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Ecology, Vol. 53, No. 4 (Jul., 1972), 661-667.

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MICRODISTRIBUTION AND DENSITY AS FACTORS AFFECTING THE DOWNSTREAM DRIFT OF MAYFLIES¹

D. M. LEHMKUHL² AND N. H. ANDERSON

Entomology Department, Oregon State University, Corvallis, Oregon 97331

Abstract. During high volume of flow in a stream that has considerable seasonal fluctuation, the microdistribution of five species of mayflies was determined by displacement of individuals by drift from rapid current areas to those with gentle or no current. The major effect of drift was dispersal, not depletion, of the mayfly population. Occurrence in drift is determined by a species-specific complex of interdependent factors including life cycle, microdistribution (both before and after the effect of spates), and the behavioral characteristic of individual species.

Downstream drift of stream invertebrates has received considerable attention in recent years but its significance to the stream biota is far from clear. Extremely high drift rates such as 10,000 individuals per hour per foot of stream width, as reported for *Baetis vagans* (McDunnough) by Waters (1962), would appear to be an important component in the dynamics of the species. On the other hand, Bishop and Hynes (1969) reported that in their study of Speed River, Ontario, only 0.0002%–0.004% of the benthos was in the drift at any one time; apparently it was this minute quantity that led Hynes (1970a) to suggest that the importance of drift may have been overstressed. Some contradictory reports on the magnitude of the drift phenomenon are obviously the result of comparisons between streams of widely different levels of productivity.

The mechanisms and importance of drift cannot be defined until more is known about the source of individuals that occur in the drift, and the factors, both biotic and abiotic, that cause the organisms to leave the substrate. The present report discusses: (1) the seasonal changes in density and microdistribution of individual mayfly species as influenced by the life cycle and fluctuations in stream discharge; (2) the associated changes in drift rate of these species; and (3) the differences in the propensity of different mayfly species to drift.

METHODS

Studies were conducted in Oak Creek, Benton County, Oregon. The field site was described by Anderson and Lehmkuhl (1968), with drift collecting methods generally following the previous methods. Samples were taken monthly. When conditions permitted, the entire creek was funneled through one drift trap; however, during the winter, when floods

¹ Technical paper 3114, Oregon Agricultural Experiment Station. We acknowledge financial support from N.S.F. grants GB 3643 and GB 7958. (Manuscript received June 28, 1971; accepted February 2, 1972.)

² Present address: Department of Biology, University of Saskatchewan, Saskatoon, Canada.

demolished the diversion wings, the traps were attached to a wooden base in the stream bed and only a portion of the water volume was collected.

Benthos samples were taken from the area above the drift trap. Collections were made by embedding the end of a length of pipe (15-cm diameter) into the substrate of the stream. The larger stones were removed by hand, and the substrate was stirred; the enclosed material was transferred to a pail with a fine mesh net (< 0.3 mm) and then later sorted. All insects isolated by the sampler were collected with little or no loss of early instars through the net; the area sampled was small enough so that it could be described in detail. Location, surface velocity of the water, water depth, and substrate type were recorded on a standardized form for each sample. Three benthos samples were taken from each of the major biotopes of the stream each month. These biotopes include: *still backwaters*, having little current during normal flow; *riffle*, having rapid current and clean rubble substrate (subdivided into mid- and edge of riffle during high water); and *glide*, having a smooth, even flow and impacted silt and rubble substrate.

Oak Creek has an extremely variable flow rate, reflecting the seasonal rainfall pattern of western Oregon. Discharge throughout the summer months is less than .03 m³/sec (1 ft³/sec), but heavy winter rains cause a series of freshets. Peak rates of 1.4–2.8 m³/sec occur during most years and in exceptional floods the discharge reaches 5.7 m³/sec or higher. Figure 1 illustrates the weekly rainfall pattern and resultant changes in stream width for 1967–68.

