The influence of current velocity and substrate on the distribution and drift of two species of mayflies (Ephemeroptera)

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The effects of substrate type and current velocity on the distribution and drift of *Baetis vagans* McDunnough and *Paraleptophlebia mollis* (Eaton) were examined in an artificial stream. Of those *B. vagans* (swimming nymphs) remaining on the substrates, most were retrieved from branches while few were found in inorganic substrates. In all cases, numbers of *B. vagans* remaining on the substrates increased as current velocities increased. *Paraleptophlebia mollis* (crawling nymphs) were most frequently associated with gravel (11.2–16 mm diameter), whereas branches were of less importance.

At 50 cm/s and during darkness, the proportion of *P. mollis* drifting from a 'least preferred' substrate was comparable with that of *B. vagans*. At lower velocities or in light, *B. vagans* drifted more frequently than did *P. mollis*, regardless of substrate type. For both species, drift was a significant mechanism in dispersal of individuals from unfavourable areas.

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L'influence du type de substrat et la vitesse du courant sur la répartition et la dérive de *Baetis vagans* McDunnough et de *Paraleptophlebia mollis* (Eaton) ont fait l'objet d'expériences dans un ruisseau artificiel. La plupart des *B. vagans* (larves nageuses), encore attachées au substrat ont été recueillies sur des branches, alors qu'un petit nombre a été retrouvé sur des substrats inorganiques. Dans tous les cas, le nombre de *B. vagans* qui s'agrippent au substrat augmente avec la vitesse du courant. *Paraleptophlebia mollis*, à larves rampantes, s'associe surtout au gravier (11.2–16 mm diamètre) et moins aux branches.

A une vitesse de 50 cm/s, à l'obscurité, la proportion des *P. mollis* qui se laissent dériver d'un substrat peu favorable est comparable à celle des *B. vagans*. Si la vitesse du courant est moins grande, ou s'il fait clair, la dérive de *B. vagans* est plus importante que celle de *P. mollis*, quel que soit le type de substrat. Chez les deux espèces, la dérive constitue un mécanisme important de dispersion des individus leur permettant de s'éloigner d'un milieu peu favorable.

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Introduction

Although changes in light intensity are known to influence significantly the periodicity of drifting organisms (Waters 1972), less is known about other factors which may also affect the drift fauna of slow-flowing waters. The importance of current velocity and substrate type in determining the benthic distribution of invertebrates in streams has been emphasized (Cummins 1966; Cummins and Lauff 1969; Hynes 1970) and yet these two factors have been somewhat neglected in behavioural drift studies.

The influence of current velocity on macroinvertebrates, however, has frequently been examined as a component of fluctuating discharge. Increasing discharges which disturb the stream bottom often result in the catastrophic downstream movement of benthic invertebrates (Anderson and Lehmkuhl 1968; Pearson and Franklin 1968; Pearson and Kramer 1972; Waters 1972; Mackay and Kalff 1973). These organisms may be displaced laterally during high flow situations rather than being transported downstream (Lehmkuhl and Anderson 1972). The sudden reduction or complete cessation of flow can induce many organisms to release their hold on the substrate and swim into the water column (Hughes 1966; Elliott 1967; Madsen 1968; Minshall and Winger 1968).

Under still-water conditions, the active departure of the mayflies *Baetis vagans* McDunnough and *Paraleptophlebia mollis* (Eaton) was found to be independent of density up to 750 nymphs/

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330 cm², which was the maximum density tested (Corkum 1976). There was also a greater tendency for the swimming nymphs *B. vagans* to leave a substrate and enter the water column than for the crawling nymphs *P. mollis* to do so.

In this study, we used an artificial stream to investigate the possibility of modifying the tendency of *B. vagans* and *P. mollis* nymphs to drift by manipulating those physical factors, current velocity and substrate, which are important in determining their benthic distribution. The first aspect of the study examines the nymphal distribution of the two species in various substrates at constant, low-level velocities. The proportion of each species drifting from those substrates which show maximal and minimal nymphal incidence is then compared over the same range of velocities.

