

Mayfly communities in a Laurentian watershed (Insecta; Ephemeroptera)

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Mayfly communities were investigated in a series of four lakes, two beaver ponds, and 13 streams in a Laurentian watershed. Forty-five taxa were collected mostly through emergence trapping of adults (76 trap-years). *Q* and *R* analyses were used to show similarities between the stations and associations between the species. The middle reaches of the mainstream harbour the richest communities which are an assemblage of a few ubiquitous species (*Baetis* gr. *pygmaeus*, *Stenonema modestum*, *Habrophlebia vibrans*, and *Paraleptophlebia volitans*), lotic species (*Baetis flavistriga*, *B. pluto*, *Stenonema vicarium*, and *Heptagenia pulla*) some of which show a restricted distribution (*Paraleptophlebia adoptiva*, *P. ontario*, *Leucrocuta hebe*, and *Stenacron interpunctatum heterotarsale*), and also lentic species (*Eurylophella verisimilis*, *Leptophlebia cupida*, *Cloeon simplex*, *C. rubropictum*, *Centroptilum album*, and *Stenacron interpunctatum frontale*). The headwater streams contain no distinct element, except perhaps *Siphonurus typicus*, but rather the more resistant or dispersive species from the mainstream, mainly Ephemerelellidae and Leptophlebiidae. The lower reaches of the mainstream are characterized by the addition of a few typical river species, *Serratella sordida* and *Epeorus vitreus*. Lacustrine communities are less diverse, comprising mostly the lentic species from the streams plus a distinctive element (*Stenacron interpunctatum canadense*, *Callibaetis ferrugineus*, and *Hexagenia limbata occulta*). Only *Leptophlebia cupida* colonizes the bog lake, and no species occur in the beaver ponds. Most congeneric species are either spatially or temporally segregated. The sections of the mainstream produce an average of some 1000 adult mayflies/m² per year; other streams are less productive and the lakes even less so (less than 100/m²). The seasonal succession of the species and the emergence patterns of the dominant species are illustrated; a classification of emergence patterns is attempted on the basis of the present data and of other recent studies.

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Les communautés d'Ephéméroptères ont été échantillonnées à l'aide de pièges d'émergence (76 pièges-années) dans un réseau hydrographique des Laurentides constitué de quatre lacs, deux étangs de barrage de castors et 13 ruisseaux. On y a dénombré 45 taxons. Des analyses en mode *Q* et en mode *R* ont permis de mettre en évidence les similarités entre les stations et d'établir les associations d'espèces. Le cours moyen du ruisseau principal possède les peuplements les plus riches constitués d'espèces ubiquistes (*Baetis* gr. *pygmaeus*, *Stenonema modestum*, *Habrophlebia vibrans*, *Paraleptophlebia volitans*), d'espèces lotiques (*Baetis flavistriga*, *B. pluto*, *Stenonema vicarium*, *Heptagenia pulla*) dont certaines possèdent une distribution restreinte (*Paraleptophlebia adoptiva*, *P. ontario*, *Leucrocuta hebe*, *Stenacron interpunctatum heterotarsale*), ainsi que d'espèces léntiques (*Eurylophella verisimilis*, *Leptophlebia cupida*, *Cloeon simplex*, *C. rubropictum*, *Centroptilum album*, *Stenacron interpunctatum frontale*). Les ruisseaux tributaires du cours supérieur n'abritent pas d'espèces particulières, à l'exception peut-être de *Siphonurus typicus*; ils sont plutôt colonisés par les espèces les plus résistantes ou les plus mobiles du cours principal, particulièrement des Ephémerelellidae et des Leptophlebiidae. Le cours inférieur du ruisseau principal est caractérisé par l'addition de quelques espèces typiques des rivières, *Serratella sordida* et *Epeorus vitreus*. Les communautés lacustres sont moins diversifiées et se composent surtout des espèces léntiques des ruisseaux, auxquelles s'ajoutent quelques espèces exclusives (*Stenacron interpunctatum canadense*, *Callibaetis ferrugineus*, *Hexagenia limbata occulta*). Seul *Leptophlebia cupida* colonise le lac tourbeux et aucune espèce n'a été récoltée dans les étangs de barrage de castors. On note une séparation dans le temps ou dans l'espace de la plupart des espèces congénériques. Le cours principal du ruisseau produit environ 1000 Ephéméroptères adultes/m² par année; les autres ruisseaux sont moins productifs et les lacs le sont très peu (moins de 100/m²). La succession saisonnière des espèces et les patterns d'émergence des espèces les plus communes sont illustrés. À partir de ces résultats, il est possible d'esquisser une classification des patterns d'émergence chez les Ephéméroptères.

Following the pioneering studies of McDunnough (1925, 1930, 1932), the mayfly fauna of Quebec was one of the best known on the continent. Since then, only four papers deal specifically with the ecology of the local fauna (Harper and Magnin 1971; Gibbs 1971, 1977; Harper and Harper 1976), although additional information is available in comprehensive studies (Mackay

1969) and in reports and theses (Pilon *et al.* 1975; Elouard 1977; Rochon 1977; Olivier 1980).

The present investigation was undertaken as part of a study of insect communities in a system of lakes and streams in the Southern Laurentian Highlands of Québec (Harper 1978). Emphasis is placed on the species composition in the various habitats, the species distribu-

tion, and their phenology. The study is based exclusively on adults which are well known taxonomically and can thus provide a precise picture of the communities.

Methods

Mayfly adults were collected through an extensive program of emergence trapping, some light trapping (black light GE F8T5/BL), and some general collecting (beating the riparian vegetation, collecting swarms, checking spider webs).

The emergence traps were of the design of Harper and Magnin (1971): a pyramidal frame covered with fibre-glass netting (7 threads/cm) which sampled an area of 0.5 m²; a sleeve fitted into one side allowed the removal of the insects with an aspirator connected to a hand-operated suction bulb. Traps set on the mainstream were emptied daily and those on the tributaries and the lakes three times a week during the entire emergence season, from early May to mid-September.

