Life history and production of mayflies, stoneflies, and caddisflies (Ephemeroptera, Plecoptera, and Trichoptera) in a spring-fed stream in Prince Edward Island, Canada: evidence for population asynchrony in spring habitats?

Michelle Dobrin and Donna J. Giberson

Abstract: We examined the life history and production of the Ephemeroptera, Plecoptera, and Trichoptera (EPT) community along a 500-m stretch of a hydrologically stable cold springbrook in Prince Edward Island during 1997 and 1998. Six mayfly species (Ephemeroptera), 6 stonefly species (Plecoptera), and 11 caddisfly species (Trichoptera) were collected from benthic and emergence samples from five sites in Balsam Hollow Brook. Eleven species were abundant enough for life-history and production analysis: *Baetis tricaudatus*, *Cinygmula subaequalis*, *Epeorus (Iron) fragilis*, and *Epeorus (Iron) pleuralis* (Ephemeroptera), *Paracapnia angulata*, *Sweltsa naica*, *Leuctra ferruginea*, *Amphinemura nigritta*, and *Nemoura trispinosa* (Plecoptera), and *Parapsyche apicalis* and *Rhyacophila brunnea* (Trichoptera). Life-cycle timing of EPT taxa in Balsam Hollow Brook was generally similar to other literature reports, but several species showed extended emergence periods when compared with other studies, suggesting a reduction in synchronization of life-cycle timing, possibly as a result of the thermal patterns in the stream. Total EPT secondary production (June 1997 to May 1998) was 2.74–2.80 g·m^{-2}·year^{-1} dry mass (size-frequency method). Mayflies were dominant, with a production rate of 2.2 g·m^{-2}·year^{-1} dry mass, followed by caddisflies at 0.41 g·m^{-2}·year^{-1} dry mass, and stoneflies at 0.19 g·m^{-2}·year^{-1} dry mass. More than half of the species found in the study stream represented new distribution records for Prince Edward Island.

Résumé : Nous avons étudié les cycles biologiques et la production de la communauté des éphéméroptères, des plécoptères et des trichoptères (EPT) en 1997 et 1998 sur une section de 500 m d'un ruisseau de source à température froide et à forte stabilité hydrologique, à l'Île-du-Prince-Édouard. Des échantillons de benthos et des récoltes de l'émergence provenant à 5 sites du ruisseau de Balsam Hollow contenaient 6 espèces d'éphémères (Ephemeroptera), 6 espèces de perles (Plecoptera) et 11 espèces de phryganes (Trichoptera). Onze des espèces étaient présentes en nombre suffisant pour permettre une analyse du cycle biologique et de la production : *Baetis tricaudatus*, *Cinygmula subaequalis*, *Epeorus (Iron) fragilis* et *Epeorus (Iron) pleuralis* (Ephemeroptera), *Paracapnia angulata*, *Sweltsa naica*, *Leuctra ferruginea*, *Amphinemura nigritta* et *Nemoura trispinosa* (Plecoptera), ainsi que *Parapsyche apicalis* et *Rhyacophila brunnea* (Trichoptera). La phénologie des cycles biologiques des EPT au ruisseau de Balsam Hollow est généralement semblable à celle observée dans d'autres études; néanmoins, plusieurs espèces ont des périodes d'émergence plus allongées, ce qui laisse croire qu'il y a une réduction du synchronisme de la phénologie des cycles biologiques, probablement occasionnée par le régime thermique du ruisseau. La production secondaire totale des EPT (de juin 1997 à mai 1998) était de 2,74–2,80 g de masse sèche·m^{-2}·an^{-1} (méthode de la fréquence des tailles). Les éphémères dominaient avec un taux de production de 2,2 g de masse sèche·m^{-2}·an^{-1}, suivies des phryganes avec 0,41 g de masse sèche·m^{-2}·an^{-1} et des perles avec 0,19 g de masse sèche·m^{-2}·an^{-1}. Plus de la moitié des espèces trouvées dans le cours d'eau étudié sont signalées pour la première fois à l'Île-du-Prince-Édouard.

