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Seasonal dynamics of a mayfly (Insecta: Ephemeroptera) community in a Laurentian stream

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The purpose of our study was to compare on a seasonal basis the emergence, the drift and the benthos on a short and uniform section (18.5 m) of a stream in the Laurentian Hills of Québec. Nineteen species occurred on this stretch, but only six were abundant: *Leptophlebia cupida* (Say), *Habrophlebia vibrans* Needham, *Baetis pygmaeus* (Hagen), *Eurylophella verisimilis* (McDunnough), *Stenonema modestum* (Banks), and *Stenonema vicarium* (Walker). Emergence was monitored for 5 years; densities differed from one trap to the next, as did species dominance, but total densities were similar. These data conform to Illies' rules of constancy and harmony. Nymphal densities were high (mean of 16000 m^{-2}). The dominant species were univoltine, except *H. vibrans* (semivoltine), and *B. pygmaeus* (polyvoltine). Larger species contributed relatively more to the production of the reach despite their low densities than did the more abundant smaller species, especially those with long life cycles. Drift was low during most of the year, except during spring and species composition varied considerably. A comparison of the three data sets (emergence, drift and benthos) shows a general agreement for the less abundant species, but for three of the dominants, *H. vibrans, L. cupida* and *E. verisimilis,* movements of individuals to and from the reach at various times in the life cycle (adult flight, nymphal drift and migration) must be taken into account in order to correlate the data. None of the methods alone gives a satisfactory picture of the community structure, each is to some extent misleading and needs to be used in conjunction with the others; the conflicting results obtained from the data sets often reveal interesting life history traits which otherwise would not have been detected.

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1. Introduction

Ever since the pioneering investigations of Needham (1908) and Ide (1940), aquatic insect emergence has been monitored for various purposes, be it inventory, phenology, zonation or productivity estimation (Illies 1974, Speir and Anderson 1974, Zwick 1984). The use of adults instead of immatures has had the advantage of lessening the problems of collecting and identification, as well as the tedium of sorting. Although a renewed interest in quantitative emergence studies is manifest (Davies 1984), the relations between emergence data and the more traditional parameters, such as nymphal density or drift, are unknown or problematical (Ide 1940, Clifford et al. 1979). It is often uncertain whether the site of the emergence of a species is that of its nymphal habitat. Also, the role of downstream drift, which is important in mayflies (Waters 1972), has seldom been assessed in this context. It is therefore difficult to determine the significance of emergence variables in life-history work.

Our study aims to compare the representations of a mayfly community generated by the concurrent sampling of the emerging adults, the bottom-dwelling nymphs, and the drifting nymphs in a short and uniform stretch of stream over a period of one year. We will also compare emergence data over 5 years.

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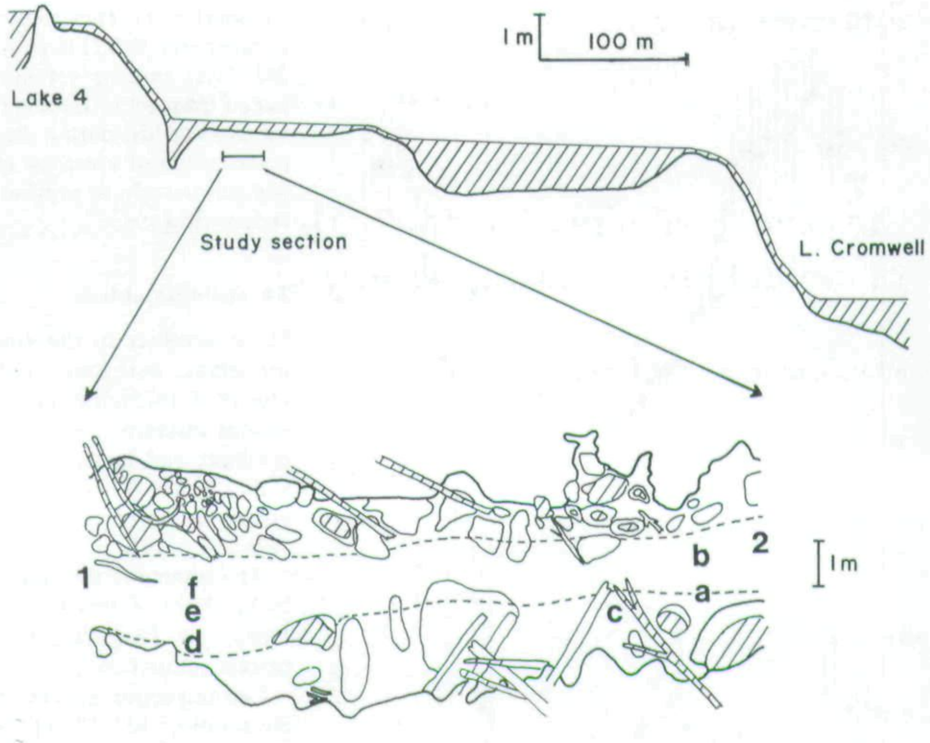
Fig. 1. Position of study area along a section of the stream reach and map of sampling stations. The letters (a–f) represent the locations of the emergence traps and the numerals (1–2) those of the drift nets. The broken lines show limits of the central erosional channel (erosional 35%, depositional 65%, in this instance). The hatched areas on bottom map are emergent.



2. Site description

The stream (see also Harper 1978, Harper and Harper 1982, Lauzon and Harper 1986) flows off the Canadian Shield towards the St. Lawrence Valley at an altitude of some 325 m through a 60-year-old second-growth white birch (*Betula papyrifera*) forest with an understory of sugar maple (*Acer saccharum*). The water is acidic (pH = 5.8–6.2), unmineralized (30 $\mu S\ cm^{-1}$), coloured (60 Pt units), and soft (< 50 mg $CaCO_3\ l^{-1}$). The section studied (Fig. 1) is a mainstream second-order reach some 85 m downstream from Lake 4, just below fast water flowing over boulders (Lake 4 is a small beaver pond some 4 km from the source and the sixth small lake along the course). The study reach is some 18.5 m long and 4–5 m wide; its depth varies from 10 to 50 cm (Fig. 2B). The substrate is of gravel and sand (0.125–32 mm, mean phi number (Krumbein 1936) with 95% confidence intervals $- 2.66 \pm 0.37$), with particulate organic matter (POM classes as in Cummins (1974); 6–1363 g dry weight m^{-2} for large POM, 17–1065 g for medium POM, and 21–1068 g for small POM). From June to April, fine sediments accumulate on the lateral gravel, while the mid-channel remains clean (Fig. 1); the % of stream bottom that is erosional varies from about 20% in summer to over 100% in spring (Fig. 2C) when the stream overflows and the whole bottom is scoured and the finer sediments carried downstream. Water temperatures range from 0 to 27°C (Fig. 2B). The proximity of the lake prevents heavy icing, except near shores.

3. Methods

3.1. Adults

Adults were collected over five seasons (1978–1982) in 6 pyramidal traps (0.5 m^2 of stream bottom; Fig. 1, sites a–f). In 1978 and 1979 the traps were of the design of Harper and Magnin (1971), but afterwards of the more convenient model of LeSage and Harrison (1979). They were emptied from 3 to 7 times a week.

3.2. Benthic nymphs

Samples were taken from June 1981 to June 1982. A surface was isolated within a PVC cylinder of either 81 (June–December) or 182 cm^2 (thereafter, because of declining populations) cross-section and 90 cm in length driven into the substrate to a depth of 20 cm. The top 10 cm of substrate was sucked up with a sampler (Roy 1979) fitted to a hand pump. The collecting chamber contained two net bags (1000 and 53 μm mesh openings), one inside the other. The outtake from the pump was flushed back into the cylinder to wash it and to scour the bottom. Since little or no water infiltrated into the cylinder from the outside, it was presumed that no contamination came from the gravel. Samples were taken every 2 (summer) to 3–6 (winter) weeks. At each date, 4 to 7 (15) samples were taken. Sites were chosen by a random stratified sampling technique (Cummins 1962). A total of 117 samples were gathered from the mid-stream, and 20 from the lateral zones.

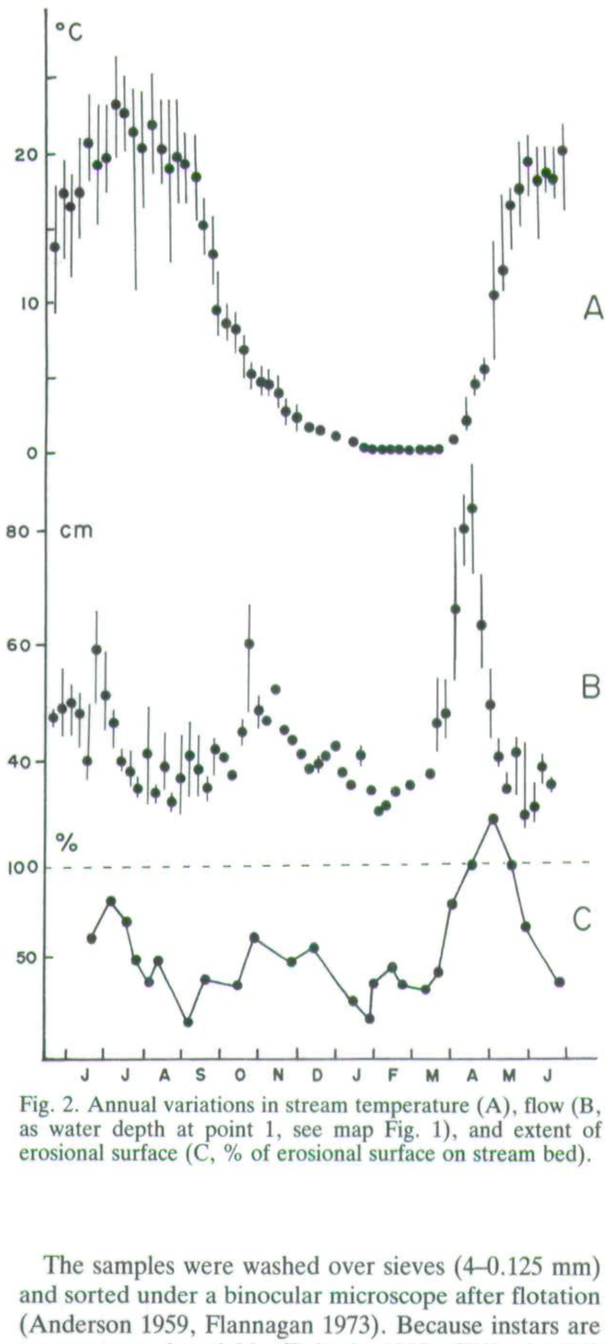


Fig. 2. Annual variations in stream temperature (A), flow (B, as water depth at point 1, see map Fig. 1), and extent of erosional surface (C, % of erosional surface on stream bed).