Identification and nomenclature follow Edmunds *et al.* (1976), but take into account the revisions of Bednaryk and McCafferty (1979), Allen (1980), and Flowers (1980).

Statistical procedures are taken from Legendre and Legendre (1979) and the data were processed on the Université de Montréal Cyber computer using the "Logiciel *r*" statistical package developed by Alain Vaudor.

Sites were compared using both the Steinhaus and the chi-square similarity indices; the former bases similarity on the common possession of the same species in similar numbers ($S = 2W/(A + B)$, where W is the sum of minimum abundances of each species in each sample pair, and A and B are respectively the sums of abundances of species in each sample); the latter uses the proportions of each species as a basis for similarity irrespective of total numbers

$$S = 1 - \left\{ \sum_i (1/y_i) [(y_{i1}/y \cdot 1) - (y_{i2}/y \cdot 2)]^2 \right\}^{1/2}$$

where y_{i1} is the number of specimens of species i in site 1, y_i the sum of all specimens of species i in all sites and $y \cdot 1$ the sum of all species in site 1. Clustering of sites resulted from hierarchical intermediate (75%) linkage procedures.

Species associations were based on the Krylov (1968) similarity coefficient $S = 1 - \text{prob}(\chi^2)$, $\nu = 1$, with the exception that if $(a + b)(a + c)/p \geq a$, S equals 0; χ^2 is calculated as $p[ad - bc] - (p/2)^2 / ((a + b)(c + d)(a + c)(b + d))$, where a, b, c, d are respectively the number of samples where both species are present (a), one is absent (b, c), and both are absent (d); p is $(a + b + c + d)$. Clustering is based on the nonhierarchical complete linkage procedure of Fager (1957), and the restrictions of Fager and McGowan (1963) and of Krylov (1968) have been taken into account.

The study site

The area chosen for this investigation is the upper Western section of the L' Achigan River drainage (Fig. 1), the site of many of our previous studies on aquatic insects (Harper and Magnin 1971; Back and Harper 1979; Harper and Cloutier 1979; Harper 1980). It comprises a mainstream arising from Lac Pilon and flowing through a series of small lakes and

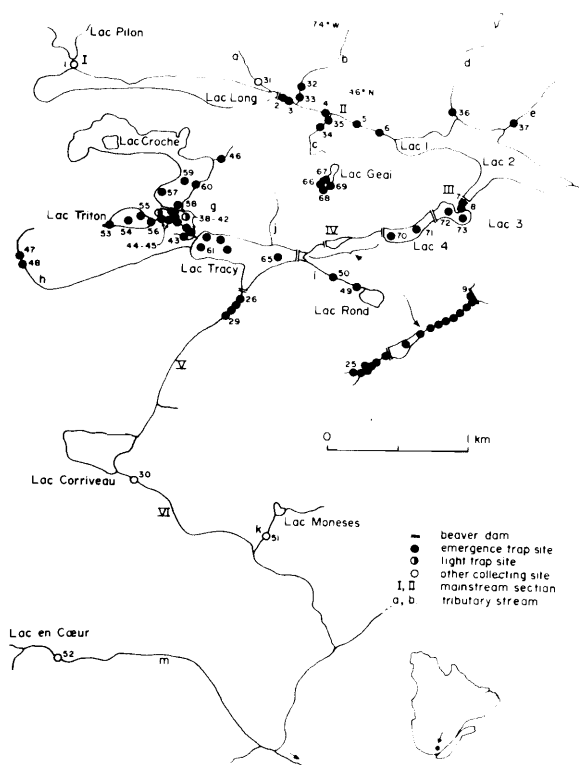


FIG. 1. Map of the study area and position of the sampling stations. The numeration of the stations begins with the mainstream (1–30), and follows with the tributaries (a–m; stations 31–52) and the lakes and ponds (53–73). The inset map of Quebec shows location of study area.

beaver ponds. The mainstream is thus divided into sections: section I is a first-order stream, sections II–IV are second order, and sections V–VI are third order. Thirteen tributary streams (a–m) were also sampled and all are first order, except stream *g* which is second order for most of its length. Collections were also made on four lakes (Triton, Croche, Tracy, Geai) and two beaver ponds (Lac 2, Lac 3). Thus 73 stations were sampled in the watershed (Table 1), 68 of them with emergence traps over one summer. Eight stations (9, 10, 12, 15, 20, 22 in mainstream section IV and 38 and 39 in tributary *g*) were sampled during two seasons.

Descriptions of many of the sites have been given elsewhere (Back and Harper 1979; Harper and Cloutier 1979; Harper 1980), so the general features are simply summarized in Table 1. The water is unpolluted, humic, soft, and slightly acid. The lakes generally freeze over from early November to early May. Precipitation averages 5–10 cm a month over the year and the winter snow accumulation is about 2–3 m. Water temperatures are maintained between 20 and 25°C during the summer, with a recorded maximum of 27°C. The surrounding vegetation is a second-growth white birch (*Betula papyrifera*) association, a successional stage leading to the sugar maple (*Acer saccharum*) – yellow birch (*B. lutea*) climax of the area.

TABLE 1. Summary of habitat conditions and sampling scheme. For each site, the corresponding station numbers are indicated, together with the frequency of collections where emergence traps were maintained. The numbers in the last column refer to individual stations

