Life history and distribution of mayflies (Ephemeroptera) in some acid streams in south central Ontario, Canada

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Life histories and distribution of mayflies (Insecta: Ephemeroptera) were investigated in 11 streams in south central Ontario that ranged from highly acidic to circumneutral. At least 29 mayfly species were recorded from the streams, with 16 common enough for life history analysis. Mayfly distribution and diversity were correlated with pH regime and stream size. No mayflies were found in the smallest, most acid stream, and numbers of mayfly species and their relative abundances generally increased with both increasing stream size and stream pH. Incorporation of life cycle information with distributional data enabled us to determine the precise stream-water pH range encountered by different mayfly life stages in the study streams. Generally, during the period of greatest acid stress in the streams (pH depressions associated with spring snowmelt) the mayflies were present in large or dormant stages, which are believed to be more tolerant of lowered pH.

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Le cycle biologique et la répartition des éphémères (Insecta : Ephemeroptera ont fait l'objet d'une étude dans 11 ruisseaux d'acidités diverses, allant de très acides à presque neutres, du centre-sud de l'Ontario. Au moins 29 espèces ont été inventoriées dans les ruisseaux et 16 d'entre elles étaient assez abondantes pour permettre l'étude de leur cycle biologique. La répartition des éphémères et leur diversité étaient en corrélation avec le pH et l'importance du ruisseau. Il n'y avait pas d'éphémères dans les ruisseaux les plus petits et les plus acides et le nombre d'espèces et leur abondance relative avaient généralement tendance à augmenter en même temps que l'importance du ruisseau et le pH. La combinaison des informations sur le cycle et des données sur la répartition nous ont permis de déterminer précisément l'échelle des pH auxquels sont soumis les divers stades larvaires dans les ruisseaux étudiés. Généralement, durant la période de stress acide maximal dans les ruisseaux (baisses de pH associées à la fonte des neiges au printemps) les éphémères sont à un stade larvaire avancé ou en stade de dormance, stades qui semblent plus tolérants aux pH faibles.

[Traduit par la rédaction]

Introduction

South central Ontario is located in a region of northeastern North America that receives significant inputs of acid precipitation (pH of rainfall ~4.2; Dilon et al. 1978). As a result, short-term pH depressions of as much as two units occur regularly in the poorly buffered Precambrian Shield streams of the region (Jeffries et al. 1979). These depressions have major effects on biota (Hall et al. 1988). Mayflies are among the most sensitive of aquatic insects to the effects of acid precipitation (Sutcliffe and Carrick 1973; Hall et al. 1980; Harriman and Morrison 1982; Mackay and Kersey 1985; Peterson et al. 1986), particularly in certain life history stages (Bell 1971; Fiance 1978; Allard and Moreau 1987; Rowe et al. 1988*a*). However, although life history information is considered to be important in interpreting toxicological responses (Buikema and Benfield 1979; Lehmkuhl 1979), few studies on the distribution of aquatic insects over chemical gradients have included information on life cycles or even the life stages present at the time of sampling.

In this study, we examined mayfly populations in 11 streams chosen to provide a gradient of mean annual pH values from 4.0 to 7.5. Our objectives were to describe mayfly life cycles and distribution in streams of varying pH, and to determine the actual stream-water pH ranges to which each species and each life stage was exposed.

Study site

The 11 study streams were located in the Muskoka–Haliburton region of south central Ontario (Fig. 1; for detailed maps of each catchment see Scheider et al. 1983). The streams were chosen on the basis of preliminary information on mayfly distribution (Mackay and Kersey 1985) and from examination of chemical data from the Ontario Ministry of the Environment, and were first- to third-order streams flowing into or out of Harp, Plastic, Dickie, Chubb, and Beech lakes. The streams are generally unnamed but have been identified by the Ontario Ministry of the Environment, so inflow streams are numbered consecutively around each lake (e.g., Harp Lake 4 and Harp Lake 5 are adjacent to each other; Scheider et al. 1983). Riparian vegetation in the area was primarily beech–maple forest (Seip et al. 1985), and the study streams generally possessed shallow, poorly developed substrates overlying granitic bedrock (details of catchment geology and soil geochemistry are provided in Jeffries and Snyder 1983). Physical characteristics of the study streams (discharge, pH, and temperature) are shown in Fig. 2, with mean values summarized in Table 1. The pH regimes varied both among streams and seasonally in all streams (Fig. 2*a*). Generally, streams were more acidic during the winter, with lowest pH readings recorded during the spring snowmelt period (Figs. 2*a* and 2*c*). In the the summer, smaller streams were generally cool (12–16°C) and larger steams were warm (22°C) (Fig. 2*b*).

Inflow streams

Harp Lake inflow 3*a* and Plastic Lake inflow 1 are usually intermittent first-order streams. Both are normally dry in summer, but flowed during the entire study period owing to an unusually wet season in 1985. Plastic Lake inflow 1 was extremely acidic (mean pH 4.4; Table 1), whereas Harp Lake inflow 3*a* was only moderately acidic (mean pH 6.0; Table 1). Both streams had a cobble–gravel–

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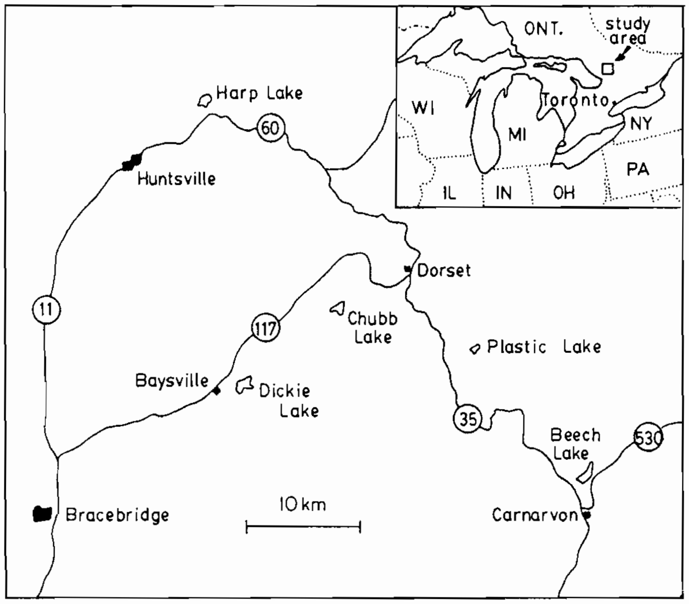

FIG. 1. Map of the study area, showing location of lakes associated with study streams. Detailed maps of each watershed can be found in Scheider et al. 1983.

sand substrate with leaf and debris packs accumulating in slower sections. Dickie Lake inflows 8 and 11 were both acidic (pH 5.0 and 4.1; Table 1), highly coloured, second-order streams which drained boggy areas. Their substrates consisted of sand, gravel, and cobble in the faster sections, and sand and silt and debris packs in slow sections.

Three sampling sites were located on Harp Lake inflow 4: station H4-1 was on a second-order branch of the stream about 300 m below a beaver pond with a mean pH of ~5.8, station H4-2 was on an adjacent first-order branch with a mean pH of 6.3, and station H4-3 was just below the confluence of the two branches, with a mean pH of 6.3 (Table 1). Harp Lake inflow 5 was a third-order stream at the sample site and had a mean pH of 5.3 (Table 1). Harp Lake inflows 4 and 5 were both clear woodland streams, with a moderate gradiant and a sand–gravel–cobble substrate. Beech Lake inflow 1 was the largest of the inflow streams studied, and had a mean pH somewhat higher than expected for the region (pH 7.4; Table 1) because of a large area of limestone bedrock in the catchment (Jeffries and Snyder 1983). The substrate in Beech Lake 1 consisted of large angular pieces of rock with some smaller cobble, gravel, and sand.

Outflow streams

The outflow streams generally drained larger areas and had higher mean discharges than the inflow streams (Table 1). The outflows were also characterized by much coarser substrates, which consisted of large, angular pieces of granitic rock (>1 m diameter) with interstices filled with sand, gravel, and cobble. Plastic, Chubb, and Dickie lake outflows had mean annual discharges (1984–1985) that ranged from 25 to 100 L · s^{-1} and drainage areas that ranged from ~100 to 300 ha, but had similar pH regimes (Table 1). Harp Lake outflow larger and possessed a pH regime considered "typical" of the pre-acidification condition (mean pH 6.5, Table 1; see Giberson and Hall 1988).