RESULTS

Seasonal pattern of benthos populations

Over 20 species of mayflies occur in Oak Creek, but only the six numerically dominant species were studied intensively: *Baetis tricaudatus* Dodds, *B. bicaudatus* Dodds, *B. parvus* Dodds, *Paraleptophlebia debilis* (Walker), *P. temporalis* (McDunnough), and *Cinygmula reticulata* McDunnough.

The total number of mayflies collected in the 12

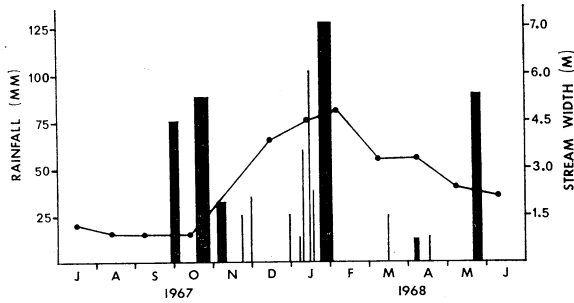


FIG. 1. Rainfall and stream width at Oak Creek sampling station June 1967 to June 1968. Solid line connecting circles shows stream width on the sampling date. Histograms indicate amount of rainfall and period during which the rain fell.

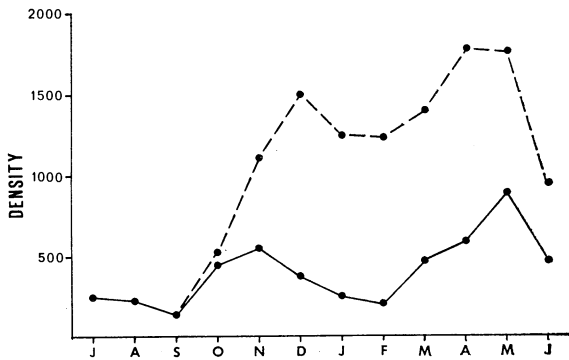


FIG. 2. Numbers of mayflies in benthos samples (solid line) (0.22 m²), compared with numbers corrected for increase in stream width (dashed line).

benthos samples each month is shown by the solid line in Fig. 2. The slight drop in density in September is a result of the emergence of *P. debilis*. Several species have a major hatching period in the late autumn, reflected in the increase in density in October and November. Winter rains caused an increase in stream velocity and stream width; concurrent with this, the apparent density of mayflies in benthos samples decreased until February. Stream flow decreased from March onward and there was an increase in the number of specimens collected until May. In June the emergence of adults of several species resulted in a rapid drop in the numbers collected.

As has been previously demonstrated (Anderson and Lehmkuhl 1968), winter floods result in a three- to fourfold increase in the incidence of insects in drift samples, and a reduction in the number of insects per unit area in the benthos. This could be interpreted as a reduction of the benthic population in the stream by drift. However, in order to assess the total effect of flooding on the population, it is necessary to take into account the increase in width of the stream or available living space. This has been done in Fig. 2. The broken line in Fig. 2 shows the density

of mayflies per unit length of stream. The number of specimens taken in a unit area sample was multiplied by the factor for increase in stream width for that month, using July–September as the base line. Thus, for example, in January the stream was approximately five times as wide as it was in July, providing five times as much living space; therefore, numbers per unit area in the benthos samples were multiplied by 5 to give the population in a segment of stream. On the basis of these data, the major effect of flooding and of the catastrophic drift was the redistribution of the population over the width of the stream bed, not a severe reduction in the population of insects in the benthos. McLay (1968) and Hynes (1970b) have also reported on the dispersal caused by spates. We shall continue this argument by examining the distribution of individual species.