Site	Stations	Frequency of emergence trapping	Habitat notes
Mainstream I	1	—	Gravel, wood debris
Mainstream II	2–6	Three per week (1972)	Gravel (2), silt (3), cobbles (4, 6), silt and ferns (5)
Mainstream III	7–8	Daily (1972)	Mossy boulders (7), cobbles (8)
Mainstream IV	9–25	Daily (1972–1973)	Mossy boulders (10, 19), cobbles (9, 11–13, 21–24), sand and silt (14, 15, 18), backwater and weeds (17, 25)
Mainstream V	26–29	Daily (1972)	Cobbles and gravel
Mainstream VI	30	—	Boulders and cobbles
Tributary <i>a</i>	31	—	Gravel and silt
Tributary <i>b</i>	32–33	Irregular	Gravel (32), silt (33)
Tributary <i>c</i>	34–35	Irregular	Cobbles and gravel
Tributary <i>d</i>	36	Irregular	Cobbles and gravel (intermittent)
Tributary <i>e</i>	37	Irregular	Gravel (intermittent)
Tributary <i>g</i>	38–42	Daily (1972–1973)	Wood debris (38), gravel and sand (39–42)
Tributary <i>ga</i>	43	Daily (1973)	Silt
Tributary <i>gb</i>	44–45	Daily (1972–1973)	Gravel (44), silt (45)
Tributary <i>gc</i>	46	Three per week (1974)	Silt and sand (intermittent)
Tributary <i>h</i>	47–48	Three per week (1974)	Gravel (intermittent)
Tributary <i>i</i>	49–50	Three per week (1973)	Cobbles (intermittent) (49), silt (50)
Tributary <i>k</i>	51	—	Gravel and cobbles
Tributary <i>m</i>	52	—	Cobbles and gravel
Lac Triton	53–56	Three per week (1973)	Pond, z_m 3m
Lac Croche	57–60	Three per week (1974)	Dimictic, vegetation scarce, z_m 10m, hypolimnetic deoxygenation
Lac Tracy	61–65	Three per week (1974)	Dimictic, vegetation abundant, z_m 9m, deoxygenation
Lac Geai	66–69	Three per week (1974)	Dimictic bog, z_m 8m
Lacs 3 and 4	70–73	Three per week (1978)	Beaver ponds, bog and pond vegetation, z_m 2m

Results

The mayfly fauna

Table 2 lists the 45 taxa collected during the study together with the numbers of specimens. It was not possible to discriminate between the females of *Baetis pygmaeus* and *B. macdunnoughi*; because the latter is parthenogenetic at our latitude (Bergman and Hilsenhoff 1978), it was assumed that when only females were collected in a station, such as in station 8, *B. macdunnoughi* was the only one present. On the other hand, when the sex ratio was 1:1, *B. pygmaeus* was considered to be dominant; in intermediate situations there was probably a mixture of both. Very few males of *Ephemera invaria* were collected: it is possible that the species is to some extent parthenogenetic. There is some indication, however, that two forms are involved, a parthenogenetic population in the small tributaries, and

a bisexual population in the lower mainstream, but the problem requires further investigation.

Distribution of the species

Thirty-nine taxa inhabit the mainstream (Table 3). Section I was sampled very irregularly and the low numbers reflect the sampling effort rather than the species richness. The three middle sections (II–IV) support some 20–30 species, a dozen or so of which are abundant. The fauna is remarkably similar in all sections and the dominant species are the same: *Baetis flavistriga*, *B. gr. pygmaeus*, *Heptagenia pulla*, *Stenonema modestum*, *S. vicarium*, *Habrophlebia vibrans*, *Paraleptophlebia volitans*, and *Eurylophella verisimilis*. Only two species appear to be restricted to the uppermost stations: *Paraleptophlebia debilis*, a headwater species, and *Litobranchea recurvata*, abundant in a

TABLE 2. Species collected, all samples pooled

	Males	Females
Family Siphonuridae		
<i>Siphonurus alternatus</i> (Say)	4	17
<i>S. typicus</i> Eaton	214	212
Family Baetidae		
<i>Baetis flavistriga</i> McDunnough	595	637
<i>B. pluto</i> McDunnough	365	382
<i>B. propinquus</i> (Walsh)	26	21
<i>B. pygmaeus</i> (Hagen) + <i>B. macdunnoughi</i> Ide	1246	4066
<i>Callibaetis ferrugineus</i> (Walsh)	2	3
<i>C. skokianus</i> Needham	1	0
<i>Centropilum album</i> McDunnough	25	23
<i>C. bellum</i> McDunnough	1	0
<i>Cloeon rubropictum</i> McDunnough	140	194
<i>C. simplex</i> McDunnough	43	108
<i>Pseudocloeon</i> sp.	1	0
Family Oligoneuriidae		
<i>Isonychia bicolor</i> (Walker)	3	4
Family Heptageniidae		
<i>Arthroplea bipunctata</i> McDunnough	6	7
<i>Epeorus vitreus</i> (Walker)	2	0
<i>Heptagenia pulla</i> (Clemens)	129	179
<i>Leucrocuta hebe</i> (McDunnough)	37	44
<i>Stenacron carolina</i> (Banks)	22	1
<i>S. interpunctatum canadense</i> (Walker)	6	9
<i>S. interpunctatum frontale</i> (Banks)	59	82
<i>S. interpunctatum heterotarsale</i> (McDunnough)	34	56
<i>Stenonema femoratum</i> (Say)	15	31
<i>S. modestum</i> (Banks)	673	724
<i>S. vicarium</i> (Walker)	216	285
Family Leptophlebiidae		
<i>Habrophlebia vibrans</i> Needham	3690	2107
<i>Leptophlebia cupida</i> (Say)	326	455
<i>L. johnsoni</i> McDunnough	13	
<i>L. nebulosa</i> (Walker)	3	
<i>Paraleptophlebia adoptiva</i> (McDunnough)	198	314
<i>P. debilis</i> (Walker)	26	30
<i>P. guttata</i> (McDunnough)	7	3
<i>P. mollis</i> (Eaton)	2	0
<i>P. ontario</i> (McDunnough)	128	131
<i>P. volitans</i> (McDunnough)	275	740
Family Ephemerellidae		
<i>Ephemerella dorothea</i> Needham	2	0
<i>E. invaria</i> (Walker)	12	168
<i>Eurylophella prudentalis</i> (McDunnough)	9	348
<i>E. temporalis</i> (McDunnough)	35	
<i>E. verisimilis</i> (McDunnough)	134	
<i>Serratella sordida</i> (McDunnough)	7	8
Family Caenidae		
<i>Caenis simulans</i> McDunnough	1	2
Family Ephemeridae		
<i>Hexagenia limbata occulta</i> (Walker)	13	21
<i>Litobrantha recurvata</i> (Morgan)	14	18

