dispersed than animals at the river margins. As the slope approaches zero, dispersal at all points in the river becomes equivalent.

The intercept and slope of the functions were adjusted to produce lateral diffusion levels of zero at the river margin transects and to allow maximum lateral dispersal values of 0.25, 0.50, 0.75, 1.00 or 1.25. Settling rate (r) was constant at all transects with a value of 0.200. Departure rates were adjusted as indicated above.

Results

Influence of Departure Rate

When both settling rates and lateral diffusion were held constant, the distribution of animals after 15 days was determined by the sign of the relationship between departure and distance from shore (Fig. 29). When departure was a positive function of distance from shore, densities at the river centre became reduced and densities increased evenly at all other transects. When departure was negatively related to distance from shore, densities increased both at the river centre and in the transects closest to shore. Densities near margins increased because animals drifting to the river edges were placed on the substrate rather than being reflected back to the river centre.

Increasing the maximum proportion of animals departing resulted in more pronounced changes in distribution after 15 days. However, the relationship was not linear. Each 0.200 increase in maximum departure rate produced a proportionately smaller change in distribution.

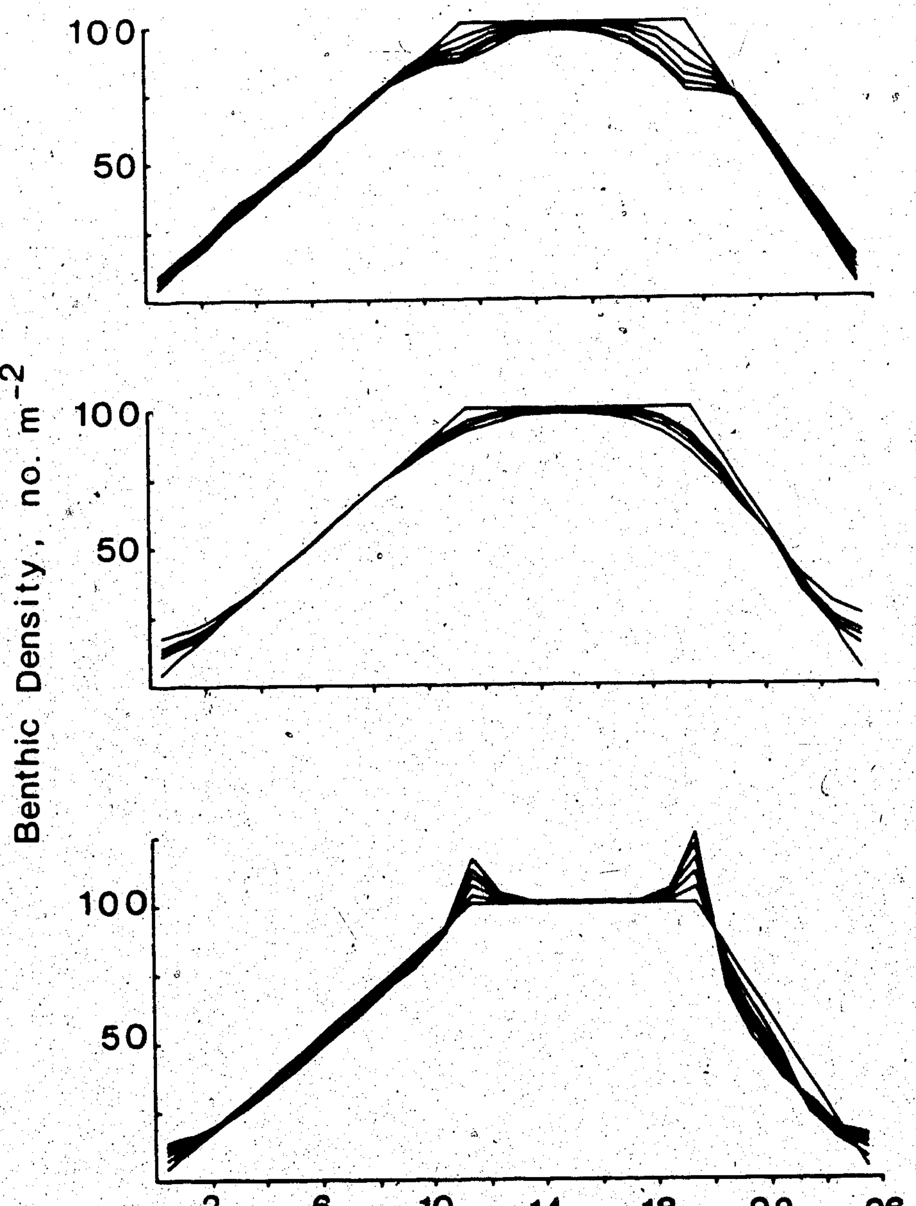

Figure 29. Effect of varying daily proportion of animals departing, on benthic distribution after 15 days; settling and diffusion parameters constant. Top, departure increases with increasing mean current velocity; centre, departure independent of mean current velocity; bottom, departure decreases with increasing mean current velocity. Lines most deviant in each figure are those with highest maximal departure rates.

Influence of Settling Rate

The influence of varying both the intercept and the exponent of the settling rate functions was to accelerate changes in distribution, which were determined by relative departure rates. Small intercept values (Fig. 30) and large negative exponent values (Fig. 31) each produced increasingly marked changes in the distributions after 15 days.

Influence of Diffusion Rate

When the relationship between lateral diffusion and distance from shore was constant, high diffusion rates resulted in more rapid changes in distribution than did low rates. The region of concentration of animals was dependent on the relationship between departure rate and distance from shore (Fig. 32). Linear increments in the diffusion values produced exponential changes in the distribution of animals after 15 days.

Increasing the slope of the functions relating lateral diffusion to distance from shore produced increasingly marked differences in distribution after 15 days (Fig. 33). Animals became increasingly abundant near river margins as slopes became greater regardless of the relationship between departure and distance from shore, although when departure was negatively related to distance from shore, some increase in density at the river centre was also evident.