The samples were washed over sieves (4–0.125 mm) and sorted under a binocular microscope after flotation (Anderson 1959, Flannagan 1973). Because instars are numerous and variable (Brittain 1982, Clifford 1982) and biomass is best estimated from total length (Smock 1980), all nymphs were measured (labrum to epiproct) and grouped into size-classes of 0.5 mm.

3.3. Drifting nymphs

Drift was sampled from June 1981 to June 1982 with nets of the design of Dance et al. (1979). The mouth of the net was a narrow vertical slit (2×100 cm) and the 2 m bag had a mesh size of 53 or (to prevent clogging during spring) 253 µm. Two nets were used, one upstream from the study section, and the other downstream (Fig. 1). They were set for periods of 3–4 days in summer and of 7–12 days in winter (41 samples covering 247 days) and the volume of water filtered was estimated from water level and velocity. One downstream sample was lost during the spring flood (Fig. 12). The combination of a narrow mouth and a large collecting bag was thought to prevent escape from the net and to reduce clogging.

3.4. Statistical methods

Mean densities in the emergence, after a log transformation, were compared with a one-way ANOVA (Nie et al. 1975) or an equality of means test for heterogenous variances (Sokal and Rolf 1983). Specific compositions and mean annual densities were compared with a G test (Sokal and Rolf 1983), and homogenous groups set up by the SCHEFFE procedure (Nie et al. 1975).

An estimate of the annual production was calculated by the Hynes-Coleman size-frequency method (Benke 1984), our data being too variable to allow a more precise calculation.

Two dispersion indices were used: "I", the variance/mean ratio, and "K", a parameter of the negative binomial distribution ($K = (X^2/S_x^2) - X$). Random distributions occur when $I < 1$ and $K > 8$, otherwise patchiness is demonstrated (Elliott 1977). The "b" parameter of the Taylor function was used as an aggregation index (Downing 1979):

$$S_X^2 = aX^b$$

where X is the mean density and S_x^2 the variance of the samples; $b > 1$ indicates a contagious distribution, $b = 1$ a random distribution, and $b < 1$ a uniform distribution.

The proportion of the benthos found in the drift is described by Elliott's (1965) formula:

$$P = x \cdot D \cdot 100/(X - xD)$$

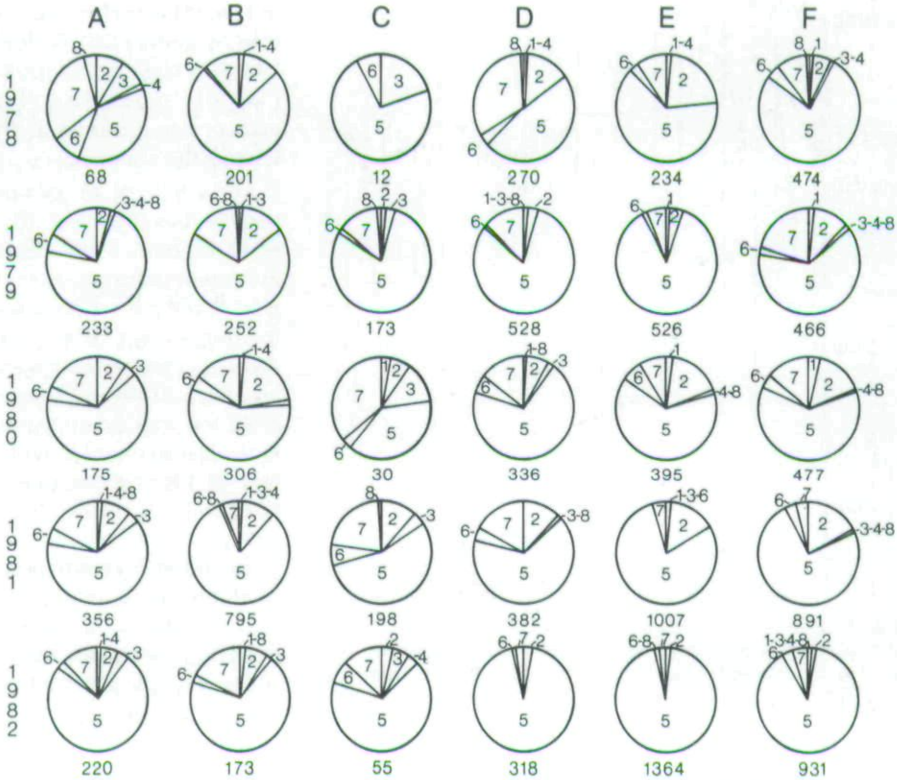
where x is the number of drifting nymphs per m^3, X the mean number of benthic nymphs per m^2 and D is the mean depth of the stream in meters. Correlation coefficients were also calculated to show relation of various parameters to drift.

4. Results

4.1. Annual and spatial variations in the emergence of the adults

Over the 5 years, 11 965 adults (1 200 samples) were collected, representing 18 species, 10 by few specimens; the rarer species were *Baetis pluto* McDunnough, *B. propinquus* (Walsh), *Brachycercus lacustris* (Needham), *Callibaetis ferrugineus* (Walsh), *Heptagenia pulla* (Clemens), *Leptophlebia cupida* (Say), *Paraleptophle-*

Fig. 3. Relative contributions of the 8 dominant species to the emergence in 6 sites (a–f) over 5 years (1978–1982). The numbers under each pie chart represent the total annual catch of the trap (N 0.5 m^{-2}). The species are (1) *B. flavistriga*, (2) *B. pygmaeus*, (3) *C. rubropictum*, (4) *E. verisimilis*, (5) *H. vibrans*, (6) *P. volitans*, (7) *S. modestum*, and (8) *S. vicarium*.



bia adoptiva (McDunnough), *P. ontario* (McDunnough), *Stenonema interpunctatum frontale* (Banks), and *Tricorythodes atratus* (McDunnough). The eight other species made up 99,7% of the total: *Habrophlebia vibrans* Needham (75.7%), *Stenonema modestum* (Banks) (10.1%), *Baetis pygmaeus* (Hagen) (9.5%), *Paraleptophlebia volitans* (McDunnough) (2.7%), *Cloeon rubropictum* McDunnough (0.75%), *Baetis flavistriga* McDunnough (0.40%), *Stenonema vicarium* (Walker) (0.34%), and *Eurylophella verisimilis* (McDunnough) (0.24%).

Habrophlebia vibrans was the dominant species (Fig. 3). The density of the emergence (traps pooled) did not vary significantly ($p > 0.05$) from year to year, nor did the densities of *H. vibrans, S. modestum, B. pygmaeus,* and *P. volitans*. On the other hand, the total emergence, as well as that of the four species aforementioned, differed significantly ($p < 0.05$) from one trap to the next (years pooled). By the SCHEFFE procedure, two groups were recognized, traps A and C and traps A, B, D, E, and F, on the basis of total numbers and of numbers of *H. vibrans, B. pygmaeus,* and *P. volitans*. Trap C differed from the others by its low catches, and trap A had intermediate densities. Trap C was set near the shore behind a clump of ferns (*Osmunda regalis*) and thus in much calmer water than the others. Trap A was set at the junction of the lateral depositional area. All the others were over gravel in erosional zones (Fig. 1).

The species composition of the catches varied signif-

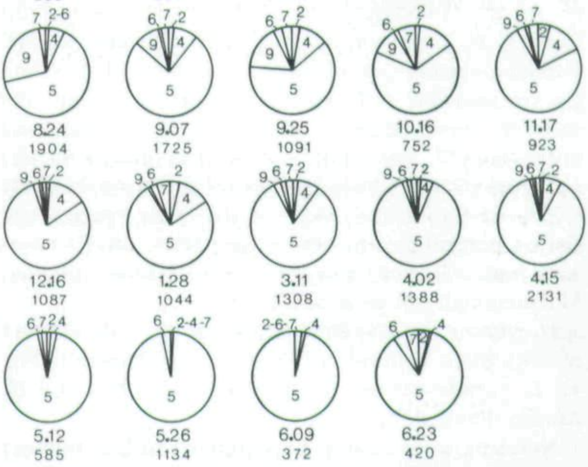


Fig. 4. Seasonal variations in the relative importance of the 5 dominant species in the 19 benthos samples. The upper numbers beneath the pie charts refer to the sampling dates and the lower numbers to the actual numbers of specimens collected. The species are: (2) *B. pygmaeus*, (4) *E. verisimilis*, (5) *H. vibrans*, (7) *S. modestum*, (8) *S. vicarium*, and (9) *L. cupida*.

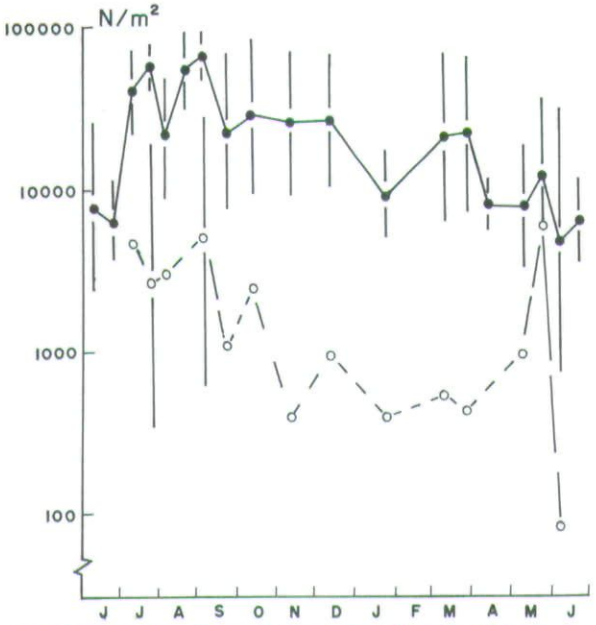


Fig. 5. Seasonal variation in the density ($N\ m^{-2}$) of the mayfly community (all species pooled) in the central erosional zones (full line) and the lateral depositional areas (broken line).

icantly from one year to the next (G = 837***) and from trap to trap (G = 593***).