TABLE 3. Numbers of each species collected from the six mainstream sections

	I	II	III	IV	V	VI
<i>Siphonurus alternatus</i>	—	2	—	6	—	—
<i>Baetis flavistriga</i>	—	17	2	1111	57	—
<i>B. pluto</i>	—	4	3	728	11	—
<i>B. propinquus</i>	—	—	—	47	—	—
<i>B. gr. pygmaeus*</i>	—	21	476	4454	234	2
<i>Isonychia bicolor</i>	—	3	—	1	—	—
<i>Callibaetis skokianus</i>	—	—	—	1	—	—
<i>Centroptilum album</i>	—	—	—	9	18	—
<i>Cloeon rubropictum</i>	—	—	—	222	3	—
<i>C. simplex</i>	4	—	41	65	1	—
<i>Pseudocloeon</i> sp.	—	—	—	—	1	—
<i>Arthroplea bipunctata</i>	1	—	—	—	—	—
<i>Epeorus vitreus</i>	—	—	—	—	—	2
<i>Heptagenia pulla</i>	—	17	21	185	11	—
<i>Leucrocuta hebe</i>	5	2	2	25	8	18
<i>Stenacron carolina</i>	—	7	—	—	—	6
<i>S. i. frontale</i>	—	—	—	30	2	—
<i>S. i. heterotarsale</i>	—	14	2	15	22	7
<i>Stenonema femoratum</i>	—	—	—	1	—	—
<i>S. modestum</i>	—	27	170	1063	135	—
<i>S. vicarium</i>	—	5	11	371	49	4
<i>Habrophlebia vibrans</i>	10	356	28	2000	1318	42
<i>Leptophlebia cupida</i>	—	2	7	197	—	1
<i>L. johnsoni</i>	—	—	—	2	—	—
<i>Paraleptophlebia adoptiva</i>	2	82	10	278	—	12
<i>P. debilis</i>	1	3	—	—	—	—
<i>P. guttata</i>	—	—	—	1	1	8
<i>P. mollis</i>	—	—	—	—	1	—
<i>P. ontario</i>	—	28	5	224	2	—
<i>P. volitans</i>	1	2	444	198	351	17
<i>Ephemerella dorothea</i>	—	—	—	—	—	1
<i>E. invaria</i>	—	—	—	11	16	1
<i>Eurylophella prudentalis</i>	—	—	—	14	—	—
<i>E. temporalis</i>	—	—	—	17	—	—
<i>E. verisimilis</i>	8	26	—	119	69	8
<i>Serratella sordida</i>	—	—	—	—	8	6
<i>Caenis simulans</i>	—	—	—	—	4	—
<i>Litobrancha recurvata</i>	—	32	—	—	—	—
No. of taxa	8	20	15	29	23	16
Specimens/m ²	—	260	1222	843	1161	—

*Includes *B. pygmaeus* and *B. macdunnoughi*.

short muddy stretch (station 5). Section IV offers a wide variety of habitats and it harbours the richest fauna. *Baetis propinquus* and *Eurylophella prudentalis* represent additional lotic elements in this section, and a number of lentic species, *Callibaetis skokianus*, *Centroptilum album*, *Stenacron i. frontale*, *Stenonema femoratum*, and *Eurylophella temporalis*, occur in the quieter reaches. *Epeorus vitreus* and *Serratella sordida* appear only in the lowermost sections V and VI and represent the riverine species of the fauna. *Paraleptophlebia guttata* and *Ephemerella dorothea*, which are

restricted to the downstream stations on the mainstream, were however collected in some tributaries.

The tributary streams (Table 4) harbour fewer species, and *Siphonurus typicus* is the only additional taxon. The dominant species tend to differ from those of the mainstream and to vary from one stream to the next. Small intermittent streams contain no species (stream gc) or only a few (streams a–e), none of which is abundant; Leptophlebiidae are most commonly encountered and may actually swim in from the mainstream at high water in the spring. Intermittent stream h harbours

TABLE 4. Numbers of each species collected from the tributary streams

	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>e</i>	<i>g</i>	<i>ga</i>	<i>gb</i>	<i>h</i>	<i>i</i>	<i>k</i>	<i>m</i>
<i>Siphonurus typicus</i>	—	—	—	4	6	—	—	—	417	—	—	—
<i>Baetis flavistriga</i>	—	—	1	—	—	22	—	1	—	—	—	—
<i>B. gr. pygmaeus</i>	—	—	—	—	—	134	—	5	—	—	—	—
<i>Centroptilum album</i>	—	—	—	—	—	21	1	1	—	—	—	—
<i>Arthroplea bipunctata</i>	—	—	1	—	—	—	—	2	—	—	—	—
<i>Stenacron carolina</i>	—	—	—	—	—	1	—	—	—	—	7	2
<i>S. i. frontale</i>	—	—	—	—	—	—	—	1	—	—	—	—
<i>S. i. heterotarsale</i>	—	—	—	—	—	—	1	—	—	—	2	2
<i>Stenonema modestum</i>	1	—	—	—	—	—	—	—	—	—	—	—
<i>S. vicarium</i>	—	—	—	—	—	2	—	1	—	5	—	1
<i>Habrophlebia vibrans</i>	—	1	—	—	—	1430	37	313	—	2	6	16
<i>Leptophlebia cupida</i>	—	4	—	—	—	8	1	188	5	8	1	4
<i>Paraleptophlebia adoptiva</i>	—	—	3	—	—	72	5	—	—	1	1	4
<i>P. debilis</i>	—	7	—	—	—	—	1	—	—	54	3	—
<i>P. guttata</i>	—	—	—	—	—	—	—	—	—	1	—	—
<i>P. mollis</i>	—	—	—	—	—	—	—	—	—	—	—	1
<i>P. volitans</i>	—	—	—	—	—	—	—	3	—	—	—	—
<i>Ephemerella dorothea</i>	—	—	—	—	—	—	—	—	—	—	—	1
<i>E. invaria</i>	—	—	—	1	—	18	27	2	3	17	—	—
<i>Eurylophella prudentialis</i>	—	—	—	—	—	—	—	2	—	—	—	—
<i>E. temporalis</i>	—	—	—	—	—	2	—	—	—	—	—	—
<i>E. verisimilis</i>	—	—	—	—	—	25	5	9	—	—	—	—
No. of taxa	1	3	3	2	1	12	8	13	3	7	6	8
Specimens/m ²	—	—	—	—	—	694	158	704	—	88	—	—