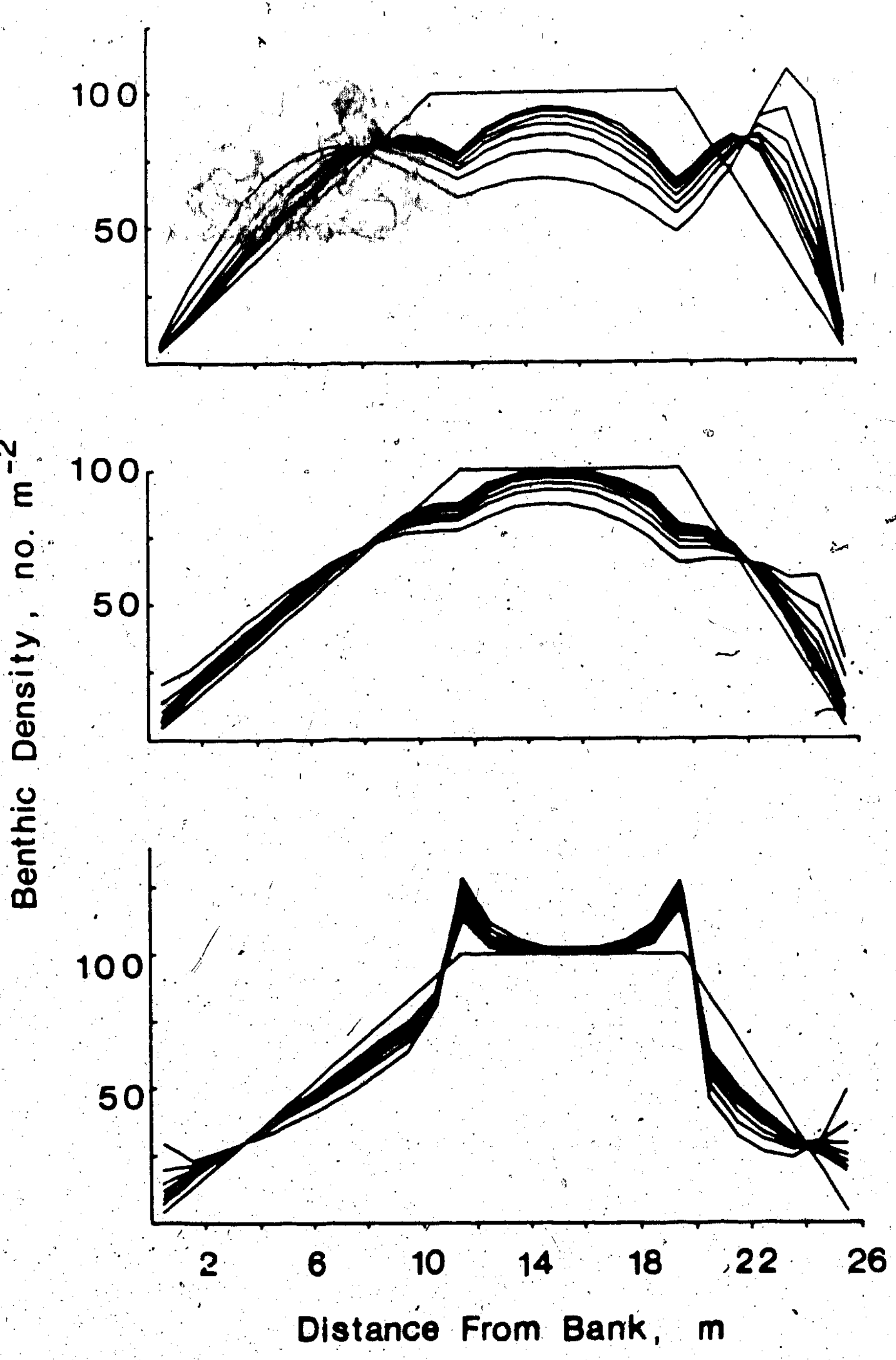

Figure 30. Effect of varying intercept of settling rate function on benthic distribution of animals after 15 days; settling exponent and lateral diffusion parameters constant. Top, centre and bottom figures as described in Fig. 29. Lines most deviant in each figure are those with lowest settling rate function intercepts.

