Hydrobiologia **199**: 43–64, 1990.

Associations of aquatic insects (Ephemeroptera, Plecoptera, and Trichoptera) in a network of subarctic lakes and streams in Québec

P. P. Harper
Département de sciences biologiques, Université de Montréal, C. P. 6128, Succ. 'A', Montréal, QC. Canada H3C 3J7

Received 12 September 1988; in revised form 16 June 1989; accepted 5 July 1989

Key words: emergence, species associations, subarctic region, lakes, streams, Ephemeroptera, Plecoptera, Trichoptera

Abstract

As part of an impact assessment of large hydroelectric projects in the James Bay drainage in Northwestern Québec, the aquatic insect communities were studied in a network of rivers, lakes and streams during the summer of 1975. Thirty-eight emergence traps operated over the ice-free season yielded 10 888 insects (5559 Ephemeroptera, 2817 Plecoptera, and 2512 Trichoptera), representing 148 species (respectively 44, 18, and 86), most of temperate and boreal afinities. There was no arctic element.

Similarity analyses and clustering procedures on the emergence series revealed the existence of distinct insect communities in the river (fast and slow sections), the streams (fast and slow), the lakes and the bogs, each characterized by a particular assemblage of species. Many of the species were more or less ubiquitous and differences between communities were marked more by changes in the dominance of the species and differences in the frequency distributions, than absolute shifts in the species lists. The yields in the traps set in fast water were much greater than those in slow running water, and these in turn greater than those of standing water.

By comparison with more southerly sites, the seasonal succession of species was retarded in the spring and early summer, but was not shortened appreciably in the fall. The usual emergence patterns associated with these taxa was observed, namely those of spring, summer and autumn species.

Introduction

The middle latitudes of the Québec-Labrador Peninsula possess an enormous potential for the generation of hydro-electrical power and have been subjected over the last decades to large-scale projects. Such developments are bound to continue, given the ever-increasing need for 'clean' energy in the Northeastern parts of the continent.

Although most of the earlier projects proceeded without much evironmental consideration, a considerable effort was made to secure baseline data during the construction of the hydro-electrical complex on the James Bay drainage begun in the early 1970s. Among such endeavours, a study was initiated in the summer of 1975 to characterize the insect communities in a wide array of aquatic habitats in the immediate vicinity of the La Grande 2 Reservoir, then under construction. The study was conducted by the Société d'Energie de la Baie James (S. E. B. J.) and involved sampling of both benthic larvae and emerging adults. A summary description of the benthos has been published (Magnin, 1977), but the adults were never studied.

This paper deals therefore with the adult stages of three orders of aquatic insects, Ephemeroptera, Plecoptera, and Trichoptera; previous studies which include material from this project are those of Pilon *et al.* (1978) on Odonata, and of Landry & Harper (1985) on Empdidae (Diptera). The objectives are to characterize the species associations inhabiting these subarctic biotopes and to describe the seasonal succesion of the species. These data are particularly relevant given the dearth of information on the ecology of aquatic insects in subarctic latitudes, especially in Eastern North America. They are also especially important because of the radical transformation the aquatic habitats are being subjected to via resource development and/or environmental pollution.

Study area

The study site was the upper drainage of Rivière du Castor, a tributary of James Bay some 40 km south of La Grande Rivière (Fig. 1), southwest of the LG2 dam, about 70 km from the coast of the Bay (Fréchette, 1976; Pilon *et al.*, 1978).

The area belongs to the Eastmain Lowlands

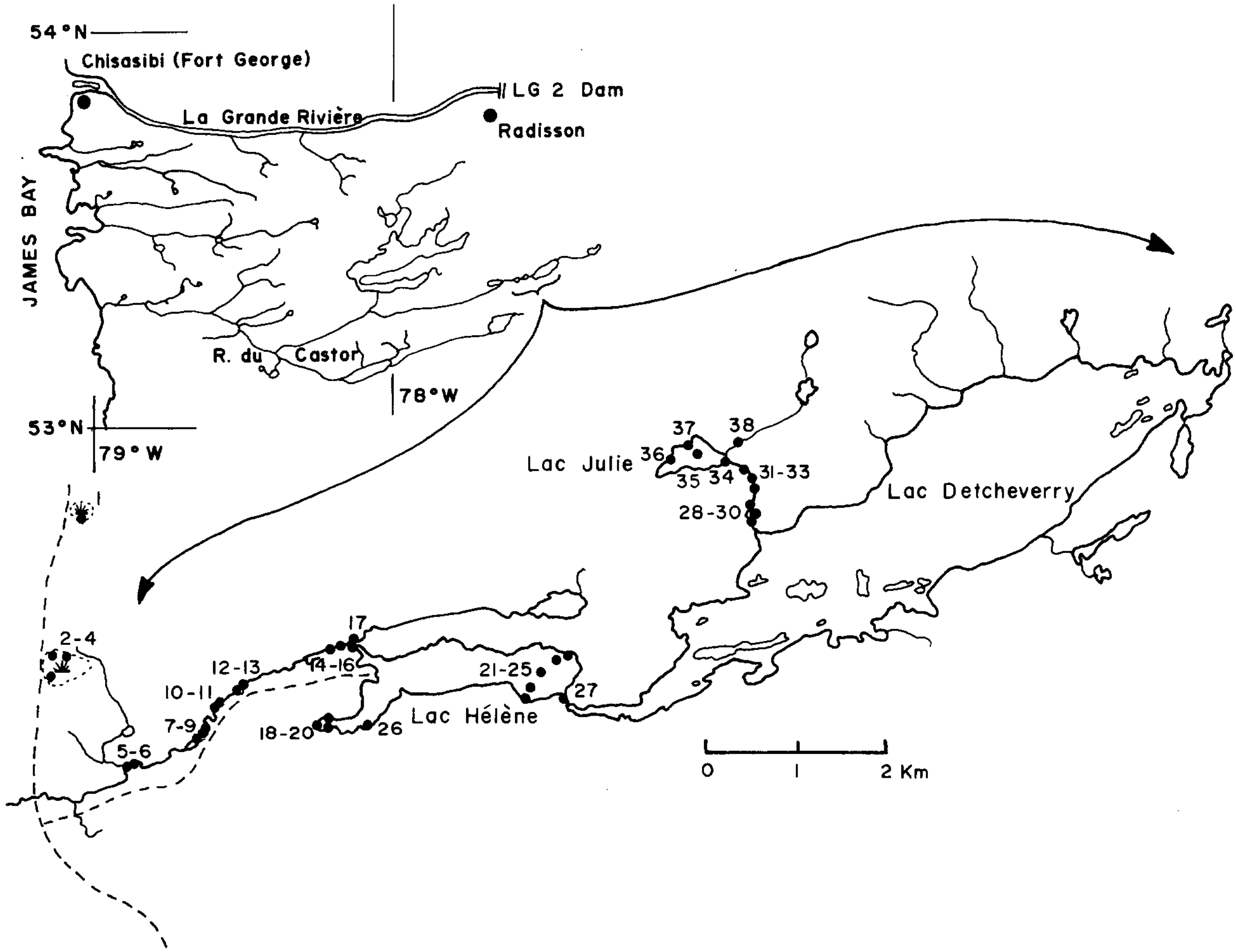

Fig. 1. Map of study area with locations of the 38 sampling stations. The upper map shows position of study area in river basin.

physiographical unit. The subsoil is gneiss and granite covered with moraine deposits and sand and silt from the Pleistocene Tyrell Sea. The climate is humid middle subarctic: a mean annual temperature of -3 °C, about 1200 degree-days (above 5 °C), and 80 frost-free days. Annual precipitation averages 60 cm, half of it as snow. Snow can be expected every month of the year, but is least likely in August. The vegetation is dominated by black spruce (*Picea mariana*) with mosses and Labrador tea (*Ledum groenlandicum*); the tree cover is less than 50% and bogs represent about 5% of the ground surface.

At the point of study, the river (stations 5–16) had an average annual flow of 1 m/s; its mean depth varied from 0,5 to 1,2 m, and its width from 5 to 12 m. The substrate ranged from slow silty reaches (5, 6, 12, 13) to fast water over cobbles and stones (7–9), with sandy and gravelly stretches (10–11). Stations 14–16 were in the lake outlet.

Two reticulated bogs were sampled. One (station 1) dominated by sedges (*Carex*) and buckbean (*Menyanthes trifoliata*) had an area of 1.8 ha and was 30 to 50 cm deep; the pH varied between 5.4 and 6.4. Temperature maxima regularly reached 20 ° and more from mid-June to mid-August, with an absolute maximum of 26 ° on several occasions. The second bog (stations 2–4) was larger (8.3 ha), more acidic (pH 3.5 to 4.3), and dominated by sphagnum and pond lilies (*Nuphar*). Temperature maxima were over 20 °C during the last two weeks of July and reached 28 ° on one occasion. Conductivity was low (25 μS/cm), but organic carbon high (26.8 mg/l). Both bogs froze to the bottom during winter (Magnin, 1977).

Lac Hélène (stations 18–26) has an area of 120 ha and its greatest depth is 8 m; the outlet is blocked by a beaver dam. The water temperature rose rapidly in May and reached its peak of 21 °C in the second half of July and then steadily declined until late October when the lake froze over; there was no stable thermocline, though deeper waters were sometimes 1–4 ° colder than the surface. Oxygen did not fall below 70% saturation. The conductivity was of the order of 38 μS/cm, pH close to neutrality (6.7), and organic carbon moderately abundant (8.1 mg/l) (Magnin, 1977). Traps were set in a small shallow bay covered with pond lilies (18–19 near shore, 20 at a depth of 1 m), along the shore over dead leaves and grasses (26), and across the deepest part of the lake (21–25, 2 littoral traps, 2 at mid-depth and one at maximum depth).

The northern tributary (station 17) of Lac Hélène is a small dark-water stream draining bog areas and a small pond. A trap was set over a slow silty section.

The eastern tributary (station 27) is the main course of the river; it drains Lac Detcheverry and forms a 500 m braided channel between the two lakes. The substrate is of cobbles and boulders.

Lac Julie (stations 34–37) is a small (13 ha) shallow (less than 2.5 m) pond; its substrate includes both rock outcrops and sandy bottoms. The thermal characteristics paralleled those of Lac Hélène. The mean pH was 6.4, the conductivity 34 μS/cm, and the organic carbon 14,1 mg/l. The maximum temperature was 23 °C in the middle and 28 near the shore. Its tributary (station 28) had a mean flow of some 0.014 m^3/s and drained two small ponds in a boggy area and was interrupted by a small beaver dam. The outlet (stations 28–33) is at first a rapid stream (31–33), then slows down and widens into a small pond (28–30).

Methods

Specimens were collected with emergence traps of the model of Harper & Magnin (1971) with a sampling surface of 1 m^2 and covered with fine muslin, except for traps 27, 28, 31, 32, 43, 36–36 which were fitted with standard mosquito netting (8 openings/cm). The traps were emptied with an aspirator either daily (traps 1–21, 25–27) or every second day (22–24,28–38), from May 25 (June 7 at Lac Julie and area) to October 10, 1975, except on Sundays.