TABLE 5. Species collected from lakes and ponds

	Lakes				Beaver ponds, lacs 3 and 4
	Triton	Croche	Tracy	Geai bog	
<i>Siphonurus alternatus</i>	—	—	1	—	—
<i>Callibaetis ferrugineus</i>	4	1	1	—	—
<i>Cloeon rubropictum</i>	15	50	—	—	—
<i>C. simplex</i>	4	—	18	—	—
<i>Stenacron i. canadense</i>	—	6	1	—	—
<i>S. i. frontale</i>	1	35	7	—	—
<i>Stenonema femoratum</i>	14	5	3	—	—
<i>S. modestum</i>	1	—	—	—	—
<i>S. vicarium</i>	1	—	—	—	—
<i>Habrophlebia vibrans</i>	—	1	—	—	—
<i>Leptophlebia cupida</i>	—	1	1	199	—
<i>Eurylophella temporalis</i>	1	8	2	—	—
<i>Hexagenia l. occulta</i>	—	5	—	—	—
No. of taxa	8	9	8	1	0
Specimens/m ²	17	56	14	100	—

a large population of *Siphonurus typicus* which survives the summer drought in small permanent pools in the stream bed. Tributaries *i*, *k*, and *m* are lake outlets and never dry up completely, although the flow may be briefly interrupted, and their fauna tends to be more diverse than in other streams. Stream *g*, the outflow of

lakes Triton and Croche, is the largest of the tributaries, and its fauna is similar to that of the mainstream; its own tributary (station 43) contains an important population of the suspected parthenogenetic form of *Ephemerella invaria*.

Few species inhabit the lakes (Table 5) and many of

these also live in the slower reaches of the streams. Three exclusive lake species, *Callibaetis ferrugineus*, *Stenacron i. canadense*, and *Hexagenia l. occulta*, together with the lentic *Cloeon* spp., *Stenacron i. frontale*, *Stenonema femoratum*, and *Eurylophella temporalis*, make up the list of dominant taxa. The three larger lakes (Croche, Tracy, Triton) have relatively similar faunas and the numbers of species are of the same order. The large burrowing *H. l. occulta* occurs only in Lac Croche. The bog lake (Geai) contains only one species, *Leptophlebia cupida*, albeit in large numbers. The beaver ponds contain no mayflies.

To assess the distribution of the species within the system, similarity and association matrices were constructed from the 60 complete emergence series.

A *Q*-type analysis based on the Steinhaus and the chi-square coefficients reveals a number of clusters. (i) Most of the fast-water stations of section III (8) and IV (9–13, 15, 19–24) of the mainstream show a high degree of similarity (Steinhaus coefficient > 60%). On the basis of the species composition only, regardless of total numbers, two subgroups can be recognized, the upper riffle stations (8–15) and the lower riffle stations (19–24) (chi-square coefficient > 0.988). (ii) At a similar level (Steinhaus coefficient > 60%), the slower stations of the middle section (15, 16), the upper (2, 3), and the lowermost sections of the mainstream (26–30), together with the stations (38–42) of the large tributary stream *g* form a distinct cluster. Here again on the basis of the species composition alone, there is a discrimination of the downstream stations (16, 26, 27, 29) from the upper stations (chi-square coefficient > 0.987). (iii) Other stations show little evidence of similarity and clustering, except on a one to one basis. These are sites with relatively few species, but with differing dominances. The only exception is a clear cluster of the Lac Geai stations (66–69) which all contain only one same species. An *R*-type analysis of descriptors (species) reveals a few distinct species associations: (i) A large group of fast-water species, including *Stenonema vicarium*, *S. modestum*, *Heptagenia pulla*, *Habrophlebia vibrans*, *Paraleptophlebia volitans*, *P. ontario*, *Baetis gr. pygmaeus*, *B. flavistriga*, *B. pluto*, and *Eurylophella verisimilis* (Krylov coefficient = 0.98). (ii) A second smaller association, again of lotic species: *Stenacron i. heterotarsale*, *Leucrocuta hebe*, and *Paraleptophlebia adoptiva* (Krylov coefficient = 0.98). (iii) An association of lake species (Krylov coefficient = 0.98) composed of *Stenacron i. canadense*, *Eurylophella temporalis*, and *Hexagenia l. occulta*. (iv) Smaller associations of only two species are also apparent, but would not be retained on the basis of "the three species minimum criterion" of Krylov (1968). Two are mentioned anyway, as they appear to be of some significance: *Leptophlebia cupida* and *Baetis*

propinquus are characteristic of the slower lotic stations, as are *Cloeon rubropictum* and *Stenacron i. frontale* which also inhabit the lakes (respective Krylov coefficients 0.9966 and 0.9997, hierarchical grouping procedure).

Although the associations group only half of the species, the species involved dominate the communities and represent more than 86% of the specimens.

The *Q* and *R* analyses represent different facets of the same phenomenon; there is indeed a concordance between the clusters of stations and the species associations. There is, for instance, a clear correspondence between the cluster of fast-water stations of the mainstream and the largest species association (*S. vicarium*). The subgroup of the lower riffle in section IV is characterized by the addition of a second association of exclusive species (*S. i. heterotarsale*).

The second cluster of lotic stations, the quieter reaches, has no special species association, but is characterized by differences in proportions and numbers.

The lake species form a distinct association of "exclusive" species (*S. i. canadense*, etc.), and a second "group" of nonexclusive species (*C. rubropictum*, *S. i. frontale*), but the lake stations show little overall similarity, probably because of the small populations and the low number of species in each station.

Distribution of the dominant taxa among habitats along the mainstream stations is illustrated in Fig. 2.

