

Life history and production of the stream-dwelling mayfly *Habrophlebia vibrans* Needham (Ephemeroptera; Leptophlebiidae)

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Habrophlebia vibrans in Québec has a 2-year cycle, a feature unexpected in a small mayfly and unreported in Leptophlebiidae. Emergence ($875/\text{m}^2$) occurred in June and was synchronous. Ovipositing females concentrated upstream (239 ± 94.7 eggs/female). Eggs hatched within 3 weeks. In summer, nymphs reached densities of $27\,500/\text{m}^2$ and a size of 1.65 mm. During the next 18 months, densities decreased ($4000\text{--}9500/\text{m}^2$). After a year, nymphs were 2.1 mm long and reached 3 mm at the end of their second summer. The final size (5.0 mm) was attained in the last weeks before emergence, and mean densities then were $648/\text{m}^2$. Nymphs lived on gravel where they preferred larger particles and scanty detritus. Drift occurred in small nymphs during August of their 1st year, in larger nymphs during spring runoff, and in mature nymphs at emergence. This resulted in a concentration of emergence in the lower reaches. Annual production was $710\text{--}829\text{ mg}/\text{m}^2$ and the production to biomass ratio was 2.5–3.2. About three-quarters of the production was due to the 2nd-year cohort, and one-half was accumulated during the last 2 months. No constant relation was found between production and drift and between production and emergence.

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Habrophlebia vibrans possède au Québec un cycle de 2 ans, une caractéristique inattendue chez une petite éphémère et inconnue chez les Leptophlebiidae. L'émergence ($875/\text{m}^2$) en juin est synchrone. Les femelles se rassemblent à l'amont et pondent $239 \pm 94,7$ oeufs. Les oeufs éclosent en moins de 3 semaines. Les larves atteignent des densités de $27\,500/\text{m}^2$ et en septembre elles mesurent 1,65 mm. Pendant les 18 mois suivants, les densités diminuent ($4000\text{--}9500/\text{m}^2$). Les larves de 1 an mesurent 2,1 mm et, après leur second été, elles atteignent 3,0 mm. Elles parviennent à leur taille finale de 5,0 mm juste avant l'émergence; les densités sont alors de $648/\text{m}^2$. Les larves vivent sur le gravier où elles préfèrent les particules grossières et les faibles accumulations de détrit. La dérive affecte les petites larves en août de leur premier été, les larves plus grandes durant la crue et les larves prêtes à émerger. La production est de $710\text{--}829\text{ mg}/\text{m}^2$ et le rapport production/biomasse se situe entre 2,5 et 3,2. Les trois-quarts de la production se réalisent dans la cohorte de 2^e année et la moitié durant les 2 derniers mois. Il n'existe pas de relation constante entre la production et la dérive et entre la production et l'émergence.

Introduction

Mayflies show a remarkable plasticity in their life histories, with variations quite common in voltinism, in adult size and colouration, in reproduction, and in phenology, especially in the smaller species (Clifford 1982; Brittain 1982). Many of these variations are still undescribed and there are few careful and quantitative studies of life histories, even of the common species (Butler 1984).

With these imperatives in mind, we initiated a quantitative investigation into the life history of *Habrophlebia vibrans* Needham, a small species of Leptophlebiidae that is locally abundant in streams of the lower Laurentians in Québec. The species has a highly synchronous emergence and prefers gravel substrates (Harper and Magnin 1971; Harper and Harper 1982). We also wished to examine various direct and indirect methods of estimating production and to determine how they could be affected by features of the life history (Waters 1979). This study focussed on the emergence, oviposition, nymphal growth, and production, with special reference to movements of nymphs and adults.

Study site

The study area is a second-order stream at Station de biologie de l'Université de Montréal in the Laurentians near St. Hippolyte, 75 km north of Montréal ($46^{\circ}0' \text{ N}$, $74^{\circ}0' \text{ W}$). As the stream has been described recently by Harper and Harper (1982) it will suffice to note that the 90-m section selected is immediately downstream from a beaver pond (Lake 4). The first 55 m below the beaver dam flows between boulders; current velocity varies from 0.05 to 2.5 m/s, and stream width decreases rapidly from 10 m at the dam to 3–4 m over most of the

section. The last 35 m has a gentle slope, the substrate consists mostly of gravel and detritus, and the water velocity varies from 0.05 to 1 m/s.

The summer is short (Fig. 1). In winter, icing is extensive in the upper section between the boulders where snow accumulates but practically absent from the lower gravel reach. Water level is generally stable, except for occasional spates and a heavy flood resulting from snowmelt in the spring (Fig. 3).