The traps were set on the river (traps 5–17) about 2 weeks after the spring ice run. On Lac Hélène, the traps were installed within 2 days of the disappearance of the ice, but on Lac Julie and associated streams, a period of up to 3 weeks elapsed.

Similarity analyses were performed on the data sets using the Steinhaus index (S_{17} of Legendre & Legendre, 1979): $S = 2W / (A + B)$, where W is the sum of minimum abundances of each species in each pair of emergence series, an A and B are respectively the sums of abundances of all species in each series. Clustering of series resulted from hierarchial intermediate (50%) linkage procedures and were processed on the Université de Montréal CDC-Cyber computer, using the 'Prologiciel r' statistical package (Vaudor, 1984). The Steinhaus index was chosen because it attributes similarity to two communities on the basis of shared species, but of equal density (e. g. numbers/m^2).

Table 1. Ephemeroptera collected in the various stations.

Stations	River 5–13	Outlet 14–16	Stream 17	Hélène 18–26	River 27	Stream 28–33	Julie 34–37	Stream 38
SIPHLONURIDAE								
Siphlonurus alternatus (Say)								
Siphlonurus quebecensis (Provancher)								
Siphlonurus rapidus McD.								
METRETOPODIDAE								
Metretopus borealis Eaton	2	7	–	1	–	–	–	–
Siphloplecton basale (Walker)	11	129	–	80	1	–	1	–
HEPTAGENIIDAE								
Arthroplea bipunctata McD.	5	11	8	–	–	2	37	–
Epeorus vitreus (Walker)	17	–	–	–	–	–	–	–
Heptagenia pulla (Clemens)	23	–	–	–	11	35	–	–
Leucrocuta hebe (McD.)	6	–	–	2	–	–	–	–
Stenacron i. canadense (Walker)	11	–	–	–	–	–	–	–
Stenonema femoratum (Say)	–	–	–	1	2	–	–	–
Stenonema vicarium (Say)	38	–	–	–	–	–	–	–
LEPTOPHLEBIIDAE								
Habrophlebia vibrans Needham	1	–	–	–	–	–	–	–
Leptophlebia cupida (Say)	48	–	–	–	–	–	–	2
Leptophlebia johnsoni McD.	4	8	6	1	–	6	8	–
Leptophlebia nebulosa (Walker)	–	235	1	14	–	24	153	1
Leptophlebia spp.	–	–	–	–	–	–	–	18
Paraleptophlebia adoptiva (McD.)	74	–	–	1	–	–	–	–
Paraleptophlebia debilis (Walker)	301	10	4	14	3	878	4	3
Paraleptophlebia mollis (Eaton)	14	–	–	–	5	–	–	–
EPHEMERELLIDAE								
Ephemerella aurivillii Bengtsson	48	–	–	–	–	–	–	–
Ephemerella excrucians Walsh	12	–	–	–	–	–	–	–
Ephemerella invaria (Walker)	10	–	–	–	24	–	–	–
Ephemerella needhami McD.	4	–	–	–	–	–	–	–
Ephemerella septentrionalis McD.	6	–	–	–	–	–	–	–
Ephemerella spp.	48	1	–	–	–	–	–	–
Eurylophella prudentalis (McD.)	1	–	–	–	–	–	–	–
Eurylophella temporalis (McD.)	4	11	–	5	–	5	15	–
Eurylophella verisimilis (McD.)	174	45	–	29	1	–	–	–
Eurylophella spp.	8	3	–	6	–	–	–	–

Table 1. Ephemeroptera collected in the various stations. (continued)

Stations	River 5–13	Outlet 14–16	Stream 17	Helene 18–26	River 27	Stream 28–33	Julie 34–37	Stream 38
BAETIDAE								
Acerpenna pygmaea (Hagen)	104	1	–	–	8	4	–	2
Baetis brunneicolor McD.	–	–	–	–	–	3	–	19
Baetis flavistriga McD.	12	–	–	–	1	11	–	–
Baetis propinquus (Walsh)	17	1	–	–	–	–	–	–
Baetis tricaudatus Dodds	17	–	–	–	5	–	–	–
Baetis spp.	510	17	3	5	276	79	1	–
Callibaetis ferrugineus (Walsh)	–	–	–	–	–	–	47	1
Centroptilum album McD.	62	12	–	26	1	48	–	38
Centroptilum rufostrigatum McD.	77	2	–	6	–	–	–	–
Cloeon rubropictum McD.	21	40	1	73	1	–	–	–
Pseudocloeon parvulum McD.	9	–	–	–	–	–	–	–
Pseudocloeon sp. 1	–	–	–	–	–	1	–	–
EPHEMERIDAE								
Ephemera simulans Walker	–	23	–	81	5	–	–	–
Hexagenia l. occulta Walker	1	–	–	1	–	2	–	–
Litobrancha recurvata (Morgan)	71	93	32	–	–	–	–	–
CAENIDAE								
Caenis forcipata McD.	–	–	–	18	–	–	–	–
Caenis simulans McD.	–	–	–	–	–	3	–	–
BAETISCIDAE								
Baetisca laurentina McD.	–	1	–	–	–	–	–	–
Total	1882	1065	86	444	364	1101	532	85
Number of species	35	21	10	19	13	13	9	8
Nb per square metre	209.4	355	86	49.4	364	183.5	133	85

Results

The data pertaining to each taxocene are listed in Tables 1–3. Each set was subjected to an independent similarity analysis and the emergence series (or stations, i. e. the total emergence from one station over the season) were grouped into clusters. There are broad agreements between the clusters generated from the three data sets. The clusters were then used to define communities and to describe the species associations. Phenology is illustrated in four of the habitats, the bogs (Fig. 2), the river (Fig 3), the streams (Fig. 4), and Lac Julie (Fig. 5).

The bogs

The bog stations (1–4) form an independent cluster characterized by the caddisfly fauna

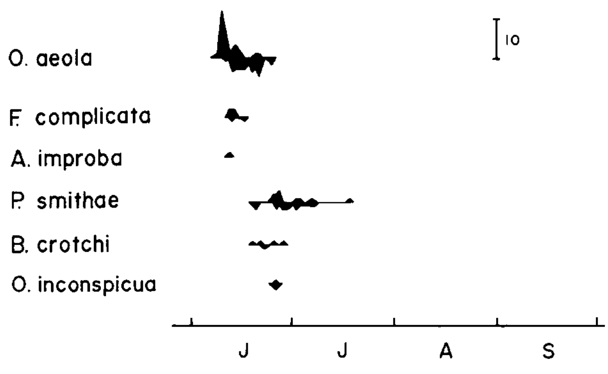

Fig. 2. Emergence patterns of Trichoptera in the bogs (stations 1–4, data pooled). Upper part of each diagram represents males, lower part females.

Table 2. Plecoptera collected in the various stations.

Stations	River 5–13	Outlet 14–16	Stream 17	Hélène 18–26	River 27	Stream 28–33	Julie 34–37	Stream 38
NEMOURIDAE								
Amphinemura linda (Ricker)	3	–	–	–	3	53	1	–
Nemoura trispinosa Claassen	–	–	–	–	–	15	–	3
Podmosta macdunnoughi (Ricker)	580	1	1	–	–	–	–	–
Shipsa rotunda (Ricker)	36	14	1	2	–	–	–	–
CAPNIDAE								
Paracapnia sp.	1	–	1	–	–	–	–	–
LEUCTRIDAE								
Leuctra ferruginea Walker	1502	1	1	–	2	3	–	1
Leuctra tenella Provancher	–	–	1	–	–	–	–	–
Leuctra tenuis (Pictet)	–	–	–	55	46	–	–	–
PTERONARCYIDAE								
Pteronarcys dorsata (Say)	2	–	–	–	–	–	–	–
PERLIDAE								
Paragnetina media (Walker)	15	–	–	–	7	–	–	–
PERLODIDAE								
Isogenoides frontalis (Newman)	5	–	–	–	5	–	–	–
Isoperla bilineata (Say)	1	–	–	–	–	–	–	–
Isoperla cotta Ricker	32	–	–	–	–	–	–	–
Isoperla frisoni Illies	250	–	–	–	–	–	–	–
Isoperla lata Frison	4	–	–	–	–	–	–	–
Isoperla marlynia N. & C.	43	–	–	–	–	–	–	–
Isoperla transmarina (Newman)	98	–	1	3	21	–	–	–
CHLOROPERLIDAE								
Alloperla atlantica Baumann	4	–	–	–	–	–	–	–
Total	2576	16	5	60	84	71	1	4
Number of species	15	3	5	3	6	3	1	2
Nb per square metre	286.2	5.3	5	6.7	84	11.8	0.3	4

(Table III), as no mayfly nor stonefly was collected. The dominance of Polycentropodidae (*Polycentropus smithae*) and Phryganeidae (*Fabria complicata*, *Agrypnia improba*, and *Banksiola crotchi*) is noteworthy, as is the importance of the microcaddisfly *Oxyethira aeola*. *Fabria complicata* is a rare northern element (Wiggins, 1961).

The number of species is small (6) and these succeed each other rapidly in early summer (Fig. 2), so much so that no species emerges after mid-July, despite the fact that favourable weather conditions continue into late September. All species have short emergence periods. A distinct protandry is apparent only in *O. aeola*. The sedge bog (station 1) is more productive (69 insects/m^2) and is dominated by *O. aeola* (90%); *P. smithae* and *Oecetis inconspicua* are also present. The sphagnum bog (stations 2–4) has a more varied fauna (5 species), but its productivity is low (10–19 insects/m^2). The dominant species are *P. smithae* (61%), *F. complicata* (22%), and *B. crotchi* (12%). Stations 3 and 4 are the most

Table 3. Trichoptera collected in the various traps.