Four taxa, *Baetis gr. pygmaeus*, *Stenonema modes-*

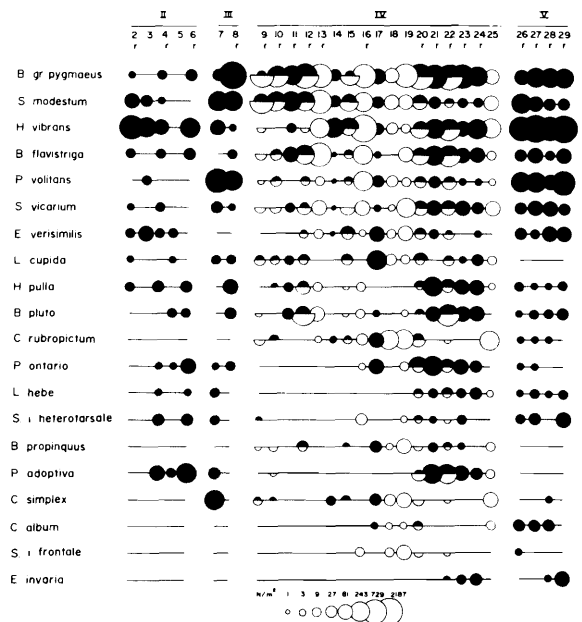


FIG. 2. Distribution of the main taxa among stations in the mainstream; *r* indicates riffles.

tum, *Habrophlebia vibrans*, and *Paraleptophlebia voltans*, are ubiquitous, occurring in most habitats, although with generally higher densities in the fast-water areas.

The majority of species are restricted to riffles or are much more abundant there; these are *Baetis flavistriga*, *B. pluto*, *Stenonema vicarium*, and *Heptagenia pulla*. *Paraleptophlebia ontario*, *P. adoptiva*, *Leucrocuta hebe*, and *Stenacron i. heterotarsale* also belong to the same group, but in section IV they are curiously restricted to the lower riffle (stations 20–24) and nearly absent elsewhere.

The slow regions are characterized by an assemblage of *Eurylophella verisimilis*, *Leptophlebia cupida*, *Cloeon simplex*, *C. rubropictum*, *Centroptilum album*, *Baetis propinquus*, and *Stenacron i. frontale*.

In most respects, Fig. 2 reveals graphically the same species associations and the same habitat distributions as the numerical indices used in the *Q* and *R* analyses, thus confirming these results.

Many congeneric species are spatially segregated: for instance, *Stenacron i. frontale* in lakes and the slow streams, *S. i. canadense* in lakes, and *S. i. heterotarsale* in fast streams; *Baetis propinquus* inhabits slower

waters than its congeners; *Siphonurus alternatus* and *Stenonema femoratum* are typically lake species, while other *Siphonurus* and *Stenonema* are lotic. In other groups, little segregation is evident (*Leptophlebia* spp., *Paraleptophlebia* spp., *Eurylophella* spp.), but temporal segregation is usually important.

Phenology

Figure 3 illustrates the emergence periods of the species collected in 1972 and 1973. The seasonal succession begins in mid-May, and new species continue to appear into August. There is no true autumnal element, although *Paraleptophlebia debilis* starts emerging after the stream temperatures have begun to decrease. The onset of the emergence was generally delayed in 1972 by comparison with 1973, particularly in the early and late species, but the emergence sequence is roughly the same for both years.

Figures 4 and 5 represent respectively for 1972 and 1973 the emergence patterns of the dominant species, as illustrated by data from a station in which each was abundant. *Paraleptophlebia adoptiva*, *Leptophlebia cupida*, *Eurylophella invaria*, *Habrophlebia vibrans*, and *P. ontario* typically have a short emergence which corresponds to Corbet's (1964) and Harper and Magnin's (1971) "synchronous" type. The other species have an emergence of the "extended" type: in some, such as *Stenonema modestum*, *Eurylophella verisimilis*,

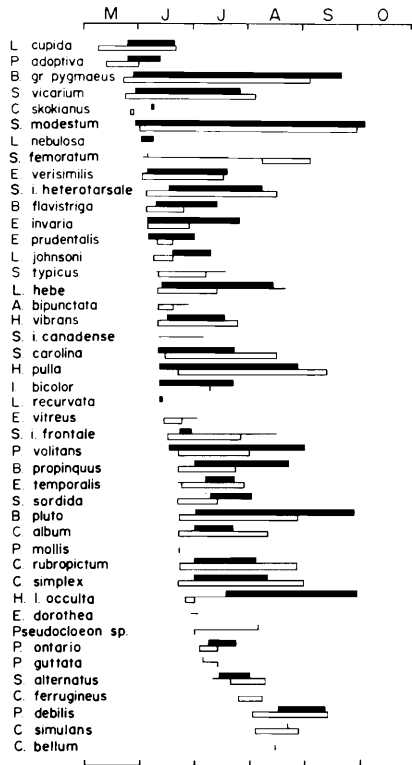


FIG. 3. Seasonal succession of the species based on a pooling of all collections; dark bars represent the 1972 data, white bars the 1973 data.

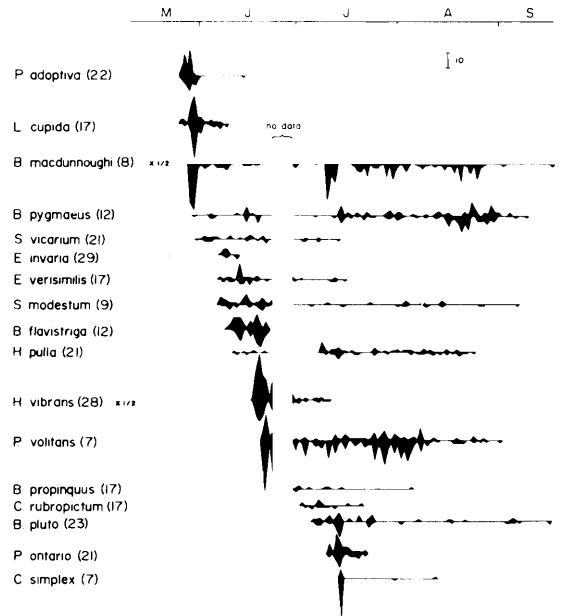


FIG. 4. Representative emergence patterns of major species in 1972; station numbers are indicated in parentheses. The upper part of each graph represents males, the lower part females. The lack of data in late June is due to the disruptions caused by Hurricane Hazel.