Materials and methods

Samples were collected by kicking substrate materials immediately upstream of a D-frame collecting net (net mesh 200 μm, net length 50 cm), so that 30 s were spent in each of three habitat zones (fast water, moderate current, slow or no current). Collections were made approximately every 2 months through the winter and every 2 weeks during the summer, but because new locations were added later in the study, the length of the study periods varied from location to location. Sampling was conducted as follows: Harp Lake inflows 3*a* and 4, Dickie Lake inflows 8 and 11, and Plastic Lake inflow 1 and outflow from October 1984 to November 1985; Harp Lake outflow from October 1984 to June 1986; Chubb and Dickie lake outflows from July 1985 to November 1985; and Beech Lake inflow 1 from July 1985 to May 1986. Samples were preserved in Kahles' solution in the field and returned to the laboratory for sorting and identification of mayfly species. Specimens were later measured using an ocular micrometer in a dissecting microscope, and the life cycles of the more abundant taxa were analyzed by constructing length–frequency histograms. The pH was determined by a combination glass electrode standardized against appropriate buffers from surface water samples collected at least weekly by the Ontario Ministry of the Environment. Water temperature was determined from maximum–minimum thermometers located near each study site, and discharge was recorded continuously at Ontario Ministry of the Environment weirs and determined from previously determined stage–discharge relationships for each stream.

Results and discussion

Diversity and distribution

Mayfly diversity has been linked to stream-water pH, with lowest diversity expected in streams with lowest pH (Sutcliffe and Carrick 1973; Hall et al. 1980; Mackay and Kersey 1985; Peterson et al. 1986). At least 29 mayfly species were found in the 11 streams in our study, and although their diversity and distribution were correlated with pH, stream size was also important (characterized here by mean annual discharge; Fig. 3). In the two first-order streams investigated, no mayflies were found in the highly acidic Plastic Lake inflow 1, but four species were recorded in the more moderately acidic Harp Lake inflow 3*a*. Mayflies were recorded from all second-order stream sites (Harp Lake inflows 4-1 and 4-2; Dickie Lake inflows 8 and 11), and diversity and abundances were lowest in the highly coloured, lower-pH Dickie Lake streams. Harp Lake inflows 4-3 and 5 were both third-order streams, but the catchment area and mean discharge for Harp Lake 5 were nearly twice those of Harp Lake 4 (Table 1), and Harp Lake 5 showed greater mayfly diversity than Harp Lake 4, despite a lower pH regime. Beech Lake inflow was the largest and least acidic of the inflow streams studied, and also had the highest mayfly diversity.

Diversity in the outflow streams appeared to be more strongly related to pH than to size of stream, all moderately acidic (pH ~5.4) outflows showing similar diversity (five or six species, Table 2) despite a 3-fold difference in size (Table 1). Harp Lake outflow had the highest diversity, 17 species, and it was the largest and least acidic of the outflow streams.

Most of the mayfly species collected from the 11 study streams were restricted in their distribution to one or two of the streams (Table 2). However, four species were widespread. *Eurylophella funeralis* McD. was most abundant in moderate-sized and heavily wooded inflow streams, though it was present in most streams with mean pH ~~≤~~≥5.3. This distribution is similar to that reported by Fiance (1978) in the Hubbard

FIG. 2. Seasonal pH (*a*), discharge (*b*), and temperature (*c*) regimes for the 11 study streams, July 1984 – November 1985 (Ontario Ministry of the Environment, unpublished data). H3*a*, Harp inflow 3*a*; P1, Plastic inflow 1; D8, Dickie inflow 8; D11, Dickie inflow 11; H4-3, Harp inflow 4, stn. 3; H5, Harp inflow 5; B1, Beech inflow 1; PO, Plastic Lake outflow; ChO, Chubb Lake outflow; DO, Dickie Lake outflow; HO, Harp Lake outflow.

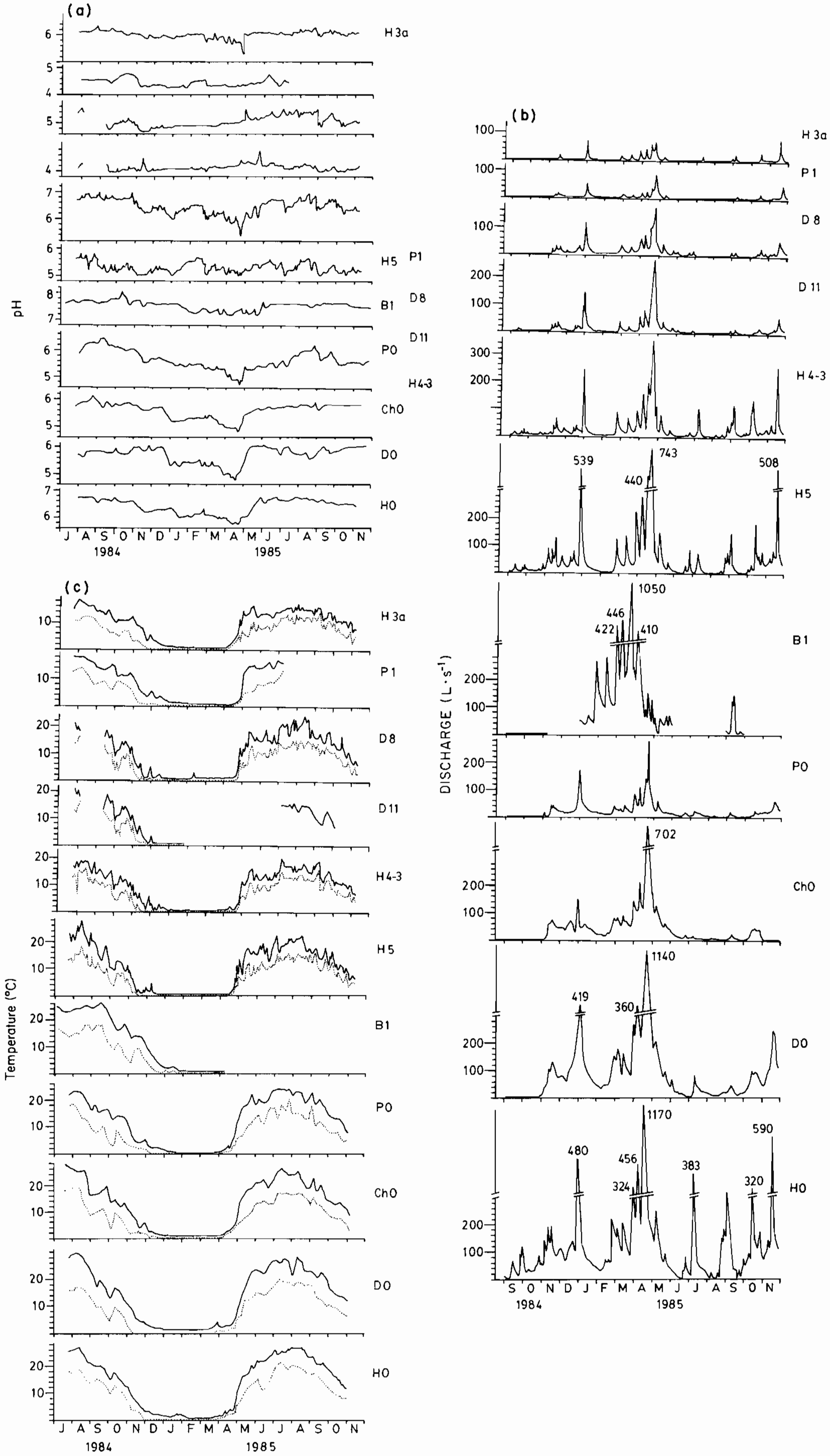
(a)
pH
H 3a
H5
P1
B1
D8
P0
D11
H4-3
ChO
DO
HO
J A S O N D J F M A M J J A S O N
1984
1985
(b)
DISCHARGE (L·s⁻¹)
H 3a
P 1
D 8
D 11
H 4-3
H5
539
743
440
508
B1
1050
446
422
410
PO
ChO
702
DO
1140
419
360
HO
1170
480
456
324
383
590
320
S O N D J F M A M J J A S O N
1984
1985
(c)
Temperature (°C)
H 3a
P 1
D8
D11
H4-3
H5
B1
PO
ChO
DO
HO
J A S O N D J F M A M J J A S O N
1984
1985

TABLE 1. Physical characteristics of 11 study streams (Ontario Ministry of the Environment, unpublished data)

	Drainage area (ha)	Mean pH, 1984–1985	Mean summer temp., 1985 (°C)	Mean discharge, 1984–1985 ($L \cdot s^{-1}$)
Harp Lake inflow 3*a*	22.4	6.0	13	4.4
Plastic Lake inflow 1	23.3	4.4	12	5.1
Dickie Lake inflow 8	71.4	5.0	15	13.9
Dickie Lake inflow 11	109.1	4.1	13	13.9
Plastic Lake outflow	124.6	5.5	20	24.3
Harp Lake inflow 4	139.1	5.8–6.3	16	25.6
Chubb Lake outflow	200.9	5.4	22	53.0
Harp Lake inflow 5	204.1	5.3	22	48.1
Dickie Lake outflow	311.9	5.4	22	101.7
Harp Lake outflow	429.1	6.3	22	121.6
Beech Lake inflow 1	571.6	7.4	22	81.8