Stations	Bog 1–4	River 5–13	Outlet 14–16	Stream 17	Hélène 18–26	River 27	Stream 28–33	Julie 34–37	Stream 38
RHYACOPHILIDAE									
Rhyacophila carolina Banks	–	13	–	–	–	–	–	–	–
Rhyacophila fuscula (Walker)	–	69	–	–	–	46	–	–	–
Rhyacophila invaria (Walker)	–	73	–	–	–	–	–	–	–
GLOSSOSOMATIDAE									
Glossosoma nigrior Banks	–	14	–	–	–	–	–	–	–
PHILOPOTAMIDAE									
Dolophilodes distinctus (Walker)	–	34	–	–	–	–	–	–	–
PSYCHOMYIIDAE									
Lype diversa (Banks)	–	16	1	–	–	–	–	–	–
HYALOPSYCHIDAE									
Phylocentropus lucidus (Hagen)	–	–	–	–	–	–	–	–	2
Phylocentropus placidus (Banks)	–	79	8	99	13	–	1	18	–
POLYCENTROPODIDAE									
Neureclipsis crepuscularis (Walker)	–	14	–	–	2	–	–	–	–
Neureclipsis valida (Walker)	–	5	50	26	1	–	–	–	–
Polycentropus albipunctus (Banks)	–	–	1	2	5	–	–	130	–
Polycentropus cf. cinereus Hagen	–	4	–	–	3	–	–	–	–
Polycentropus flavus (Banks)	–	2	1	–	–	–	–	–	–
Polycentropus iculus Ross	–	25	–	–	–	–	–	–	–
Polycentropus maculatus Banks	–	–	–	–	–	–	2	–	–
Polycentropus pentus Ross	–	–	–	–	–	–	2	–	–
Polycentropus remotus Banks	–	2	1	7	2	–	–	31	–
Polycentropus smithae Denning	27	–	–	–	1	–	–	–	–
HYDROPTILIDAE									
Oxyethira aeola Ross	62	112	–	1	–	–	–	–	–
Oxyethira allagashensis Blickle	–	13	–	–	–	–	42	–	–
Oxyethira rivicola Blickle & Morse	–	3	–	–	–	–	–	–	–
HYDROPSYCHIDAE									
Cheumatopsyche campyla Ross	–	–	–	–	–	2	–	–	–
Cheumatopsyche gracilis (Banks)	–	86	–	–	–	2	–	–	–
Hydropsyche alhedra Ross	–	13	–	1	–	–	–	–	–
Hydropsyche alternans (Walker)	–	–	18	8	1	2	–	–	–
Hydropsyche slossonae Banks	–	–	–	–	–	2	–	–	–
Hydropsyche sparna Ross	–	38	–	–	–	–	–	–	–
PHRYGANEIDAE									
Agrypnia colorata (Milne)	–	–	–	–	3	1	–	–	–
Agrypnia deflata (Milne)	–	2	30	8	–	–	–	1	–
Agrypnia improba (Hagen)	1	–	–	1	7	–	–	33	–
Agrypnia straminea Hagen	–	–	6	–	1	–	–	–	–
Banksiola crotchi Banks	5	–	1	–	–	–	–	1	–
Fabria complicata (Banks)	9	–	1	–	–	–	–	–	–
Oligostomis pardalis (Walker)	–	6	–	–	–	–	–	–	–

Table 3. Trichoptera collected in the various traps. (continued)

Stations	Bog 1–4	River 5–13	Outlet 14–16	Stream 17	Hélène 18–26	River 27	Stream 28–33	Julie 34–37	Stream 38
Phryganea cinerea Walker	–	–	–	1	1	1	–	2	–
Ptilostomis ocellifera (Walker)	–	1	–	–	–	–	2	–	–
Ptilostomis semifasciata (Say)	–	6	–	–	–	–	2	–	–
LIMNEPHILIDAE									
Anabolia bimaculata (Walker)	–	10	6	1	1	–	17	–	–
Anabolia consocia (Walker)	–	–	–	–	–	–	73	–	4
Arctopora pulchella (Banks)	–	–	1	–	1	–	–	–	–
Asynarchus curtus (Banks)	–	5	–	2	1	–	5	–	–
Glyphopsyche irrorata (Fabricius)	–	6	–	–	–	–	2	–	–
Hesperophylax designatus Banks	–	–	2	–	20	2	–	–	–
Hydatophylax argus (Harris)	–	10	–	–	–	–	–	–	–
Limnephilus argenteus Banks	–	1	2	–	6	–	1	5	–
Limnephilus canadensis Banks	–	–	–	–	–	1	162	–	11
Limnephilus externus Hagen	–	5	1	1	–	–	1	–	–
Limnephilus extractus Walker	–	–	1	–	1	–	–	–	–
Limnephilus infernalis (Banks)	–	–	1	–	2	–	–	11	–
Limnephilus minusculus (Banks)	–	2	–	–	–	–	–	–	–
Limnephilus nimmoi Roy & Harper	–	–	–	–	–	–	–	4	–
Limnephilus ornatus Banks	–	1	–	–	–	–	–	–	–
Limnephilus parvulus (Banks)	–	1	–	–	–	–	–	–	–
Limnephilus rhombicus (Linnaeus)	–	16	–	2	–	–	–	–	1
Neophylax aniqua Ross	–	1	–	–	–	–	–	–	–
Neophylax concinnus Maclachlan	–	8	1	–	–	–	–	–	–
Neophylax nacatus Denning	–	13	–	–	–	–	–	–	–
Neophylax oligius Ross	–	7	–	–	–	–	–	–	–
Onocosmoecus unicolor (Banks)	–	12	–	6	–	–	–	–	–
Phanocelia canadensis (Banks)	–	–	–	–	–	1	–	–	–
Platycentropus amicus (Hagen)	–	6	4	3	–	–	–	–	–
Platycentropus radiatus (Say)	–	–	2	–	–	–	–	–	–
Psychoglypha subborealis (Banks)	–	–	–	–	–	–	3	–	6
Pycnopsyche guttifer (Walker)	–	261	1	–	4	–	–	–	–
Pycnopsyche limbata (Maclachlan)	–	63	2	2	–	–	–	–	9
LEPTOCERIDAE									
Ceraclea albosticta (Hagen)	–	2	–	–	–	–	–	–	–
Ceraclea ancylus (Vorhies)	–	1	–	–	–	4	1	–	–
Ceraclea annulicornis (Stephens)	–	2	1	–	–	–	–	–	–
Ceraclea cancellata (Betten)	–	–	–	–	–	–	2	–	–
Ceraclea diluta (Hagen)	–	12	–	–	–	–	–	–	–
Ceraclea excisa (Morton)	–	2	–	–	1	–	32	–	–
Ceraclea resurgens (Walker)	–	9	–	–	–	–	–	–	–
Mystacides interjecta (Banks)	–	–	–	–	2	–	–	–	–
Mystacides sepulchralis (Walker)	–	7	6	–	2	2	–	–	–
Oecetis immobilis (Hagen)	–	–	–	–	2	–	–	–	–
Oecetis inconspicua (Walker)	5	1	1	–	2	–	–	–	–
ODONTOCERIDAE									
Psilotreta indecisa (Walker)	–	7	–	–	–	–	–	–	–

Table 3. Trichoptera collected in the various traps. (continued)

Stations	Bog 1–4	River 5–13	Outlet 14–16	Stream 17	Hélène 18–26	River 27	Stream 28–33	Julie 34–37	Stream 38
MOLANNIDAE									
Molanna blenda Sibley	–	21	–	–	–	–	–	1	4
Molanna flavicornis Banks	–	2	–	–	4	–	–	–	–
Molanna tryphena Betten	–	1	–	–	–	–	–	–	–
LEPIDOSTOMATIDAE									
Lepidostoma modestum (Banks)	–	4	–	–	–	–	–	–	–
Lepidostoma prominens (Banks)	–	1	–	1	–	–	–	–	1
Lepidostoma strophis Ross	–	3	7	–	–	–	–	–	–
Lepidostoma swannanoa Ross	–	82	–	–	–	4	–	–	–
Lepidostoma unicolor (Banks)	–	39	–	–	–	–	–	–	–
HELICOPSYCHIDAE									
Helicopsyche borealis (Hagen)	–	–	–	1	26	8	–	–	–
Total	109	1254	157	173	115	78	350	237	39
Number of species	6	58	27	19	27	14	17	11	9
Nb per square metre	27.3	166.6	52.3	173	12.8	78	71.1	59.3	39

similar (S = 0.66), followed by 2 (S = 0.45); station 1 (sedge bog) is only marginally related to the first cluster (S = 0.24).

The river

The river fauna (stations 5–16) is by far the most diverse and productive. Thirty-five species of mayflies, 15 of stoneflies, and 58 of caddisflies were collected from the river; the lake outlet had fewer species, respectively 21, 3, and 27, but of these 3 mayflies and 10 caddisflies were not present in the river proper. In all, 121 of the total 148 species occured in these stations

The cluster analyses segregate three groups of stations: (1) the fast water stations (8, 9, 10, 11) characterized by their Plecoptera (overall S = 0.57) and Ephemeroptera faunas (S = 0.47) and less so by their Trichoptera (S = 0.17); (2) the slower water stations (5, 6, 7, 12, 13) more loosely joined and generally forming overlapping clusters of 2–3 stations of higher similarity (S = 45–50) joined together by lower similarities (S = 0.10); the same pattern is generated by the 3 data sets; (3) the outlet stations (15, 16, 17) set apart by their Ephemeroptera and Trichoptera faunas (S = 0.35), particularly stations 15 and 17.

The dominant mayflies in the river (Table 1) are *'Baetis'* spp. (27%), *Paraleptophlebia debilis* (16%), *Eurylophella verisimilis* (9%), *Acerpenna pygmaea* (6%), *Siphlonurus quebecensis* (5%), *Paraleptophlebia adoptiva* (4%), *Centroptilum rufostrigatum* (4%), *Litobrancha recurvata* (4%), and *Centroptilum album* (3%); the remaining 26 species add up to 22%. Other species, less abundant, but restricted to or more common in the river, include *Siphlonurus rapidus*, *Epeorus vitreus*, *Leucrocuta hebe*, *Stenacron i. canadense*, *Stenonema vicarium*, *Leptophlebia cupida*, *Ephemerella aurivillii*, and *Serratella excrucians*.