Methods

Adults were collected from 1978 to 1983 in six pyramidal emergence traps set on two transects of three traps at 75 and 85 m downstream from the dam in the gravel reach. The traps were those designed by Harper and Magnin (1971) for the first 2 years and the more convenient model of LeSage and Harrison (1979) for the other years; each sampled a surface area of 0.5 m^2 . In 1982, additional traps of a similar design, but covering only 0.16 m^2 , were set in midstream at 4, 8, 18, 25, and 45 m downstream from the dam. All traps were emptied three or four times weekly from May to the end of August. Oviposition was monitored three or four times a week in June and July 1982 with floating trays containing water and detergent, which retained adults touching the water surface (Williams and Hynes 1976). The surface of these was 0.16 m^2 for the traps set at 4, 8, 15, 25, 45, 55, and 85 m from the dam, and 0.5 m^2 for those at 75 and 90 m.

Eggs taken from ovipositing females were incubated in Petri dishes in a stream near the laboratory that maintained temperature conditions similar to those of the study area.

Nymphs were collected from the downstream gravel section every 2nd week from June 1981 to June 1982, except during winter when intervals were 3 to 6 weeks (a total of 19 series, Fig. 2). The upstream boulder area was impossible to sample quantitatively. We used a modified suction pump (Roy 1979). From June to December, each sample represented 81 cm^2 of stream surface; afterwards, the surface

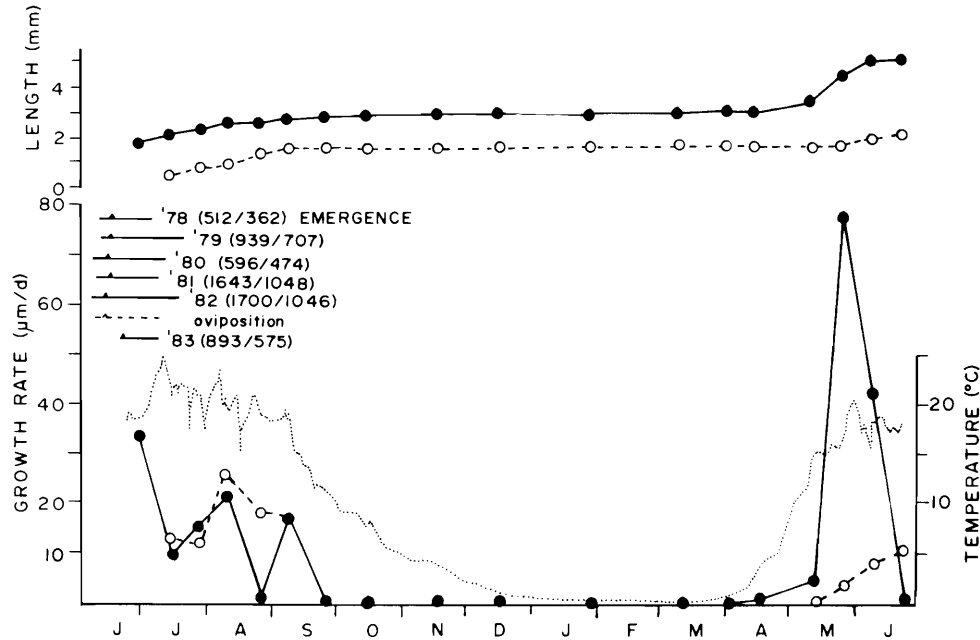


FIG. 1. Emergence, oviposition, and growth of *Habrophlebia vibrans*. Duration of the emergence (1978–1983) and oviposition periods (1982) are given in the legend; the numbers in parentheses indicate numbers of males/females and the small triangles represent 50% emergence or oviposition. Also shown are the median lengths (mm) of nymphs of cohort 1 (○---○) and cohort 2 (●—●), and growth rates of nymphs ($\mu\text{m}/\text{day}$) in cohorts 1 (○) and 2 (●) in relation to water temperature (····) from June 1981 to June 1982.

was increased to 182 cm^2 to compensate for declining populations. At each date, 4 to 7 samples were taken, except in mid-April when 15 were collected. Samples were preserved in formalin, floated in a solution of CaCl_2 , and sorted under a dissecting microscope. The total length of each nymph was measured from the margin of the clypeus to the end of the tenth abdominal segment. Lengths were grouped into 12 classes of 0.5 mm.

Multiple regressions following a logarithmic transformation of the data were used to show relations between density and substrate characteristics on 27 samples collected in midwinter. Substrate particle size was determined by weighing fractions after sieving on a mechanical shaker according to the phi scale of Krumbein (1936) (phi value = $-\log_2 X$, where X is particle size in mm.) Organic matter was removed by elutriation and separated into three fractions, SPOM (small particulate organic matter, 0.075–0.250 mm), MPOM (medium, 0.25–1.0 mm), and LPOM (large, 1–4 mm), as recommended by Cummins (1974), and weighed after oven-drying at 105°C.