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Introduction

Springs and springbrooks are unique freshwater habitats that exhibit generally low hydrologic and thermal variability compared with non-spring habitats (Williams 1983; Williams and Hogg 1988). Water temperature and water-temperature variation are two of the most important environmental factors influencing life-history patterns, especially growth rates and seasonal timing of aquatic insects (Sweeney 1984). Some insects, particularly many mayflies, appear to cue into

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seasonal temperature changes to synchronize their life cycles (either alone or in concert with photoperiodic cues; Sweeney and Vannote 1981), whereas others require certain temperature minima to grow and develop (Mecom 1972; Sweeney 1984; Elliott 1991, 1992). The low temperature variability in springs, plus the generally low temperatures found in cold springs, have been hypothesized to restrict the species-composition patterns found there, and also do affect life-history strategies and productivity (Williams and Hogg 1988; Wallace and Anderson 1996). For example, Williams and Hogg (1988) suggested that cold springs should possess more taxa showing non-synchronous emergence and recruitment than nearby runoff streams of similar size, owing to a lack of temperature cues needed to synchronize development. They proposed that species which are found in both types of stream should be more asynchronous in cold springs than in runoff streams. Other researchers (e.g., Sweeney 1984) have shown that many species require minimum summer temperatures or degree-day accumulations to complete development, restricting their ability to colonize cold springs.

Aquatic insects are important in energy flow in aquatic systems, since they constitute an important link between the algal/detrital food base and the higher trophic levels, including benthivorous fish (Benke 1984). Secondary production is a measure of biomass creation over time and depends on individual growth and life-history attributes as well as population abundance and survivorship (Benke 1984; Huryn and Wallace 2000).

Although many studies on the life history and production of aquatic invertebrates have been carried out around the world (see the review by Huryn and Wallace 2000), relatively few studies have focussed on springs, and very few on springs in northeastern North America (Williams 1983; Williams and Hogg 1988). Cold springs are widespread on Prince Edward Island (Somers et al. 1999), so this region offers an excellent opportunity to study the population and energy dynamics of aquatic insects in these poorly known systems. The objective of this study was to examine the life history and production of a component of the aquatic insect community (Ephemeroptera, Plecoptera, and Trichoptera; EPT) in a springbrook system on Prince Edward Island, and to examine these patterns in the context of previous hypotheses about thermally stable habitats.

Study site

Balsam Hollow Brook (46°29′10.6″N, 63°22′56.5″W) is a small (4 km long) spring-fed stream in north-central Prince Edward Island (Fig. 1). The stream originates as a cold spring in open agricultural land and is fed by numerous spring inputs along its length, most of which is within the boundaries of Prince Edward Island National Park. In the study area, the stream runs through mixed hardwood forest (the Acadian Forest subregion of the Appalachian Forest) and a golf course before entering a series of ponds and crossing a system of coastal sand dunes to empty into the Gulf of St. Lawrence.

Five stream sites were located along a 500 m long reach within the national park and adjacent to the golf course, to

represent a range of substrate and flow types and riparian conditions. Three of the sites were heavily shaded and the riparian vegetation was composed of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), yellow and white birches (*Betula alleghaniensis* and *Betula papyrifera*), mountain ash (*Sorbus americana*), balsam poplar (*Populus balsamifera*), and downy alder (*Alnus crispa*). The two sites that possessed more open canopies were partially shaded by shrubs (mainly downy alder), grasses, sedges, and herbs. Two of the sites possessed cobble substrates, one open site was primarily gravel, and the remaining two sites had substrates dominated by sand and silt (Hynes' (1970) substrate-size classification). Sites were separated by at least 50 m; each site included sections of fast and slow water, and both habitat types were sampled. Stream width and water temperature (Table 1) did not vary significantly along the 500 m long section of stream.

Methods

Physical-habitat characteristics

Several physical-habitat characteristics were measured at Balsam Hollow Brook in 1997 and 1998. Mean channel width and depth were measured at several transects at each study site in August 1997 and 1998. Water temperature was monitored weekly from May to early November in 1997 and 1998 (and intermittently during the winter months) using maximum/minimum thermometers to determine whether temperature varied along the length of the stream. At one of the sites, temperature was also monitored continuously from early June to early November in both years, using a temperature logger. Stream pH and conductivity were measured using a pH/conductivity meter, and were recorded weekly throughout the summer and fall of 1997, bimonthly throughout the winter of 1997–1998, weekly throughout the summer of 1998, and biweekly in the fall of 1998. In addition, water samples that were collected on three occasions for a subsequent study were tested for a variety of chemical parameters through the water-testing laboratory of the Prince Edward Island Department of the Environment. These were not collected concurrently with this study, but are included here to show that water chemistry varied little, either seasonally or along the length of the stream.