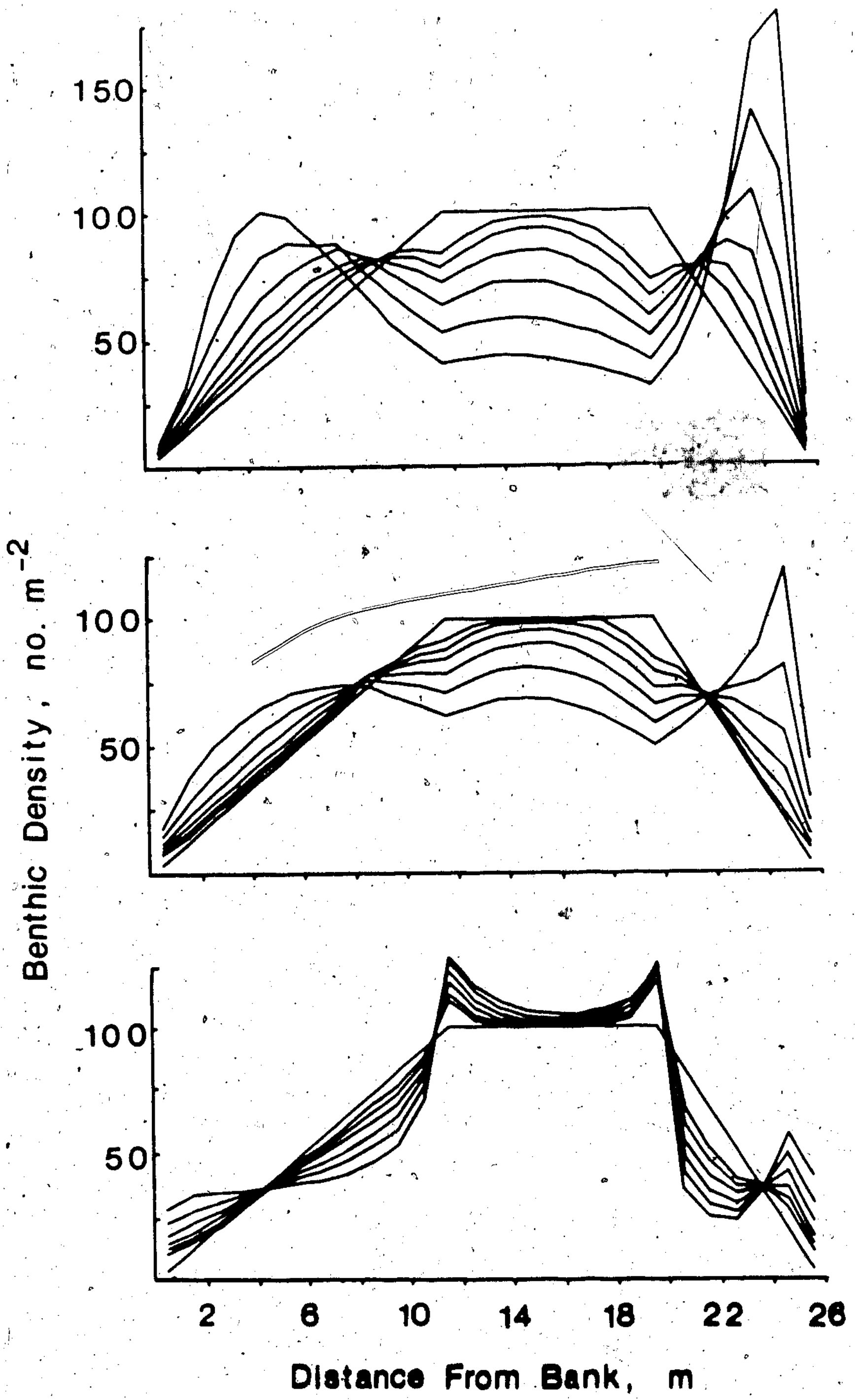

Figure 31. Effect of varying exponent of settling rate function on benthic distribution of animals after 15 days; settling intercept and lateral diffusion parameters constant. Top, centre and bottom figures as described in Fig. 29. Lines most deviant in each figure are those with largest negative settling function exponent values.