Drift was sampled during 45 periods of approximately 1 week over the year with a continuous sampler as designed by Dance *et al.* (1979); sampling periods were usually less than a week in summer and longer in winter (see Fig. 3). The entrance of the net was vertical (2×100 cm, extending from the substrate to above the water surface) and led into a 2-m net (53- μm mesh). The mesh was increased to 253 μm to prevent clogging during the spring flood. Two nets were used, one upstream from the benthos sampling stations at 70 m, and a second net downstream at 90 m, both in similar conditions of substrate and discharge. The volume filtered was calculated from the water level and current velocity. The tendency to drift was calculated for each size class by using the (inverted) index of Fjellheim (1980), which is the ratio of the percent of the class in the drift to the percent in the benthos.

Production was estimated by the average cohort method, the growth increment summation method, and the instantaneous growth rate method, as described in Downing and Rigler (1984). For the first method, the suggestions and corrections of Hamilton (1969), Menzie (1980), and Benke and Wallace (1980) were followed. Biomass was calculated from a dry mass to length relationship (Fig. 5); three series of nymphs (3–100) from each size class were oven-dried at 105°C and weighed on an analytical microbalance (precision 1.0 μg), and an average mass was determined.

Results

Adults

The mean duration of the emergence period was 31 days (range, 19–42, $n = 6$ years). It extended from June 6 at the earliest to July 15 at the latest (Fig. 1). There was a slight protandry, as illustrated previously by Harper and Magnin (1971). Three to 8 days after the onset, 50% of the population had emerged. The mean annual density of the emergence was 875 adults/ m^2 (range, 437–1393). Every year, there were significantly more males than females (sex ratio, 1.26 to 1.63; mean, 1.46) in the traps ($\chi^2 = 13.9$, $p < 0.005$).

In 1982, the oviposition period was shorter than the emergence period (Fig. 1) and the cumulative 50% of ovipositing females in the traps occurred at the same time (day 3) as 50% of emerging females. A higher proportion of females was collected in the trays than in the emergence traps and the sex ratio was 1.02.

The longitudinal distribution of emergence and oviposition along the study reach are illustrated in Table 1. Maximum emergence occurred between 45 and 85 m, while oviposition was concentrated upstream (4–8 m). A mean of 851 females/ m^2 was collected from the oviposition trays, with a maximum of 6867 individuals/ m^2 at 8 m.

Each female laid a mean of 239 eggs (± 94.7 , 99% CI, $n = 12$). The eggs were oval, 197 μm (± 11.2) \times 79.3 μm (± 11.2). The first eggs hatched 17 days after being laid, and most eggs hatched within 3 weeks of oviposition. Hatching was highly synchronous.

Growth of the nymphs

The nymphs lived some 23 months. During the emergence period in June, many nymphs only 1.5 to 2.5 mm long were present; these still had much growing to do and could not emerge within the short emergence period (Fig. 2, June 29). In mid-July, the hatchlings appeared and two size classes were

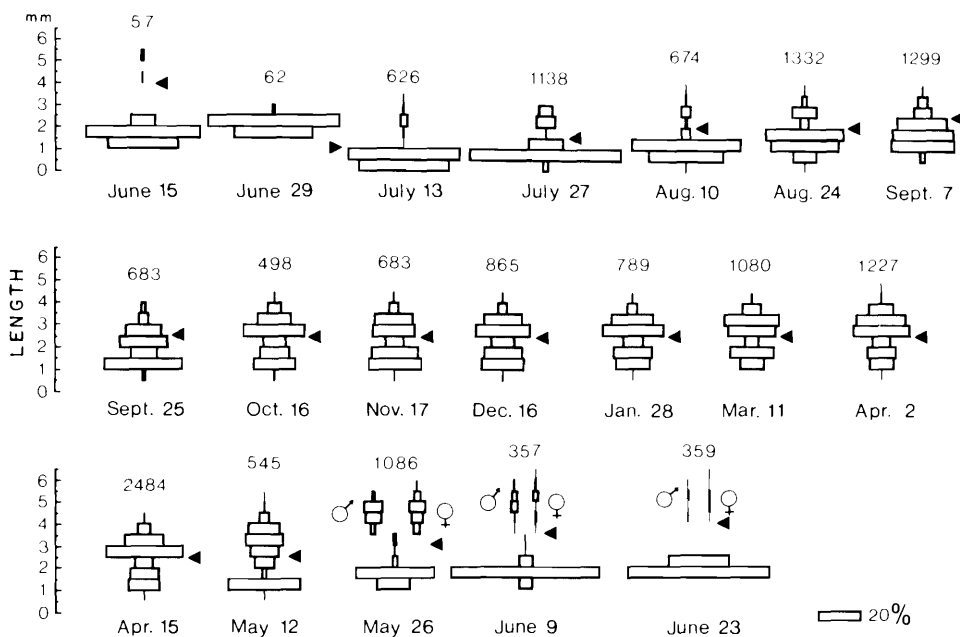


FIG. 2. Relative frequencies (%) of various size classes of nymphs in benthos samples from June 15, 1981, to June 23, 1982. The black triangles indicate limits of the two cohorts and the number of nymphs in each sample is given above each graph.