The temporal patterns of emergence are not illustrated here, but they agree totally with those illustrated by Harper and Magnin (1971) and Harper and Harper (1982). *Habrophlebia vibrans* had a short emergence, others have the extended pattern characteristic of summer species.

4.2. Seasonal variations in the nymphal populations

Some 22 000 nymphs were collected belonging to 8 taxa: *H. vibrans* (74.5%), *L. cupida* (11.6%), *E. verisimilis* (6.6%), *B. pygmaeus* (2.7%), *S. modestum* (2.7%), *Paraleptophlebia* spp. (1.3%), *S. vicarium* (0.5%), and *Caenis simulans* (0.005%). These are generally the same as above, despite differences in sequence and proportions: *L. cupida* did not occur in the emergence; *E. verisimilis* represented 6.6% of the nymphs, but only 0.24% of the adults. Most of the other species had similar percentages in both series; some rarer species were not collected as nymphs, and *Caenis simulans* McDunnough not as an adult.

H. vibrans was dominant except for the early summer of 1981 when *Leptophlebia cupida* was abundant (Fig. 4). *L. cupida* did not reappear in June 1982, and *H. vibrans* dominated.

Numbers were highest during mid and late summer when most species were hatching (Fig. 5), and declined steadily thereafter as mortality, migration and emergence progressed. The highest densities were observed in the central channel (to a mean maximum of 40 000); in the littoral areas, densities were of at least one order of magnitude lower. The contribution of each species is related to its size, its body shape, and its life cycle. Length-weight relationships are of the form $W = bL^k$ (Tab. 1); while values of k are similar b varies considerably. *E. verisimilis* is the stockiest species, and *H. vibrans* the slimmest.

The adults of *H. vibrans* emerged synchronously in mid- to late June (Fig. 6). The hatchlings were present as early as mid-July. Growth proceeded directly and maximum densities were reached in September. Nymphal development extended over 2 years and ended in a final spurt just before emergence. Two cohorts were therefore present throughout (a detailed life-cycle is given in Lauzon and Harper 1986). Because of the small body size and the concentration of much of the growth in the last weeks of nymphal life, biomass remained low despite the high densities, except shortly before the emergence. Nevertheless, the species predominated the stream section, both in numbers and biomass. The long cycle and slow growth pattern account for the relatively small production and the low turnover ratio (3.2).

The eggs of *L. cupida* hatched in June and the nymphs grew rapidly thereafter (Fig. 7); maximum density was reached in August and then decreased rapidly; the species disappeared completely from the reach, some 2–3 weeks before its synchronous emergence in late-May (Harper and Harper 1982). Emerging adults could be collected in great numbers some 100 m downstream, chiefly in backwaters. Growth proceeded during winter, though smaller nymphs straggled along and their relative importance increased as the larger ones left. The production was relatively high as indicated by the turnover-ratio of 9.8.

E. verisimilis was abundant only from September to March. The adults emerged in early June, but downstream from the study section. The eggs hatched rapidly (Fig. 8). Growth proceeded until October and resumed in May. Maximum biomass and densities occurred in autumn. A few nymphs grew much faster than the others and the larger nymphs left the study area for the downstream sections where they normally emerge. Production was high, with a turnover ratio of 7.

Because of its large size, *S. modestum* is an important component of the community, despite its low densities. The adults were on the wing from June to September (Harper and Harper 1982) and recruitment of hatchlings extended throughout the summer (Fig. 9). Growth was rapid in late summer and autumn and most individ-

Tab. 1. Length-weight relationships in 5 species of mayfly. Length is in mm and dry weight in µg.

H. vibrans	$W = 2.8355\ L^{2.4876}$
**L. cupida*	$W = 4.5\ \ L^{2.23}$ and $= 0.2\ L^{4.01}$
***S. modestum*	$W = 4.7359\ L^{2.8193}$
E. verisimilis	$W = 5.0543\ L^{2.4419}$
B. pygmaeus	$W = 3.9523\ L^{2.3775}$

* from Clifford et al. (1979).
**used also for *S. vicarium*.

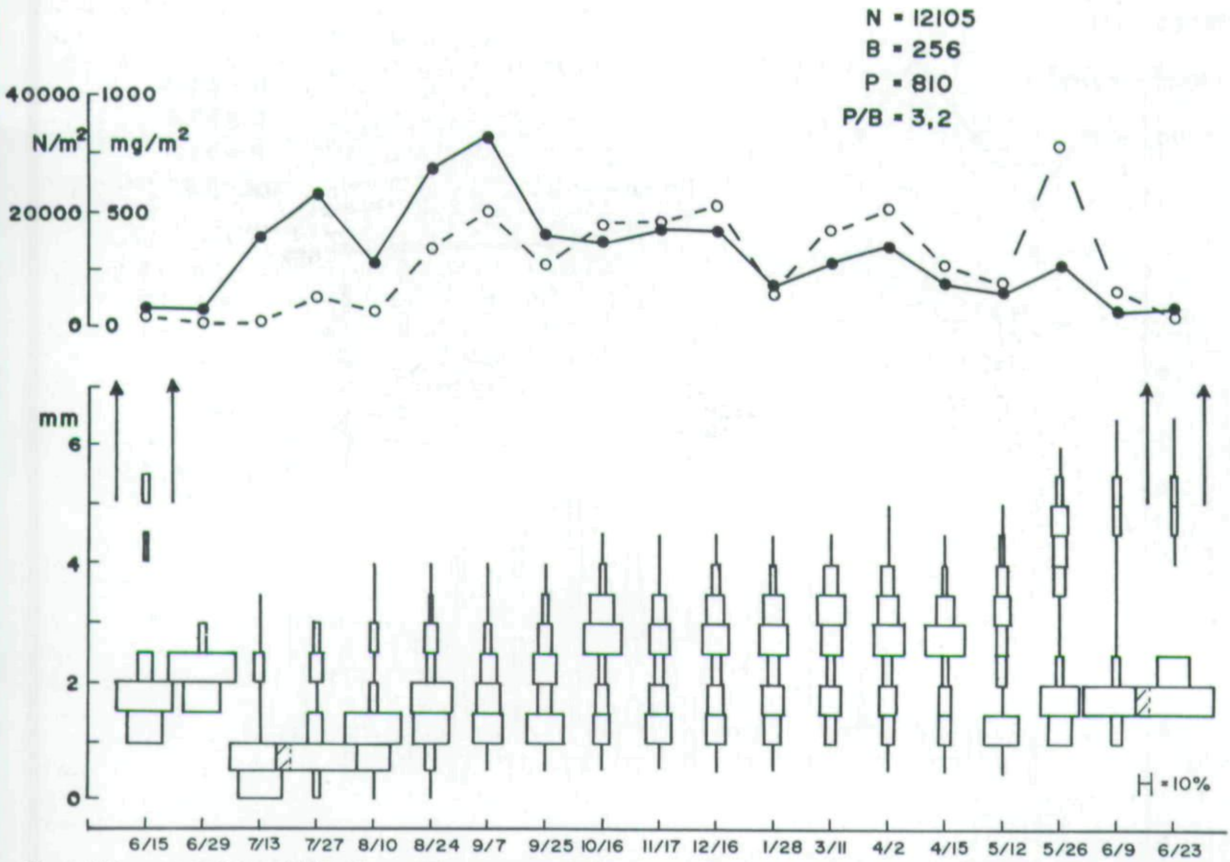


Fig. 6. Life cycle of *Habrophlebia vibrans*. The upper graph shows annual variation in density (N m^{-2}; full line) and biomass (mg m^{-2}, dashed line); mean density, biomass, and production (mg m^{-2} yr^{-1}) are indicated. The lower graph illustrates the distribution of the relative frequencies of the size classes of nymphs; arrows mark the emergence period.

uals were ready to emerge by June; most of the population emerges within the first two weeks and stragglers keep maturing irregularly throughout the summer (Harper and Magnin 1971, Harper and Harper 1982). Maximum biomass was attained in early winter. The turnover-ratio was average (4.7) and the annual production important (781 mg m^{-2} yr^{-1}). Only *H. vibrans* contributed more (810 mg m^{-2} yr^{-1}) and only barely.

Baetis pygmaeus was multivoltine (Harper and Harper 1982), but the nymphs were abundant only in June when the winter and summer cohorts overlapped (Fig. 10). The summer generation had twice the importance of the winter generation in terms of numbers, biomass and production. There could have been two summer generations (Harper and Harper 1982), in which case the production values would be underestimated.

Stenonema vicarium maintained a low density, but its large size made its contribution to the system of some significance in terms of biomass and production. The adults emerged from late-May to mid-June. Recruitment of nymphs occurred throughout the summer and growth proceeded rapidly until early winter (Fig. 11). Densities were too small in winter for a detailed description of the population structure, but there appeared to be a wide range of size-classes present. The turnover-ratio was average (5.3).

The other species were either too rare or their presence too haphazard to warrant a special discussion.

H. vibrans, L. cupida, E. verisimilis, and *B. pygmaeus* all had patchy distributions (Tab. 2). The slope (b) of the power function between the variance and the mean for the combined species of mayflies is 2.042 ($S_X^2 = 0.369\ X^{2.042}$; $r^2 = 0.98^{***}$, n = 62). This value is much greater than that calculated by Downing (1979) for mayflies dwelling in lakes and large rivers (b = 1.339).