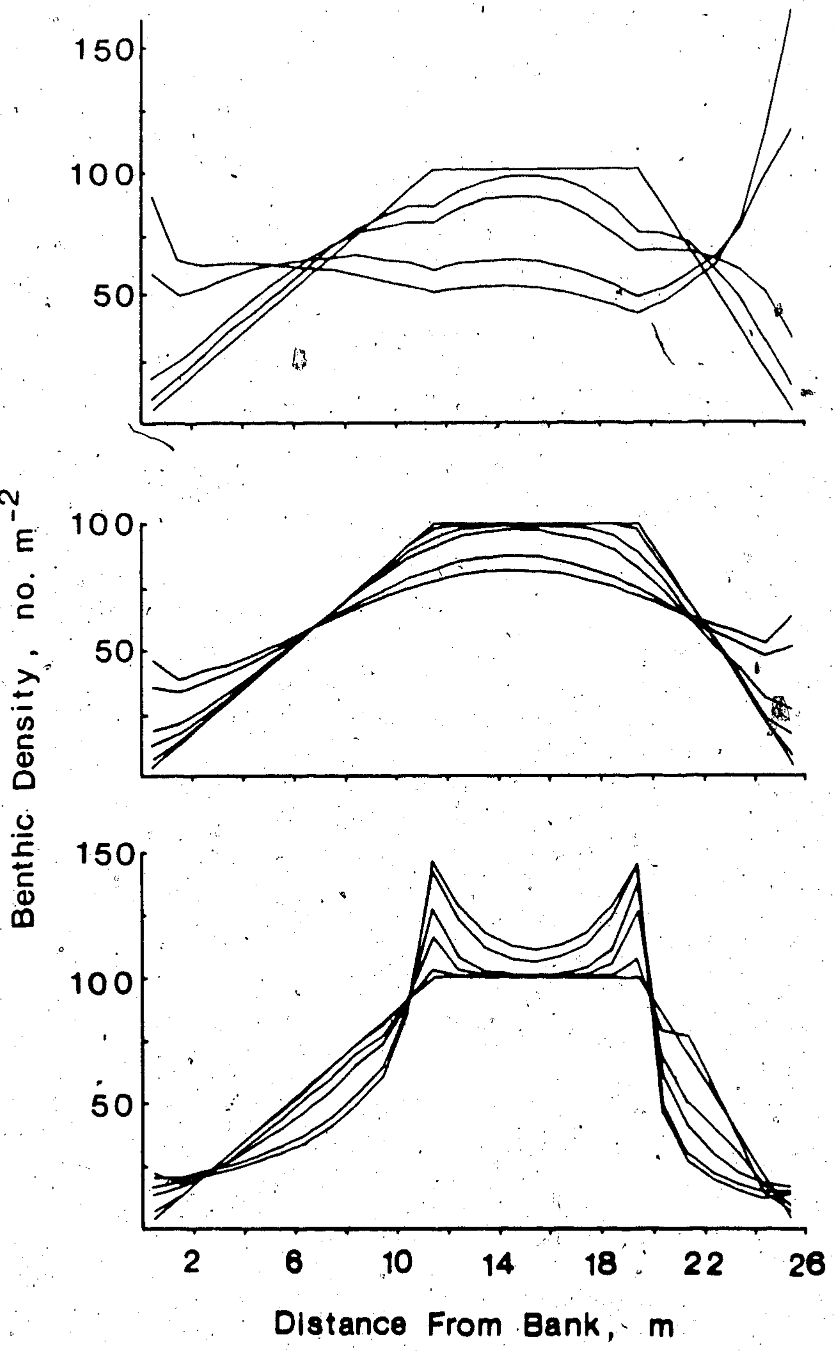

Figure 32. Effect of varying intercept of lateral diffusion function on benthic distribution of animals after 15 days; lateral diffusion slope and settling rate parameters constant. Top, centre and bottom figures as described in Fig. 29. Lines most deviant have largest lateral diffusion function intercepts.