TABLE 1. Numbers of adults collected in emergence and oviposition traps at various distances downstream from the dam

Distance (m)	Emergence trap (N/m^2)		Oviposition trap (N/m^2)	
	♂	♀	♂	♀
4	80	40	778	756
8	30	30	3889	2978
15	490	460	844	1733
25	850	600	1822	2644
45	1630	870	133	44
55	—	—	22	22
75	829	520	78	33
90	123	75	33	11

clearly seen in the nymphal population. The cycle is therefore semivoltine. From September to April, the two cohorts overlapped to some extent and were not easily discriminated. By spring, however, the second cohort, composed of 22-month-old nymphs, started growing very rapidly and the two cohorts were again distinctly separated (Figs. 1 and 2).

The hatchlings measured 0.46 mm and grew rapidly during the latter part of the summer. By the end of September, the mean size of the nymphs of this cohort was 1.65 mm (Fig. 1). When water temperatures decreased to about 9–15°C, growth stopped and resumed only in mid-May when temperatures ranged between 12 and 17°C (Fig. 1). After 1 year, these nymphs had a median length of 2.1 mm. The nymphs of the second cohort grew little during their second summer; their growth was slow and irregular (Fig. 1). Growth of both cohorts 1 and 2 stopped in the fall. The median length of the nymphs at the end of their second summer was 3.0 mm (Fig. 1). At the beginning of their third summer, the nymphs resumed growth early and increased very rapidly in size, reaching their full development (median length, 5.0 mm) by early June; some of the largest females were

6.1 mm. In the last 7 weeks of their 95-week nymphal life, the nymphs doubled in length and reached maturity. At this stage, males could be distinguished from females by their larger eyes and their genital buds. The sex ratio was close to 1 (300 males, 312 females; $\chi^2 = 0.24$, $p > 0.05$). The nymphal period lasted approximately 702 days.

Drift

Most of the drift (87%) occurred during spring (Fig. 3). In summer, drift of the first cohort was very low except for a short outburst in August. Little drift was apparent in the second cohort from the end of June to early April of the following year. In April, drift densities increased rapidly and reached 218 nymphs/1000 m^3 during the 1st week of May. Densities then decreased only to rise again sharply in early June (239 nymphs/1000 m^3), and fell again. The nymphs of the first cohort experienced the May peak of drift but at a much reduced level (maximum of 25 nymphs/1000 m^3), and there was no indication of a second peak in June. Drift activity was similar in both the upstream and the downstream nets, although drift density did vary. There was no significant correlation between water level and density of drift for either cohort or in either net. More nymphs drifted in the upstream station than at the downstream site and there was a dominance of males.

Table 2 compares the distributions of nymphs in the drift and bottom samples between April 2 and June 26, the period of maximum drift. The two distributions differ significantly for both cohort 1 ($\chi^2 = 230$, $p < 0.001$) and cohort 2 ($\chi^2 = 250$, $p < 0.001$). The tendency to drift, as measured by the Fjellheim index, was greatest in the largest nymphs (class 12), followed by classes 8, 7, 6, 11, 9, 5, 10, 3, and 4. Nymphs from cohort 2 drifted more readily than those of cohort 1 (except for size class 10). For lack of sufficient material, classes 1 and 2 were not included in the analysis.

Substrate–benthos relationships

The relationships between the density of nymphs (D , in N/m^2), the median size of the mineral substrate ($md\phi$, in phi units), and the quantity of organic matter (FPOM, in g/m^2) are