Brook Experimental Forest in New Hampshire; there the highest populations were found at the higher-pH sites with the most organic cover, and the species was absent in two permanent streams with pH ≤5.5. One of the *Baetis* species (*Baetis* near *brunneicolor* McD.) showed a similar distribution pattern, though *Baetis* spp. are generally considered to be the most susceptible to the effects of lowered pH (Sutcliffe and Carrick 1973; Simpson et al. 1985; Peterson et al. 1986; Allard and Moreau 1987). *Habrophlebia vibrans* Needham was recorded from every outflow stream except Dickie Lake and from the largest inflow streams (Harp Lake 5 and Beech Lake 1). Lauzon and Harper (1988) reported this species to be very abundant in a moderately large Canadian Shield stream in Quebec. Stream size may be more important than pH in determining the distribution of *H. vibrans* in the study area, at least above pH 5.4. *Leptophlebia cupida* (Say) was generally the most abundant and widespread mayfly in the study area and was recorded from small, highly acidic streams as well as from the larger outflow streams with more moderate pH regimes. However, it was present in the small acidic streams only for a brief period in the spring, at a time when nymphs were apparently migrating upstream into warmer marshy areas where they are reported to emerge (Neave 1930; Clifford 1969; Clifford et al. 1979). *Leptophlebia cupida* is distributed across northern North America from north central Alberta (Clifford 1969) to Ontario and Quebec (Coleman and Hynes 1970; Harper and Harper 1982), where it is found at pH values ranging from 4.1 (this study) to >8.0 (Clifford 1969).

The distribution of other mayfly species was more restricted. *Paraleptophlebia* occurred in six of the sites with pH >5.3, but in most cases a single, different species was present in each stream (Table 2). Five heptageniid species were recorded, including three *Stenonema* species from smaller streams with pH as low as 5.4, and *Arthroplea bipunctata* (McD.) at pH 4.2. The greatest abundance amongst the heptageniids was noted for *S. modestum* (Banks) nymphs in Harp Lake outflow (Table 2; see also Fig. 7). Baetids were most diverse and abundant in streams with higher pH, though *Baetis pygmaeus* (Hagen) was fairly common in Harp Lake inflow 5, with a mean pH of only 5.3 (Table 2). Ephemerellids were not common in even moderately acidic streams, with the exception of *Eurylophella funeralis*, mentioned above, and an unidentified *Eurylophella* species from Dickie Lake outflow (specimens were too small to identify but were not *E. funeralis*), though at least five species were found in the higher-pH streams (Table 2). Finally, the two siphlonurid species that were common, *Siphlonurus* probably *typicus* Eaton (nymphs keyed to *S. quebecensis* in Burks 1953, but adults captured in the area were identified as *S. typicus*) and *Ameletus ludens* Needham, were found only in small headwater streams with higher pH.

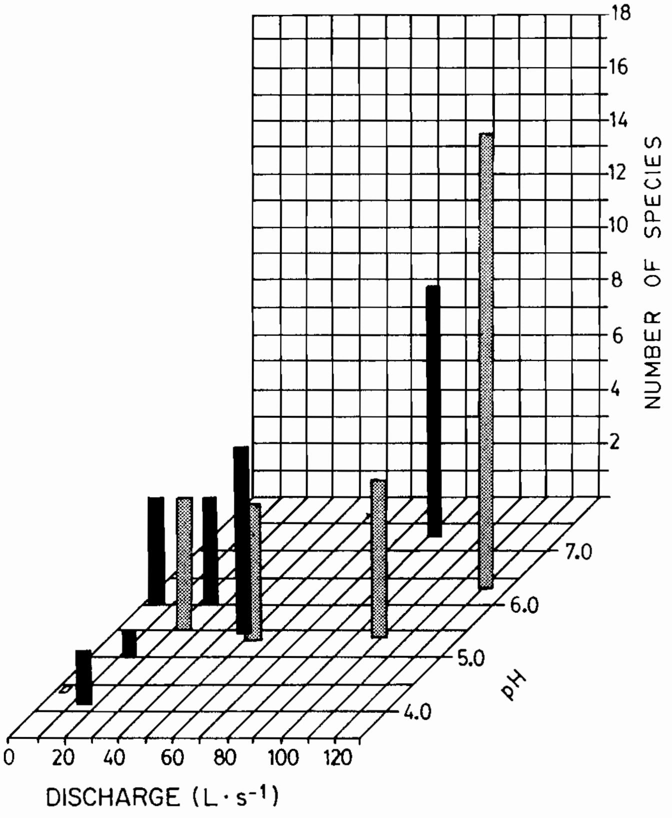

FIG. 3. Mayfly species diversity as a function of mean annual pH and stream size (expressed as mean discharge) for the 11 study streams, 1984–1985. Solid bars represent inflow streams and stippled bars outflows; open square represents site where no mayflies were found.

So far, the distributional data have been correlated with pH

TABLE 2. Life cycle types and relative abundances of mayflies in 11 streams in south central Ontario, and the pH ranges of the stream(s) during the period when species were present in the nymphal stage

		Location													
	Life cycle[a]	D11 (4.1)	P1 (4.4)	D8 (5.0)	H5 (5.3)	ChO (5.4)	DO (5.4)	P0 (5.5)	H4-1 (5.8)	H3*a* (6.0)	H4-2 (6.3)	H4-3 (6.3)	HO (6.3)	B1 (7.4)	pH range[b]
Siphlonurus probably *typicus* Eaton	U_w	—	—	—	—	—	—	—	—	A	—	—	—	—	5.7–6.4
Ameletus ludens Needham	U_w	—	—	—	—	—	—	—	—	—	M	—	—	—	5.4–7.1
Baetis near *brunneicolor* McD.	U_s	—	—	—	R	—	—	R	M	M	—	A	M	—	5.4–7.1
Baetis flavistriga McD.	?	—	—	—	—	—	—	—	—	—	—	—	R	—	6.5–6.8
Baetis pygmaeus (Hagen)	MB_{ws} or MP	—	—	—	M	—	—	—	—	—	—	—	A	R	5.0–6.0
Baetis spp.	?	—	—	—	—	—	—	—	—	—	—	—	—	M	7.2–7.8
Cloeon sp.	?	—	—	—	—	—	—	—	—	—	—	—	R	—	6.5–6.8
Centoptilum sp.	?	—	—	—	—	—	—	—	—	—	—	—	R	—	6.5–6.8
Isonychia bicolor (Walker)	?	—	—	—	—	—	—	—	—	—	—	—	R	—	5.7–6.8
Stenonema femoratum (Say)	U_w	—	—	—	—	—	M	—	—	—	—	—	R	—	5.5–6.8
Stenonema modestum (Banks)	U_w	—	—	—	—	R	R	—	—	—	—	—	M	R	5.6–6.8
Stenonema vicarium (Walker)	?U_w	—	—	—	—	—	R	—	—	—	—	—	R	R	5.4–7.8
Stenacron interpunctatum (Say)	U_w	—	—	—	—	—	—	—	M	R	M	R	—	—	5.4–7.0
Arthroplea bipunctata (McD.)	?U_s	R	—	—	—	—	—	—	—	—	—	—	—	—	4.2
Habrophlebia vibrans Needham	?2 yr	—	—	—	R	R	—	M	—	—	—	—	M	M	4.8–6.8
Leptophlebia cupida (Say)	U_w	S	—	R–S	M	M	M	M	—	—	—	R	A	—	4.2–6.8
Paraleptophlebia adoptiva (McD.)	U_w	—	—	—	—	—	—	—	—	—	—	—	A	—	5.7–6.8
Paraleptophlebia debilis (Walker)	U_s	—	—	—	R	—	—	—	A	—	—	R	—	—	5.0–6.8
Paraleptophlebia mollis Eaton	U_w	—	—	—	—	—	—	—	—	—	—	—	—	A	7.2–7.8
Paraleptophlebia moerens McD.	U_w	—	—	—	—	—	—	A	—	—	—	—	—	—	4.7–6.4
Paraleptophlebia sp.	?	—	—	—	—	—	—	—	—	—	—	—	—	M	7.2–7.8
Eurylophella funeralis McD.	2 yr	—	—	—	A	R	—	M	A	R	R	M	M	—	4.7–7.1
Eurylophella temporalis McD.	?	—	—	—	—	—	—	—	—	—	—	—	R	—	5.7–6.8
Eurylophella verisimilis McD.	U_w	—	—	—	R	R	—	—	—	—	—	—	A	—	5.7–6.8
Eurylophella spp.	?	—	—	—	—	—	R	—	—	—	—	—	R	R	5.5–6.8
Ephemerella spp.	?	—	—	—	—	—	—	—	—	—	—	—	R	M	5.7–7.8
Caenis sp.	?	—	—	—	—	—	R	—	—	—	—	—	—	—	5.5–6.0
Total no. of species		2	0	1	7	5	6	5	4	4	3	5	17	9	

NOTE: Locations are as follows: D11, Dickie Lake inflow 11; P1, Plastic Lake inflow 1; D8, Dickie Lake inflow 8; H5, Harp Lake inflow 5; ChO, Chubb Lake outflow; DO, Dickie Lake outflow; H4-1, Harp Lake inflow 4 (stn. 1); H3*a*, Harp Lake inflow 3*a*; H4-2, Harp Lake inflow 4 (stn. 2); H4-3, Harp Lake inflow 4 (stn. 3); HO, Harp Lake outflow; B1, Beech Lake inflow 1. Numbers in parentheses show mean pH at that location. Abundances are classified as follows: A, abundant; M, moderately abundant; R, rare; S, absent, except briefly in spring; R–S, rare, except briefly abundant in spring.