Materials and Methods

Distribution and drift studies of *B. vagans* and *P. mollis* nymphs were conducted in the laboratory using an elliptical, artificial stream in which dechlorinated water was circulated by a motor-driven paddlewheel. A water depth of 10 cm above the substrate was maintained in all experimental trials, the total volume circulated being 1944 litres.

Water temperatures in the artificial stream were regulated to correspond to those at the sample site each time nymphs were collected. A refrigerating unit (Frigid Units Inc., Toledo, OH; Min-O-Cool, BHL-909A) installed within the stream reservoir was able to cool the water to a minimum of 7°C. When lower temperatures were required, refrigerated dechlorinated water was added to the stream and the level was maintained by an overflow drain. At 2-week intervals, the stream was drained, sponged clean, and hosed with water.

Fluorescent tubes and incandescent bulbs, mounted 1.32 m above the stream, provided a light intensity of 2200 lx at the stream bottom. To simulate natural sunset and sunrise, fluorescent dimming controls were installed to provide a gradual change of about 20-min duration at dusk and dawn.

An experiment was designed to determine which of 10 substrates retained the highest and lowest number of nymphs at mean current velocities of 0, 10, 20, 30, 40, and 50 cm/s. Water flow was measured using an Ott C-1 current meter (A. Ott Kempten Co., West Germany). Gravel was gathered from the Credit River, Peel County, Ont., washed, dried, and hand-sieved with a U.S. standard sieve series (Anonymous 1969). Sufficient gravel of each of nine particle sizes, ranging from 4 to 90.5 mm, was sieved in $\frac{1}{2}$ phi (ϕ) gradations (see Cummins and Lauff (1969)) to fill two sets of nine aluminum trays (21.5 cm by 21.5 cm and 2.5 cm deep). In addition, branches were collected from the river and cut to fit snugly into a 10th tray. Branches varied in diameter from 2 to 6 cm.

The 10 trays containing substrates were autoclaved between experiments to eliminate most food sources and then cooled and placed in a double row in the stream channel. The contents of adjacent trays were spread over the edges, making a continuous gravel pathway to permit tray to tray movement by the nymphs. A rectangular aluminum frame supporting a 1-m-long Nitex net bag (mesh opening: 0.423 mm), which tapered to a screw-cap catchment jar, was inserted directly downstream from the last pair of trays. The substrate sizes were arranged by tray with reference to the direction of water flow: fine to coarse material in one trial series, coarse to fine in a second, and random in a third. In one random tray series, the branches were omitted and replaced with an inverted empty tray, the bottom of which had been roughened. Two trials were conducted for each substrate tray arrangement at each of the six current velocities for a total of 36 experiments per species.

To reduce the likelihood of behavioural changes associated with size differences among nymphs, Clifford's (1970) scheme of developmental classification was adopted. Only stage III individuals were used: those nymphs without black wing pads but whose mesothoracic wing-pad lengths were greater than the distance between them. On each day of an experiment, stage III nymphs were collected from a site near the Forks of the Credit River, Peel County, Ont., and transported to the laboratory in widemouthed thermos bottles containing river water. A distribution study of *Baetis* spp. and *P. mollis* nymphs at various current velocities had been previously conducted in the East Credit River about 200 m upstream from the Forks (Corkum 1976).

On returning to the laboratory, 15 nymphs were placed by pipette (5 mm in diameter) into still water a few centimetres above each of the 10 substrate trays ($\Sigma n = 150$) in the laboratory stream. The current velocity was then increased at a rate of 10 cm/s min⁻¹ until the desired level was reached. This current velocity was maintained for 24 h after which it was reduced to zero at the same rate at which it had been raised. The light sequence simulated natural conditions. Nymphs which left the substrate during the experiment were trapped in the downstream net, which was sampled and inspected for nymphs at the conclusion of each experiment. The substrate trays were then carefully removed from the stream and the water from each was poured through an aquarium net to trap any nymphs.