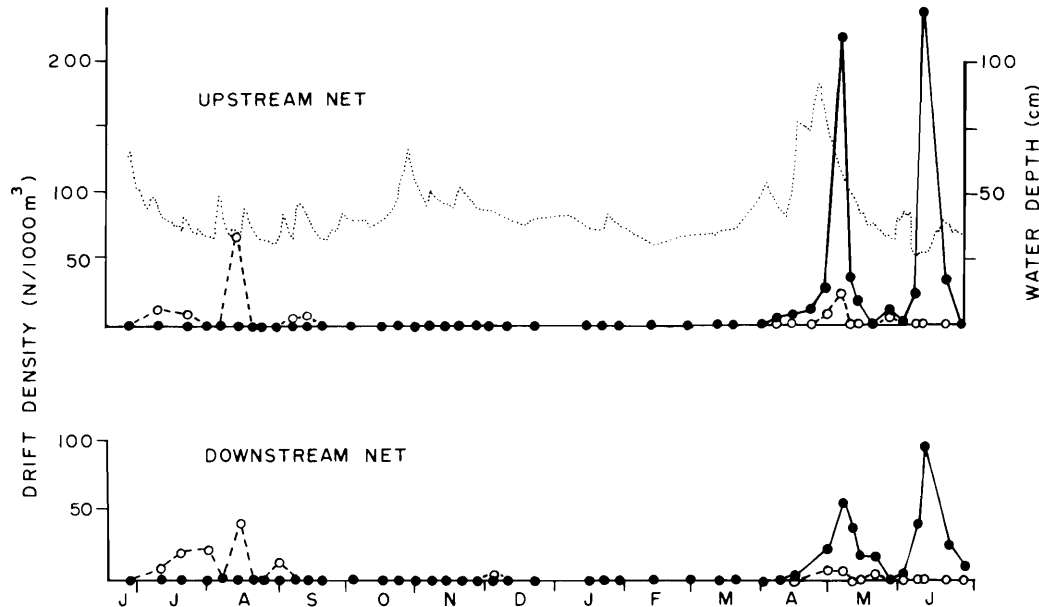


FIG. 3. Density of drifting nymphs ($N/1000 \text{ m}^3$) in cohorts 1 (○) and 2 (●) in relation to water level (....) from June 1981 to June 1982 in the upstream and the downstream nets.

TABLE 2. Tendency of nymphs of size classes 3–12 (1.5–6.0 mm) to drift

	Size class									
	3	4	5	6	7	8	9	10	11	12
N in benthos	824	1462	487	833	722	390	260	228	98	23
% in benthos	15.5	27.4	9.1	15.6	13.5	7.3	4.9	4.3	1.8	0.4
N in drift	7	5	76	240	211	157	71	22	27	98
% in drift	0.8	0.6	7.4	26.5	23.3	17.4	7.9	2.4	3.0	10.8
Fjellheim index ⁻¹	0.05	0.02	0.8	1.7	1.7	2.4	1.6	0.6	1.7	27.0

NOTE: The modified (reciprocal) Fjellheim index is the ratio of the percent nymphs of a given size class in the drift to the percent nymphs of the same class in the benthos.

shown in the following equation:

$$D = 4.93 \times 10^{-0.84 \text{ mdf}} \times 10^{-0.14 \text{ FPOM}}$$

This equation accounts for 40% of the variance ($r = 0.64$, $p = 0.02$, $n = 27$). Nymphal density tends to be greater when mdf is small, and thus when particle sizes are larger, and also when quantities of FPOM are small. No significant relationships were found with other classes of organic matter (MPOM and LPOM).

Seasonal variations in density, biomass, and production

The maximum density recorded was 27 554 nymphs/ m^2 in the first cohort in September (Fig. 4). In winter (October–April), densities of both cohorts were of the same order of magnitude, 3888 to 9531 nymphs/ m^2 . Immediately before emergence, cohort 2 was represented by some 648 nymphs/ m^2 . No details of the intersample variations in the densities are given in Fig. 4, but indications are available in Lauzon (1985) as part of a discussion of seasonal dynamics of mayfly communities in the same stream.

Biomass of cohort 2 was usually greater than that of cohort 1, particularly from October to June (Fig. 4). Variations were similar in both cohorts, except in late May and June when the biomass of cohort 2 increased rapidly to the maximum of 725

mg/ m^2 before emergence. Cohort 1 had a biomass of 13.9 mg/ m^2 in July, reached a maximum of 318 mg in September, but then decreased during the winter to between 39 and 97 mg.

Production varied with the season (Fig. 4). There was no production from September to June in cohort 1 and from November to early May in cohort 2. In May and June of their last year, the nymphs of the second cohort completed 74.9% of their annual production and, in fact, 54.2% of their total production. During summer (July to September), production of cohort 1 was higher than that of cohort 2. From June to November, production of cohort 2 was somewhat irregular. Annual production calculated by the mean cohort method with CPI (cohort production interval) correction was estimated at 812 mg/ m^2 per year; with the growth increment summation method, the estimate was 710 mg/ m^2 per year, and with the instantaneous growth method it was 817 mg/ m^2 per year (Table 3). The corresponding production to mean biomass ratios varied from 2.52 to 3.22.