Benthic sampling

A modified Hess sampler (mesh size 200 µm, area 0.07 m^2) was used to quantitatively sample running-water habitats to provide data for calculating secondary productivity and determining life cycles. Three samples were collected on each sampling date in the running-water habitats at each of the four sites in Balsam Hollow Brook. Samples were collected approximately monthly during the spring–summer–fall growth periods in 1997 and 1998 (June–October 1997 and April–May 1998), and a single winter sample was collected in December.

Emergence and light-trap sampling

Adult insects were sampled to confirm species identifications and determine emergence and flight periods. Emergence was monitored directly using emergence traps suspended over

Fig. 1. Balsam Hollow Brook, Prince Edward Island. The rectangle shows the stream area sampled and the dots indicate the study sites. Shaded polygons represent forest and broken lines indicate the boundaries of the golf course. The solid square in the inset map shows the location of the stream on Prince Edward Island.
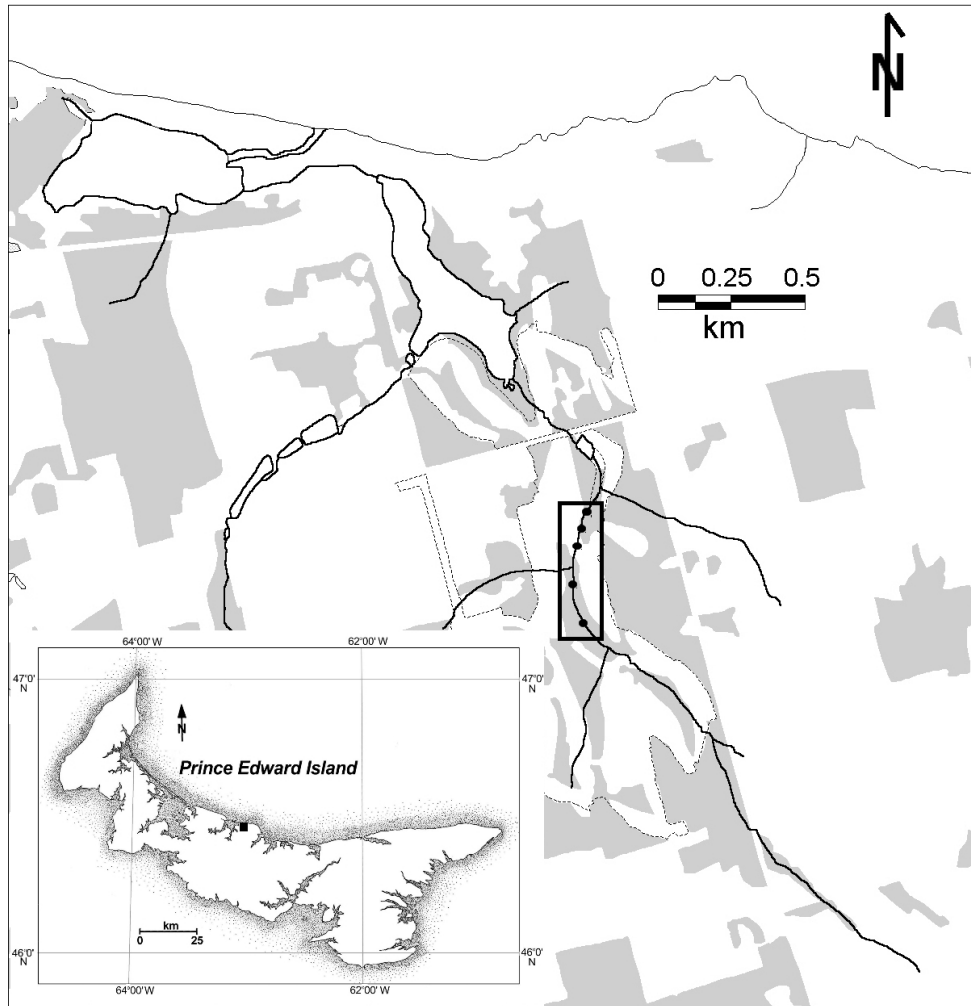
the water. The emergence trap (Giberson and Garnett 1996) was a cone-shaped trap (basal area 0.07 m^2, mesh size 300 μm) suspended from a plastic collecting jar containing 70% ethanol. Three emergence traps were set up at each riffle site in Balsam Hollow Brook at the end of May in 1997 and 1998, and were emptied at weekly (summer) and biweekly (fall) intervals until the end of November in 1997 and the end of October in 1998. Emergence samples were also collected from pool habitats (3 traps) in 1997 at Balsam Hollow Brook. A light trap was also set up on a hiking trail along the stream between the two upstream sites three times during the summer of 1997 (10 June, 8 July, and 4 August) to collect adults that may have avoided the emergence traps.