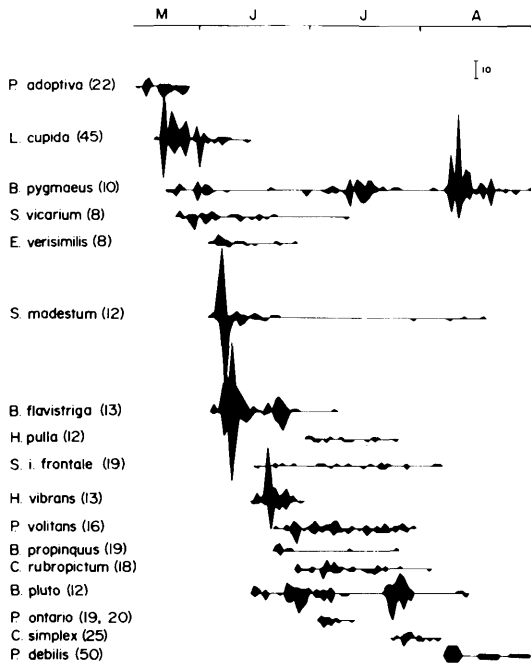


FIG. 5. Representative emergence patterns of major species in 1973; station numbers are indicated in parentheses. The upper part of each graph represents males, the lower part females.

and *Baetis flavistriga*, most of the population emerges within a fortnight, but with a few stragglers over the following weeks or even months. In species such as *Stenonema vicarium*, *Heptagenia pulla*, *Stenacron i. frontale*, *Paraleptophlebia volitans*, and *Cloeon rubropictum*, the emergence is spread over many weeks without any definite mode except perhaps at midemergence. Finally in some species of *Baetis*, the extension of the emergence seems to be related to polyvoltinism: three distinct peaks occur in *Baetis pygmaeus* and *B. macdunnoughi*, and two in *B. pluto*.

Generally the patterns for the same species for both years are similar and the differences can be related to particular weather conditions. Cool temperatures in May 1972 (Back and Harper 1979) led to the late appearance of the early species (*P. adoptiva*, *L. cupida*), but also to a more synchronized emergence. On the other hand, the cool wet summer of 1972 obscured the patterns of the later emerging species, particularly the polyvoltine *B. pygmaeus* and *B. pluto*.

Discussion

Species richness

Our record of some 40 stream species and a dozen lake species fall within the order of magnitude of other similar inventories (Sprules 1947; Oliver and Danks 1975). Evidently, mayflies are primarily adapted to

running-water habitats where the primitive species live and where they reach their greatest diversity among the manifold available habitats. Few groups are restricted to lakes, and indeed most of the lentic species can also inhabit the slower sections of streams.

Density

The average yield of 1000 to 1200 adults/m² per year in some stream stations is higher than usual, particularly if the maximum yield of 2816 in trap 15 is taken into account. Sprules (1947) in a similar system records a maximum of 3604 (as 3037/yard² (1 yard = 0.914 m)) and Ide (1940) collected up to 6500/m² in southern Ontario. Indeed in our own stream, during a previous study (Harper and Magnin 1971) up to 6032 mayflies/m² were recorded. More commonly, values of the order of 300–1500 (in several German and Austrian streams (Illies 1971, 1978, 1980; Sandrock 1978)), 600 (Oregon (Kraft 1964)), and 300 (Alberta (Boerger and Clifford 1975)) are encountered. In lakes, yields are usually much lower and our results are particularly so, but this may be a general characteristic of the unproductive Laurentian lakes. Comparative values from other areas include 40/m² in Lake Heming (Flannagan and Lawler 1972), 423/m² in Dundas Marsh (Judd 1953), 80–800/m² in oligotrophic Lake Pääjärvi (Paarsivirta 1975), and 392–2635/m² in a small Scottish loch (Morgan and Waddell 1961). Such values, while indicative of the productivity of a water body, are subject to much variation from year to year, by a factor of up to seven (Illies 1978).

Bélanger (1978), who compared bottom samples of nymphs (taken by conventional methods) and our emergence trap yields in 1973, calculated an average standing crop of nymphs which was smaller than the yield of adults by a factor of two; Ide (1940) had made similar observations in southern Ontario. These discrepancies are no doubt due to the still inadequate sampling methods for immatures or, to some extent, the migration of mature nymphs prior to emergence. The mean standing crop reported for mayflies in the Holarctic is 375/m² and the maximum is 1448 (Clifford 1980).

Species zonation

The distinction between stream and lake species is well documented; however, a large number of lentic species inhabit both the littoral areas of lakes and the slower reaches of streams.

There does not appear to be a distinct headwater fauna in this instance, except for *Siphonurus typicus* in stream *h* and *Paraleptophlebia debilis* in a few others. This may be due to the fact that the streamlets we investigated are either the outlets of small lakes and ponds, or runoff-fed streams; none is truly spring fed. In the spring-fed West Creek on Mont Saint-Hilaire in south-

ern Quebec, Mackay (1969) found a very typical fauna of nine species (mainly *Ameletus* spp., *Paraleptophlebia moerens*, *Ephemerella dorothea*, *Eurylophella funeralis*) only one of which occurs in our streams, in small numbers. By contrast, the fauna of our headwater streams is composed essentially of the most tolerant or dispersive species of the mainstream, particularly Ephemerellidae, Leptophlebiidae, and Baetidae, with the addition of species characteristic of temporary habitats, such as *Arthroplea bipunctata*; Bogoescu and Rogoz (1973) noted a similar faunal assemblage in Balkan streamlets. Needham (1928) suggested that, as a rule, small streams are most productive in benthic invertebrates per unit area than larger streams; this is probably incorrect when headwaters are taken into account, and Sprules (1947) and Kamler (1962) have shown that middle-sized streams are most productive.

The lower reaches of the mainstream appear poorer and the number of species decreases despite the addition of riverine elements, such as *Serratella sordida* and *Epeorus vitreus*.