Nymphs clinging to the substrates were recovered from each tray using a sugar flotation technique (Anderson 1959) and added to those decanted from the appropriate trays. The nymphs from each tray were counted and preserved as were those collected from the downstream net. Experiments with *B. vagans* were conducted during the fall of 1974; those with *P. mollis* were conducted in the spring of 1974 and 1975. All experimental trials were randomized.

Further experiments were conducted with the two substrates which supported the greatest and least number of nymphs of each species. These substrates were placed separately in aluminum trays with a total surface area of about 0.25 m². Drift experiments were conducted to determine whether the proportion of nymphs leaving the stream bed changed either with substrate type or with current velocity. The drift net was positioned in the stream channel in the same manner previously described. Individuals were collected from the sample site on the day of an experiment and 100 nymphs were pipetted onto the

substrates in still water. The current velocity was then gradually increased to one of six preselected levels. Two trials were conducted at each current velocity for each of the two substrates selected for a total of 24 experiments per species.

The duration of each of these experiments was 10 h (5 h light – 5 h dark (5L–5D)). Drift was monitored at 30-min intervals, drifting nymphs being counted and preserved. After 10 h, the current velocity was reduced to zero, the trays were removed, and net and stream channel were inspected for nymphs. Again, the flotation technique was used to recover nymphs from the substrate trays. Trials with nymphs of *B. vagans* were conducted in April 1975; those for *P. mollis* were conducted in June 1975. All experiments were randomized.

Results

A chi-square test for k independent samples (Siegel 1956) was used to test for nonrandom distribution of the nymphs resulting from the arrangement of substrate trays with reference to the water current (Cummins and Lauff 1969). The distribution of *P. mollis* nymphs was random ($P > 0.05$). The distribution of *B. vagans* nymphs, however, was significantly biased with respect to tray arrangement ($P < 0.05$). In subsequent analyses, therefore, the incidence of *B. vagans* nymphs on the substrates within trays was grouped with reference to current: fine to coarse, coarse to fine, and random. The numbers of nymphs remaining on each of 10 substrate trays at six current velocities after 24 h were recorded for each species. The data $(x + 1)$ were log transformed and then analyzed as a 10×6 factorial analysis (ANOVA; Sokal and Rohlf 1969).

During each 24-h experiment, most *B. vagans* nymphs entered the water column and were collected in the downstream net. In contrast, most *P. mollis* nymphs remained in the substrate (Fig. 1).

Substrate and current velocity were both significant ($P < 0.05$) in determining the occurrence of *B. vagans* for all tray arrangements. *Baetis vagans* nymphs were most numerous on branches, whereas their incidence on all inorganic substrates was low. The fewest *B. vagans* nymphs were found in gravel particle sizes of 16–22.6 mm (-4ϕ). The abundance of *B. vagans* nymphs in the substrate increased with increasing current velocities, i.e., fewer nymphs entered the water column (Fig. 1). Between 16 and 46 of a possible 150 nymphs remained in trays at 30 to 50 cm/s as compared with between 4 and 20 nymphs remaining at lower current velocities.

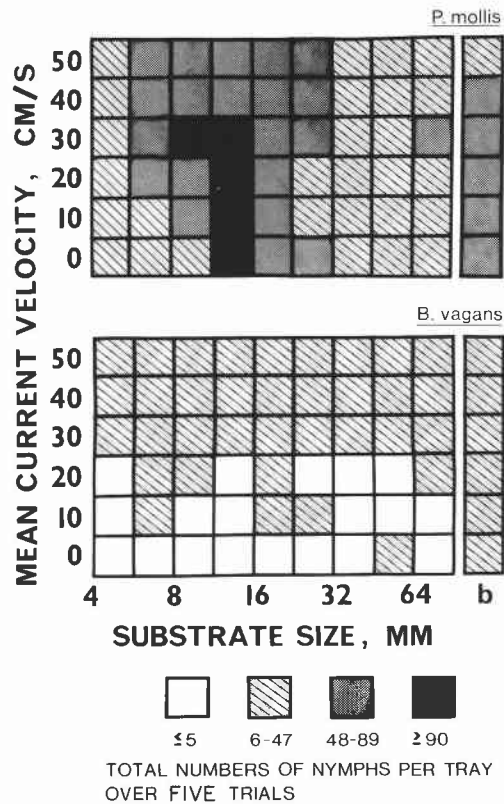Substrate, current velocity, and the interaction