In the outlet stations (4–16), the dominant species are *Siphlonurus quebecensis* (35%), *Leptophlebia nebulosa* (22%), *Siphloplecton basale* (12%), *Litobrancha recurvata* (9%), *Eurylophella verisimilis* (4%), *Cloeon rubropictum* (4%), and *Siphlonurus alternatus* (4%); the other 14 species make up the remaining 10%. A few species are

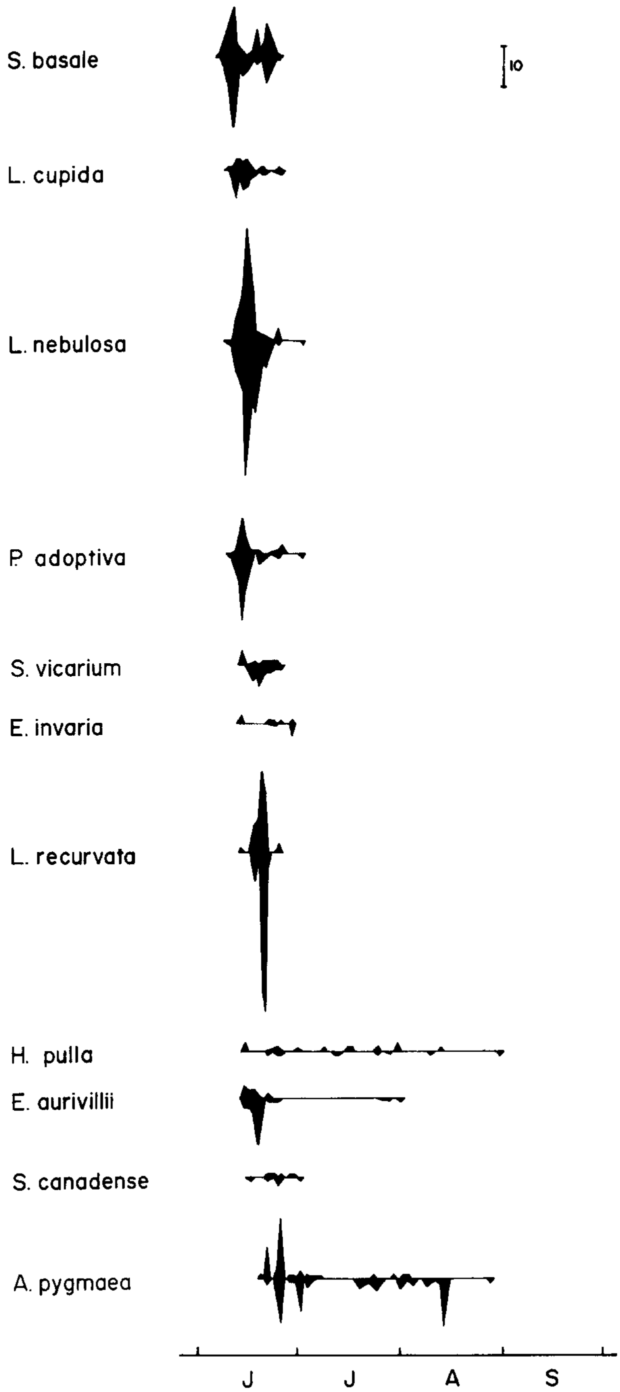

Fig. 3a.

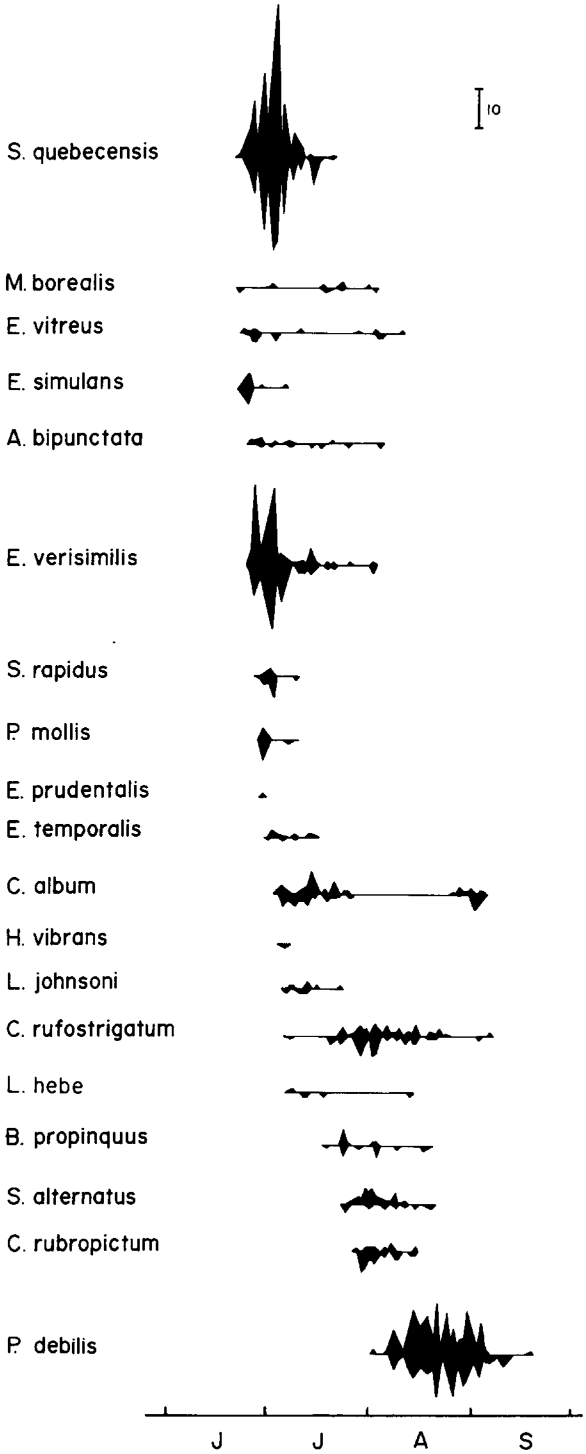

Fig. 3b.

Fig. 3. Emergence patterns of Ephemeroptera (a, b), Plecoptera (c), and Trichoptera (d, e, f) in the river and the outlet of Lac Hélène (stations 5–16, data pooled). Upper part of each diagram represents males, lower part females.

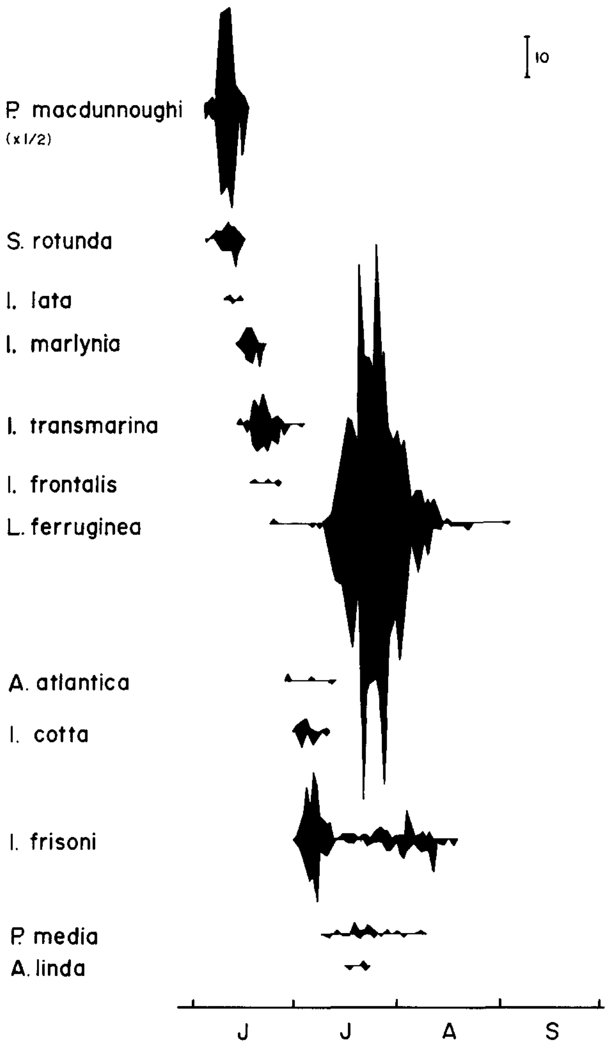

Fig. 3c.

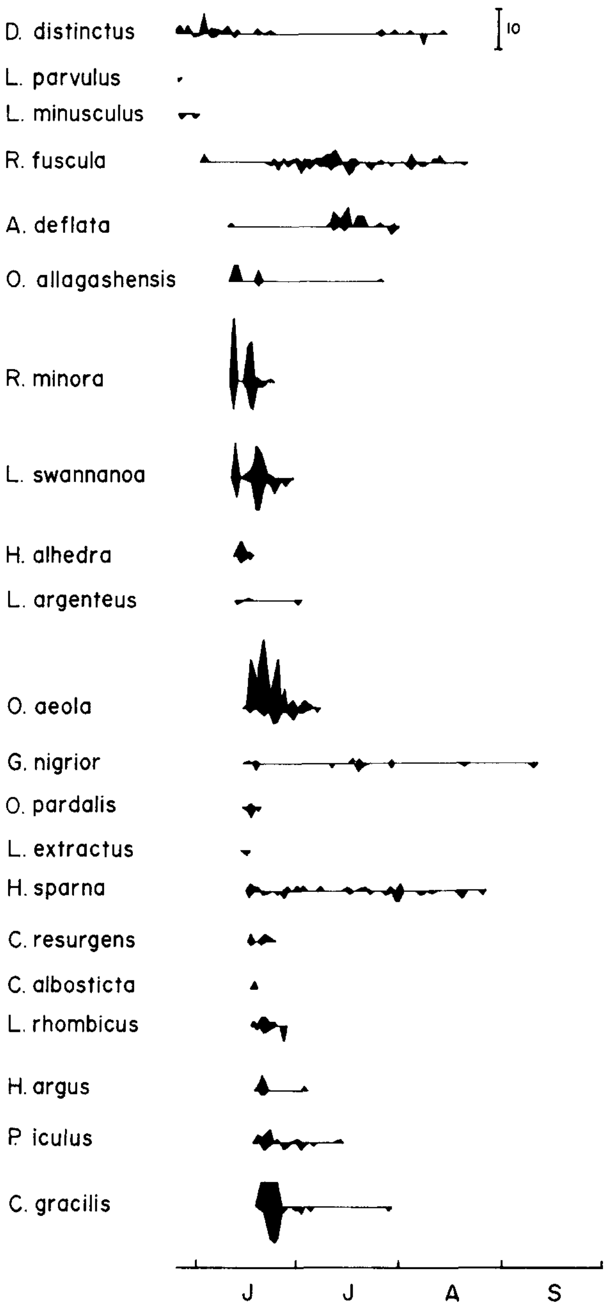

Fig. 3d.

characteristic of the outlet area: these are *Siphlonurus quebencensis*, *Metretopus borealis*, *Siphloplectum basale*, *Leptophlebia nebulosa*, *Cloeon rubropictum*, *Ephemera simulans*, and *Litobrancha recurvata*.

A mean of 209.4 mayflies/m^2 (151 at St. 6–284 at st. 12) emerged from the river stations, and 355/m^2 (148 at st. 15–670 at st. 14) from the outlet sites.