The bog Lac Geai supports a large population of *Leptophlebia cupida*, its sole mayfly species. A similar situation occurs in European bogs, where *Leptophlebia vespertina* is the equivalent species (McLachlan and McLachlan 1975). Both species are ubiquitous and capable of supporting the humic and acid waters (Bagge and Salmela 1968).

Neither of the two beaver ponds harboured any mayflies; this is somewhat unexpected, since Sprules (1947) had shown that the damming of a stream by beavers had caused a marked reduction in the mayfly populations, but not their elimination. On the other hand, this may be a phenomenon common to older beaver ponds which are depauperate in some taxa (G. Pritchard, University of Calgary, personal communication).

The other lakes support similar faunas; despite the small numbers collected, there appear to be differences in the frequencies of the species between the lakes, and some species are restricted to a particular lake (e.g., *Hexagenia l. occulta* in Lac Croche).

Spatial distribution

The distribution of the species among the various habitats (Fig. 3) and the comparison of the stations on the basis of their respective faunas provide a picture which is in accord with the present knowledge of the environmental requirements of the species (Leonard 1965; Bergman and Hilsenhoff 1978; Flowers and Hilsenhoff 1978). The only unusual feature is the difference observed between the two riffles in mainstream section IV; indeed the lower riffle harbours large populations of species (*Paraleptophlebia adoptiva*, *Leucocuta hebe*, and *Stenacron i. heterotarsale*) not

found in the upper riffle. Given the proximity of the two riffles (about 400 m) and their overall physiographical similarity, the situation of the upper riffle as a lake outlet is doubtless of significance; lake outlets have long been recognized as special habitats with a specialized community (Illies 1956).

Temporal segregation

Most congeneric species are temporally segregated, for instance the various species of *Stenonema* (*vicarium*, *modestum*) and of *Paraleptophlebia* (*adoptiva*, *volitans*, *ontario*, *debilis*), and the species and cohorts of *Baetis* (*pygmaeus*, *flavistriga*, *propinquus*, *pluto*). This is generally the case in mayflies, but exceptions have been reported (Langford 1975): Many congeners are also spatially segregated; this is the case of the three subspecies of *Stenacron interpunctatum* which behave here as true species.

Emergence types

From investigations in the same stream system, Harper and Magnin (1971) postulated that emergence patterns in mayflies fell into two fundamental types. More recent studies and the present data allow us to update this discussion. (i) There is a very distinct spring fauna composed of univoltine and semivoltine species (and the early cohort of some polyvoltine species) which emerge soon after the water warms up in the spring. Typically their emergence is very synchronous, especially in climates with well-marked seasons such as ours. *Paraleptophlebia adoptiva* and *Leptophlebia cupida* are perfect examples. (ii) The summer species must first complete their nymphal growth and start emerging in early and midsummer; their emergence pattern tends to be more dispersed, probably because water temperatures are then more stable. This group is far from homogenous and distinctions are necessary.

The more characteristic species start to emerge near or after the summer solstice, during the period of maximum water temperature. The environmental conditions are stable and the emergence is spread over a long period with a maximum near the middle of the period. *Paraleptophlebia volitans* belongs here.

Also included are species exhibiting a pattern intermediate between the two types: the emergence is extended, but the maximum occurs early. This appears to be the case in our data on *Stenonema modestum* (see however data in Harper and Magnin (1971) showing a pattern with a central maximum).

There is the particular case of species which, although univoltine, show a distinct bimodal pattern, viz., *Isonychia bicolor* in Harper and Magnin (1971). Such is also the case of *Ameletus inopinatus* in Great Britain in which two cohorts are separated by an interruption of hatching during the winter (Gledhill 1959). A division

of the population into cohorts has been used to explain complex growth or emergence patterns in species which otherwise appear to be univoltine; in some instances, tendencies towards polyvoltinism are demonstrated. The European *Ecdyonurus torrentis* and the North American *Stenacron interpunctatum* are thought to complete the growth of three cohorts in 2 years (Harker 1952; McCafferty and Huff 1978).

There are further the polyvoltine species which are spring species for their first generation, then complete one or more summer generations, such as *Baetis pygmaeus* and *B. macdunnoughi*. Others undergo only summer generations, e.g., *Baetis pluto*. In the simplest situation, the cohorts and generations are discrete and successive, but in recent analyses many species have been shown to possess overlapping cohorts, for instance *Baetis lutheri* and *B. alpinus* in Austria which can mature 10–11 cohorts in 30 months (Humpesch 1979). Furthermore, under special circumstances, polyvoltine species can become univoltine (Illies and Masteller 1977); in our stream, *Baetis flavistriga* is univoltine, while in Wisconsin it is said to be bivoltine (Bergman and Hilsenhoff 1978).

Finally there are the autumnal species which start emerging when both photoperiod and temperature are declining, such as *Paraleptophlebia debilis*. Autumnal species are little affected by climatic conditions and emerge in a similar pattern each year (Thibault 1971). The maximum occurs early in the emergence period, but a late maximum is described for *Paraleptophlebia guttata* (Carlson 1973).

Emergence in mayflies is thus more plastic than would appear at first glance and much could be gained from the accumulation of additional data from areas different from the cold temperate regions where most studies have been conducted up to now. Patterns may even vary from one site to the next in the same area for the same species (for example, *Siphonurus lacustris* in Norway (Brittain 1979)).

There is also an indication in Brittain's (1979) data that there may be an inverse relation between the synchrony of the emergence and the density of the local population; Sprules' (1947) data on *Paraleptophlebia debilis* point to the same phenomenon. This is certainly worth investigating.

Variations in the emergence patterns of individual species over a wide geographical gradient are poorly known; *Habrophlebia vibrans* which in our stream possesses one of the shortest and most synchronous emergences has an extended emergence of some 13–17 weeks in South Carolina (Carlson 1973).

Emergence patterns thus reflect the overall success and strategy of the species and cannot be studied irrespective of the other life-cycle features. The syn-

chronous and the extended patterns reflect two different life-history strategies and, particularly if they are related in some way to population density, they become parameters of significant ecological interest.

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