FIG. 1. Accumulated incidence of *B. vagans* and *P. mollis* nymphs in trays of 10 different substrates ($b =$ branches) after a 24-h exposure to each of six mean current velocities. One random series, in which the branches were replaced with an inverted pan, is excluded.

of the two variables were all highly significant ($P < 0.005$) in determining the occurrence of *P. mollis* nymphs for all tray arrangements. Largest numbers of nymphs occupied substrate particle sizes of 11.2–16 mm ($-3\frac{1}{2} \phi$), whereas smallest numbers of nymphs occurred on particle sizes of 45.3–64 mm ($-5\frac{1}{2} \phi$). With initial densities of 150 nymphs, 78–139 nymphs remained in the 10 trays over the examined range of current velocities. The lower nymphal numbers in the substrates were recorded in still water and at 50 cm/s.

The distribution of the nymphs of both species were compared to determine if the organic substrate (branches) influenced the distribution of nymphs among the inorganic particles. There was no difference in the distribution of *P. mollis* nymphs among the particle sizes ($P > 0.05$) in trials where no organic substrate was available. Although the distribution of *B. vagans* did vary significantly ($P < 0.05$), there were very few
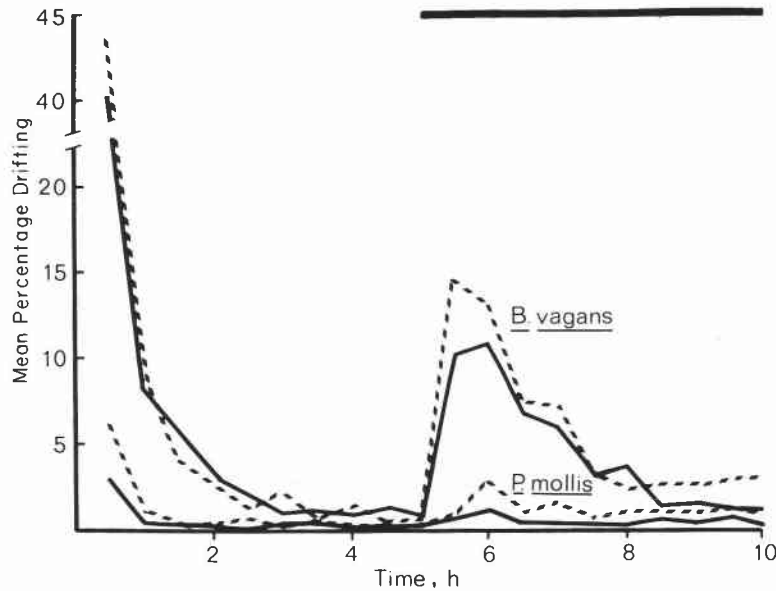
FIG. 2. Mean percentage of *B. vagans* and *P. mollis* nymphs drifting from the most preferred (—) and least preferred (- - -) substrates in relation to time (5 h of light followed by 5 h of dark). Horizontal black line indicates dark interval.

nymphs remaining in the substrate and this renders the findings questionable.

The proportion of nymphs drifting from substrates with low and high incidences of nymphs was examined at each of six different current velocities for 10 h (5L–5D). Initially, the number of nymphs drifting during each $\frac{1}{2}$-h interval was pooled for all current velocities.

Figure 2 shows that more *B. vagans* nymphs drifted than did nymphs of *P. mollis*. Regardless of substrate type or species concerned, nymphs did not leave the stream bottom in a random manner with respect to time (Kolmogorov-Smirnov test of goodness of fit, $P < 0.001$; Sokal and Rohlf 1969).

The proportion of *B. vagans* nymphs drifting in the light decreased during the initial 150 min of each experiment and then levelled off until a change in light intensity occurred. The nymphs subsequently exhibited an increase in drift during the first $\frac{1}{2}$ h after the onset of darkness. The drifting of *P. mollis* nymphs decreased over the 1st h of light and then remained constant until dark. The nocturnal drift peak for *P. mollis* was reached at the end of the first full hour of darkness and thereafter a lower drift level was maintained (Fig. 2).