Distribution among biotopes

Figure 3 compares the numbers of individuals of four species collected in backwater, glide, and riffle biotopes at four times during the year. (Data are available for all months but graphed for only four for brevity.) In October, before the heavy rains begin, all are most numerous in the riffle with over 95% of the individuals occurring in this area. From November to February, when flooding activity is

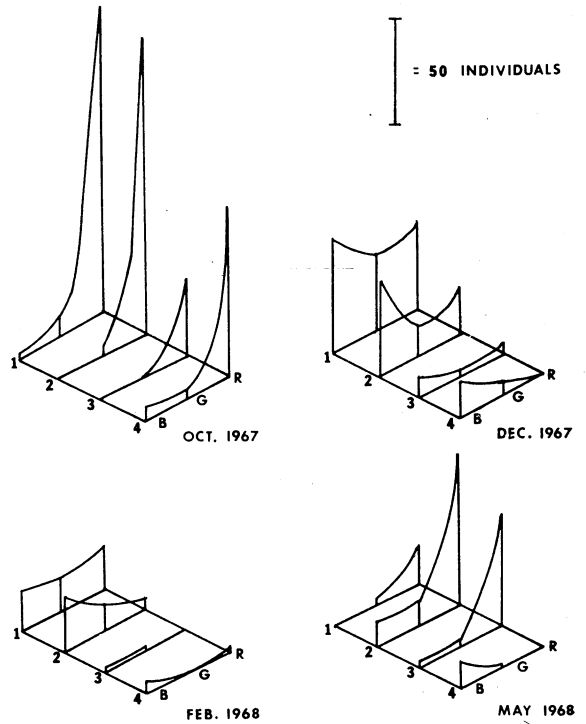


FIG. 3. Distribution of four species of mayflies between biotopes in different seasons in Oak Creek: 1 = *Cinygmula reticulata*, 2 = *Baetis parvus*, 3 = *B. tricaudatus*, 4 = *Paraleptophlebia temporalis*; B = backwater, G = glide, R = riffle.

great, no species is concentrated in the riffle area and only 25% of the population occurs there. By May, when the water levels have subsided, three of the four species are again concentrated in the riffle. The data indicate the general relationship between microdistribution and volume or velocity of water flow. That is, "typical" riffle insects are displaced by floods to atypical situations for a considerable period of the year. This supports our previous conclusion that a major effect of flooding is redistribution of the population.

Distribution in relation to physical factors

A weakness of the previous discussion concerning microdistribution is that "backwater, glide, and riffle" indicate points in space. Since over a period of time

conditions change at a given point, one could argue, for example, that the glide of October becomes, in terms of physical conditions, a riffle in December; comparisons would therefore be invalid. To check this the distributions of species are plotted in terms of current velocity and substrate type in Fig. 4-6. The area of concentration (that yielding more than 60% of the individuals) was determined for each species each month. Substrate was ranked on a somewhat subjective numerical scale for particle size and organic matter. The particle size ranged from 1 (silt) to 5 (fist-sized stones); the amount of organic matter was inversely related to particle size, and ranged from 1 (rotting wood and leaves) through decreasing amounts to 5 (no detritus).

In October *P. temporalis* was found in the riffle (Fig. 3), in rapid current, and in clean substrate (Fig. 4). In December and February the species was found mainly in the glide and backwaters and in considerably slower current than in October. Thus, the response of the species to high-water conditions has not only been a change of location in space, but also a change in physical conditions. This species emerges from April to June and remains in slow water (May, Fig. 3 and 4). *Baetis tricaudatus* occurred in the riffle (Fig. 3) and in fast water and clean substrate (Fig. 5) in October; it was distributed evenly over the stream bed and displaced toward slower water in December and February, but returned to the riffle and fast water in May. This analysis can be repeated for other species, and our previous conclusion that high volume of flow displaces "riffle" species to non-riffle habitats is reaffirmed.

Distribution and life cycles

Three general types of life cycles can be recognized for the five species. In the first, eggs hatch in fall and winter, nymphs develop through the winter, and adults emerge in the spring. The summer period of low water and high temperature is passed in the egg stage. This type of cycle is shown by *P. temporalis* and *C. reticulata* (Lehmkuhl and Anderson 1971a, b) (both with emergence periods from April to June) and less clearly by *B. parvus*, which emerges from April to October. With *P. debilis*, the eggs hatch in the spring and the adults emerge in the summer and fall, from June to November. The winter period of high water and low temperatures is passed in the egg stage. *Baetis tricaudatus* was the only multivoltine species. Discrete generations cannot be detected since most size classes of nymphs occur throughout the year and adults were collected in all months except February and March.