The succession of the species is illustrated in Fig. 3a, b. *Siphloplecton basale* is the first species to emerge in early June and is highly synchronized; it is followed shortly by a sequence of species with similar patterns, the last of which is *Siphlonurus quebecensis* in late June. A few of the intervening species have extended emergence patterns, such as *Heptagenia pulla* and *Acerpenna pygmaea*. In July and August, the patterns are extended somewhat. *Paraleptophlebia debilis* re-

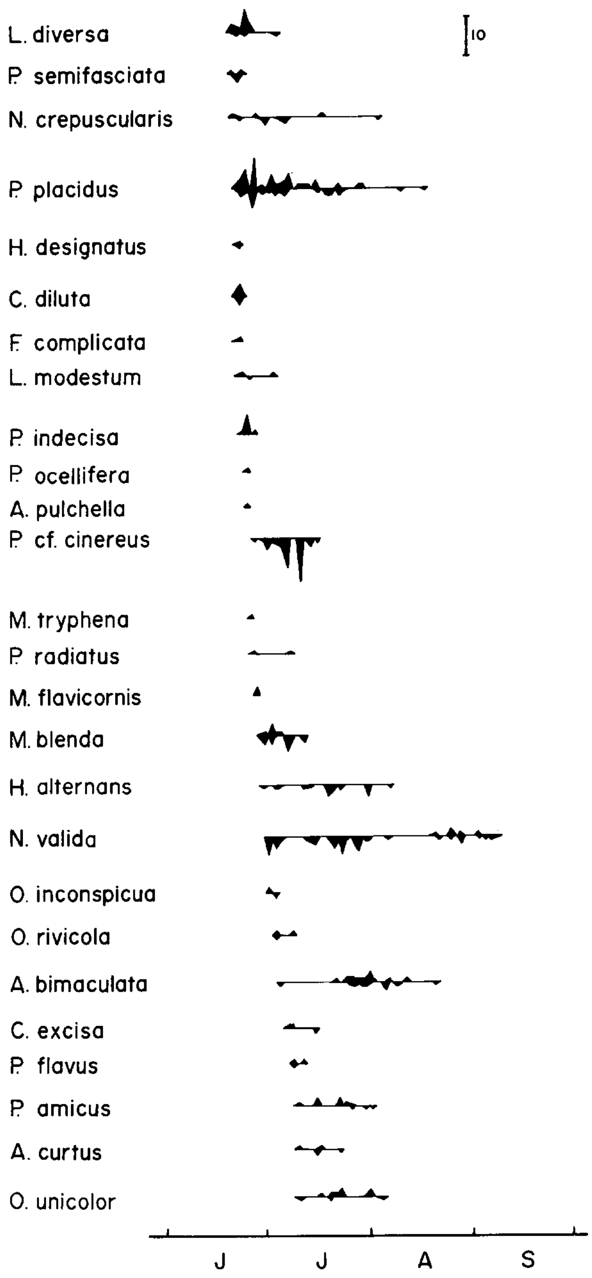

Fig. 3e.

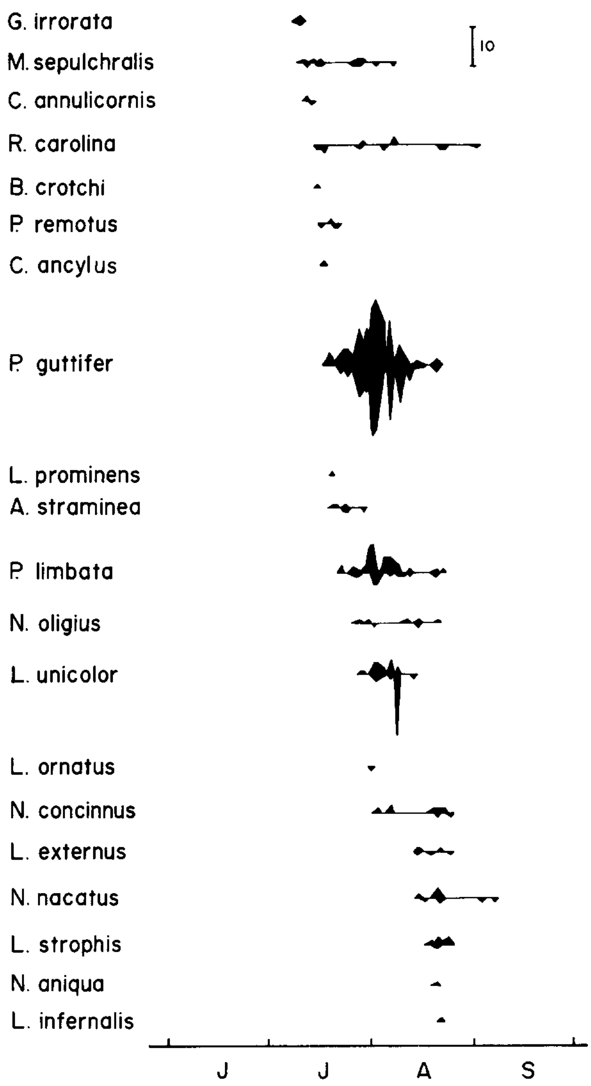

Fig. 3f.

presents the only autumnal element and emerges in August, extending into September. Males and females emerge at the same periods. There is little evidence of bivoltinism, except in Baetidae (*Acerpenna pygmaea* and *Centroptilum album*).

The stoneflies (Table 2) are similarly well represented. Fifteen of the 18 species collected occur there. The fauna is dominated by *Leuctra ferruginea* (58%), *Podmosta macdunnoughi* (23%), *Isoperla frisoni* (10%), and *Isoperla transmarina* (4%); the others amount to 5%. All of the 15 species, except *Amphinemura linda*, are more numerous in the river than in any other station. The mean annual yield is of 286,2/m^2 (11–96 at

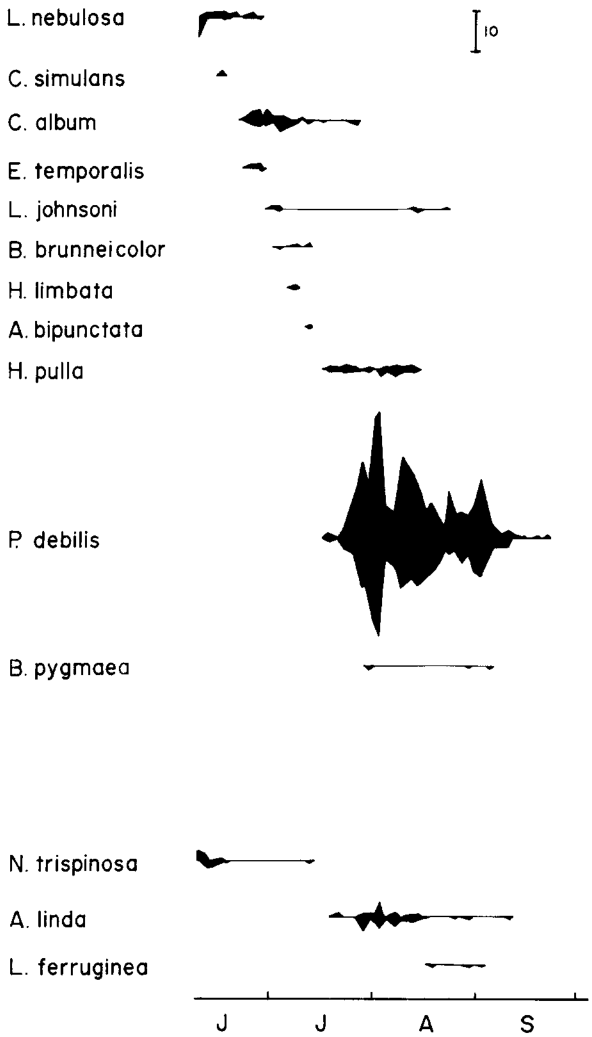

Fig. 4a.

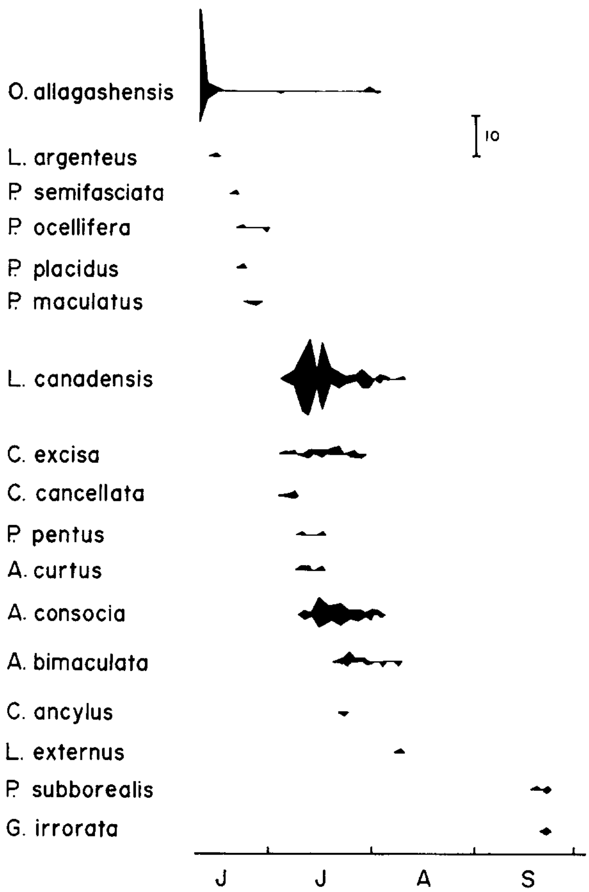

Fig. 4b.

Fig. 4. Emergence patterns of Ephemeroptera, Plecoptera (a), and Trichoptera (b) in outlet stream of Lac Julie (stations 28–33, data pooled). Upper part of each diagram represents males, lower part females.

the slower sites, 255–778 at the faster). The outlet stations present more lentic conditions and their stonefly fauna is consequently reduced; three species were collected, only *Shipsa rotunda* in any numbers; the annual yield is a mere 5,3 (0–14) insects/m^2.

The seasonal succession of the species (Fig. 3c) shows a sequence of 6 early species with short synchronous emergence periods, to which the later species *Alloperla atlantica* and *Isoperla cotta* can be added. The other species are summer species emerging mostly in July; among these, two patterns are evident; the first, that of *Leuctra ferruginea* with a maximum in mid-summer, the second, that of *Isoperla frisoni* with a clear maximum at the beginning of the period. This latter pattern can be classified as intermediate between the two others which are more characteristic. No autumnal species is present. Both sexes emerge together.