The relation between drift (D , in $N/1000 \text{ m}^3$ per sampling interval) and production, as calculated by the growth increment method (P , in mg/ m^2 per sampling interval), is described for cohort 1 by the equation

$$D = 0.173P^{0.541} \quad (r^2 = 0.62, p = 0.00015, n = 18)$$

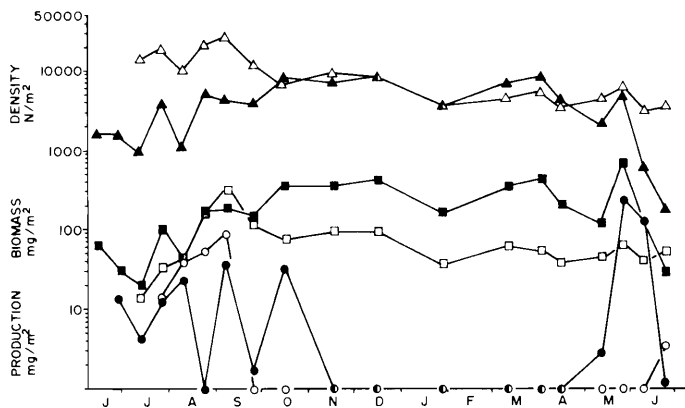


FIG. 4. Densities of nymphs (N/m^2) of cohorts 1 (Δ) and 2 (\blacktriangle), biomass (mg dry weight/ m^2) of cohorts 1 (\square) and 2 (\blacksquare), and production (increment summation method) of cohorts 1 (\circ) and 2 (\bullet) between June 1981 and July 1982.

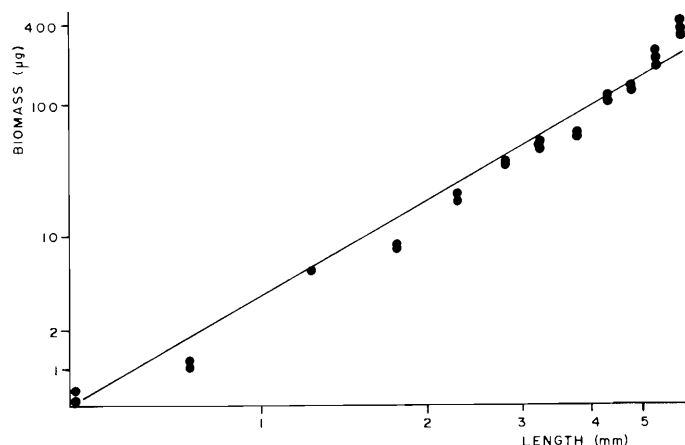


FIG. 5. Relationship between the length of nymphs (mm) and their dry weight (μg).

TABLE 3. Comparison of production estimates and production to biomass ratios (P/B) calculated by three methods

	Production (mg/m^2)			P/B
	Cohort 1	Cohort 2	Total	
Increment summation	196	514	710	2.5
Instantaneous growth rate	215	602	817	2.9
Average cohort	—	—	812	3.2

and for cohort 2:

$$D = 0.148P^{0.385} \quad (r^2 = 0.23, p = 0.2, n = 18)$$

The ratio between mean production ($514 \text{ mg}/m^2$ per year for cohort 2; 710 mg for both cohorts) and mean emergence ($404 \text{ mg}/m^2$ per year) is 1.3 or 1.8, depending on whether only the second or both cohorts are considered.

Discussion

Life cycles

Among the 29 species of Leptophlebiidae with known life cycles (Clifford 1982), *H. vibrans* is the first species reported to be semivoltine. This is particularly unexpected since *H. vibrans* is one of the smallest species in the family, and because semi-

voltinism is usually associated with large insects. Other similar species, such as European *H. lauta* Eaton, have repeatedly been shown to be univoltine (Pleskot 1953; Landa 1968; Thibault 1971; Sowa 1975); *H. fusca* (Curtis) is also said to be univoltine, perhaps with a long egg diapause (Jop 1981).

The duration of the emergence is unusually short and our results contrast markedly with the observations of Carlson (1973) on the same species in Wildcat Creek, North Carolina; he indicates a 13- to 17-week emergence period with a midpoint at 1–3 weeks, whereas we noted a 3- to 7-week emergence with a peak between the 3rd and 8th day. In Harper and Magnin's (1971) classification, the emergence is highly synchronous. Mackey (1978) and Edmunds and Edmunds (1979) suggest that such synchrony may be an adaptive strategy to minimize predation by saturating predators. This is perhaps significant since emergence is diurnal; 97% of individuals emerge, mate, and oviposit during daylight hours, particularly between 1000 and 1600 (Harper *et al.* 1983). Potential exposure to insect and bird predators is particularly high in midday.