Paraleptophlebia debilis and *P. temporalis* occur over a range of substrate types and velocities throughout their life cycles, with *P. debilis* tending to occur in

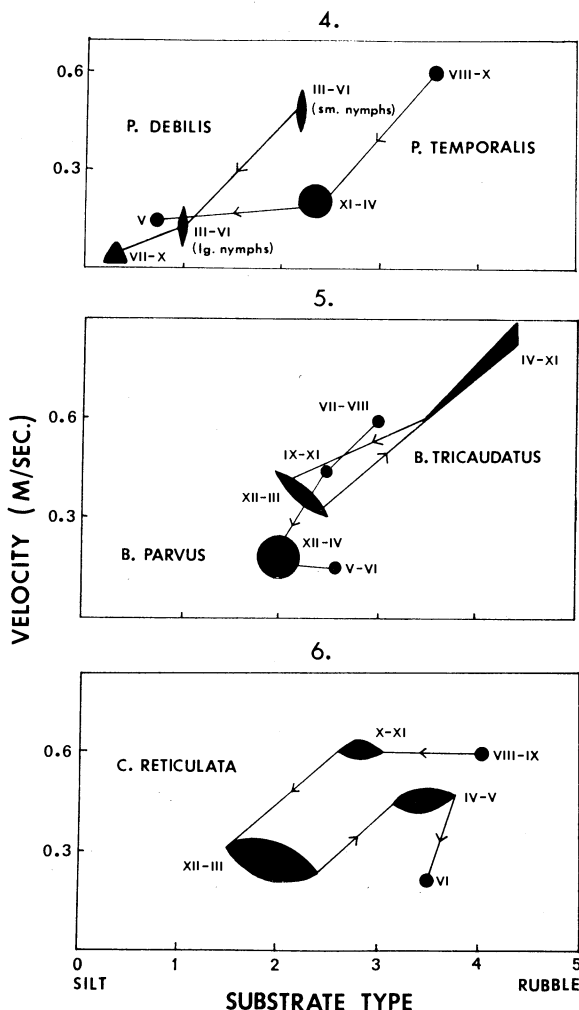


FIG. 4-6. Schematic representation of seasonal changes in area of concentration of five species of mayflies in relation to current velocity and substrate type. Months are indicated by Roman numerals. Blackened areas indicate concentration of nymphs with respect to current velocity (ordinate) and substrate type (abscissa). Arrows indicate sequence of movements by nymphs.

the more sheltered areas even in times of low volume of flow (Fig. 4). This species occurs in the egg stage during the period of high water (Lehmkuhl and Anderson 1971b). The eggs are apparently deposited and hatch in the riffle area, since many small specimens were found there; however, the larger nymphs were found only in areas with a current velocity of less than 30 cm/sec and in silty substrate. *Paraleptophlebia temporalis* also hatched in the riffle area, but the nymphs were present during the autumn and winter and were displaced from the riffles to slower water during the winter. In the spring the species was found chiefly in slow water areas. This was probably a shift in habitat preference occurring prior to emergence.

The distributions of *B. tricaudatus* and *B. parvus* are shown in Fig. 5. *Baetis parvus* is a slow-water species compared to *B. tricaudatus* and was the species most quickly displaced by increased velocity. *Baetis tricaudatus*, which is multivoltine, is typically a fast-water species although it occurs in a wide range of velocities. *Baetis tricaudatus* was displaced to areas of 30–45 cm/sec in winter but again became concentrated in areas of above 60 cm/sec when water volume decreased. It appears that under stable conditions the species selects an area of rapid current, but during spates and floods it cannot maintain itself in the areas of optimum current.