The caddisfly fauna (Table 3) is varied and 58 species were collected, though the yield is not correspondingly high, 166.6 (27–373) insects/m^2/year in the river and 52.3 (13–143) m^2 in the

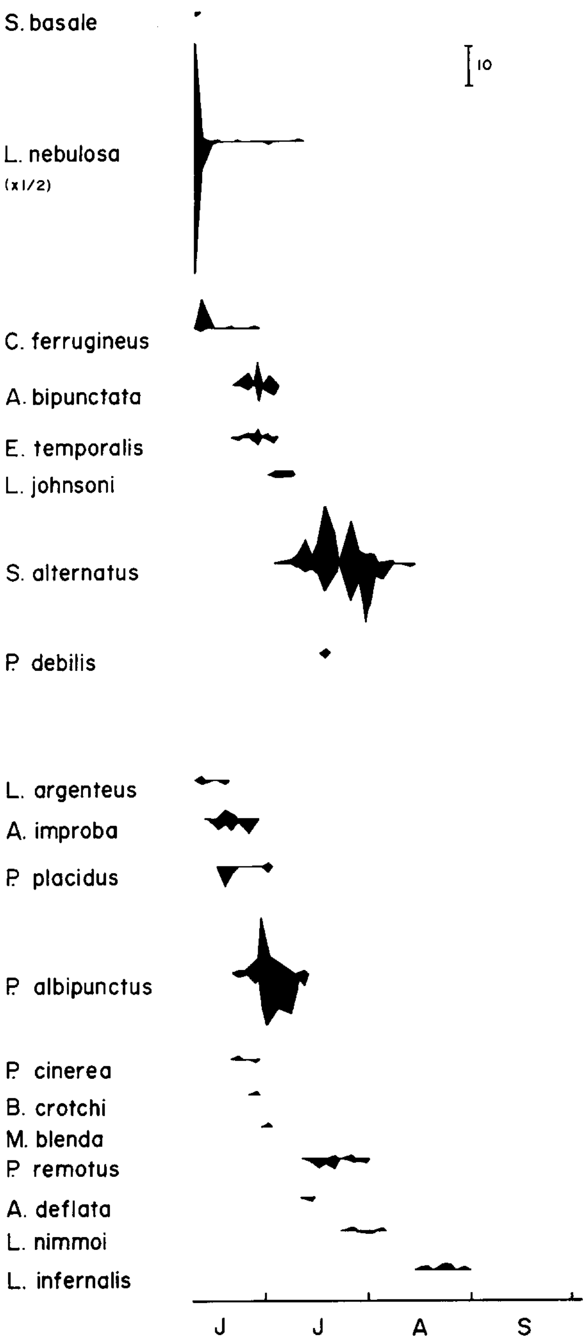

Fig. 5. Emergence patterns of Ephemeroptera and Trichoptera in Lac Julie (stations 34–37, data pooled). Upper part of each diagram represents males, lower part females.

outlet. The dominant taxa are *Pycnopsyche guttifer* (21%), *Oxyethira aeola* (9%), *Cheumatopsyche gracilis* (7%), *Rhyacophila fuscula* (6%), *Rhyacophila minora* (6%), *Phylocentropus placidus* (6%), and *Pycnopsyche limbata* (5%). Most of the taxa are characteristic of the river and many (32) are more abundant there than at the other stations. The outlet stations have half as many species (27) and the dominants are different: *Neureclipsis valida* (32%), *Agrypnia deflata* (19%), *Hydropsyche alternans* (11%). In addition to the last two species, the characteristic species include *Agrypnia straminea* and *Lepidostoma strophis*. The large number of *Oxyethira aeola*, particularly at station 12, is surprising as this is a species shared with one of the bog habitats. The other abudant species are typical dwellers of running waters, *Phylocentropus placidus* and *Pycnopsyche* spp. on slow substrates and *Rhyacophila* spp., *Lepidostoma* spp. and Hydropsychidae in the rapid reaches.

The emergence patterns (Fig. 3d–f) are more varied than those of the other two orders, and synchronous and dispersed patterns succeed each other throughout the season. There is no clear indication of more than one generation a year in any of the species. Contrary to the previous groups, new species continue to appear until late August so that a distinct autumnal fauna is evident (*Pycnopsyche* spp., *Neophylax* spp., and specialized *Limnephilus* and *Lepidostoma*). A few species emerge throughout the summer season, such as *Dolophilodes distinctus*, *Rhyacophila fuscula*, *Glossosoma nigrior*, and *Neureclipsis valida*, and probably comprise overlapping cohorts.

The mainstream station linking Lac Detchevery to Lac Hélène (station 27) has a fauna reduced in diversity (Tables I–IV), but not in density. The dominant species *Baetis* spp. (81%) and *Ephemerella invaria* (7%) in the mayflies, *Leuctra tenuis* (55%) and *Isoperla transmarina* (25%) in the stoneflies, and *Rhyacophila fuscula* (59%) in the caddisflies are species common at the other river stations, except *L. tenuis* which occurs only in the adjacent part of Lac Hélène.

Table 4 summarizes the composition of the faunas in the 3 river situations, rapid water over cobbles, rapid water over gravel, and slow water. The dominance of the stoneflies and Baetidae in the fast waters is evident and the abundant caddisflies belong to lotic genera, such as *Rhyaco-*

Table 4. Dominant species in the river stations. Up to ten pecies are given in each category with corresponding percentages. The characteristics of each habitat and the stations involved are given above each column, the number of specimens per square metre and the total number of species (broken into E-P-T, Ephemeroptera-Plecoptera-Trichoptera) listed below.

RIVER Fast water boulders, cobbles stn 8–9	RIVER Fast water gravel, sand stn 7, 10–11	RIVER Slow water sand, silt stn 5–6, 12–13	RIVER Fast water cobbles stn 27
P L. ferruginea 41.2	P L. ferruginea 27.7	E P. debilis 13.7	E 'Baetis' spp. 58.9
E 'Baetis' spp. 19.8	P P. macdunnoughi 15.3	E E. verisimilis 9.7	P L. tenuis 8.7
P I. frisoni 9.7	E 'Baetis' spp. 11.5	P L. ferruginea 7.3	T R. fuscula 4.7
P P. macdunnoughi 9.1	T P. guttifer 6.8	I P. guttifer 6.2	E E. invaria 4.4
T R. fuscula 2.6	P I. transmarina 3.3	T O. aeola 5.2	P I. transmarina 4.0
T R. minora 1.9	P I. frisoni 3.2	E C. rufostrigatum 4.1	E H. pulla 2.1
E P. adoptiva 1.8	T C. gracilis 2.8	T P. placidus 3.8	T H. borealis 1.5
T D. distinctus 1.4	T L. swannanoa 2.5	E C. album 3.6	P P. media 1.3
T C. gracilis 1.1	E P. debilis 2.4	P P. macdunnoughi 3.3	P I. frontalis 1.0
E E. vitreus 1.0	E S. quebecensis 1.9	E S. quebecensis 2.7	E P. mollis 1.0
659–1092 54 sp (18-11-25)	465–1183 80 sp (24-15-41)	274–550 78 sp (28-11-39)	526 33 sp (13-6-14)
STREAM Fast water stn 31–33	STREAM Slow water stn 28–30	TRIBUTARY STREAM Slow water stn 38	
E P. debilis 61.9	T O. allagashensis 27.2	E C. album 29.7	
T L. canadensis 11.4	E C. album 13.9	E Leptophlebia spp. 16.4	
E 'Baetis' spp. 6.3	E L. nebulosa 11.9	E 'Baetis' spp. 15.6	
T A. consocia 5.3	E P. debilis 11.9	T L. canadensis 8.6	
P A. linda 3.8	E 'Baetis' spp. 7.9	T P. limbata 7.0	
E H. pulla 2.3	P N. trispinosa 6.6	T P. subborealis 4.7	
T R. excisa 2.3	T L. canadensis 4.6	T A. consocia 3.5	
E C. album 2.0		T M. blenda 3.5	
T A. bimaculata 1.0		P N. trispinosa 2.3	
		E P. debilis 2.3	
218–755 24 sp (11-1-12)	35–63 23 sp (10-3-10)	118 19 sp (8-2-9)	

phila, *Dolophilodes*, and *Cheumatopsyche*. On finer substrates, appear genera such as *Pycnopsyche* and *Lepidostoma* adapted to moderate currents. In slow reaches, the lotic species are replaced by more lenitic groups. The annual yield is highest in the faster waters, but the number of species is lower and the dominance much enhanced.

The streams

Three streams were sampled during this investigation.

One (station 17) is a small tributary reaching Lac Hélène just as it flows out into rivière du Castor. Both the diversity of the species (10 mayflies, 5 stoneflies, and 19 caddisflies) and the productivity are low (annual yield 86 mayflies, 5 stoneflies) except in caddisflies (173 per m^2). The mayflies are essentially those inhabiting the lake

Table 5. Dominant species in the lake stations. Up to ten species are given in each category with corresponding percentages. The characteristics of each habitat and the stations involved are given above column, the number of specimens per square metre and the total number of species (broken into E-P-T, Ephemeroptera-Plecoptera-Trichoptera) listed below.

Lac Hélène Shore stn 18–21, 25, 26	Lac Hélène Centre stn 22–24	Lac Hélène Outlet stn 14–17
E E. simulans 14.4	P L. tenuis 44.3	E S. quebecensis 26.0
E S. basale 14.0	T P. cinerea 14.4	E L. nebulosa 15.7
E C. rubropictum 13.1	T P. placidus 12.4	E S. basale 8.6
E S. alternatus 11.6	T P. guttifer 5.2	E L. recurvata 8.3
E C. album 7.5	E E. verisimilis 5.2	T N. valida 3.3
E E. verisimilis 5.5	E P. debilis 2.1	E S. alternatus 2.7
T H. borealis 4.5		E C. rubropictum 2.6
T H. designatus 3.6		E E. verisimilis 2.4
E C. forcipata 3.3		T A. deflata 2.0
P L. tenuis 2.7		E E. simulans 1.5
42–157	15–46	264–685
42 sp (17-3-22)	20 sp (8-1-11)	55 sp (19-5-31)

Lac Julie Shore stn 34	Lac Julie Mid-depths stn 36–37	Lac Julie Centre stn 35
E L. nebulosa 50.8	E S. alternatus 43.1	E S. alternatus 29.4
E A. bipunctate 30.6	T P. albipunctus 20.3	T A. improba 27.5
E L. johnsoni 7.6	E L. nebulosa 14.7	T P. albipunctus 19.6
E E. temporalis 5.9	E C. ferrugineus 5.6	E P. debilis 7.8
T L. nimmoi 1.7	T P. remotus 5.1	E C. ferrugineus 3.9
	T A. improba 3.1	
	T P. placidus 2.0	
	T L. infernalis 1.7	
118	183–422	51
8 sp (4-1-3)	16 sp (5-0-11)	11 sp (4-1-6)

outlet. The presence of the stoneflies is fortuitous. The caddisflies are more numerous due to the presence of two species, both filter feeders, *Phylocentropus placidus* (57%) and *Neureclipsis valida* (15%), adapted to slow running water conditions (Wiggins, 1977). In Table 5, these data have been compiled with those of the lake outlet stations; in the similarity analysis, station 17 tends to cluster with station 5.

Another first order stream (station 38) flows into Lac Julie. The species richness (8 mayflies, 2 stoneflies, and 9 caddisflies) is low and so is the yield (respectively, 85, 4, and 39 insects/m^2). The only species of any importance is *Centroptilum album*. This station is closest to the slow stations of the outlet stream of Lac Julie, particularly station 30. The richest stream is that draining Lac Julie into Lac Detcheverry (stations 28–33). Thirteen mayflies, 3 stoneflies, and 17 caddisflies have been collected. The yields are moderate, respectively 183.5, 11.8, and 71.1/m^2. The dominant species are *Paraleptophlebia debilis* (80%), *Baetis* spp. (7%), and *Centroptilum album* (4%) in the mayflies, *Amphinemura linda* (71%) and *Nemoura trispinosa* (21%) in the stoneflies, *Limnephilus canadensis* (46%), *Anabolia consocia* (21%), *Oxyethira allaghashensis* (12%), and *Ceraclea excisa* (9%) in the caddisflies. This species composition is highly original and differs from that of the other lotic environments sampled. Of particular interest are the species of boreal distributions (*Amphinemura linda*, *Limnephilus argenteus*, *Limnephilus canadensis*, and *Ceraclea excisa*). The similarity analysis discriminated between the lenitic and the lotic stations in this reach. The more lenitic habitats (stations 28–30, Tab. 4) are dominated by *Oxyethira allagashensis* and *C. album*, whereas the other dominants aforementioned are prevalent on faster substrates (stations 31–33).