[a] U_w, univoltine winter; U_s, univoltine summer, 2 yr, 2 years; MB_{ws}, seasonal bivoltine (winter + summer); MP, seasonal polyvoltine (three or more generations per year).

[b] Determined from a comparison of the figures illustrating life cycles with Fig. 2*a*.

only on the basis of the annual mean for the stream. However, since pH was monitored regularly for each stream throughout the year (Fig. 2*a*), it was possible to look at the precise range of stream-water pH values during specific life cycle stages of the individual species. The actual surface water pH values recorded when nymphs of each species were present (based on the life cycle analysis) in the study streams are shown in Table 2. For most species the range is equal to the total annual pH range for the stream(s) in which they are found. However, some species (e.g., *Paraleptophlebia debilis* (Walker) and *Baetis* near *brunneicolor* McD.) were present only as nymphs during summer, and were not exposed (as nymphs) to the relatively severe pH depressions that occurred in spring. Furthermore, by referring to detailed life cycle information for each species (Figs. 4–11), pH ranges encountered by given nymphal stages in each stream (e.g., early-stage versus later-stage nymphs) could be determined. This is important because small, actively growing stages are particularly susceptible to the effects of lowered pH (Bell 1971; Allard and Moreau 1987; Rowe et al. 1988*a*). In fact, a comparison of the size distributions over time (Figs. 4–11) with the pH and temperature data (Figs. 2*a* and 2*c*) indicates that most of the mayflies in our study encountered the lowest pH in each stream as large, nearly mature nymphs in dormant or semidormant (nongrowing) stages at low winter temperatures. Mechanisms of pH toxicity in mayflies are still poorly understood, but probably relate to ionoregulatory responses (Berrill et al. 1987; Rowe et al. 1988*a*). For example, Rowe et al. (1988*a*) found the ionoregulatory response of *Stenonema femoratum* to be highly seasonal, so that individuals were in a dormant phase (regardless of size class), and least susceptible to lowered pH, during snowmelt, the period of greatest acid stress. Therefore, mayflies may be able to withstand brief exposures to pH values far below an annual mean, especially when they are exposed during a tolerant phase in the life cycle.

Life cycles of abundant taxa

Sixteen mayfly species were abundant enough for analysis of life cycle patterns. We show the length–frequency histograms for each stream in Figs. 4–11 to facilitate community comparisons, but each species is discussed individually here, along with notes on stream-water pH regimes at which they were found. Harp Lake outflow had the most diverse mayfly fauna, 17 species, 8 of which were common enough for life cycle analysis. Most of the mayfly species in the study streams had univoltine winter cycles (after Clifford 1982), the populations overwintering as nymphs and reproducing during the summer (Table 2; see also Figs. 4–11). Three species had

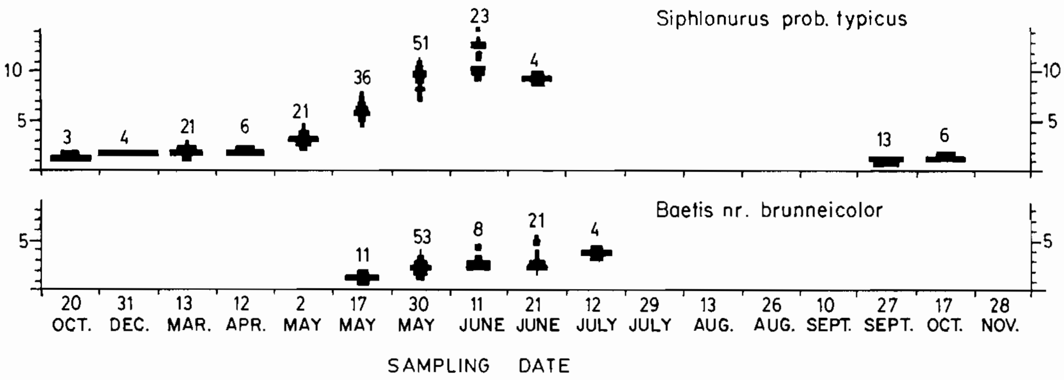

FIG. 4. Life histories of common mayfly species in Harp Lake inflow 3*a*, October 1984 – November 1985 (numbers above length–frequency distributions show number of individuals collected on each date).

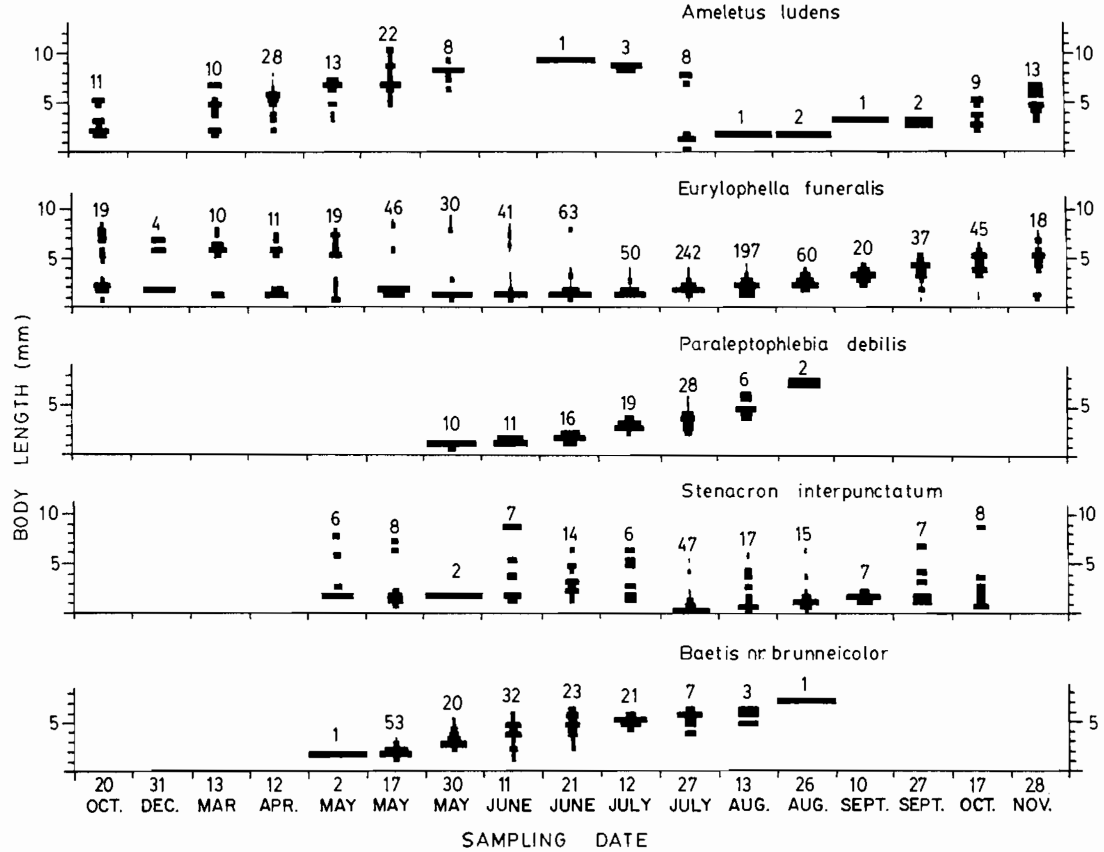

FIG. 5. Life histories of common mayfly species in Harp Lake inflow 4, October 1984 – November 1985 (numbers above length–frequency distributions show number of individuals collected on each date).

univoltine summer cycles, hatching, growth, emergence, and reproduction all occurring during summer. At least one of the baetid species was multivoltine. Only two species had a 2-year cycle. Emergence was highly synchronous for most species, with the exception of the heptageniids and some multivoltine baetids, which emerged continuously during the summer.