Cinygmula reticulata (Fig. 6) occurred in fast water after hatching in the autumn but was displaced to slower waters by freshets; they then returned to the riffles in April and May.

Composition of the drift

Although over 20 species of mayflies were collected in the drift and benthos samples, six species accounted for 85% of the individuals in most months. In this section we compare the drift of individual species as components of the total mayfly drift and relate drift rate to the distributions and life cycles discussed in the previous section. The percentage composition of the drift is given for 10 months in Table 1. The miscellaneous species, accounting for 35% of the drift in January and February, were

largely of the family Heptageniidae (*Epeorus*, *Cinygmula*, and *Rhithrogena*), and *Ephemerella* and *Ameletus*. *Baetis tricaudatus* was always the dominant species in the drift (40%–80% of the total). In early summer it accounted for 84% at a time when most of the nymphs were small (< 3 mm) and the species was concentrated in the riffle areas. As the flow regime was relatively stable at this time of the year, the high drift rate cannot be ascribed to high water conditions; it must be related to the behavior of the species. The species fell to below 50% of the total drift during the high-water period (after November), when it was dispersed to all biotopes (Fig. 3, December and February).

Baetis bicaudatus was an important drift component only during March and April, which was a period of active growth of the species. The majority of specimens in the drift were less than half-grown in the March collection and about 50% were near emergence in the April collection. A summer generation of *B. bicaudatus* did not mature in Oak Creek, probably because of high summer temperatures (Lehmkuhl 1969). This species was found concentrated in faster water than any of the other mayflies. In field sites where nymphs of *B. bicaudatus* occur year-round (such as in the Cascade Mountains; Lehmkuhl 1969), this species would probably be as abundant as *B. tricaudatus* in the drift.

In contrast to its congeners, *B. parvus* was usually a minor component of the drift. A high percentage (11) occurred in December and the largest numbers of *B. parvus* drifted in May and June as mature nymphs.

Paraleptophlebia temporalis increased from 13% to 28% of the total mayfly drift from September to October; thereafter, there was a continuous decrease in its percentage contribution throughout the winter and spring. This species provided a major contribution to drift when the small nymphs were in the riffle areas and when floods displaced them to the slower water. It was an important component of the "catastrophic drift" in a previous study, listed as *Paraleptophlebia* sp. (Anderson and Lehmkuhl 1968). In an unpublished experiment, *P. temporalis* ac-

TABLE 1. Ephemeroptera in drift (proportion) in Oak Creek, Benton Co., Oregon (T = <1%)

Ephemeroptera	Month									
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
<i>B. tricaudatus</i>	.75	.58	.46	.41	.41	.46	.39	.54	.59	.84
<i>B. parvus</i>	.06	.01	.01	.11	.04	.02	.01	.00	.14	.06
<i>B. bicaudatus</i>	.00	.00	.00	T	.02	.09	.34	.30	.00	.00
<i>P. temporalis</i>	.13	.28	.17	.09	.08	.04	.01	.00	T	.02
<i>P. debilis</i>	T	.01	T	.00	.00	.00	.01	.00	.15	.04
<i>C. reticulata</i>	.02	.08	.27	.24	.10	.04	.14	.02	.02	.02
Others	.03	.04	.10	.15	.35	.35	.11	.14	.08	.02
Total no./24 hr	1,045	970	983	332	408	432	450	350	1,114	1,614

counted for 40% of the mayflies in the drift after the first autumn freshet. *Paraleptophlebia temporalis* nymphs in inclined troughs with a mesh substrate, exposed to a range of velocities from 20 to 100 cm/sec, made no attempt to grasp the substrate and demonstrated no ability to withstand current (Lehmkuhl 1969). Thus when this species occurs in the drift it is probably passively transported. However, habitat selection in this species concentrates it in areas from which drift will be minimal. The shift in area of concentration to still backwaters (Fig. 4) in the spring, when the species nears maturity, results in a minimal increase in drift rate during the period of rapid growth prior to emergence.