4.3. Drifting of the nymphs

The drift study yielded 8761 nymphs. The species were *L. cupida* (70.9%), *H. vibrans* (15.1%), *S. modestum* (6.9%), *E. verisimilis* (2.8%), *B. pygmaeus* (2.8%), *S. vicarium* (1.4%), and *Baetis* spp. (0.11%).

Both nets, that above and that below the study section, yielded similar results (Fig. 12). In winter, the species composition of the drift varied little and *L.*

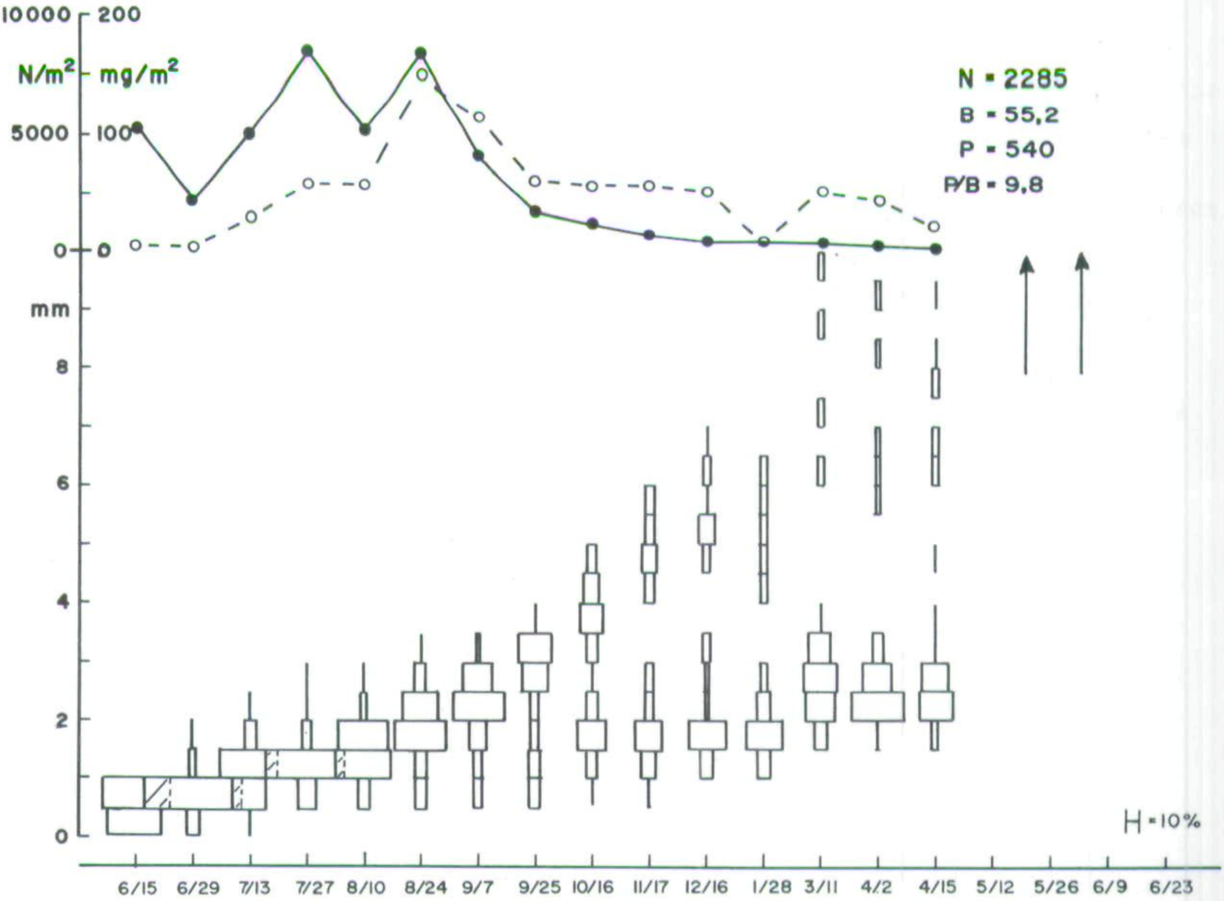


Fig. 7. Life cycle of *Leptophlebia cupida*. Legends as in Fig. 6.

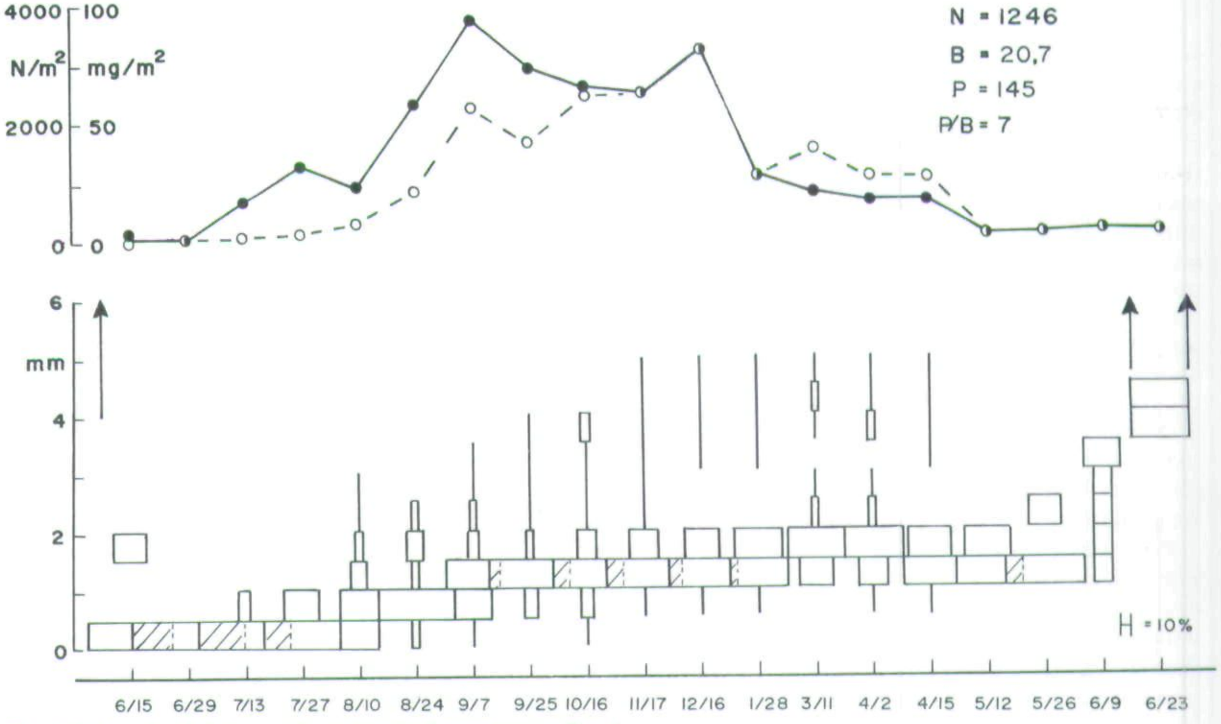


Fig. 8. Life cycle of *Ephemerella verisimilis*. Legends as in Fig. 6.

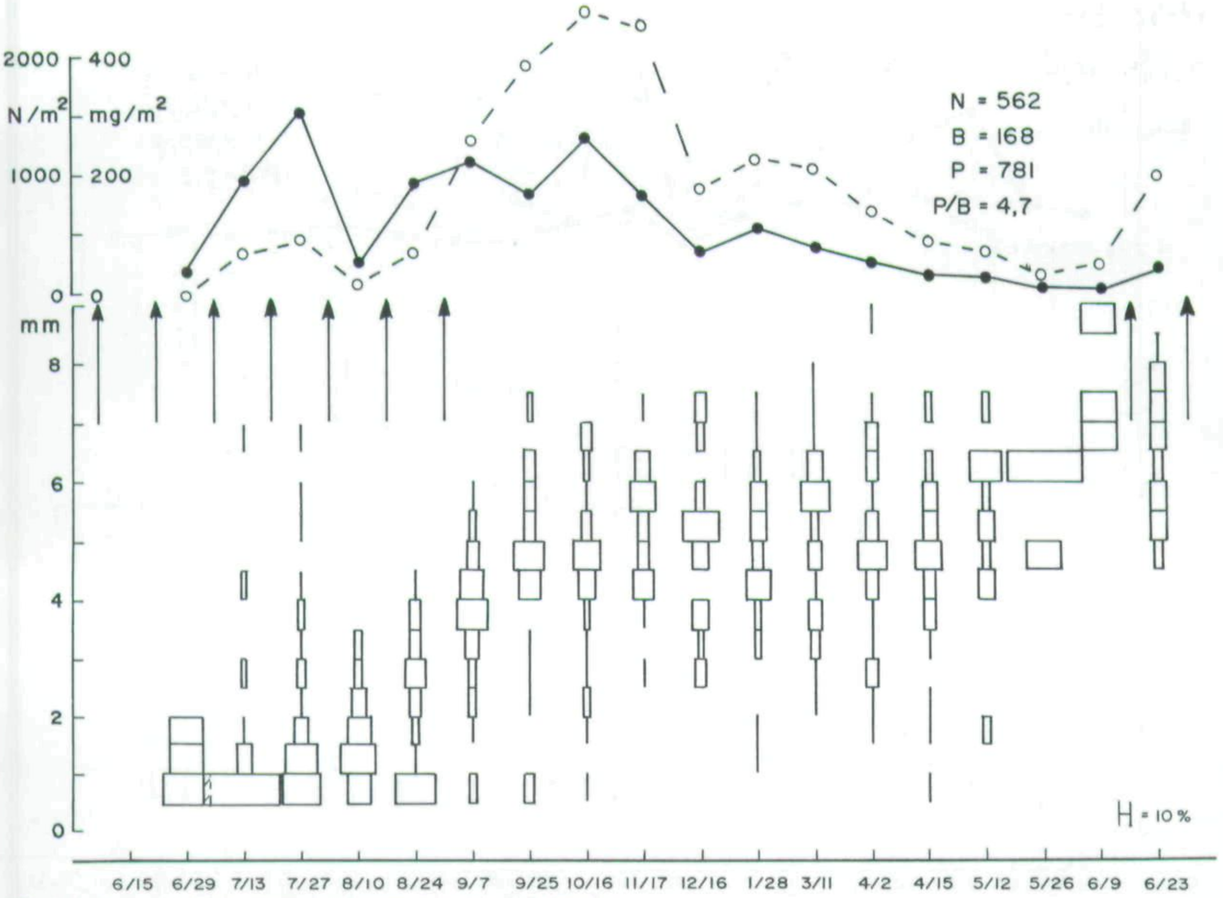


Fig. 9. Life cycle of *Stenonema modestum*. Legends as in Fig. 6.