Siphlonurus probably *typicus* Eaton

Siphlonurus probably *typicus* was found only in Harp Lake inflow 3*a* (Table 2; Fig. 4). Nymphs were collected from small riffles with gravel substrates until about 4 weeks prior to emergence (June), when they congregated in pools and backwaters. Young nymphs were first noted in September, suggesting a long embryonic period or a summer diapause, which may be an adaptive response for an intermittent stream habitat. Growth was slow during the fall and winter, then very rapid in spring prior to emergence. *Siphlonurus typicus* exhibited a similar life cycle pattern in a headwater stream in Quebec, although it was believed that they spent the summer drought period as small nymphs in small permanent pools in the stream bed (Harper and Harper 1982). Nymphs were present in Harp Lake 3*a* at stream-water pH values ranging from 5.7 to 6.4

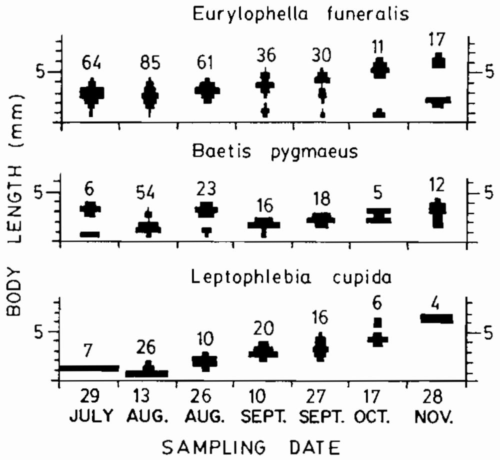

FIG. 6. Life histories of common mayfly species in Harp Lake inflow 5, July–November 1985 (numbers above length–frequency distributions show number of individuals collected on each date).

(Table 2). Stream-water pH did not fall below pH 5.9 when nymphs were in their smallest (and presumably most vulnerable) stages.

Ameletus ludens Needham

Ameletus ludens was moderately abundant in only one upstream reach in Harp Lake inflow 4 (stn. H4-2, Table 2), where it was univoltine (Fig. 5). Emergence began in late May, probably extending into July, and recruitment began in late July, indicating an egg development period of about 2 months. Sprules (1974) reported this species in nearby Algonquin Park, where the main emergence period extended from the end of May to the 1st week of June. Mackay (1969) reported a similar growth pattern for the nymphs in a stream near Montreal, Quebec (as *Ameletus* sp. C), where stream-water pH ranged from 6.5 to 7.4. Stream-water pH at stn. H4-2 ranged from about 5.4 to 7.1 while *A. ludens* was present in the nymphal stages (Table 2), but did not drop below 6.3 when the early-stage nymphs were present.

Baetis near *brunneicolor* McD.

This species was found only during the summer months in the Harp Lake watershed (Table 2; Figs. 4, 5, and 7). Recruitment occurred in early spring, followed by rapid nymphal growth during the summer, adult emergence in August, and an apparent egg diapause during the winter. This relatively large (6–7 mm) *Baetis* sp. was uniformly brown and keyed to *B. brunneicolor* in Morihara and McCafferty (1979). However, Burks (1953) and Sprules (1947) reported a flight period for *B. brunneicolor* adults in spring and early summer that does not correspond with the life cycle pattern observed in this study. Nymphs were found when stream-water pH ranged from 5.4 to 7.0, but they reached their greatest abundance in streams where pH did not fall below 6.4. Young nymphs were only present in the streams when pH was >5.9.

Baetis pygmaeus (= *Acerpenna pygmaeus*, Waltz and McCafferty 1987)

Baetis pygmaeus was probably trivoltine in Harp Lake outflow (Fig. 7) and Harp Lake inflow 5 (Fig. 6), with one winter generation and two summer generations. Lauzon and Harper (1988) and Harper and Harper (1982) reported a multivoltine cycle for this species in Quebec. *Baetis pygmaeus* was found in both Harp Lake 5 (moderately acidic) and Harp Lake outflow (slightly acidic), so nymphs of this species encountered a pH range of 5.0–7.1 over their life cycle.

Stenonema femoratum (Say)

Stenonema femoratum was abundant in Dickie Lake outflow (Table 2; Fig. 8). Unfortunately, samples in this stream were not collected for a long enough period to allow adequate characterization of the life cycle, though a wide range of size classes was found on most sample dates. The species was largely univoltine in another stream system in south central Ontario, with emergence occurring from June to August and recruitment throughout the year (Rowe et al. 1988*a*). A bivoltine cycle was reported in southern Ontario (Rowe and Berrill 1989) and in Wisconsin (Flowers and Hilsenhoff 1978). Laboratory studies by Rowe et al. (1988*a*, 1988*b*) and Berrill et al. (1987) showed *S. femoratum* to be tolerant of low pH, and in our study it was found when stream-water pH values ranged from 5.5 to 6.8. However, the pH of stream water in Dickie Lake outflow dropped to 4.8–5.4 during winter and spring (Fig. 2*a*), so it is likely that *S. femoratum* nymphs were exposed to a pH range of 4.8–6.8 during their life cycle. No samples were collected in this stream in the winter–spring period, so actual tolerance at pH values <5.5 cannot be confirmed.

Stenonema modestum (Banks)

Stenonema modestum was moderately abundant in Harp Lake outflow, where stream water was only slightly acidic (pH 5.6–6.8, Table 2), although specimens were occasionally found in Chubb Lake outflow when pH was >5.6. *Stenonema modestum* was univoltine in Harp Lake outflow (Fig. 7). Emergence began in early June, but extended throughout the summer, and the major recruitment period was in midsummer. However, small stages were present all winter, and recruitment may have continued through the winter months. A similar nymphal growth pattern was found in Quebec (Lauzon and Harper 1988) and southern Ontario (Rowe and Berrill 1989). Harper and Magnin (1971) and Harper and Harper (1982) recorded emergence through the summer for *S. modestum* in Quebec.

Stenacron interpunctatum (Say)

Growth of *Stenacron interpunctatum* nymphs in Harp Lake 4 (all stations, Fig. 5) was similar to that of *Stenonema modestum*, with all size classes collected throughout most of the year except for a brief period in midsummer, when the smallest size classes dominated. *Stenacron interpunctatum* is probably univoltine in Harp Lake 4, with continuous reproduction during the summer and recruitment occurring all year. This species emerged throughout the summer in Quebec (Harper and Harper 1982; Harper et al. 1983), but had two emergence peaks in Wisconsin (Flowers and Hilsenhoff 1978). The life cycle was univoltine in southern Ontario (Rowe and Berrill 1989) and ranged from 1/year to 3 generations/2 years in Indiana (McCafferty and Huff 1978). In this study, all size classes were present over a stream-water pH range of 5.4–7.0.

Leptophlebia cupida (Say)

Leptophlebia cupida was recorded from 7 of the 11 study streams (Table 2), although in the two Dickie Lake inflow streams it was found only during a brief period in the spring. Nymphs are known to undergo spring migrations from larger streams and lakes into small tributaries and marshy areas just