Paraleptophlebia debilis was abundant in the drift only during May and June. Drift-collected specimens were of medium age classes but slightly smaller than the mean size of specimens from benthos collections at that time. This species may be important in the drift during the summer months but data are not available. Since *P. debilis* occurs as mature nymphs in very slow waters near shore, it would be very prone to the flushing action of the autumn freshets; but, most adults have emerged by that time.

Cinygmula reticulata occurred in low numbers in the drift most of the year but accounted for about 25% of the mayflies in November and December, when the nymphs were 1–2 mm long. In March there was a slight increase (14%) that consisted of specimens of all size classes.

Thus, each species has an individual pattern of drift, and the difference can in part be correlated

with life histories and distribution in the stream. However, the correlation between density in the benthos and drift is still not clear. The question remains whether certain species drift more because they occur at higher densities in the substrate or simply because they have a greater tendency to drift.

Drift-benthos relationships

Waters (1969) has suggested that the best measure of the propensity to drift for various taxa would be an estimate of the total daily drift rate (standardized by dividing by the total discharge) relative to an estimate of bottom fauna density in the area upstream from the drift sampling. The drift trap collections are now compared with composite benthos samples (i.e., density estimates). We have arbitrarily selected for comparison the units, drift per 100 m³ to a benthos area of 0.1 m². The drift net had mesh openings of 0.333 mm. While this is a small mesh size, it still may allow the escape of very small specimens and thus < 1 mm nymphs may be underrepresented in our drift samples.

Figure 7 compares the drift and benthos samples for *B. tricaudatus*, *B. parvus*, *C. reticulata*, and *P. temporalis*. Different drift-benthos patterns are apparent. *Baetis tricaudatus* always drifts in very high numbers compared to its occurrence in benthos samples. This is a vagile species comparable to *B. vagans*, as studied by Waters (1962, 1965) and *B. rhodani*, as studied by Elliott (1967) and Ulfstrand (1968). It is very different from its congener *B. parvus* in this respect, the latter having a much lower drift:

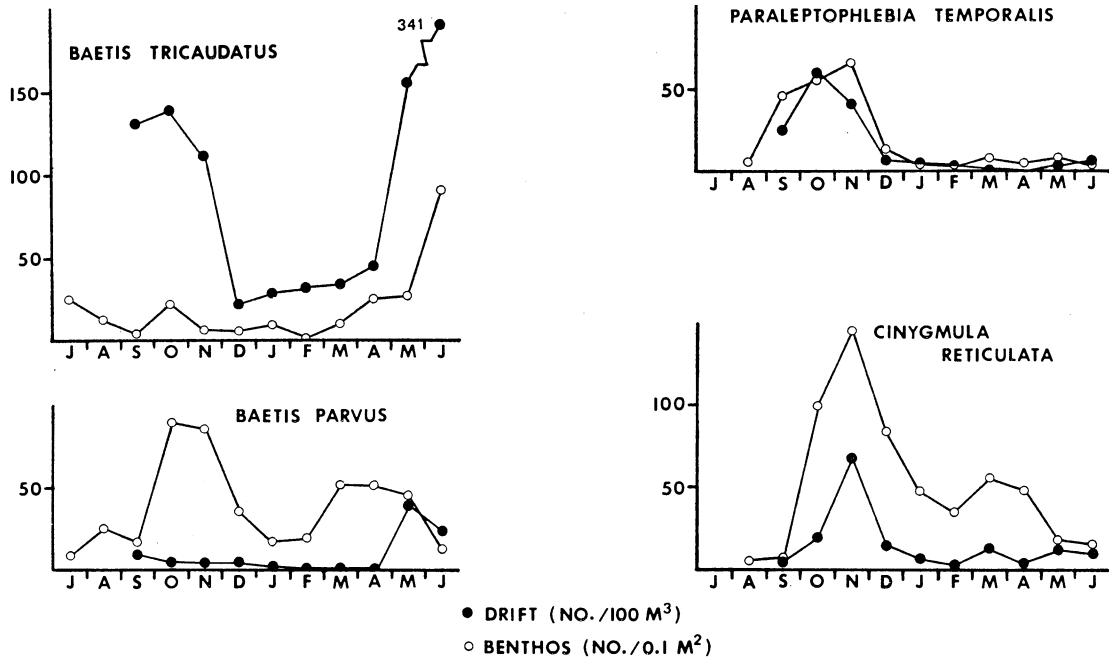


FIG 7. Comparison of numbers of mayflies collected in drift and benthos samples in Oak Creek, July 1967–June 1968.