The influence of species type, substrate type, and current velocity on the proportion of

nymphs drifting was analyzed for light and for dark conditions using a $2 \times 2 \times 6$ factorial analysis (Sokal and Rohlf 1969). The mean proportion of *B. vagans* nymphs drifting during the *light* was significantly greater than that of *P. mollis* nymphs ($P < 0.001$). The significant interaction between species and current ($P < 0.005$) as well as between species and substrate ($P < 0.025$) suggests that the two species react differently. Consequently, a 2×6 ANOVA was performed separately for each species. Although current velocity had an overall significant influence on drift ($P < 0.01$), neither substrate type nor the interaction of current with substrate appeared significant in the overall analysis.

The proportion of *B. vagans* drifting during the light period was significantly influenced by current velocity ($P < 0.01$). *Baetis vagans* drifted less at 50 cm/s than at lower current velocities (Fig. 3). The proportion of *P. mollis* nymphs drifting during the light period was significantly influenced by both current velocity ($P < 0.001$) and substrate type ($P < 0.05$). At the higher current velocities of 30, 40, and 50 cm/s, more *P. mollis* nymphs drifted from the substrate which was previously shown to be 'least preferred' than from the 'most preferred' substrate (Fig. 3).
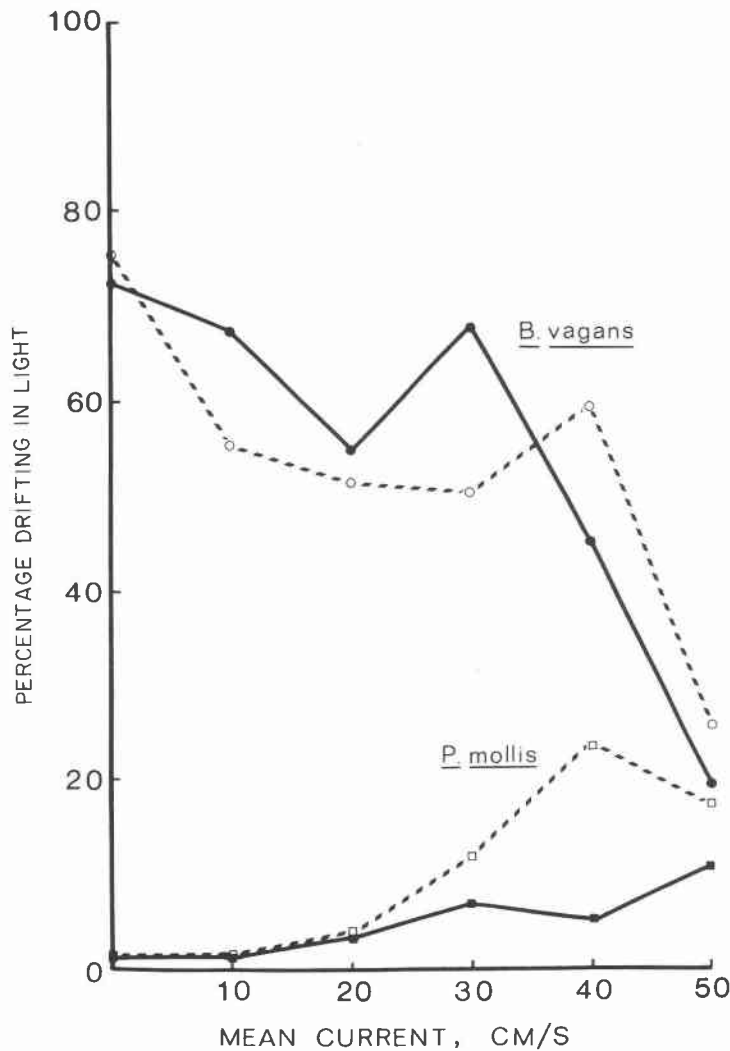
The mean proportion of *B. vagans* nymphs

FIG. 3. Mean percentage of *B. vagans* (○, ●) and *P. mollis* (□, ■) nymphs drifting, after 5 h of light, from the most preferred (—) and least preferred (- - -) substrates in relation to mean current velocities.

drifting during the *dark* (numbers drifting in dark divided by numbers present in the substrate at the beginning of the dark period) was significantly greater than that of *P. mollis* nymphs ($P < 0.001$). All other factors were significant to a lesser degree (i.e., $0.05 > P < 0.005$).