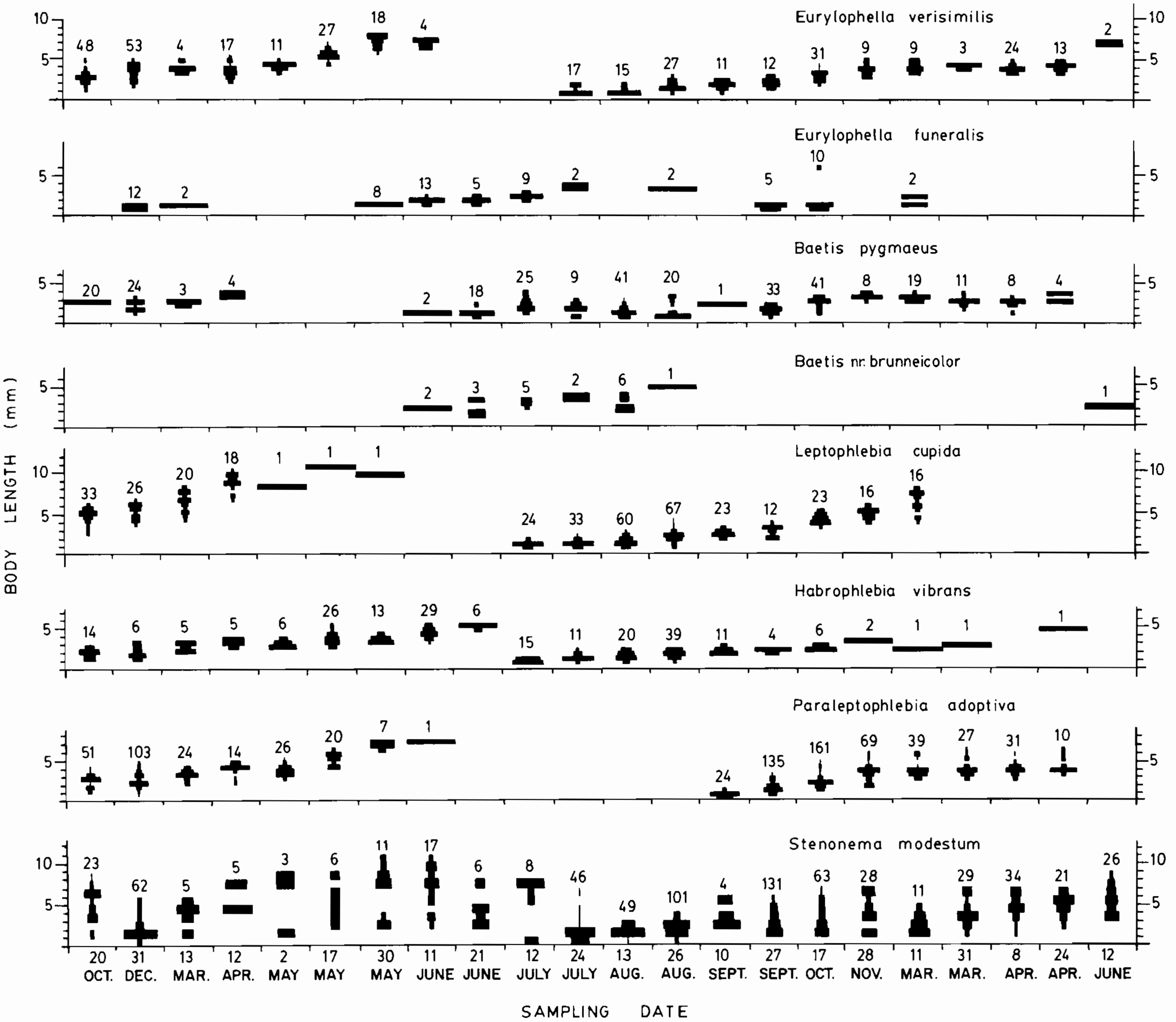

FIG. 7. Life histories of common mayfly species in Harp Lake outflow, October 1984 – June 1986 (numbers above length–frequency distributions show number of individuals collected on each date).

prior to emergence (Neave 1930; Clifford 1969; Clifford et al. 1979). Small *L. cupida* nymphs were found in both Dickie Lake (D. Giberson, unpublished data) and Dickie Lake outflow (Fig. 8), so those that were collected from Dickie Lake 8 and 11 were presumably moving upstream to emerge.

The annual life history pattern is best seen in Harp Lake outflow (Fig. 7) and Plastic Lake outflow (Fig. 9), but the pattern was consistent for populations in Harp Lake 5 (Fig. 6), Dickie Lake outflow (Fig. 8), and Chubb Lake outflow (Fig. 10). The life cycle of *Leptophlebia cupida* was univoltine, with little variation between sites. Adults emerged early in May and early-stage nymphs were first noted in samples collected in early July. Growth was rapid during the fall, but slowed during winter. About 3–4 weeks before emergence, nymphs virtually disappeared from the study reaches as they apparently migrated into pools or tributaries to emerge. This pattern was also reported for populations in Alberta (Clifford

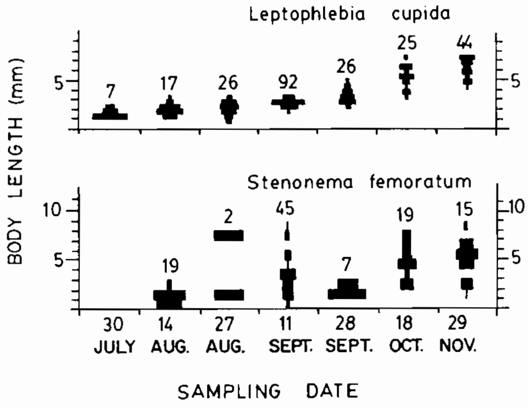

FIG. 8. Life histories of common mayfly species in Dickie Lake outflow, July–November 1985 (numbers above length–frequency distributions show number of individuals collected on each date).

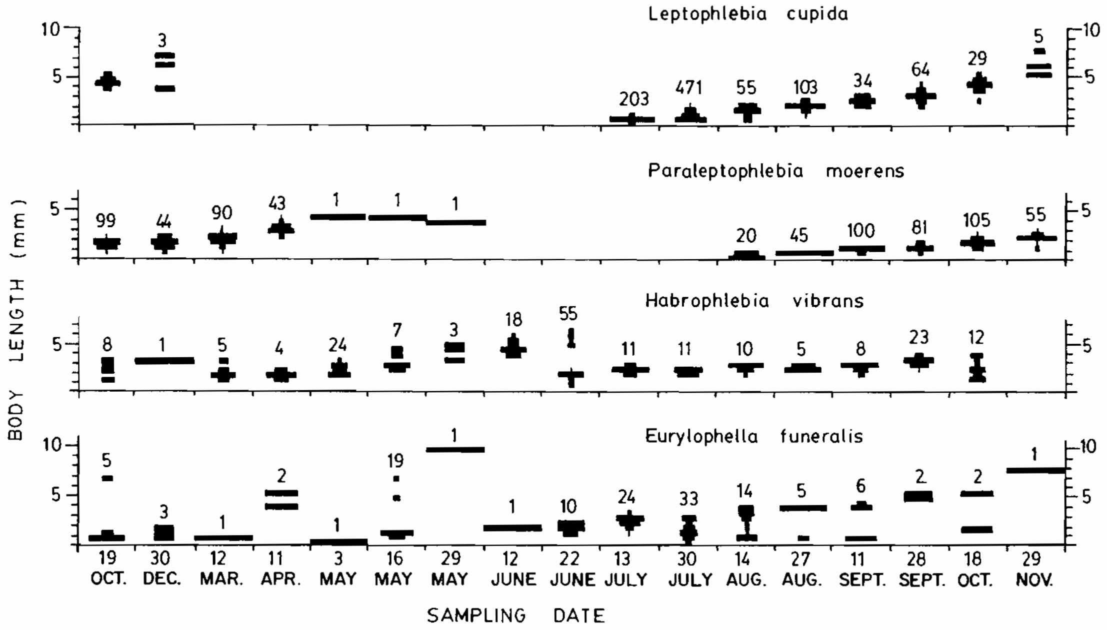

FIG. 9. Life histories of common mayfly species in Plastic Lake outflow, October 1984 – November 1985 (numbers above length–frequency distributions show number of individuals collected on each date).

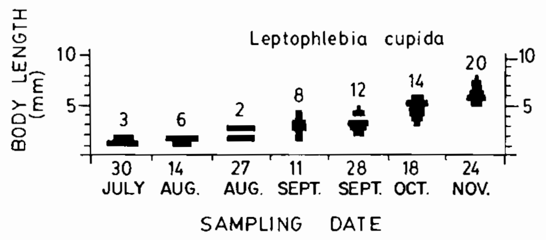

FIG. 10. Life histories of common mayfly species in Chubb Lake outflow, July–November 1985 (numbers above length–frequency distributions show number of individuals collected on each date).

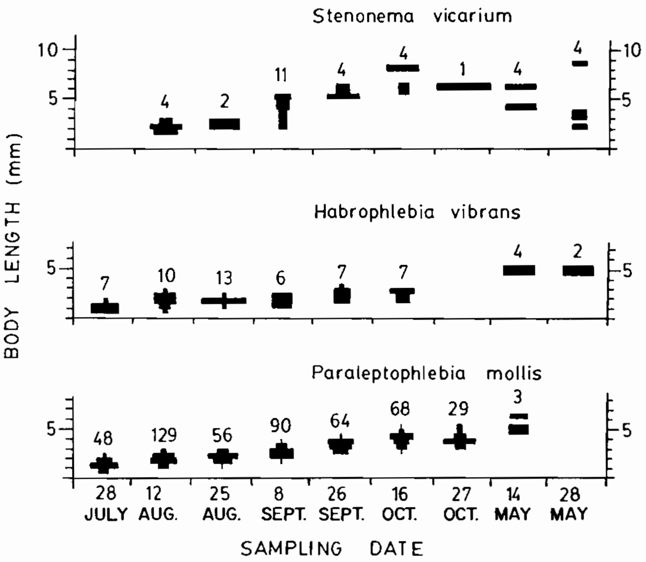

FIG. 11. Life histories of common mayfly species in Beech Lake inflow 1, July 1985 – May 1986 (numbers above length–frequency distributions show number of individuals collected on each date).

et al. 1979) and southern Ontario (Coleman and Hynes 1970). Egg development took 8–10 weeks under field conditions, but eggs probably did not enter diapause, sinced eggs begin hatching in 10–14 days at 20°C in the laboratory (Clifford et al. 1979; Rowe et al. 1988*b*). Stream pH ranged from 4.2 to 6.8 in the study streams during the period when *L. cupida* nymphs were present, though small stages were always found when pH was >5.2.