Sample processing

Aquatic insect larvae and other aquatic invertebrates found in benthic samples were preserved in 4% formalin, then washed into 70% ethanol for storage. All specimens were sorted from the gravel and detritus using a dissecting microscope, then the EPT taxa were separated and identified to species using the keys of Flint (1961), Edmunds et al. (1976), Stewart and Stark (1988), Edmunds and Waltz (1996), Morse

and Holzenthal (1996), Stewart and Harper (1996), and Wiggins (1996a, 1996b). Adults were collected directly into 70% ethanol and identified using the keys of Needham et al. (1935), Ross (1944, 1956), Hitchcock (1974), Edmunds et al. (1976), Schmid (1981), Marshall and Larson (1982), Parker and Wiggins (1985), Burian (1990), Ruiter (1995), Edmunds and Waltz (1996), Morse and Holzenthal (1996), Stewart and Harper (1996), and Wiggins (1996a, 1996b). Adults were associated with larvae on the basis of life-history analysis to confirm larval species identifications.

EPT larvae from benthic samples were measured using an ocular micrometer in a stereoscopic dissecting microscope, and were placed into 1-mm size (body length) categories for life-cycle analysis. Size-frequency histograms were plotted for each species and compared among sampling dates. Body lengths were converted to body mass for secondary-productivity calculations using dry mass – length equations given in Benke et al. (1999). Individuals from all sites were combined to provide a large enough sample for production analysis. Secondary productivity was calculated using the size-frequency method for all species and the instantaneous growth rate method for species where cohorts could be reliably

Table 1. Physical-habitat variables measured at Balsam Hollow Brook, Prince Edward Island, during the 1997 and 1998 sampling seasons.

	1997		1998	
	Mean	Range	Mean	Range
Channel width (m)[a]	1.8	1.0–2.8	1.8	1.2–2.8
Channel depth (m)[a]	0.07	0.05–0.18	0.10	0.07–0.20
Water temperature (°C)	10.2	6–17	9.9	7–14
Total summer degree-days (°C)[b]	1576		1578	
Stream pH	7.7	7.5–8	7.6	7.1–7.9
Stream conductivity (µS/cm)	230	180–350	194	110–220

[a]Averaged over several transects in the study reach in August of each year.
[b]Degree-days >0°C calculated from 28 May to 31 October 1997 and from 1 June to 1 November 1998.

Table 2. Summary of water-chemistry analysis of water from Balsam Hollow Brook in the summer and winter of 2000–2001.

	22 June 2000 (upstream)	22 June 2000 (downstream)	9 Aug. 2000 (upstream)	1 Feb. 2001 (upstream)	1 Feb. 2001 (downstream)	Mean
pH	7.5	7.5	7.8	7.7	7.9	7.7
Total alkalinity (mg/L $CaCO_3$)	98.5	98.8	83.4	94.8	92	93.5
Hardness (mg/L $CaCO_3$)	—	—	102	124	114	113.3
Conductance (µS/cm)	285	287	—	—	—	286
Turbidity (JTU)	1.8	1.9	—	—	—	1.85
Nitrate-N (mg/L NO_3)	2.6	2.5	<0.2	4.2	2.4	2.38
Chloride (mg/L)	18.2	18.3	24	20.6	19.8	20.18
Calcium (mg/L)	30	29	22.5	31.5	29	28.4
Cadmium (mg/L)	—	—	<0.005	<0.005	<0.005	<0.005
Chromium (mg/L)	—	—	<0.05	<0.05	<0.05	<0.05
Copper (mg/L)	—	—	<0.02	<0.02	<0.02	<0.02
Iron (ext.) (mg/L)	—	—	0.12	0.64	0.25	0.34
Iron (diss.) (mg/L)	—	—	—	<0.1	—	<0.1
Potassium (mg/L)	1.47	1.48	1.82	1.87	1.41	1.61
Magnesium (mg/L)	10.4	10.2	11.1	10.83	10.1	10.53
Manganese (mg/L)	—	—	0.17	0.15	0.08	0.13
Sodium (mg/L)	10	10.1	10.5	10.14	9.75	10.10
Nickel (mg/L)	—	—	<0.05	<0.05	<0.05	<0.05
Phosphorus (mg/L)	0.06	0.06	0.06	0.07	0.06	0.06
Lead (mg/L)	—	—	<0.002	<0.002	0	<0.002
Sulfate (mg/L SO_4)	5.26	5.26	6.94	5.57	5.51	5.71
Zinc (mg/L)	—	—	0.03	<0.02	<0.02	0.02