For *B. vagans*, the mean proportion of nymphs drifting in the dark was significantly different over different current velocities ($P < 0.005$). Neither the influence of substrate nor the interaction of substrate with current was significant. In flowing water, the maximum drift of *B. vagans* nymphs occurred at 10 cm/s and then decreased with increasing current velocities (Fig. 4). The

mean proportion of *P. mollis* nymphs drifting from the two substrates in the dark was significantly different ($P < 0.005$). More nymphs drifted from the $-5\frac{1}{2}\,\phi$ substrate than from the $-3\frac{1}{2}\,\phi$ substrate, but neither current velocity nor the interaction of substrate and current velocity significantly influenced the drift (Fig. 4).

Discussion

This study was limited in its scope to substrate types of a homogeneous nature and non-fluctuating current velocities of 50 cm/s or less. Clearly, preferences which may be exhibited in the laboratory may not be directly applicable
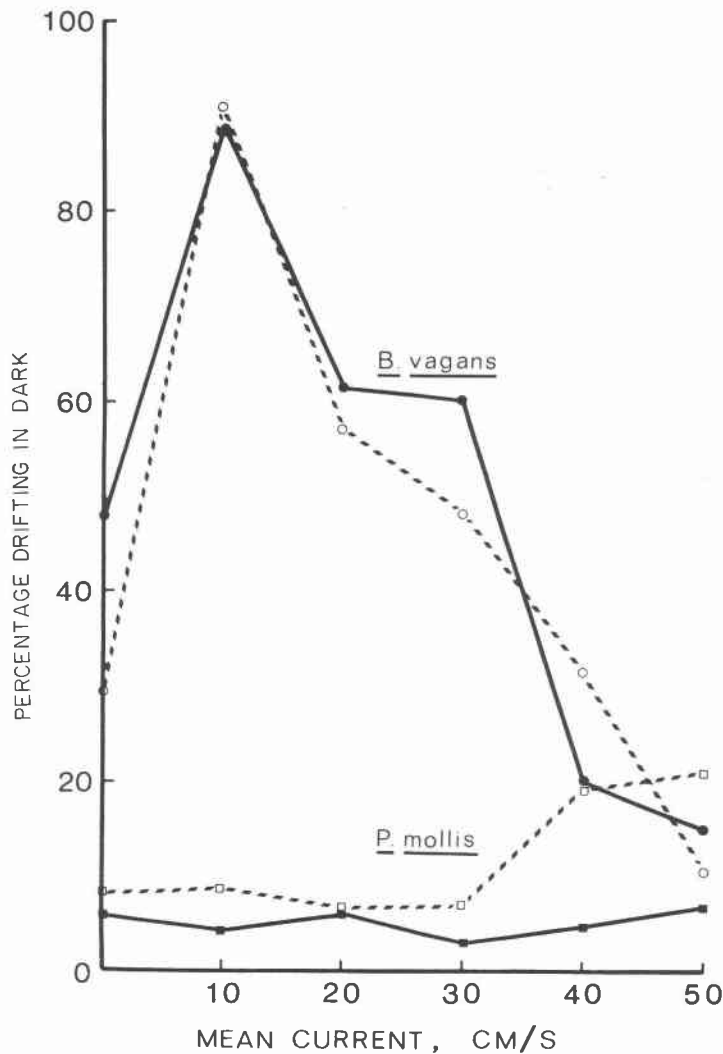
Fig. 4. Mean percentage of *B. vagans* (○, ●) and *P. mollis* (□, ■) nymphs drifting, after 5 h of darkness, from the most preferred (—) and least preferred (- - -) substrates in relation to mean current velocities.

to situations at the sample site where substrates are heterogeneous and current velocities may exceed 1 m/s. Furthermore, the term 'preference' is used with caution, since a nymph rather than selecting one site may actually be avoiding another. In spite of these limitations, the laboratory findings demonstrate which of the physical factors examined will likely influence the distribution and drift of *B. vagans* and *P. mollis* in field situations.