Habrophlebia vibrans Needham

Habrophlebia vibrans was recently studied in detail by Lauzon and Harper (1988), who identified a 2-year life cycle for a population in Quebec. In contrast, in this study, *H. vibrans* was apparently univoltine in at least two of the streams where it was numerous enough for life history analysis (Harp Lake outflow, Fig. 7; Beech Lake 1, Fig. 11). Only one cohort was noted on any sample date, and no other small leptophlebiid nymphs were present that could have confused identification in the very early stages. The pattern in Plastic Lake outflow, however, does suggest a 2-year cycle, since more than one cohort can be separated on some sample dates (Fig. 9). Furthermore, some early-stage nymphs identified as *Paraleptophlebia moerens* may have been confused with *H. vibrans* during the summer months (before the development of the distinctive gills that are characteristic of *H. vibrans*). Plastic Lake outflow was slightly cooler than the other streams (Fig. 2*b*), so apparent differences in voltinism may be temperature-related, or may be an incorrect interpretation due to low population numbers. Alternatively, Rowe et al. (1988*b*) recently determined that *H. vibrans* eggs took up to twice as long to develop at Ph 5.0 as at pH 6.5, so the lower pH regime found in Plastic Lake outflow may have resulted in longer developmental times for *H. vibrans* in that stream. However, it is likely that the life cycles are similar in all creeks, since the emergence period was the same for all three streams, occurring in mid to late June, with early-stage nymphs noted soon afterwards. Growth was slow through the summer and winter, but rapid in the spring just prior to emergence. *Habrophlebia vibrans* nymphs were exposed to a pH range of 4.8–6.8 in the study area, though small stages were only recorded above pH 5.3.

Paraleptophlebia debilis (Walker)

Paraleptophlebia debilis was found only during the summer months in Harp Lake inflows 4 and 5 (Fig. 5; Table 2). Nymphs were first noted in samples in early May, and they grew rapidly through the summer months to emerge in August. *Paraleptophlebia debilis* is also a summer species in Alberta, with growth, emergence, and reproduction all occurring between June and August (Clifford 1969). The winter is probably spent in the egg stage. The pH range encountered by nymphs of *P. debilis* in Harp Lake 4 and 5 was 5.0–6.0, though early-stage nymphs were only present when the pH was >5.4.

Paraleptophlebia mollis (Eaton)

Paraleptophlebia mollis is common in southern Ontario at slightly alkaline sites, where nymphs are univoltine, first appearing in July or August and emerging in mid to late May (Coleman and Hynes 1970; Corkum 1978). In this study they were also found at a slightly alkaline site (range 7.2–7.8), Beech Lake inflow 1 (Fig. 11), where the life history pattern was the same as was reported in southern Ontario.

Paraleptophlebia adoptiva (McD.)

Paraleptophlebia adoptiva was the only *Paraleptophlebia* species found in the species-rich Harp Lake outflow reach (Table 2), though it has been reported as co-occurring with *P. mollis* and *P. moerens* in slightly alkaline streams in southern Ontario (Coleman and Hynes 1970; Corkum 1978). It was univoltine in Harp Lake outflow (Fig. 7). Emergence began in early May, but young nymphs were not found in samples until September. Growth was rapid during the fall, but slowed or stopped during the cold months, before resuming in spring prior to emergence. This pattern was consistent with that reported for a southern Ontario population by Corkum (1978). The pH range encountered by *P. adoptiva* nymphs in Harp Lake outflow was 5.7–6.8, though young nymphs were found only when stream-water pH was >6.4.

Paraleptophlebia moerens McD.

Paraleptophlebia moerens was abundant in Plastic Lake outflow, where it was univoltine (Fig. 9), which is consistent with the life cycle reported by Coleman and Hynes (1970) for a slightly alkaline southern Ontario stream. Adults began emerging very early in the spring, and early-stage nymphs were first noted in August. Egg development, therefore, required approximately 4 months in the field, suggesting a summer dormancy or diapause. Nymphs grew quickly in the fall, but growth stopped or slowed during winter before resuming in spring just prior to emergence. Stream-water pH in Plastic Lake outflow when *P. moerens* nymphs were present was 4.8–6.4, although young stages were only found when pH was >5.6.

Eurylophella funeralis McD.

Eurylophella funeralis is univoltine and bisexual in the southern portions of its range (Hamilton and Tarter 1977; Sweeney and Vannote 1981; Sweeney and Vannote 1987) and semivoltine (Fiance 1978) and largely or completely parthenogenic in the north (McDunnough 1931; Sweeney and Vannote 1987). In this study, *E. funeralis* was abundant in medium-sized, woodland streams (Harp Lake inflows 4 and 5, Harp Lake outflow, and Plastic Lake outflow; Figs. 5, 6, 7, and 9), where nymphs needed 2 years to develop and populations consisted only of females. Emergence began at the end of May and young nymphs were noted as early as July in Plastic Lake outflow (Fig. 9), suggesting an egg development time of at least 2 months. Nymphal growth was slow in the 1st year of the development, and most of the growth occurred in the autumn months of the 2nd year. This pattern was consistent with that reported by Fiance (1978) in New Hampshire. All sizes of *E. funeralis* were found at stream-water pH values that ranged from 4.7 to 7.1.

Eurylophella verisimilis McD.

Eurylophella verisimilis was found only in Harp Lake outflow, where it was moderately abundant and univoltine (Fig. 7). Adults began emerging in late May and early June, and after an egg development period of ~6–8 weeks, nymphs grew rapidly through the autumn before growth stopped in winter. Similar patterns were reported for populations in Pennsylvania (Sweeney and Vannote 1987) and Quebec (Lauzon and Harper 1988). *Eurylophella verisimilis* nymphs were found over a stream-water pH range of 5.7–6.8; young nymphs were found when pH was >6.4.

Conclusion

At least 29 mayfly species, in 15 genera, were found in the 11 streams investigated. Our results show a trend of decreasing mayfly diversity with decreasing pH, already documented by Sutcliffe and Carrick (1973), Hall et al. (1980), Mackay and Kersey (1985), Peterson et al. (1986), and others. However, these data also indicate how important it is to consider stream size when looking at distribution patterns. In addition, we show the importance of species-level indentifications in assessing distribution patterns relative to stresses, including the presence of toxicants. For example, five species of *Paraleptophlebia* were found in the study streams, over a pH range of 4.7–7.8, suggesting that this group has a wide pH tolerance. However, only one of the five species (*P. moerens*) was actually found at the lowest pH; the remainder were only found at stream-water pH values >5.4. Similarly, only one *Eurylophella* species (*E. funeralis*) was found over a wide pH range, though three other species were found at higher pH.

Five mayfly species were common in more than one stream (*Baetis pygmaeus*, *Baetis* near *brunneicolor*, *Habrophlebia vibrans*, *Leptophlebia cupida*, and *Eurylophella funeralis*), resulting in some of these species being exposed to widely varying pH ranges. Lowered pH has previously been reported to affect developmental rates in some mayflies (e.g., *Eurylophella funeralis* nymphs, Fiance 1978; and *Habrophlebia vibrans* eggs, Rowe et al. 1988*b*), though not in others (e.g., *Baetis pygmaeus* eggs and *Leptophlebia cupida* eggs or nymphs (Berrill et al. 1987; Rowe et al. 1988*b*). Life cycle patterns reported in this study were apparently unaffected by pH regime, with the possible exception of that of *H. vibrans*, which appeared to be univoltine in the higher-pH streams and semivoltine in the more acid Plastic Lake outflow. However, *H. vibrans* was also semivoltine in a Quebec stream that was only slightly acid (Lauzon and Harper 1986), so this apparent variation in voltinism is probably an artifact of sampling, or is related to the temperature conditions in the streams.

Including life cycle information as well as distribution data in considering pH effects allowed us to state precisely the pH ranges encountered during the life cycle of the component species. This resulted in patterns slightly different from those that may have been evident when distribution was correlated with total annual pH regimes. For example, *Paraleptophlebia debilis* was common in an upstream site of Harp Lake inflow 4 (H4-1), where the pH ranged from 5.0 to 6.3, but nymphs were only present during the summer, when the pH was generally >5.5. Similarly, *Baetis* near *brunneicolor* was found in streams where pH ranged from 4.7 to 7.1, but again, nymphs were only present when the pH was >5.4.