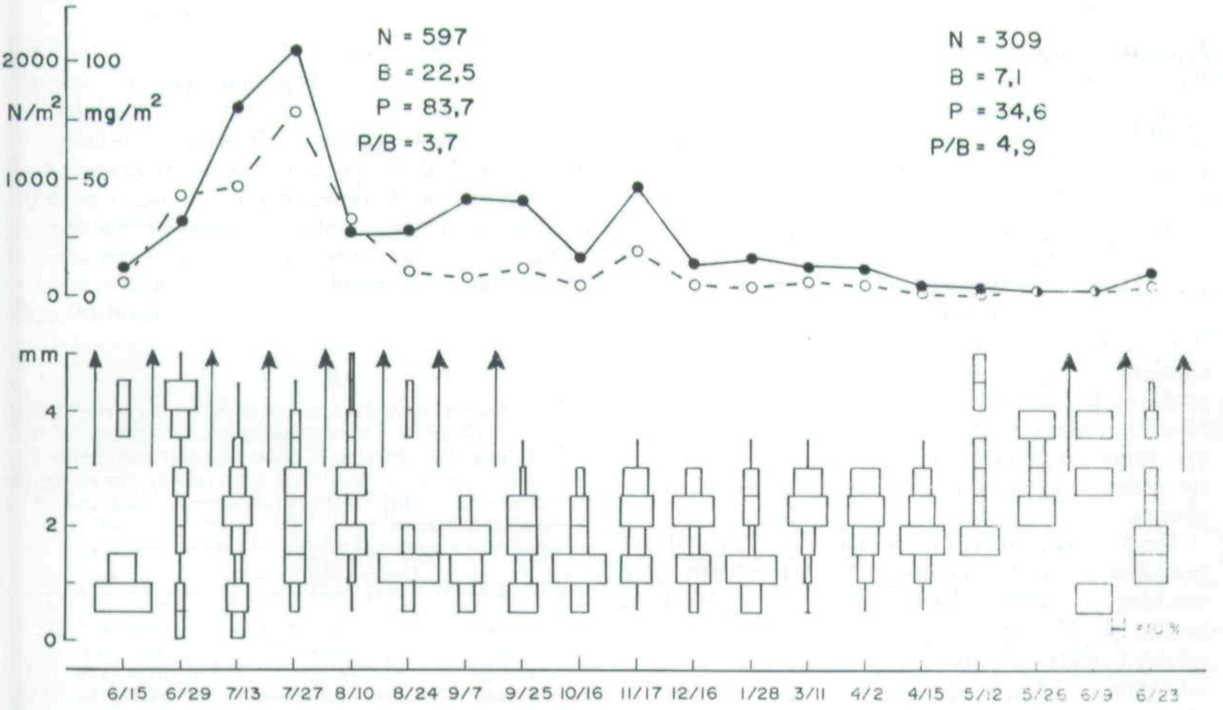


Fig. 10. Life cycle of *Baetis pygmaeus*. Legends as in Fig. 6.

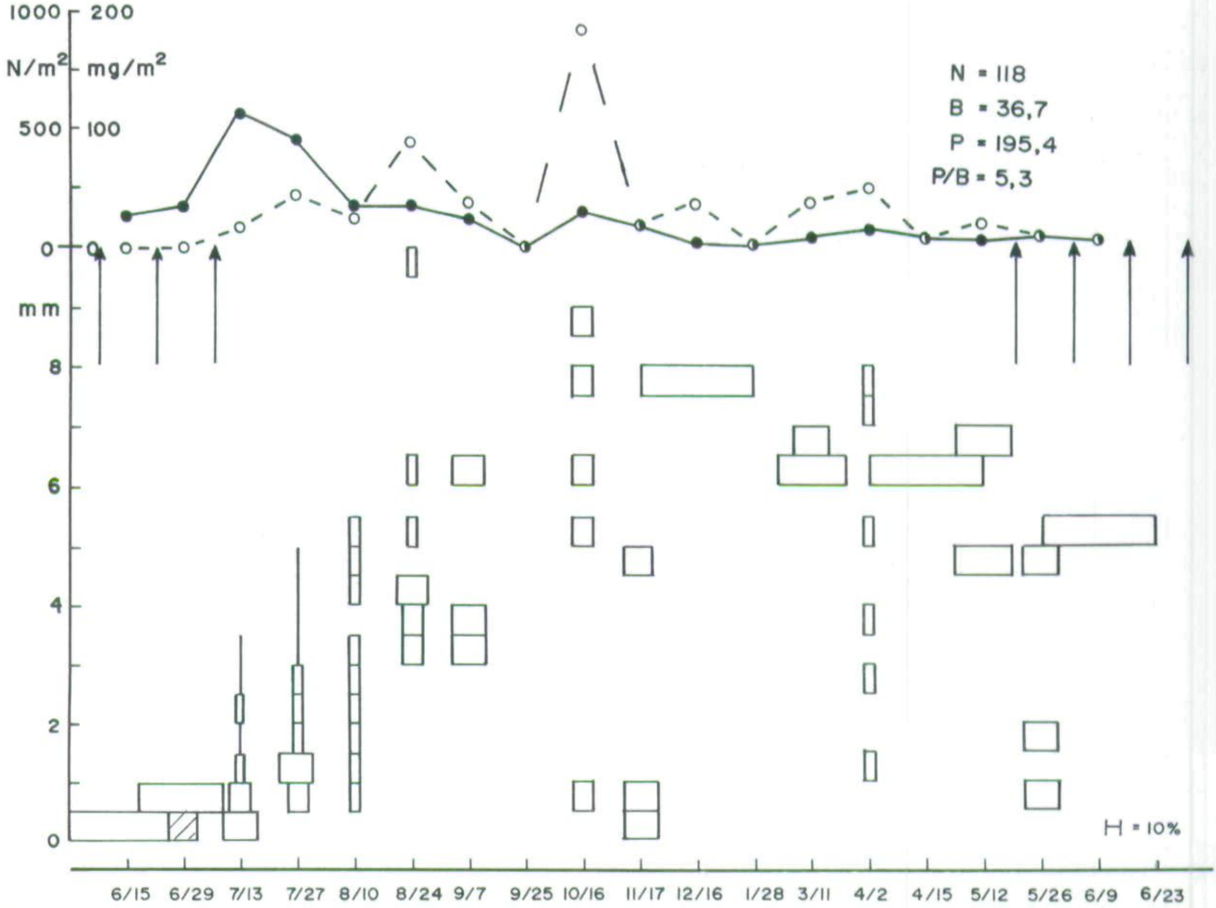


Fig. 11. Life cycle of *Stenonema vicarium*. Legends as in Fig. 6.

cupida predominated. From May to October, most of the other species were also present.

The densities varied from minima of 3 to 48 nymphs per 1000 m^3 in autumn and winter to a maximum of 900 in spring. During summer, the levels were intermediate (20 to 300). The spring thaw (15 April – 12 May, 1982) accounted for 36% of the annual density of the drift and 51% of the drifting biomass; such drift qualifies as "catastrophic drift" in Water's (1972) terminology.

The proportions of nymphs of any one species in the drift were always inferior to 0.07% except in two instances in the spring when *L. cupida* was observed only in the drift (none in the benthos). Proportions were lower in winter (generally $< 0.001\%$), and increased in the spring during the thaw and in early summer due to the resumed nymphal growth and the onset of emergences.

The first generation of *H. vibrans* (Fig. 12, no. 5) was prevalent in the drift in July and August shortly after hatching; the second generation drifted in great numbers in May and June of the last year just before emergence. Drifting *E. verisimilis* (no. 4) were abundant in late summer (August, September); they were present during the winter and increased in number towards the spring. Both generations of *B. pygmaeus* (no. 2) drifted readily. *L. cupida* (no. 9) appeared in the drift throughout; it formed the bulk of the low drift of winter and became very abundant in April, which coincided with the migration of the species out of the study area. Both *S. modestum* and *S. vicarium* (no. 7, 8) occurred in the drift, albeit in small numbers, especially in summer.

We have attempted to relate drift with variables of the habitat, some simple (AFDW of drifting organic matter, water level, mean temperature), others com-

Tab. 2. Dispersion coefficients calculated on the series of samples of nymphs of the 4 most common species. I is the variance/mean ratio and K a parameter of the binomial distribution. For each are given the mode (when appropriate), the range (in parentheses) and the proportion of samples which indicate a clumped distribution.