Note: "Upstream" and "downstream" refer to water-sampling sites near the upper part of the stream within the national park boundary and the lower sampling reach, respectively.

separated (Benke 1984). Only the size-frequency method results are reported here, as they were virtually identical with those from the instantaneous growth rate method.

Results and discussion

Physical-habitat characteristics

Balsam Hollow Brook is a small stream (≈4 km long) with a channel width of ≈2 m and a mean depth of ≈10 cm in the study reach during summer low flow (Table 1). The stream is fed by multiple groundwater-spring inputs along its length, so water temperature varied by <0.5°C along the entire 750 m long study reach, regardless of canopy cover. Seasonal water-temperature data showed only minimal fluctuations, as expected in a spring-fed stream (Hynes 1970; Williams and Hogg 1988). Winter minima in Balsam Hollow Brook generally approach 5°C (D.J. Giberson, unpublished

data), so total annual variation in temperature was 13°C in 1997 and 9°C in 1998 (Table 1). On a weekly basis, maximum and minimum temperatures never varied by more than 3°C. In contrast, annual temperature variations in nearby non-spring stream habitats are commonly ≥25°C (D.J. Giberson, unpublished data). Williams and Hogg (1988) reported an annual temperature variation of 11°C near the source of Valley Spring in Ontario, although some other studies (e.g., on Root Spring, Massachusetts; Teal 1957) report much smaller fluctuations. Total accumulated degree-days (>0°C for the 5 warmest months) for the stream were virtually identical for both years, despite the differences in seasonal pattern in the 2 years (Table 1).

Balsam Hollow Brook is a slightly alkaline, generally low-conductivity stream, and is similar in water chemistry to other spring-fed streams on Prince Edward Island (Tables 1, 2; Brandon 1966; Somers et al. 1999). Prince Edward Island

Table 3. Relative abundance (percentage of total individuals of each species in each EPT order and the total numbers of invertebrates captured in 1997 and 1998) in Balsam Hollow Brook.

	Benthos		Adults	
	% of order	% of total	% of order	% of total
Ephemeroptera (total no.)	13 541		246	
Baetis tricaudatus	61.34	8.62	58.54	0.62
Cinygmula subaequalis	32.12	4.51	4.88	0.05
Epeorus (*Iron*) spp.	5.42	0.76	23.17	0.25
Paraleptophlebia debilis	0.44	0.06	13.41	0.14
Paraleptophlebia volitans	0.68	0.10	a	a
Plecoptera (total no.)	7 924		1 042	
*Paracapnia angulata**	28.66	2.36	a	a
*Leuctra ferruginea**	38.26	3.15	59.60	2.69
*Paraleuctra sara**	1.15	0.09	0.29	r
Nemoura trispinosa	24.87	2.04	8.34	0.38
Amphinemura nigritta	6.21	0.51	31.38	1.42
Sweltsa naica	0.85	0.07	0.29	r
Trichoptera (total no.)	777		132	
Rhyacophila brunnea	69.11	0.56	18.05	0.10
*Parapsyche apicalis**	28.70	0.23	3.76	r
*Frenesia missa**	a	a	0.75	r
*Hesperophylax designatus**	a	a	1.50	r
*Hydatophylax argus**	a	a	1.50	r
*Limnephilus rhombicus**	a	a	0.75	r
*Onocosmoecus unicolor**	0.13	r	6.03	r
*Psychoglypha subborealis**	a	a	65.41	0.38
*Pycnopsyche gentilis**	a	a	0.75	r
Lype diversa	a	a	0.75	r
*Neophylax aniqua**	2.06	r	0.75	r
Overall total	96 404		23 102	