Another advantage of using life cycle information in conjunction with water chemistry data is that particular life stages could be associated with periods of potential stress. For most species the larger stages were present during spring snowmelt, the period of greatest acid stress, and early-stage nymphs were generally only present when the streams were at their highest pH levels. The presence of larger (and presumably more tolerant) stages during the periods of lowest pH is probably simply a coincidence of life cycles that have adapted over long periods to other factors, such as seasonal food and discharge patterns. This pattern has also been noted for mayfly populations in other parts of eastern North America that are not experiencing acid stress.

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ALLARD, M., and MOREAU, G. 1987. Effects of experimental acidification on a lotic macroinvertebrate community. Hydrobiologia, **144**: 37–49.

BELL, H. L. 1971. Effect of low pH on the survival and emergence of aquatic insects. Water Res. **5**: 313–319.

BERRILL, M., ROWE, L., HOLLETT, L., and HUDSON, J. 1987. Response of some aquatic benthic arthropods to low pH. *In* Ecophysiology of acid stress to aquatic organisms. *Edited by* H. Witters and O. Vanderborght. Ann. Soc. R. Zool. Belg. **117** (Suppl. 1): 117–127.

BUIKEMA, A. L., JR., and BENFIELD, E. F. 1979. Use of macroinvertebrate life history information in toxicity tests. J. Fish. Res. Board Can. **36**: 321–328.

BURKS, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. Ill. Nat. Hist. Surv. Bull. **26**.

CLIFFORD, H. F. 1969. Limnological features of a northern brownwater stream, with special reference to the life histories of the aquatic insects. Am. Midl. Nat. **82**: 578–597.

——— 1982. Life cyles of mayflies (Ephemeroptera), with special reference to voltinism. Quaest. Entomol. **18**: 15–90.

CLIFFORD, H. F., 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 Plecoptera and Ephemeroptera in a southern Ontario stream. Can. J. Zool. **48**: 1333–1339.

CORKUM, L. D. 1978. The nymphal development of *Paraleptophlebia adoptiva* (McDunnough) and *Paraleptophlebia mollis* (Eaton) (Ephemeroptera: Leptophlebiidae) and the possible influence of temperature. Can. J. Zool. **56**: 1842–1846.

DILLON, P. J., JEFFRIES, D. S., SNYDER, W., REID, R., YAN, N. D., EVANS, D., MOSS, J., and SCHEIDER, W. A. 1978. Acidic precipitation in south-central Ontario: recent observations. J. Fish. Res. Board Can. **35**: 809–815.

FIANCE, S. B. 1978. Effects of pH on the biology and distribution of *Ephemerella funeralis* (Ephemeroptera). Oikos, **31**: 332–339.

FLOWERS, R. W., and HILSENHOFF, W. L. 1978. Life cycles and habitats of Wisconsin Heptageniidae (Ephemeroptera). Hydrobiologia, **60**: 159–171.

GIBERSON, D. J., and HALL, R. J. 1988. Seasonal variation in faunal distribution within the sediments of a Canadian Shield stream, with emphasis on responses to spring floods. Can. J. Fish. Aquat. Sci. **45**: 1994–2002.

HALL, R. J., LIKENS, G. E., FIANCE, S. B., and HENDREY, G. R. 1980. Experimental acidification of a stream in the Hubbard Brook experimental forest, New Hampshire. Ecology, **61**: 976–989.

HALL, R. J., BAILEY, R. C., and FINDEIS, J. 1988. Factors affecting survival and cation concentration in the blackfly *Prosimulium hirtipes* complex and the mayfly *Leptophlebia cupida* during spring snowmelt. Can. J. Fish. Aquat. Sci. **45**: 2123–2132.

HAMILTON, D. A., and TARTER, D. C. 1977. Life history of *Ephemerella funeralis* McDunnough (Ephemeroptera: Ephemerellidae) in a small West Virginia stream. Am. Midl. Nat. **98**: 458–462.

HARPER, F., and MAGNIN, E. 1971. Émergence saisonnière de quelques éphéméroptères d'un ruisseau des Laurentides. Can. J. Zool. **49**: 1209–1221.

HARPER, F., MAGNIN, E., and HARPER, P. 1983. Diel periodicity of emerging mayflies (Insecta: Ephemeroptera) in a Laurentian stream. Aquat. Insects, **5**: 21–31.

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

HARRIMAN, R., and MORRISON, B. R. S. 1982. Ecology of streams draining forested and non-forested catchments in an area of central Scotland subject to acid precipitation. Hydrobiologia, **88**: 251–255.

JEFFRIES, D. S., and SNYDER, W. 1983. Geology and geochemistry of the Muskoka–Haliburton study area. Data Rep. No. 83/s, Ontario Ministry of the Environment, Toronto.

JEFFRIES, D. S., COX, C. M., and DILLON, P. J. 1979. Depressions of pH in lakes and streams in central Ontario during snowmelt. J. Fish. Res. Board Can. **36**: 640–646.

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.

——— 1988. Seasonal dynamics of a mayfly (Insecta: Ephemeroptera) community in a Laurentian stream. Holarct. Ecol. **11**: 220–234.

LEHMKUHL, D. M. 1979. Environmental disturbance and life histories: principles and examples. J. Fish. Res. Board Can. **36**: 329–334.

MACKAY, R. J. 1969. Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. J. Fish. Res. Board Can. **26**: 1157–1183.

MACKAY, R. J., and KERSEY, K. E. 1985. A preliminary study of aquatic insect communities and leaf decomposition in acid streams near Dorset, Ontario. Hydrobiologia, **122**: 3–12.

MCCAFFERTY, W. P., and HUFF, B. 1978. The life cycle of the mayfly *Stenacron interpunctatum* (Ephemeroptera: Heptageniidae) Great Lakes Entomol. **11**: 209–216.

MCDUNNOUGH, J. 1931. The bicolor group of the genus *Ephemerella*, with particular reference to the nymphal stages (Ephemeroptera). Can. Entomol. **63**: 30–42, 61–68.

MORIHARA, D. K., and MCCAFFERTY, W. P. 1979. The *Baetis* larvae of North America (Ephemeroptera: Baetidae). Trans. Am. Entomol. Soc. **105**: 139–217.

NEAVE, F. 1930. Migratory habits of the mayfly *Blasturus cupidus* Say. Ecology, **11**: 568–576.

NEEDHAM, J. G., TRAVER, J. R., and HSU, Y. C. 1935. The biology of mayflies with a systematic account of North American species. Comstock Publications, Ithaca, NY.

PETERSON, R. H., GORDON, D. J., and JOHNSTON, D. J. 1986. Distribution of mayfly nymphs (Insecta: Ephemeroptera) in some streams of eastern Canada as related to stream pH. Can. Field-Nat. **99**: 490–493.

ROWE, L., and BERRILL, M. 1989. The life cycles of five closely related mayfly species (Ephemeroptera: Heptageniidae) coexisting in a small southern Ontario stream. Aquat. Insects, **11**: 73–80.

ROWE, L., BERRILL, M., and HOLLETT, L. 1988*a*. The influence of season and pH on mortality, molting and whole-body ion concentration in nymphs of the mayfly *Stenonema femoratum*. Comp. Biochem. Physiol. A, **90**: 405–408.

ROWE, L., HUDSON, J., and BERRILL, M. 1988*b*. Hatching success of mayfly eggs at low pH. Can. J. Fish. Aquat. Sci. **45**: 1649–1651.

SCHEIDER, W. A., COX, C. M., and SCOTT, L. D. 1983. Hydrological data for lakes and watersheds in the Muskoka–Haliburton study area (1976–1980). Data Rep. No. DR 83/6, Ontario Ministry of the Environment, Toronto.

SEIP, H. M., SEIP, R., DILLON, P. J., and DEGROSBOIS, E. 1985. Model of sulphate concentration in a small stream in the Harp Lake catchment, Ontario. Can. J. Fish. Aquat. Sci. **42**: 927–937.

SIMPSON, K. W., BODE, R. W., and COQUHOUN, J. R. 1985. The macroinvertebrate fauna of an acid-stressed headwater stream system in the Adirondack Mountains, New York. Freshwater Biol. **15**: 671–681.

SPRULES, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. Univ. Toronto Stud. Biol. Ser. No. 69.

SUTCLIFFE, D. W., and CARRICK, T. R. 1973. Studies on mountain streams in the English Lake District. 1. pH, calcium, and the distribution of invertebrates in the River Duddon. Freshwater Biol. **3**: 437–462.

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

——— 1987. Geographic parthenogenesis in the stream mayfly, *Eurylophella funeralis* in eastern North America. Holarct. Ecol. **10**: 52–59.

WALTZ, R. D., and MCCAFFERTY, W. P. 1987. New genera of Baetidae for some Nearctic species previously included in *Baetis* Leach (Ephemeroptera). Ann. Entomol. Soc. Am. **80**: 667–670.