TABLE 2. Drift:benthos ratios of four species of mayflies in Oak Creek, Benton Co., Oregon (ratio based on drift per 100 m³ and benthos samples of 0.1 m²)

	<i>B. tricaudatus</i>	<i>B. parvus</i>	<i>C. reticulata</i>	<i>P. temporalis</i>
Mean (10 mo.)	5.31	0.32	0.24	0.47
May 5-8	3.57	0.46	0.33	0.51
Sept. 20-24	2.50	—	0.01	0.14

benthos (D:B) ratio. There is a suggestion that *B. parvus* has a high summer drift rate in that the May, June, and September samples were high; we do not have data for the remainder of the summer. The drift and benthos curves for *C. reticulata* and *P. temporalis* show a consistent relationship for the entire collecting period. The D:B ratio was more constant for *C. reticulata* over 10 months than for the other five species. It was slightly high in November (0:5:1) when this species was dispersed to all habitats (Fig. 3 and 6). There was a small increase in drift numbers during May and June in the emergence period, but in general this species drifts in low numbers and in direct proportion to the numbers in the benthos.

Drift:benthos ratios under various conditions are given in Table 2. The first line summarizes the results in the previous graphs, giving the mean D:B ratio based on one 24-hr collection per month for 10 consecutive months. It is apparent that *B. tricaudatus* is markedly different from the other three species. In the second line, a D:B ratio based on the mean for 4 consecutive days of drift sampling in May is given. The ratio is slightly lower for *B. tricaudatus* and slightly higher for each of the other three species. This difference is attributed to the fact that the three univoltine species are approaching maturity at this time of the year; it has been previously demonstrated that drift rate increases near maturity (e.g., Elliott 1967). The last line gives D:B ratios for a period in the autumn on a riffle that was blocked with a net at the upstream end. *Baetis parvus* is omitted because of the scarcity of nymphs of this species in September. The very marked difference in propensity to drift of *B. tricaudatus* is evident in this comparison as in the previous ones. *Cinygmula reticulata* and *P. temporalis* had particularly low ratios at this time while benthos densities were high because eggs were hatching.

DISCUSSION

We have attempted to examine the phenomenon of drift from a number of viewpoints. It is clear that the source of individuals that enter into the drift will depend upon the time of the year (life cycle), volume of flow, and a complex of other factors. Microdistribution and drift rate are interrelated; drift

partially determines the pattern of microdistribution and, conversely, the microdistribution at a particular time will affect the drift rate of a species. The effects of the autumn freshets are similar in all species in that the populations became dispersed throughout all biotopes. While it is generally accepted that spates decrease the benthic population (Tebo 1955, McLay 1968, Hynes 1970a), this decrease may be more apparent than real. Our data indicate that density is reduced, but this is partially compensated for by the increased living space that becomes available when the area of the stream bed increases.

Drift:benthos ratios demonstrate marked differences between species, and it is noteworthy that striking differences may be found within the same genus (*Baetis* spp.). Hynes (1970b) has suggested that generalizations concerning the drift phenomenon based on studies of *Baetis* or the amphipod *Gammarus* may be inappropriate when applied to stream invertebrates in general since some species of these two taxa are particularly liable to drift. It is apparent that drift relationships are species-specific characteristics; the importance of drift in the dynamics of stream ecosystems will be understood only when quantitative studies have been made on the movements and microdistributions of a range of stream invertebrates.

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