	I			K		
H. vibrans	–	(2.3–187.2)	19/19	2	(1.0–11)	17/19
L. cupida	–	(1.4–54.6)	15/15	0	(0.4–5.1)	15/15
E. verisimilis	4	(0.5–26.9)	15/18	1	(0.3–56.6)	13/15
B. pygmaeus	1	(0.3–3.8)	16/19	1	(1.0–11.3)	14/15

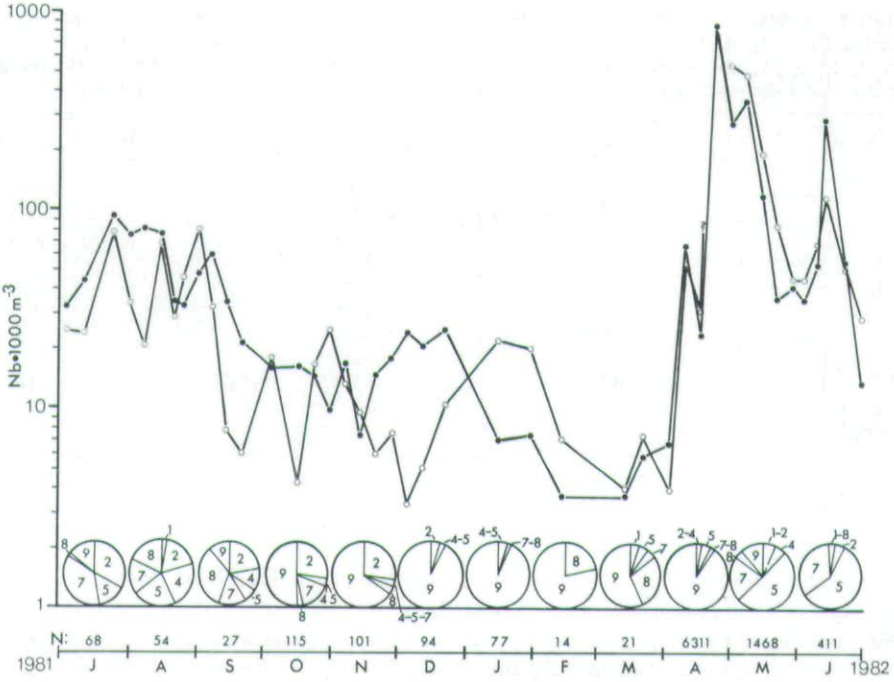


Fig. 12. Variations in drift over the year. Dots represent upstream net, open dots the downstream net. Pie charts give the relative species composition for each month, the numbers (N) the actual number of specimens collected; species as in Figs 3 and 4.

plex (density of benthos, biomass of benthos, mean size and growth rate of nymphs).

Drift can be either independent (linear realitionship) or dependent (curvilinear relationship) on benthic densities (Hildebrand 1974, Walton et al. 1977). We calculated the correlations between the benthic and the drifting densities for the 6 species and their respective cohorts before and after log transformation of the data (Tab. 3). Only for *B. pygmaeus, H. vibrans,* and *S. modestum* were significant relationships discovered. In the first year cohort of *H. vibrans* and the summer cohort of *B. pygmaeus,* the relationship was linear (best fit from untransformed data), and drift in both these groups is interpreted as density-independent, which suggests that the densities of these populations have not reached the carrying capacities of the habitat. By contrast, for *S. modestum* and the second-year cohort of *H. vibrans,* the relationship is curvilinear (best fit from log transformation) and negative. If both cohorts of *H. vibrans* or of *B. pygmaeus* are pooled, the relations are no longer statistically significant; this confirms the importance of the recommendation of Cowell and Carew (1976) that each cohort be considered separately.

Simple correlations were calculated between drift and habitat parameters before and after logarithmic transformations, and those giving the best fit were retained (Tab. 4). The greatest number of significant relationships were found with such variables as total seston (>0.250 mm), medium seston (0.250–2 mm), and coarse seston (> 2 mm) (classification from O'Hop and Wallace 1983). The strongest relations are found with *L. cupida,* the main drifter, which suggests that as particles are carried away in the drift, the nymphs associated with them are also taken into the drift. Such a relation is

Tab. 3. Relationship between the density (Y, as N 1000 m^{-3}) of nymphs in the drift and the corresponding density (X, as N m^{-2}) in the benthos. Asterisks mark the degree of statistical significance of the parameters (a, b). Non-significant relationships are not given.

B. pygmaeus (sum.)	$Y = 0.067 + 0.005^{*} X$,	$r^2 = 0.68^{*}$
B. pygmaeus (winter)		$r^2 = 0.004$
B. pygmaeus (all)		$r^2 = 0.05$
E. verisimilis		$r^2 = 0.01$
H. vibrans (gen. 1)	$Y = -1.27 + 0.00053^{**} X$,	$r^2 = 0.41^{*}$
H. vibrans (gen. 2)	$\text{Log } Y = 3.56^{**} - 0.883^{**} \text{ Log } X$,	$r^2 = 0.37^{*}$
H. vibrans (all)		$r^2 = 0.05$
L. cupida		$r^2 = 0.01$
S. modestum	$\text{Log } Y = 2{,}45 - 7.31^{**} \text{ Log } X$,	$r^2 = 0.32^{**}$
S. vicarium		$r^2 = 0.05$
Ephemeroptera (all)		$r^2 = 0.04$

Tab. 4. Pearson correlation coefficients between the density of drift and various habitat parameters, ash-free dry mass of medium seston (Sm, mg m^{-3}), of coarse seston (Sc, mg m^{-3}), and of total seston (St, mg m^{-3}), mean water temperature (T, °C), mean water level (W, cm), mean biomass of the benthos (B, mg m^{-2}), nymphal growth, rate (G, µm d^{-1}) and mean size of nymphs (L, mm). Asterisks mark degree of statistical significance. Non-significant values are marked by a dash (–).

	Sm	Sc	St	T	W	B	G	L
B. pygmaeus (S)	–	–	–	0.87**	–	0.75*	–	–
$^+$*B. pygmaeus* (W)	–	0.54**	0.45*	–	–	–	–	–
$^+$*B. pygmaeus*	0.61**	–	0.57**	0.43*	–	–	–	–
$^+$*E. verisimilis*	–	–	0.40*	–	–	–	–	–
$^+$*H. vibrans* (1)	0.55*	–	0.52*	0.55*	–	–	0.67**	–0.44*
H. vibrans (2)	–	0.56**	0.49**	–	–	–	–	0.79**
$^+$*H. vibrans*	0.68***	0.54***	0-74***	0.61**	–	–	–	–
L. cupida	–	0.89***	0.70***	–	0.69**	–	–	–
$^+$*S. modestum*	0.53*	0.43*	0.55**	0.46*	–	–0.46*	–	–
$^+$*S. vicarium*	–	–	–	–	–	0.41*	–	–
Ephemeroptera	–	0.90***	0.75***	–	0.58**	–	–	–

$^+$Log transformation of data.

still better illustrated by the correlation between the biomass of total mayflies in the drift and the weight of the mid-size seston.

Only in *L. cupida* (and in total mayflies), does the drift show any relation with water depth (Tab. 4). In a Western Canadian river, the nymphs of this species leave the riffles during the winter for the slower pool areas; in the spring, in response to high water, they migrate into tributaries and flooded shores to emerge (Hayden and Clifford 1974). No such upstream migration was observed in our stream; indeed the nymphs seem to drift downstream at high water and were observed to emerge some 100 m downstream from our section in an area of slow current (Delorme-Harper 1967).

With variables such as water temperature, growth rate and mean size of the nymphs, few significant relationships were observed, and no general tendency was apparent. There was a relationship with mean water temperature in a number of taxa, particularly *B. pygmaeus*. *Habrophlebia vibrans* was the only species which exhibited distinct behavioral drift (in Water's 1972 terminology). The drift of the first cohort was positively correlated with the growth rate and negatively with mean sizes in the benthos (Tab. 4). So, the smaller they were, the more the nymphs of the first generation occurred in the drift. However, for the second cohort, the inverse relation is true, and the bigger the nymph, the greater its propensity to drift. It is necessary to separate cohorts in order to assess the determinant factors on drift in a semivoltine insect.

4.4. Comparisons of emergence, benthos and drift

The concurrent sampling of the emergence, the benthos, and the drift in the same populations in a short stretch of stream permits a comparison of the data sets (Fig. 13). Relative densities in the benthos and the emergence are similar for *B. pygmaeus*, *P. volitans*, *S. modestum*, and *S. vicarium*. This is not so however for some of the more common species, *H. vibrans*, *E. versimilis*, and *L. cupida*. Most of the nymphs of *E. verisimilis* and nearly all those of *L. cupida* left the sampling area by drifting in the spring and emerging downstream (Harper and Magnin 1971); on the other hand, many nymphs of *H. vibrans* entered the section from upstream at the same period. The interpretation of the sole emergence data would have lead to distorsions in the descriptions of community structure on this stretch. The population of *H. vibrans* would have been overestimated, while that of *E. verisimilis* would have been underestimated, and that of *L. cupida* would not have been detected at all.

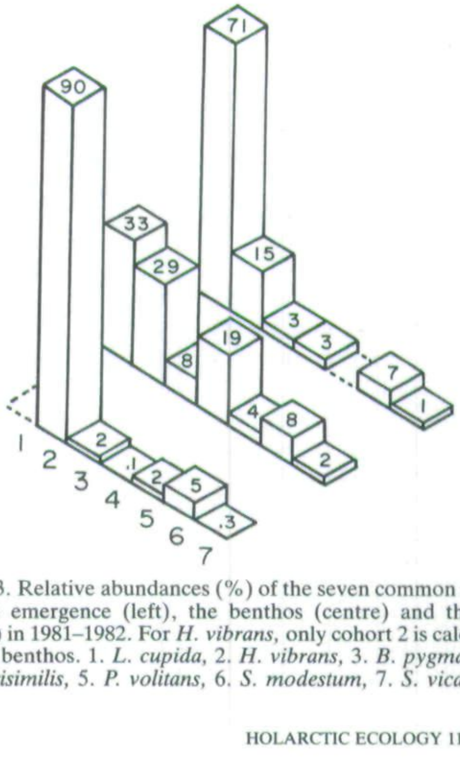


Fig. 13. Relative abundances (%) of the seven common species in the emergence (left), the benthos (centre) and the drift (right) in 1981–1982. For *H. vibrans*, only cohort 2 is calculated in the benthos. 1. *L. cupida*, 2. *H. vibrans*, 3. *B. pygmaeus*, 4. *E. verisimilis*, 5. *P. volitans*, 6. *S. modestum*, 7. *S. vicarium*.

5. Discussion

The total numbers of emerging mayflies are similar from year to year in any one area and this seems to be a general feature of many streams. Illies' (1983) has put forward a "rule of constancy" which holds that the colonization cycle (Müller 1974) of insects ensures a steady presence of the species so that total densities (all species pooled) vary relatively little over the years. Species compositions however are more variable and this led Illies to formulate a "rule of harmony" which states that the annual densities of species fluctuate more widely, but that decreases in some species are compensated by corresponding increases in others. Our results although based on fewer data are consistent with both these rules.