The number of eggs produced by the female is lower than that listed for any species in Clifford and Boerger's (1974) survey of 65 species. On the basis of the fecundity versus size relationship provided by these authors, at least twice as many eggs would have been expected. In the European *H. lauta*, the number of eggs is between 450 and 790, and in the related *Habroleptoides* spp., the numbers vary from 932 to 2324. However, egg size is comparable to that of *H. fusca* and *H. lauta* ($185 \times 75 \mu m$ and $190 \times 72 \mu m$), but smaller than that of *H. consiglioi* Biancheri ($230 \times 97 \mu m$) (Gaino and Mazzini 1984). The reproductive period is very short, which is common in semivoltine species (Clifford 1982).

Synchrony and nymphal development

The highly synchronized emergence is unexpected, given the rather asynchronous growth pattern of the nymphs. Oviposition and egg hatching are limited to a very short period. During nymphal growth, much of this synchrony is lost and nymphs of many sizes are present throughout the year. By the end of their second year, the nymphs, still half grown, experience a period of very rapid growth just before emergence and then regain much of their uniformity in size, thus leading to the highly synchronized emergence.

In most species possessing a very synchronous emergence, emergence occurs in the spring, the period during which the water warms up (Corbet 1964). How synchronization is achieved so late in the summer in *H. vibrans* is not clear. Photoperiod is probably not involved as it varies relatively little during this time of year; the same applies to temperature, which has reached its summer maximum. Only experimental work can solve this riddle. In more southerly latitudes, *H. vibrans* does not appear to have a synchronous emergence (Carlson 1973; Berner 1977). We speculate that the differences in emergence patterns reflect differences in the life cycle. In North Carolina the species is probably univoltine (or with multiple univoltine cohorts), since the climate is less seasonal and the periods favourable for growth are longer. There are no synchronization mechanisms, and oviposition spread over the summer contributes to maintain the asynchrony.

Drift

Drifting behaviour differs considerably in the two cohorts. That of cohort 1 nymphs can be grossly correlated with their growth rate and the water temperature (Figs. 1 and 3), while

drifting behaviour of cohort 2 is correlated with the size of the nymphs (Figs. 1 and 3).

The modified Fjellheim (1980) index illustrates differences in the tendency to drift. The mature nymphs (size class 12) drift more readily than others (27 times more, Table 2). Such behaviour at the end of nymphal growth has been observed in Baetidae (Müller 1966), and it has generally been suggested that larger nymphs have a greater tendency to drift, particularly during periods of high growth (Elliott 1967; Hall *et al.* 1980; Stewart and Szczytko 1983). This probably also explains at least in part the high drift rates of the nymphs of cohort 2 in early spring (April to mid-May). On the other hand, Bishop and Hynes (1969) noticed that larger nymphs often were less abundant than smaller (<5 mm) ones in the drift, a phenomenon they suggest is due to selective fish predation on the larger insects. In our stream the decrease in drift observed in the second half of May and the low tendency of the nymphs present at that time to drift (class 10, 4.5–5 mm; Table 2) could be related to the presence of a large number of minnows (*Notropis cornutus*, *Semotilus atromaculatus*) spawning in the stream. However, examination of stomach contents of some of the fish showed no remains of *Habrophlebia*. This does not necessarily mean that they are not preyed upon, because their small size and poor sclerotization could explain their rapid disappearance from the gut.

Pre-emergence drift into the downstream area probably explains why the number of emerging adults (875/m²) is greater than the mean density of nymphs just before the emergence period (648/m²). Similarly, the greater density in the upstream net as compared with the downstream net and the changes in the sex ratios (a dominance of males in the drift and during emergence, and equal proportions of males and females in the benthos) suggest the importance of an overall downstream movement of nymphs. No upstream return movement, as suggested in the colonization cycle theory (Müller 1982), was directly observed, but the concentration of oviposition in the upper reaches near the dam is indicative of such an upstream compensation flight.

Substrate–nymph relationships

An increase in density of nymphs with an increase in mean diameter of substrate particles has been observed in other lotic Ephemeroptera, but the particle range was much greater (Pennak and Van Gerpen 1947; Allan 1975; Shelly 1979; Reice 1980). Indeed, Rabeni and Minshall (1977) found the maximum number of organisms on substrates with 1- to 3.5-cm particles, the same size range as in our study. It would seem that *H. vibrans* is negatively affected by the accumulation of fine particles; a similar situation is described by Cummins and Lauff (1969) for *Ephemera simulans*.