In a natural situation, *B. vagans* nymphs occupy all sides of a substrate, especially the upper surfaces, and they tend to occur more frequently in areas of high current velocity. Conversely, *P. mollis* nymphs inhabit the lower surfaces of substrates only and so it would seem are not influenced in their distribution by current velocity (Corkum 1976).

While most *B. vagans* nymphs were retained on the organic substrate (branches), the numbers found on any of the inorganic substrates were extremely low and this probably reflects a general lack of preference for any particular inorganic substrate type among those which were offered. In all cases, however, more *B. vagans* nymphs remained within the substrates at high current

velocities than at low. Waters (unpublished data cited in Waters (1969)) similarly observed an increase in the drift of "rheophilic organisms (*Baetis*)" at very low current velocities.

Paraleptophlebia mollis nymphs were most frequently associated with gravel sizes 11.2–16.0 mm in diameter; branches were less important to this species. Most of these crawling nymphs remained within the substrates of each tray. This tendency for leptophlebiid crawling nymphs to be found below the surface of the stream bed has been frequently reported (Coleman and Hynes 1970; Bishop 1973).

The laboratory drift experiments indicated that *B. vagans*, a swimming nymph, drifted much more frequently than did *P. mollis*, a crawling nymph, regardless of substrate type. Both the swimming behaviour of *B. vagans* and its distributional proximity to the water column probably contribute to the more common occurrence of this species in the drift. Anderson and Lehmkuhl (1968) reported that *Paraleptophlebia debilis* and *P. temporalis* as well as *Baetis* spp. were major components of downstream drift during freshets, *Paraleptophlebia* spp. occurring less frequently in the drift.

The onset of darkness was a significant factor increasing the drift of both species. Holt and Waters (1967), Chaston (1969), and Bishop (1969) have outlined the importance of light intensity to the drift periodicity of many aquatic invertebrates. Light, or its absence, however, did not influence the relative preference for any particular substrate type in either species.

The numbers of both *B. vagans* and *P. mollis* nymphs which left the scrubbed, autoclaved substrates are probably comparable in magnitude with the highest drift levels that would occur in the field under moderate flow conditions. At the sample site, many *B. vagans* nymphs were associated with rocks having vegetation which likely provides a source of cover. Barber and Kevern (1973) reported that mayfly nymphs were often associated with macrophytic growths and they suggested that vegetation acted as a sieve by reducing the amount of drift from a stream section. Reduced food sources have been shown to increase the drift levels of some representative mayfly species (Hildebrand 1974).

Although this study indicates that generally a larger proportion of the swimming nymphs, *B. vagans*, enter the water column than do crawling nymphs, *P. mollis*, there are instances in which the habitat may be moderately altered so that the crawling nymphs may enter the water column as readily as swimming nymphs. In the laboratory, at flowing water conditions of 50 cm/s and during dark periods, the proportion of crawling *P. mollis* nymphs which left a 'least preferred' substrate was comparable with that of *B. vagans* nymphs leaving any substrate type. Evidently, the larger pore sizes of an aggregation of rocks 45.3–64 mm in diameter did not provide a suitable habitat site for crawling nymphs at higher current velocities. *Paraleptophlebia mollis* nymphs have been reported to crawl to the top of rock surfaces (>64 mm in diameter) at night in flowing water and under any light condition in still water (Corkum 1976). Perhaps there is less migration to the top surfaces of other substrates which provide *P. mollis* with a more suitable pore size.

This study reiterates the overall importance of both current velocity and substrate type as influences on the distribution of stream macroinvertebrates. Drift appears to be a significant mechanism in effecting the redistribution of individuals from unfavourable areas. It is evident that the favourability of a microhabitat to a particular species is not a static quantity, but varies with the prevailing conditions of the environment. Since both substrate type and current velocity of a portion of a river are in a continuous state of flux, there must be a continual movement of individuals throughout the river. This is manifested in the steady contribution of benthic populations to the drift fauna.