Yearly fluctuations are doubtless reflections of changes in weather patterns and stream conditions, particularly flow and substrate. Nonetheless, the dominant species are the same every year, although changes in the dominance sequence do occur (Zwick 1984). This confirms Illies' (1983) conclusion that emergence data, even from only one year, are important and significant parameters of a stream community.

Adult densities (110–2728 m^{-2}) are high and comparable to those of other local streams (Harper and Harper 1982). The number of species however is rather low, but this is doubtless related to the homogeneity of the reach.

Mean densities of nymphs are substantial (of the order of 16 000 m^{-2}, the maximum ca 40 000). These values contrast with those reported for the Holarctis by Clifford (1980) who considers any density above 10 000 "very large" and rather exceptional. They can be explained by the dominance in our stream of a tiny species (*H. vibrans*) and by our effort to collect quantitatively the smaller nymphs.

The larger species, because of their biomass, contribute substantially to the productivity of the community despite their low numbers. *H. vibrans* which accounts for approximately 3/4 of the mean density provides only 1/3 of the production; this is no doubt due to its slow growth and long life cycle. By contrast, a similar-sized *B. pygmaeus* which represents some 5% of the mean density also provides 5% of the production; it achieves this by being bivoltine or multivoltine.

The distribution of the mayflies is patchy, as appears in both the emergence and benthos data. The density of *H. vibrans* correlated positively with the presence of gravel and negatively with that of detritus (Lauzon and Harper 1986) and this is consistent with its higher densities in the middle channel. The same applies no doubt to the other species, for the densities in the middle channel were always higher, except in May and June when the spring flood had washed away the fine deposits. No doubt, many of the nymphs migrate towards the shores either to avoid their being carried away by the spring run (Olsson and Söderström 1978, Ciborowski and Clifford 1983), or to exploit the newly uncovered habitats (Olsson 1983). Also, patchy distributions are typical of species in which one or more habitat parameters influence greatly the spatial distribution (Alley and Anderson 1968). As well, the choice of a sampler, the sorting methods, and the biology of the species have some influence on the patterns (Resh 1977). The patchiness is however greater than that observed in lakes. Downing (1979) suggested that stream-dwelling mayflies should be more aggregated; he also noticed that aquatic invertebrates living on gravel tended to be more highly aggregated than on other substrates. Our results confirm his predictions.

The life cycles described from our data generally correspond to the outlines published anteriorly for *B. pygmaeus* (Bergman and Hilsenhoff 1978), *E. verisimilis* (Sweeney and Vannote 1981), *L. cupida* (Coleman and Hynes 1970, Clifford et al. 1979), *S. modestum* (Flowers and Hilsenhoff 1978 as *S. rubrum,* Kondratieff and Voshell 1980), and *S. vicarium* (Richardson and Tarter 1976, Flowers and Hilsenhoff 1978 as *S. fuscum,* Kruger and Cook 1984). Notable exceptions are apparent for *L. cupida* and *E. verisimilis* in which the later instars are missing from our charts, doubtless due to their leaving the study area as they mature.

Drift rates are low except during spring. This is consistent with the low grade of the section and with the dominance by bottom dwelling and clinging species. The species composition of drift reflects that of the benthos, except for the prevalence of *L. cupida* (our results are high by comparison to those of Bishop and Hynes (1969) and Clifford (1972)) and the underrepresentation of *E. verisimilis*. The percentage of *Baetis* is surprisingly low in comparison to other similar studies (Stoneburner and Smock 1979, Stewart and Szczytko 1983), given the propensity of Baetids to be overrepresented in the drift (Bailey 1981). *Stenonema* occurs in moderate proportions in comparison to published records (Bishop and Hynes 1969, Cowell and Carew 1976); it is not known as a good drifter (Walton 1980).

Such drift rates and periodicity are a common occurrence and have been described elsewhere (Waters 1969, Clifford 1972, O'Hop and Wallace 1983). Only a very small percentage of the benthos occurs at any one time in the drift (Hemsworth and Brooker 1979).

Many investigators have attempted to relate drift to factors of the habitat or the biology of the nymphs, either in a cause-effect relationship (Waters 1972, Müller 1974, Keller 1976) or in a predictive equation using easy to measure variables (O'Hop and Wallace 1983). Conflicting results have been reported in the literature. Reisen and Prins (1972) found no relation between the drift and benthos densities in a southern population of *Habrophlebia* sp. (they did not indicate voltinism). Linear relationships were reported many times for *Baetis* spp. (Pearson and Kramer 1972, Cowell and Carew 1976, Corkum 1978, Stoneburner and Smock 1979, Hensworth and Brooker 1979). Other studies have showed either no relation (Bhole 1978, Ciborowski 1983) or a distinct curvilinear relationship (Pearson and Franklin 1968, Gyselman 1980).

Few significant relationships (in our results as well as in the literature) have been obtained, and the majority of these are linear; this suggests that drift in mayflies is seldom determined by biological density-dependent factors. Nonetheless, some curvilinear relationships indicate that in a few populations, drift is an active phenomenon, determined at least in part by biological imperatives (Pearson and Franklin 1968, Reisen and Prins 1972, Walton et al. 1977, Gyselman 1980).

Among habitat parameters responsible for drift, temperature is sometimes mentioned (Pearson and Franklin 1968), but is often not a significant factor (Reisen and Prins 1972, Stewart and Szczytko 1983).

A relation between drift and growth rates has been observed by Elliott (1967) on a variety of species, except in very small nymphs. This restriction does not apply to our data, since drift is important in small nymphs, at least in *H. vibrans* (Lauzon and Harper 1986). Large mature nymphs tend to drift more than other stages in the life cycle (Müller 1966, Anderson 1967, Madsen 1976), and this is particularly so just prior to emergence (Thomas 1970, Lauzon and Harper 1986). Hall et al. (1980) have postulated, from the data of Resh (1977) and Siegfried and Knight (1978), that in species which possess a synchronous hatching of their eggs and a synchronous emergence of adults, drift is concentrated over a short time, for instance during the emergence or pre-emergence periods, or during the spring thaw. Such a pattern fits our data, except that a second period of high drift (dispersion) is observed in the small nymphs of some species, such as *H. vibrans* (Lauzon and Harper 1986).

The most interesting conclusion of our study concerns the comparisons of the pictures of the mayfly community generated by the three sampling procedures. In some species, particularly the least numerous, there appears to be little discrepancy; this may be due to the low numbers and the high variability involved. On the other hand, for three of the major species the patterns are quite different. The importance of *H. vibrans* is brought forward by all methods, though it is difficult to patch together all the data; for instance, although densities of nymphs are consistently high, there is a decrease in the population of larger nymphs in the weeks preceding emergence and it is necessary to invoke either upstream migration or drift from upstream sites to account for the numbers emerging (Lauzon and Harper 1986). The case of *L. cupida* is clearer: the decrease in the population in the spring and the absence of emerging adults is related to the high drift rates in April and with observations of an emergence concentrated downstream from the study site. A similar situation was observed in an Alberta stream by Clifford et al. (1979) who estimated that *L. cupida* made up only 8% of the mayfly community at emergence, but that it accounted for 39% in the benthos. The case of *E. verisimilis* is similar, although the lower drift rates may not totally explain the disappearance of the species from the study zone; the species is a crawler and perhaps the nymphs have a greater tendency to walk away rather than swim, as seems to be the case in *L. cupida.*

No one sampling scheme can therefore provide a complete picture of the life history of a species nor does it account for the dynamics of a whole community. Each species has requirements and habits peculiar to each of the phases of its cycle and these often explain the conflicting results generated by different sampling schemes. One should therefore be wary of generalizations based on particular data or on the sampling of only one stage or one feature of the life-history. In fact, the methods are complementary, and it is often when their results do not fit one with the other that interesting life history traits are revealed. None of the methods alone would have been so enlightening.

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References

Alley, W. P. and Anderson, R. F. 1968. Small-scale patterns of spatial distribution of Lake Michigan macrobenthos. – Proc. Conf. Great Lakes Res. 11: 1–10.

Anderson, N. H. 1967. Biology and downstream drift of some Oregon Trichoptera. – Can. Ent. 99: 507–521.

Anderson, R. D. 1959. A modified technique for sorting bottom fauna samples. – Limnol. Oceanogr. – 4: 223–225.

Bailey, C. E. 1981. Insect drift in Condor Creek, Australian Capital Territory. – Austr. J. Mar. Freshwat. Res. 32: 111–120.

Benke, A. C. 1984. Secondary production in aquatic insects. – In: Resh, V. H. and Rosenberg, D. M. (eds), The ecology of aquatic insects. Praeger, New York, pp. 289–322.

Bergman, E. A. and Hilsenhoff, W. L. 1978. *Baetis* (Ephemeroptera: Baetidae) of Wisconsin. – Great Lakes Ent. 11: 125–135.

Bishop, J. E. and Hynes, H. B. N. 1969. Downstream drift of the invertebrate fauna in a stream ecosystem. – Arch. Hydrobiol. 66: 56–90.

Bhole, H. W. 1978. Beziehungen zwischen dem Nahrungsangebot, der Drift und der reaumlichen Verteilung bei Larven von *Baetis rhodani* (Pictet). – Arch. Hydrobiol. 84: 500–525.

Brittain, J. E. 1982. Biology of mayflies. – Ann. Rev. Ent. 27: 118–147.

Ciborowski, J. J. H. 1983. Influence of current velocity, density and detritus on drift of two mayfly species (Ephemeroptera). – Can. J. Fish. Aquat. Sci. 40: 2025–2029.

– and Clifford, H. F. 1983. Life histories, microdistribution and drift of two mayfly (Ephemeroptera) species in the Pembina River, Alberta, Canada. – Holarct. Ecol. 6: 3–10.