Note: "a" indicates that a species was absent and "r" denotes <0.01%. Species marked by an asterisk are new records for Prince Edward Island, including *Epeorus* (*Iron*) *fragilis*, which is shown here combined with *Epeorus* (*Iron*) *pleuralis* as *Epeorus* (*Iron*) spp.

is dominated by crop agriculture, resulting in relatively high nitrate and phosphorus levels in ground and surface waters (Somers et al. 1999). Water-chemistry values were generally stable spatially (along the study reach) and temporally (Table 2).

Community patterns

Species richness of the EPT community was relatively low over the 2 years, with only 23 species (Table 3), compared with nearby non-spring habitats in Prince Edward Island and New Brunswick (Giberson and Garnett 1996; D.J. Giberson, unpublished data). Many of the species, especially in the Trichoptera, were extremely rare (Table 3). The pattern of low diversity in springs has been widely reported (Williams 1983; Williams and Hogg 1988) and is often attributed to the temperature patterns found in springs. Many temperate-zone aquatic insect species have low-temperature minima of 8–10°C for development (Mecom 1972; Elliott 1991, 1992) and so are effectively eliminated from cold-water habitats such as cold springs. Over half of the 23 species (13) represented new provincial records for Prince Edward Island (Table 3).

Eleven EPT species were abundant enough for analysis of their life-cycle and production dynamics. These included 4 mayfly species (*Baetis tricaudatus, Cinygmula subaequalis,*

Epeorus (*Iron*) *fragilis, Epeorus* (*Iron*) *pleuralis*), 5 stonefly species (*Paracapnia angulata, Sweltsa naica, Leuctra ferruginea, Amphinemura nigritta,* and *Nemoura trispinosa*), and 2 caddisfly species (*Rhyacophila brunnea* and *Parapsyche apicalis*).

Life-history and production patterns

The EPT species were an important component in Balsam Hollow Brook. They made up 20–40% of the total number of benthic invertebrates collected each year in Balsam Hollow Brook, with chironomids making up most of the remainder (Dobrin 2000). Chironomids also dominated the emergence samples.

EPT production in Balsam Hollow Brook was dominated by the mayflies, which made up >80% of the production for the group (Table 4). *Baetis tricaudatus* and *C. subaequalis* were the most productive taxa (38 and 33% of total EPT production, respectively), and *E.* (*I.*) *pleuralis* and *R. brunnea* each contributed about 10%. The collector functional feeding group dominated the production of the EPT taxa (>50%) and shredders made up the smallest proportion (<6%) (Table 4). Overall production of the EPT community in Balsam Hollow Brook (June 1997 to May 1998) was estimated to be 2.74 g·m^{-2}·year^{-1} dry mass (size-frequency method). This is considerably higher than the total aquatic invertebrate com-

Table 4. Summary of secondary production for Ephemeroptera, Plecoptera, and Trichoptera (EPT) in Balsam Hollow Brook from June 1997 to May 1998.

	Functional feeding group[a]	Production (P)[b] ($g·m^{-2}·year^{-1}$)	P/B[c] (annual)
Ephemeroptera			
Baetis tricaudatus	Collector/gatherer, scraper	1.03	5.4
Cinygmula subaequalis	Scraper, collector/gatherer	0.9	5.9
Epeorus (*I.*) *pleuralis*	Collector/gatherer, scraper	0.3	6.9
Epeorus (*I.*) *fragilis*	Collector/gatherer, scraper	0.028	7.8
Total		2.258	
Plecoptera			
Paracapnia angulata	Shredder	0.07	8.8
Leuctra ferruginea	Shredder	0.052	3.4
Amphinemura nigritta	Shredder	0.019	3.9
Nemoura trispinosa	Shredder	0.022	5.7
Swetsa naica	Predator	0.015	3.7
Total		0.178	
Trichoptera			
Parapsyche apicalis	Collector/filterer	0.078	
Rhyacophila brunnea	Predator	0.313	
Total		0.391	
Total EPT		2.74	

[a]Designations are derived from Merritt and Cummins (1996); in the case of multiple groups, the first category listed is the one that was considered to be most important.