Our observed decrease in density of *H. vibrans* with an increase in the quantity of substrate organic matter does not correspond to findings in earlier studies (Egglisshaw 1964, 1969; Rabeni and Minshall 1977; Williams and Mundie 1978). This could be due to the great abundance of detritus in some sections of our stream. On the other hand, correlations between invertebrate abundance and organic matter are often either weak or nonexistent (Winterbourn 1978; Reice 1980; Ciborowski and Clifford 1983). Minshall and Minshall (1977) found no relation between the density of invertebrates and various levels of detritus (121, 484, and 847 g/m²) and Barber and Kevern (1973) showed that on fine sediments (as in our stream), artificial substrates containing high levels of organic matter

(847 g/m²) supported smaller populations of mayflies than those containing less organic matter (484 and 121 g/m²); they explain their results by speculating that at high detritus levels aggregates of detritus are formed and the interior of these is not available for colonization. Recently, Culp *et al.* (1983) have shown that in 16 of the 19 invertebrates they studied, there was no significant difference in the distribution of densities or biomass over a wide range of substrate types that differed in water velocity, contact surface, and interstitial space but that all had a standardized amount of detritus. They conclude that while sedimentation is a major factor in explaining invertebrate microdistributions, detritus is probably a more important factor than mineral particle size distribution. Our results also agree with those of Malmqvist *et al.* (1978) who showed that when the fine fraction of detritus (SPOM) was taken into account, their results did not agree with those of Egglisshaw (1964, 1969).

In our results, as in Rabeni and Minshall's (1977), there is a correlation between the median size of mineral particles (md ϕ , in ϕ units) and the quantity of particulate organic matter (POM, 0.125–4.0 mm, in g/m²) according to the equation

$$\text{POM} = 44.24 + 9.90 \text{ md}\phi \quad (r = 0.39, p = 0.018, n = 27)$$

It is therefore not possible to discriminate between the effects of particle size and those of the quantity of detritus, since the smaller the mean particle size, the greater the abundance of detritus. Nonetheless, the high densities of *H. vibrans* are associated with gravel substrates that have lower quantities of detritus; the sand substrates with very high concentrations of detritus support only small populations. These observations are perhaps best explained by an intolerance of nymphs to silting.

Production

The biomass and production estimates were calculated from preserved material; had they been from fresh material, the estimates would have no doubt been 15 to 25% higher (Hall *et al.* 1980).

Our estimates of annual production vary from 710 to 829 mg/m², depending on the method used. Such values are at the lower end of the scale of reported values in mayflies (120–4450 mg/m², Waters 1977; and 8560 mg/m², Hall *et al.* 1980). Production is restricted to the warm season and is concentrated in the last weeks of the life cycle.

The increase in mean individual biomass through time follows a sigmoid curve. This causes a bias in the use of the instantaneous growth method, which assumes exponential growth (Cushman *et al.* 1977). This method gave an estimate 13.5% higher than the increment summation method, and the differences are highest during the period of maximum growth of the second cohort (333.6 mg/m² from May 12 to 26 vs. 253.0 mg/m²). Ideally, both methods should provide similar estimates (Gillespie and Benke 1979). The average cohort method often overestimates production by a factor of 15–23% (Cushman *et al.* 1977) and its use is best reserved for multispecies populations and communities where specific life-cycle patterns cannot be discriminated. As Waters (1981) suggested, the few (three) very large specimens were included in the penultimate class, but the sexes were not determined given the minimal dimorphism in size in this species.

The annual *P/B* ratios (2.5–3.2) are in the range expected for a semivoltine species (Waters 1977) and are similar to those recorded for the semivoltine mayfly *Hexagenia limbata* (Serville) by Riklik and Momot (1982; *P/B* = 2.1–2.6). The variations in the *P/B* ratio are essentially due to differences in

production and (or) mean biomass estimates from one method to the other.

Waters (1961) suggests that drift might be a useful parameter from which to estimate production, since there appears to be a relationship between drift and production and because drift is much less tedious to measure. Recently, Waters (1981) observed such a relation in an amphipod. In *H. vibrans*, such a relation was found for the first cohort, though not for the second. Behavioural patterns seem to be much more important, and drift cannot in this instance serve as an indirect measure of production.

Speir and Anderson (1974) suggest using emergence data as an estimator of production, since they observed a relatively constant value of 4–5 in the ratio of the production of larvae to emergence of adults in black fly populations. In our species, such a ratio has a value of 1.3–1.8, which is due to the increased emergence following the downstream drift of mature nymphs. If the ratio is calculated from the number of mature nymphs (before the drift and with an arbitrary 10% mortality at emergence), it has a value of 3.0, still below the values obtained by Speir and Anderson. This ratio can only be used in species that are relatively sedentary and is obviously biased by migrations prior to emergence.

Life history features, such as the movements of animals during their cycle, are therefore of prime importance and cannot be ignored in assessing such parameters as production. Indirect measurements in particular should be used only with great caution.

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