Clifford, H. F. 1972. A year's study of the drifting organisms in a brown water stream of Alberta, Canada. – Can. J. Zool. 50: 975–985.

– 1980. Numerical abundance values of mayfly nymphs from the Holarctic region. – In: Flannagan, J. F. and Marshall, K. E. (eds), Advances in Ephemeroptera biology. Plenum Press, New York, pp. 503–509.

– 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. – Quaest. Ent. 18: 15–90.

– , Hamilton, H. and Killins, B. A. 1979. Biology of the mayfly *Leptophlebia cupida* (Say) (Ephemeroptera: Leptophlebiidae). – Can. J. Zool. 57: 1026–1045.

Coleman, M. J. and Hynes, H. B. N. 1970. The life histories of some Plectoptera and Ephemeroptera in a southern Ontario stream. – Can. J. Zool. 48: 1333–1339.

Corkum, L. D. 1978. The influence of density and behavioural type on the active entry of two mayfly species (Ephemeroptera) into the water column. – Can. J. Zool. 56: 1201–1206.

Cowell, B. C. and Carrew, W. C. 1976. Seasonal and diel periodicity in the drift of aquatic insects in a subtropical Florida stream. – Freshwat. Biol. 6: 587–594.

Cummins, K. W. 1974. Structure and function of stream ecosystems. – BioScience 24: 631–641.

Dance, K. W., Hynes, H. B. N. and Kaushik, N. K. 1979. Seasonal drift of solid organic matter in two adjacent streams. – Arch. Hydrobiol. 87: 139–151.

Davies, I. J. 1984. Sampling aquatic emergence. – In: Downing, A. J. and Rigler, F. H. (eds), A manual on methods for the assessment of secondary productivity in freshwaters. IBP Handbook no. 17 (2nd ed.), Blackwell, pp. 161–227.

Delorme-Harper, F. 1967. Etude de l'émergence des Ephéméroptères d'un ruisseau de la Station de Biologie de l'Université de Montréal à Saint-Hippolyte (comté de Terrebonne, Qué.). – M. Sc. Thesis, Univ. Montréal.

Downing, J. A. 1979. Aggregation, transformation, and design of benthos sampling programs. – J. Fish. Res. Bd Can. 36: 1454–1463.

Elliott, J. M. 1965. Invertebrate drift in a mountain stream in Norway. – Norw. Ent. Tidskr. 13: 97–99.

– 1967. The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. – J. Anim. Ecol. 36: 343–362.

– 1977. Some methods for the statistical analysis of samples of benthic invertebrates. – Freshwat. Biol. Ass., Sci. Publ. 25: 1–156 (2nd ed.).

Flannagan, J. F. 1973. Sorting benthos using flotation media. – Fish. Res. Bd Can., Tech. Rep. 354: 1–14.

Flowers, R. W. and Hilsenhoff, W. L. 1978. Life cycles and habits of Wisconsin Heptageniidae (Ephemeroptera). – Hydrobiologia 60: 159–171.

Gyselman, E. C. 1980. The mechanisms that maintain population stability of selected species of Ephemeroptera in a temperate stream. – In: Flannagan, J. F. and Marshall, K. E. (eds), Advances in Ephemeroptera biology. Plenum Publishing, New York, pp. 309–320.

Hall, R. J., Waters, T. F. and Cook, E. F. 1980. The role of drift dispersal in production ecology of a stream mayfly. – Ecology 61: 37–43.

Harper, F. and Magnin, E. 1971. Emergence saisonnière de quelques Ephéméroptères d'un ruisseau des Laurentides. – Can. J. Zool. 49: 1209–1221.

Harper, P. P. 1978. Variations in the production of emerging insects from a Quebec stream. – Verh. Int. Verein. Limnol. 20: 1317–1323.

– and Harper, F. 1982. Mayfly communities in a Laurentian watershed (Insecta: Ephemeroptera). – Can. J. Zool. 60: 2828–2840.

Hayden, W. and Clifford, H. F. 1974. Seasonal movements of the mayfly *Leptophlebia cupida* (Say) in a brown-water stream of Alberta, Canada. – Am. Midl. Nat. 91: 90–102.

Hemsworth, R. J. and Brooker, M. P. 1979. The rate of downstream displacement of macroinvertebrates in the Upper Wye, Wales. – Holarct. Ecol. 2: 130–136.

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

Ide, F. P. 1940. Quantitative determination of the insect fauna of rapid water. – Univ. Toronto Stud., Biol. Ser. 47: 5–20.

Illies, J. 1974. Emergenzschwankungen – ein produktionsbiologisches Problem. – Verh. Ges. Oekol. (Saarbrücken 1973) 131–140.

– 1983. Oekosystemforschung an einem Mittelsgebirgsbach (Emergenzanalyse). – Verh. Ges. Oekol. (Mainz 1981) 10: 247–253.

Keller, V. A. 1976. The drift and its ecological significance. Experimental investigation on *Ecdyonurus venosus* (Fabr.) in a model stream. – Schweiz. Z. Hydrol. 37: 294–331.

Kondratieff, B. C. and Voshell, Jr, J. R. 1980. Life history and ecology of *Stenonema modestum* (Banks) (Ephemeroptera: Heptageniidae) in Virginia, USA. – Aquat. Insects 3: 177–189.

Kruger, C. C. and Cook, E. F. 1984. Life cycles, standing stocks, and drift of some Megaloptera, Ephemeroptera, and Diptera from streams in Minnesota, U.S.A. – Aquat. Insects 6: 101–108.

Krumbein, W. C. 1936. Application of logarithmic moments to size frequency distributions of sediments. – J. Sediment. Petrol. 6: 35–47.

Lauzon, M. and Harper, P. P. 1986. Life history and production of the stream-dwelling mayfly *Habrophlebia vibrans* Needham (Ephemeroptera; Leptophlebiidae). – Can. J. Zool. 64: 2038–2045.

LeSage, L. and Harrison, A. D. 1979. Improved traps and techniques for the study of emerging aquatic insects. – Ent. News 90: 67–78.

Madsen, B. L. 1976. Population dynamics of *Brachyptera risi* nymphs (Plecoptera). – Oikos 27: 281–287.

Müller, K. 1966. Die Tagesperiodik von Fliesswasserorganismen. – Z. Morphol. Oekol. Tiere 56: 93–142.

– 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. – Ann. Rev. Ecol. Syst. 5: 309–323.

Needham, J. G. 1908. Report of the Entomological Field Station conducted at Old Forge, N. Y., in the summer of 1905. – N. Y. State Mus. Bull. 124: 167–172.

Nie, N. H., Hull, C. H., Jenkins, J. G., Steinbrenner, K. and Bent, D. H. 1975. Statistical package for the social sciences. 2nd ed. – McGraw-Hill, New York.

O'Hop, J. and Wallace, J. B. 1983. Invertebrate drift, discharge and sediment relations in a southern Appalachian headwater stream. – Hydrobiologia 98: 71–84.

Olsson, T. I. 1983. Seasonal variation in the lateral distribution of mayfly nymphs in a boreal river. – Holarct. Ecol. 6: 333–339.

– and Söderström, O. 1978. Springtime migration and growth of *Parameletus chelifer* (Ephemeroptera) in a temporary stream in northern Sweden. – Oikos 31: 284–289.

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

– and Kramer, R. H. 1972. Drift and production of two aquatic insects in a mountain stream. – Ecol. Monogr. 24: 365–385.

Reisen, W. K. and Prins, R. 1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. – Ecology 53: 876–884.

Resh, V. H. 1977. Habitat and substrate influence on population and production dynamics of a stream caddisfly. – Freswat. Biol. 7: 261–277.

Richarson, M. Y. and Tarter, D. C. 1976. Life histories of *Stenonema vicarium* (Walker) and *S. tripunctatum* (Banks) in a West Virginia stream (Ephemeroptera: Heptageniidae). – Am. Midl. Nat. 95: 1–9.

Roy. D. 1979. Echantillonneur benthique d'eaux courantes peu profondes utilisant une pompe hydraulique à moteur. – Ann. Limnol. 14: 289–294.

Siegfried, C. A. and Knight, A. W. 1978. Aspects of the life history and growth of *Acroneuria (Calineuria) californica* in a Sierra Nevada foothill stream. – Ann. Ent. Soc. Am. 71: 149–154.

Smock, L. A. 1980. Relationship between body size and biomass in aquatic insects. – Freshwat. Biol. 10: 375–383.

Sokal, R. R. and Rolf, F. J. 1983. Biometry. – W. H. Freeman, San Francisco.

Speir, J. A. and Anderson, N. H. 1974. Use of emergence data for estimating annual production in aquatic insects. – Limnol. Oceanogr. 19: 154–156.

Stewart, K. W. and Szczytko, S. W. 1983. Drift of Ephemeroptera and Plecoptera in two Colorado rivers. – Freshwat. Invert. Biol. 2: 117–131.

Stoneburner, D. L. and Smock, L. A. 1979. Seasonal fluctuations of macroinvertebrate drift in a South Carolina Piedmont stream. – Hydrobiologia 63: 49–56.

Sweeney, B. W. and Vannote, R. L. 1981. *Ephemerella* mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. – Ecology 62: 1353–1369.

Thomas, E. 1970. Die Drift von Plecopterenlarven in Beziehung zum larvalen Wachstum und zur Schlupzeit. – Oikos, Suppl. 13: 65–69.

Walton, O. E. Jr. 1980. Active entry of benthic macroinvertebrates into the water column. – Hydrobiologia 74: 129–139.

– , Reice, S. R. and Andrews, R. W. 1977. The effects of density, sediment particle size and velocity on drift of *Acroneuria abnormis* (Plecoptera). – Oikos 28: 291–298.

Waters, T. F. 1969. Invertebrate drift-ecology and its significance to stream fishes. – In: Northcote, T. G. (ed.), Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, 1969, pp. 121–134.

– 1972. The drift of stream insects. – Ann. Rev. Ent. 17: 253–272.

Zwick, P. 1984. Stability and changes of biomass of emerging insects and their possible causes. – Verh. Int. Verein. Limnol. 22: 2037–2041.

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