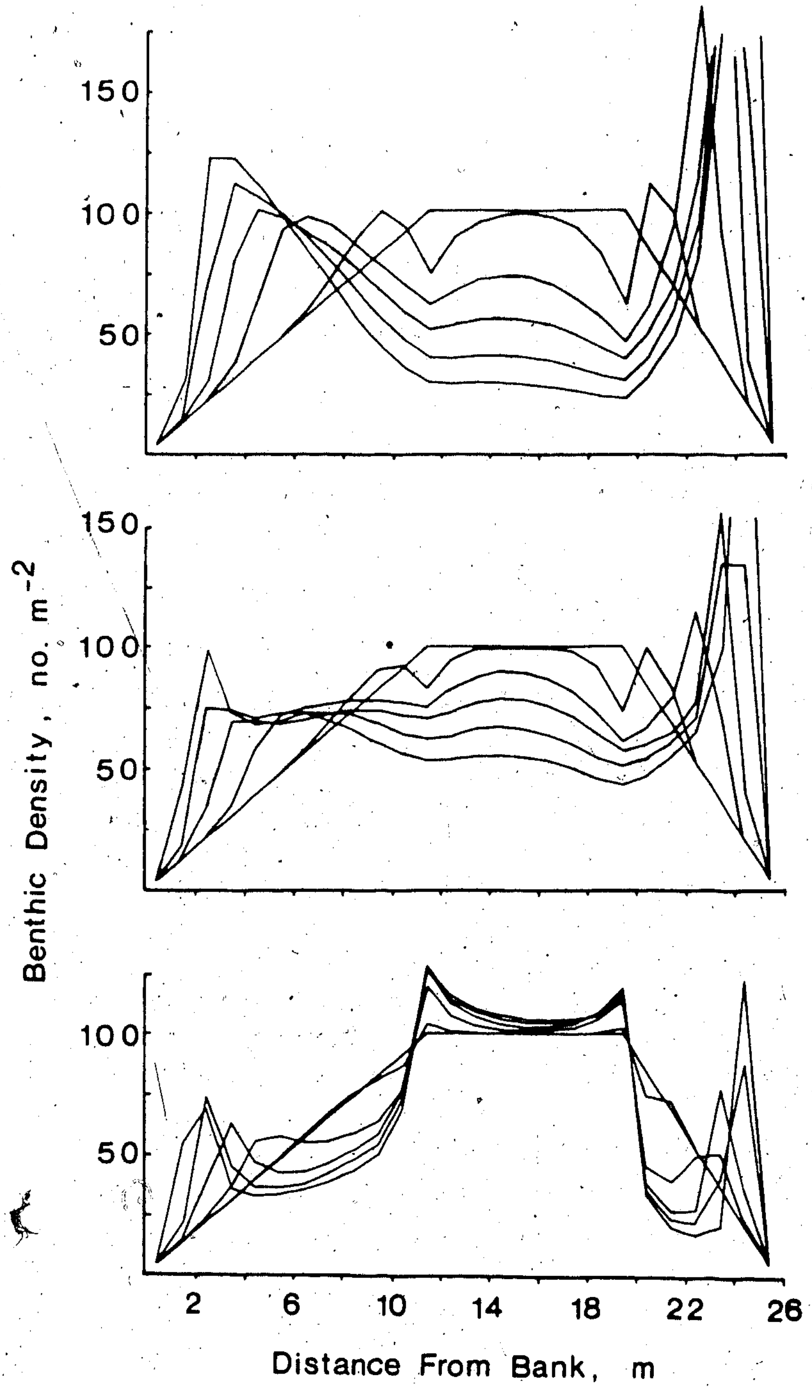

Figure 33. Effect of varying slope of lateral diffusion function on benthic distribution after 15 days; lateral diffusion intercept and settling rate parameters constant. Top, centre and bottom figures as described in Fig. 29. Lines most deviant have largest lateral diffusion function slopes.

Synopsis

Departure, settling and lateral diffusion all appear to be integral in determining the benthic distribution of animals in the model river. Whether or not animals become concentrated at the river centre depends on the sign of the relationship between departure rate and distance from shore. When a greater proportion of animals depart from shoreward areas than from the centre, populations will increase at the centre. When departure proportions are greatest at the centre, populations will become most concentrated at the margins. The process of redistribution is accelerated when animals have consistently low settling rates or consistently high lateral diffusion values, or both. Increasing the difference in settling rates between river margin and centre also accelerates the rate of redistribution. The degree of change of the lateral diffusion values from river margin to centre is of critical importance to eventual benthic distribution. If values of this parameter are very small at either river margin, it is inevitable that the corresponding transect will eventually collect and retain all drifting animals in the river. This is because a small lateral dispersal value can produce an absorbing state in the final transition matrix. Thus, once animals settle in corresponding transects, the probability of their transport by drift from these regions is zero. In such cases, variations in departure or settling parameters can only accelerate or retard the rate of accumulation in these areas.