The apparent seasonal distribution of the species (Fig. 4a, b) was curtailed by the late installation of the traps. Nevertheless, the tail end of the emergence of the early species is apparent (*Leptophlebia nebulosa*, *Nemoura trispinosa*, *Oxyethira allagashensis*). The most striking characteristic is the presence of an important late summer or autumnal fauna (*Paraleptophlebia debilis*, *Amphinemura linda*, *Psychoglypha subborealis*, and *Glyphopsyche irrorata*). The emergence patterns are of the usual types, and among the abundant species, *Oxyethira allagashensis*, *Leptophlebia nebulosa*, and perhaps *N. trispinosa* are synchronous spring (early summer) species. *Centroptilum album*, *Heptagenia pulla*, *Limnephilus canadensis*, *Ceraclea excisa*, *Anabolia consocia*, and *Anabolia bimaculata* are typical summer species with an emergence extending over several weeks. There is little difference between the emergence patterns of the sexes.

The lakes

The largest lake sampled was Lac Hélène (stations 18–26). The number of species collected is relatively high for a lenitic environment (19 mayflies, 3 stoneflies, and 27 caddisflies). However, the density of the mean annual emergence is rather low (49.4 mayflies, 6.7 stoneflies, and 12.8 caddisflies/m^2). The dominants are *Ephemera simulans* (18%), *Siphloplecton basale* (18%), *Cloeon rubropictum* (16%), *Siphlonurus alternatus* (15%), and *Centroptilum album* (6%) in the Ephemeroptera, *Leuctra tenuis* (92%) in the Plecoptera, *Helicopsyche borealis* (23%), *Hesperophylax designatus* (17%), *Phylocentropus placidus* (11%), and *Agrypnia improba* (6%) in the Trichoptera. All except the stoneflies are typical slow water dwellers. All are widespread species and none is particularly boreal in distribution, except perhaps *Limnephilus argenteus* which is not very abundant. The littoral stations, but no distinct clustering is apparent in the similarity analysis, except for the 3 deeper stations which are listed separately in Table 5. The shore stations are therefore heterogeneous and there is a distinct faunal difference between the isolated western bay (stations 18–20) dominated by *Siphloplecton basale*, *Siphlonurus alternatus*, and *Agrypnia improba*, and the lake stations proper (21–25) where more lotic elements predominate especially near shore (*Helicopsyche borealis*, *Hesperophylax designatus*, *Eurylophella verisimilis*, *Ephemera simulans*, and *Leuctra tenuis*); the deeper stations are characterized by low densities and the presence of *Phryganea cinerea*. One shore station (26) harbours the only population of *Caenis forcipata*.

The phenology of the species is not illustrated because of the low density of most of the species, particularly the Trichoptera; the few more abundant species have their patterns illustrated elsewhere and they do not differ in Lac Hélène. The only original element is *Caenis forcipata* which emerges in the last week of June.

Lac Julie (stations 34–37) is nothing more than a pond. The three deeper stations (35–37) show a high similarity ($S = 40–58$). The fauna (Tab. 1–3, 5) contains 9 mayfly species and 11 caddisflies (the collection of one specimen of stonefly is fortuitous). The mayflies are represented by *Siphlonurus alternatus* (52%), *Leptophlebia nebulosa* (29%), *Arthroplea bipunctata* (7%), and *Callibaetis ferrugineus* (7%), the caddisflies by *Polycentropus albipunctus* (55%), *Agrypnia improba* (14%), and *Polycentropus remotus* (13%). These are all lenitic species abundant in the littoral area and it is in this environment that they are the most numerous. *Arthroplea bipunctata* is abundant near the outlet and inlet streams (station 34) and *Agrypnia improba* in the centre of the lake (station 35). Other characteristic species include the Trichoptera *Limnephilus argenteus* and *Limnephilus infernalis*. Here again, only the last of the spring emergers have been collected (*Siphloplecton basale* and *Leptohlebia nebulosa*). There is an important mid-summer fauna (most of the species above) with typical extended emergence patterns and at least one distinct autumnal element (*Limnephilus infernalis*).

Discussion

The fauna inhabiting these subarctic habitats has temperate and boreal affinities, and no arctic element is evident; this holds true for the aquatic insect fauna of the James Bay drainage in general (Harper, 1989). There are nonetheless taxa characteristic of northern habitats, as witnessed by the increased importance and diversity of Limnephilidae (Schmid, 1980) in the Trichoptera and the prevalence of Siphlonuridae in lake mayflies (Saettem & Brittain, 1985). The boreal element is better represented in the outlet stream of Lac Julie than in all other habitats; by comparison, other habitats, particularly the river, have a rather commonplace fauna.

The lotic and lentic faunas show differences mainly in dominance and in proportion of species, rather than in species composition. Even the Plecoptera, which are restricted almost exclusively to running waters in temperate latitudes, maintain small populations in the lakes. This is probably due to the generally cool temperature and high oxygenation in the lakes throughout the year which allow species with high oxygen requirements to complete their cycle there. Few of the species, none of them abundant, are restricted to the lakes.

In the streams, there is little evidence of a distinct headwater fauna of the type common in southern Québec (Mackay, 1969) and dominated by Appalachian elements. The streams studied here seem mainly fed by runoff from bogs and muskeg areas and have little grade; these are not particularly suitable for such faunas. Investigation of headwaters in this area would be interesting. There are nonetheless particularities in the stream fauna (Table 4).

The number of species encountered in this study is relativly high and compares favourably with other similar investigations at more temperate latitudes (Anderson & Wold, 1972; Harper & Harper, 1984; Singh *et al.*, 1984a, b). The decrease of temperate species is largely compensated by a large boreal element (Harper, 1989). Such a diversity observed in a subarctic situation should fuel the ongoing discussions on the comparision of diversity patterns in the tropics and in temperate climates (Wolda & Flowers, 1985).

There is a general agreement between these results and the concurrent benthos studies at the same sites (Magnin, 1977). On the whole, the insects represent 73.5% of the benthos density; the mayflies make up 11.1%, the Plecoptera 2.0%, and the Trichoptera 5.7%. This is a ratio of 5.3/1/2.7; by contrast, the emergence data gives a ration of 2.0/1/0.9. The stoneflies are therefore somewhat overrepresented in the emergence relative to the benthos; this is not surprising since the benthos was collected mainly in summer when many stoneflies would have emerged.

The lack of stoneflies and mayflies in the bogs is confirmed by the benthos studies (Magnin, 1977), although a few unidentified mayfly nymphs are reported for Station 1. The dominance of Phryganeidae and Polycentropodidae is characteristic of many bogs (Harper & Cloutier, 1985).

The benthos of the river compares well with the emergence except that large populations of Hydropsychidae were present. These do not appear in the emergence traps, probably because the fastest waters were not adequently sampled.

In Lac Hélène, the heterogeneity of the benthos confirms that observed in the emergence; similarity, the densities are lower by approximately one order of magnitude. The presence of stone flies in the eastern part of the lake is confirmed; unfortunately no identification of these nymphs is provided. The dominance of Ephemeroptera in the lake as well as in lake Julie is also confirmed.

Finally, in the outlet stream of Lac Julie, the differences in density and composition of the communities of fast and slow water are also apparent.

The yields of the traps are rather on the low side by comparision with studies in temperate areas, but compare favourably with data originating from other northern sites (Boerger & Clifford, 1975). Taking the Ephemeroptera for instance (Table I), the normal annual yield per trap per square metre appears to be of the order of 200–300 individuals in temperate streams (Illies, 1978, 1980; Sandrock, 1978), though Harper & Harper (1982) observed higher values (1000–1200) probably because they worked in streams which were mainly lake oulets in a temperate environment. The Trichoptera yields are very low (Table 3), by comparision with the few data available (Anderson & Wold, 1972; Singh *et al.*, 1984b) but comparable to others (Masteller & Flint, 1980). The same holds true for Plecoptera (Harper & Pilon, 1971; Singh *et al.*, 1984a). Such low productivity, as reflected in the adult emergence (Illies, 1978), is not unexpected, given the short summer season, the cool temperatures, and the low productivity of the adjoining forest.

In the lakes the numbers are even lower, but again they compare with results from similar sites (Flannagan & Lawler, 1972; Harper & Harper, 1982). Saettem & Brittain (1985) appear to have collected large populations of emerging mayflies from a cool Norwegian lake, but they do not give details.

In this study, the river appears to be more productive than the streams; Needham (1928) had suggested that per unit surface, smaller running-water habitats should be more productive, but this has often proven to be false (Harper & Harper, 1982). Although emergence does provide a measure of productivity particularly in small streams where the emergence traps covers the stream from shore to shore (Illies, 1972), in larger habitats an important bias may be introduced when the traps are set near the shore where insects aggregate before emergence. The values obtained may then be some extent (or even greatly) overestimated.

Similarly, the rapid waters both in the river and the stream (Table 4) yield more specimens. This is in accord with the findings of Huryn & Wallace (1987) who, on the basis of larval studies, demonstrated a much higher productivity in boulder-outcrop areas than in riffles and in pools. As is observed here, they also described an increased dominance, hence a lower diversity, in the boulder-outcrop areas and the existence of a specialized fauna in the faster waters. By contrast, the productivity in pool areas was more evenly distributed between the taxa (higher diversity) and the percentage of carnivores (engulfers) was increased. In reference to the latter point, it must be recalled that they also studied Odonata an essentially carnivorous group, which is not the case here. Nevertheless, Pilon *et al.* (1978) indicate that *Ophiogomphus colubrinus* is the dominant species in the rapids, while a dozen or so species inhabit the slower reaches. The carnivorous Plecoptera (*Isoperla*) and Trichoptera (*Rhyacophila*) were more abundant in the faster waters (Table 4). Most of the sites were dominated by shredders (e. g. *Paraleptophlebia*) and collector-gatherers (e. g. *Baetis*).

Huryn (1986) indicates that Trichoptera are more adaptable to the scope of available habitats than are either the Ephemeroptera or the Plecoptera; he attributes this to the lower respiratory requirements of the caddisfly larvae. In this study, the Trichoptera colonize all the habitats and present a wide range of species, but very few of them seem to be able to reach dense populations (Table 3). The low numbers of filter-feeding Hydropsychidae has been mentioned above.

It must also be stressed that emergence densities are but an indirect measure of the population production and also of the community composition, as was demonstrated recently by Lauzon & Harper (1988). One should not make generalizations without first obtaining data on the immature stages and the dynamics and other aspects of the life-histories of species involved.