ANDERSON, N. H., and D. M. LEHMKUHL. 1968. Catastrophic drift of insects in a woodland stream. Ecology, **49**: 198–206.

ANDERSON, R. O. 1959. A modified flotation technique for sorting bottom fauna samples. Limnol. Oceanogr. **4**: 223–225.

ANONYMOUS. 1969. Testing sieves and their uses. W. S.

Tyler Co. of Canada Ltd., St. Catharines, Ont. Handb. 53.

BARBER, W. E., and N. R. KEVERN. 1973. Ecological factors influencing macroinvertebrate standing crop distribution. Hydrobiologia, **43**: 53–75.

BISHOP, J. E. 1969. Light control of aquatic insect activity and drift. Ecology, **50**: 371–380.

—— 1973. Observations on the vertical distribution of the benthos in a Malaysian stream. Freshwater Biol. **3**: 147–156.

CHASTON, I. 1969. The light threshold controlling the periodicity of invertebrate drift. J. Anim. Ecol. **38**: 171–180.

CLIFFORD, H. F. 1970. Variability of linear measurements throughout the life cycle of the mayfly *Leptophlebia cupida* (Say) (Ephemeroptera: Leptophlebiidae). Pan-Pac. Entomol. **46**: 98–106.

COLEMAN, M. J., and H. B. N. HYNES. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnol. Oceanogr. **15**: 31–40.

CORKUM, L. D. 1976. A comparative study of behaviour relating to differential drift of two species of mayflies. Ph.D. Thesis, Univ. Toronto, Toronto, Ont.

CUMMINS, K. W. 1966. A review of stream ecology with special emphasis on organism–substrate relationships. Pymatuning Symp. Ecol. Spec. Publ. **4**: 2–51.

CUMMINS, K. W., and G. H. LAUFF. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. Hydrobiologia, **34**: 145–181.

ELLIOTT, J. M. 1967. Invertebrate drift in a Dartmoor stream. Arch. Hydrobiol. **63**: 202–237.

HILDEBRAND, S. G. 1974. The relation of drift to benthos density and food level in an artificial stream. Limnol. Oceanogr. **19**: 951–957.

HOLT, C. S., and T. F. WATERS. 1967. Effect of light intensity on the drift of stream invertebrates. Ecology, **48**: 225–234.

HUGHES, D. A. 1966. On the dorsal light response in a mayfly nymph. Anim. Behav. **14**: 13–16.

HYNES, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto, Ont.

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

MACKAY, R. J., and J. KALFF. 1973. Ecology of two related species of caddis fly larvae in the organic substrates of a woodland stream. Ecology, **54**: 499–511.

MADSEN, B. L. 1968. A comparative ecological investigation of two related mayfly nymphs. Hydrobiologia, **31**: 337–349.

MINSHALL, G. W., and P. V. WINGER. 1968. The effect of reduction in stream flow in invertebrate drift. Ecology, **49**: 580–582.

PEARSON, W. D., and D. R. FRANKLIN. 1968. Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. Ecology, **49**: 75–81.

PEARSON, W. D., and R. H. KRAMER. 1972. Drift and production of two aquatic insects in a mountain stream. Ecol. Monogr. **24**: 365–385.

SIEGEL, S. 1956. Non-parametric statistics for the behavioural sciences. McGraw-Hill, New York, Toronto, London.

SOKAL, R. R., and F. J. ROHLF. 1969. Biometry. W. G. Freeman and Co., San Francisco, CA.

WATERS, T. F. 1969. Invertebrate drift-ecology and significance to stream fishes. *In* Symposium on salmon and trout in streams, H. R. MacMillan lectures in fisheries, Vancouver. *Edited by* T. G. Northcote. Univ. British Columbia, Vancouver, B.C. pp. 121–134.

—— 1972. The drift of stream insects. Annu. Rev. Entomol. **17**: 253–272.