The phenology of the species follows the usual patterns, except that the onset of the emergence season is retarded in the spring by a few weeks by comparision with more southerly latitudes (Harper & Harper, 1982); however, in the fall and late summer the emergence periods are comparable, and the autumnal fauna just as important if not more. The patterns recall those illustrated by Boerger & Clifford (1975). The early stonefly fauna emerging at the first breakup of the ice is missing, though a few stragglers (*Paracapnia*) were collected. The late onset of summer is due to the latitude, but also to the proximity of James Bay which heats up very slowly; conversely, the Bay acts as a heat reservoir in late summer, which explains the rather mild weather an August and September.

The maximum emergence seems to occur in late June and early July just after the summer solstice, although the warmest period is not before the end of July end the beginning of August.

The usual emergence patterns can be observed in the Ephemeroptera and the Plecoptera: a succesion of early ('spring') species characterized by a short and synchronous emergence; intermingled with these are a number of species, many of which start to emerge early but do not reach their peak before a few weeks then continue until late summer ('summer species'); finally, a small number of late 'autumnal' species which appear in August, emerge within a few weeks, but with a few stragglers maturing until late September. Such patterns have been observed elsewhere with the same taxa (Harper & Magnin, 1971; Harper & Harper, 1982, 1984, Singh *et al.*, 1984a).

In Trichoptera, the situation is not so clear. There are many species with short synchronous emergence periods spread over the whole summer and it is not possible to define all of them as spring species; perhaps this is due to the small densities of most of the populations which make the patterns uncertain. Many of the species have extended emergence periods of one or two months and this may be a consequence of mutivoltinism or perhaps more probably of overlapping cohorts. A characteristic of the fauna is the richness of the autumnal element by comparison with the two other orders. Why should the Trichoptera succeed in maintaining such a rich and diverse late season fauna when it is so depauperate in the other orders in not known. This is particularly intriguing in the Plecoptera where the autumnal element is limited to a few species of *Leuctra* and *Amphinemura linda* in Eastern North America, while it is very rich both in Western North America (Ricker, 1943) and in Western Europe (Aubert, 1959).

Much has been written about the temporal segregation of congeneric species as a means to reduce competition (Mackay, 1969; Singh *et al.*, 1984b); the usual examples can be observed here and a distinct temporal succesion occurs in the species belonging to large genera, such as *Isoperla*, *Limnephilus*, *Lepidostoma*,... but in others, such as *Pycnopsyche* and *Neophylax* this is obviously not the case, and ecological segregation is doubtless based on more subtle differences (Mackay, 1977).

Little or no sexual differences appear in the emergence patterns. This contrasts with other accounts from temperate habitats (Harper & Pilon, 1970; Harper & Magnin, 1971), but even there protandry was never more than a few days.

Conclusions

This investigation of the communities of Ephemeroptera, Plecoptera and Trichoptera in a network of lakes and streams in northwestern Québec by means of 38 emergence traps indicates that

(1) There is a rich and diversified fauna of 148 species (44 mayflies, 18 stoneflies, and 86 caddisflies). None of these is arctic; the bulk of the species are widespread northeastern species with some boreal elements. Many of the abundant species belong to the latter group. Such species richness compares well with that of similar habitats in temperate latitudes.

(2) The annual yields of the traps are not particularly high, but are comparable to other boreal and some temperate data sets.

(3) The mayflies are the dominant group, particularly in slower waters. The stoneflies occur mainly in running water, but small populations are maintained in lenctic situations. The caddisflies are the most diverse group, but they tend to maintain low densities; the inadequate sampling of the fast water filterer species may partly explain this underrepresentation.

(4) The faster waters, both in the river and in the streams, are more productive than the slower reaches. These in turn yield more specimens then the lakes, particularly the deeper waters.

(5) The main habitats are characerized by particular faunal assemblages. The bogs support only caddisflies, the lakes both mayflies and caddisflies, and the running waters all three groups. The bogs and the outlet stream have the most original faunas, with boreal elements, while other habitats, particularly the river, contain mainly widespread species. Differences between communities are often more a question of dominance and proportions of the species than in distinct species lists.

(6) Emergence patterns follow the usual sequence: an important 'spring' fauna composed of species emerging synchronously in close sequence in early summer; a 'summer' fauna of species emerging throughout the summer; a small contingent of 'fall' species appearing in August. The autumnal element is best represented in the Trichoptera. Differences between spring and summer patterns are less clear in Trichoptera than in the other two orders. By comparision with temperate latitudes, the onset of the emergence is retarded by about 3 weeks, but the end of the period is not affected. Little protandry in the emergence patterns is evident.

Acknowledgements

The field work was conducted by the S. E. B. J. personnel, in particular Jean-Louis Fréchette, Guy Boivin, and André Ahern, under the supervision of Prof. Jean-Guy Pilon of the Université de Montréal. Daniel Roy helped with the identifications; so did Françoise Harper who also performed the statistical analyses.

References

Anderson, N. H. & J. L. Wold, 1972. Emergence traps collections of Trichoptera from an Oregon stream. Can. Entom. 104: 189–201.

Aubert, J., 1950. Plecoptera. Fauna Helvetica 1: 1–140.

Boerger, H. & H. F. Clifford, 1975. Emergence of mayflies (Ephemeroptera) from a northern brown-water stream of Alberta, Canada. Verh. int. Ver. Theor. Angew. Limnol. 19: 3022–3028.

Flannagan, J. F. & G. H. Lawler, 1972. Emergence of caddisflies (Trichoptera) and mayflies (Ephemeroptera) from Heming Lake, Manitoba. Can. Entom. 104: 173–183.

Fréchette, J. L., 1976. Programme S. E. B. J., Rapport 55, Etude spéciale des insectes 1975. Société d'Energie de la Baie James, Direction Construction, Lac Hélène, Division Relevés techniques, 38 P. + annexes.

Harper, F. & P. P. Harper, 1984. Phenology and distribution of mayflies in a southern Ontario lowland stream. Proc. IVth Int. Conf. Ephemeroptera (V. Landa *et al.*, edits.), 243–251.

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

Harper, P. P., 1989. Zoogeographical relationships of aquatic insects from the eastern James Bay drainage. (Submitted).

Harper, P. P. & L. Cloutier, 1985. Composition et phénologie de communautés d'insectes du Lac Geai, un lac dystrophe des Laurentides (Québec). Nat. Can. 112: 405–415.

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

Harper, P. P. & J. G. Pilon, 1970. Annual patterns of emergence of some Québec stoneflies (Insecta: Plecoptera). Can. J. Zool. 48: 681–694.

Huryn, A. D., 1986. Secondary production of the macroinvertebrate community of a high-elevation stream in the southern Appalachian mountains. Ph. D. Dissertation, Univ. Georgia, Athens. (Cited by Huryn & Wallace, 1987).

Huryn, A. D. & J. B. Wallace, 1987. The exopterygote insect community of a mountain stream in North Carolina, USA: life histories, production, and functional structure. Aquat. Insects 9: 229–251.

Ide, F. P., 1935. The effect on the distribution of the mayfly fauna of a stream. Univ. Toronto Stud., Biol. Ser. 39: 3–76.

Illies, J., 1972. Emergenzmessung als neue Methode zur produktionsbiologischen Untersuchnungen von Fliessgewässern. Verh. Deut. Zool. Ges. 65: 65–68.

Illies, J., 1978. Vergleichende Emergenzmessung im Breitenbach 1969–1976. Arch. Hydrobiol. 90: 217–229.

Illies, J., 1980. Ephemeropteren-Emergenz in zwei Lunzer Bächen (1972–1977). Arch. Hydrobiol. 90: 217–229.

Landry, B. & P. P. Harper, 1985. The aquatic dance fly fauna of a subarctic river system in Québec, with the description of a new species of *Hemerodromia* (Diptera; Empididae). Can. Entom. 117: 1379–1386.

Lauzon, M. & P. P. Harper, 1988. Seasonal dynamics of a mayfly (Insecta: Ephemeroptera) community in a Laurentian stream. Holarct. Ecol. 11: 220–234.

Legendre, L. & P. Legendre, 1979. Ecologie numérique 2. La structure des données écologiques. Masson, Paris, 335 p.

Mackay, R. J., 1969. Aquatic insect communities of a small stream on Mont St. Hilaire, Québec. J. Fish. Res. Bd. Can. 26: 1157–1183.

Mackay, R. J., 1977. Behaviour of *Pycnopsyche* (Trichoptera; Limnephilidae) on mineral substrates in laboratory streams. Ecology 58: 191–195.

Magnin, E., 1977. Ecologie de eaux douces du territoire de la Baie James. Société d'Energie de la Baie James, Montréal, 430 p.

Masteller, E. C. & O. S. Flint, Jr., 1980. Emergence phenology of Trichoptera from Six Mile Creek, Erie County, Pennsylvania, U. S. A. Aquat. Ins. 2: 197–210.

Needham, P. R., 1928. Quantitative studies on the fish food supplies in selected areas. New York State Conservation Department, Annual Report, Supplement, pp. 220–232.

Pilon, J. G., G. Boivin & J. L. Fréchette, 1978. Les Odonates d'une région du bassin versant de la Baie James située entre La Grande Rivière et la rivière Eastmain. Ann. Soc. Entom. Qué. 23: 3–29.

Ricker, W. E., 1943. The stoneflies of southwestern British Columbia. Indiana Univ. Publ., Sci. Ser. 12: 1–145.

Saettem, L. M. & J. E. Brittain, 1985. Life cycles and emergence of Ephemeroptera and Plecoptera from Myrkdalsvatn, an oligotrophic lake in Western Norway. Aquat. Ins. 4: 229–241.

Sandrock, F., 1978. Vergleichende Emergenzmessung an zwei Bächen des Schlitzerlandes (Breitenbach und Rohrwiesenbach 1970–1971). Arch. Hydrobiol. Suppl. 54: 328–408.

Schmid, F., 1980. Genera des Trichoptères du Canada et des Etats adjacents. Ins. Arachn. Canada 7: 1–296 (Agriculture Canada, Div. Rech., Publ. 1692).

Singh, M. P., S. M. Smith & A. D. Harrison, 1984a. Emergence patterns of stoneflies (Plecoptera) from a wooded stream in southern Ontario. Aquat. Ins. 6: 233–243.

Singh, M. P., S. M. Smith & A. D. Harrison, 1984b. Emergence of some caddisflies (Trichoptera) from a wooded stream in southern Ontario. Hydrobiologia 112: 223–232.

Vaudor, A., 1984. Le prologiciel r. Centre de calcul, Université de Montréal.

Wiggins, G. B., 1961. The rediscovery of an unusual North American phryganeid, with some additional records of caddisflies from Newfoundland (Trichoptera). Can. Entom. 93: 695–702.

Wolda, H. & R. W. Flowers, 1985. Seasonality and diversity of mayfly adults (Ephemeroptera) in a 'nonseasonal' tropical environment. Biotropica 17: 330–335.