[b]Total production was calculated using both size-frequency and instantaneous growth rate methods, but the values were virtually identical, so only size-frequency values are recorded here.

[c]P/B is the turnover ratio (B is annual mean biomass).

munity production reported in Valley Spring in Ontario ($\approx 0.7–1.9$ $g·m^{-2}·year^{-1}$ dry mass (converted from wet mass using an equation from Waters 1977)). However, it is similar to the EPT production reported for other springs and small shaded streams (e.g., 3.02 $g·m^{-2}·year^{-1}$ dry mass in a Danish stream (Iversen 1988) and 1.93–8.8 $g·m^{-2}·year^{-1}$ dry mass in three small shaded streams in Minnesota that varied in water chemistry (Krueger and Waters 1983; converted from wet mass using an equation from Waters 1977)). These values are considered to be in the "low production" range when compared globally with those from other larger and nutrient-rich streams (Huryn and Wallace 2000).

Life-cycle patterns of the common EPT taxa included 7 species with univoltine cycles (3 mayflies, 3 stoneflies, and 1 caddisfly), 1 with a bivoltine or multivoltine cycle (*B. tricaudatus*), and 3 with a 2-year cycle (*S. naica*, *L. ferruginea*, and *R. brunnea*). Detailed life-history information for the common species is given below.

Ephemeroptera

Four species of mayflies (*B. tricaudatus*, *C. subaequalis*, *E.* (*I.*) *fragilis*, and *E.* (*I.*) *pleuralis*) were sufficiently abundant in benthic and emergence samples at Balsam Hollow Brook for life-cycle analysis. Two leptophlebiid species (*Paraleptophlebia debilis* and *Paraleptophlebia volitans)* were too rare in benthic samples to be analysed, although *P. debilis* was collected in emergence traps in the fall of both 1997 and 1998 (Fig. 2), a fall-emergence pattern also noted by Giberson and MacKay (1991).

Baetis tricaudatus Dodds (Baetidae) was the most abundant mayfly at Balsam Hollow Brook (Fig. 3). Investigation of size-frequency histograms (Fig. 3) suggests that *B. tricaudatus*

had at least 2 generations per year. This pattern was consistent with the results of most other studies on the species (Ide 1935; Coleman and Hynes 1970; Corkum and Pointing 1979; Clifford 1982), though some studies have reported up to 4 generations a year (Waters 1966). At Balsam Hollow Brook, most of the abundant overwintering generation emerged and oviposited in late spring (June; Fig. 2), with recruitment in the summer and a second emergence peak in late summer and fall (Figs. 2, 3). Eggs of the overwintering generation hatched in the fall, and larvae grew at different rates through the winter, resulting in a variable size distribution in the spring and an extended and overlapping emergence period (Fig. 2).

Cinygmula subaequalis (Banks) (Heptageniidae) was not well known previously (Burian and Gibbs 1991), but univoltine life cycles have been reported for other *Cinygmula* species (Clifford 1982). The species is clearly univoltine in Balsam Hollow Brook, with synchronous development. Overwintering larvae of *C. subaequalis* emerged in June and July (Fig. 2) and new recruits were first seen in late August. Larvae grew slowly through the winter, then rapidly in the spring (Fig. 3), completing the cycle.

Two species of *Epeorus* (Heptageniidae) were found at Balsam Hollow Brook in 1997 and 1998: *E.* (*I.*) *fragilis* (Morgan) and *E.* (*I.*) *pleuralis* (Banks). The 2 species were impossible to distinguish as larvae and adult females, but examination of adult males indicated that 2 species were present. The size-frequency distributions (Fig. 3) showed two cohorts, suggesting that the 2 species coexisted in the stream and did not overlap temporally. The pattern was confirmed by examining adult males. Male imagos of *E.* (*I.*) *pleuralis* were only found in late June, and male imagos of *E.* (*I.*)

Fig. 2. Emergence phenologies of Ephemeroptera, Plecoptera, and Trichoptera collected in emergence traps in 1997 and 1998 in Balsam Hollow Brook. The numbers beside the bars indicate the total number of individuals collected over the entire sampling season. The vertical lines on the bars indicate peak emergence time. Note that the emergence period for *Epeorus* (*Iron*) spp. is for a combination of 2 species, *E.* (*I.*) *fragilis* and *E.* (*I.*) *pleuralis*, which could not be reliably separated as females.
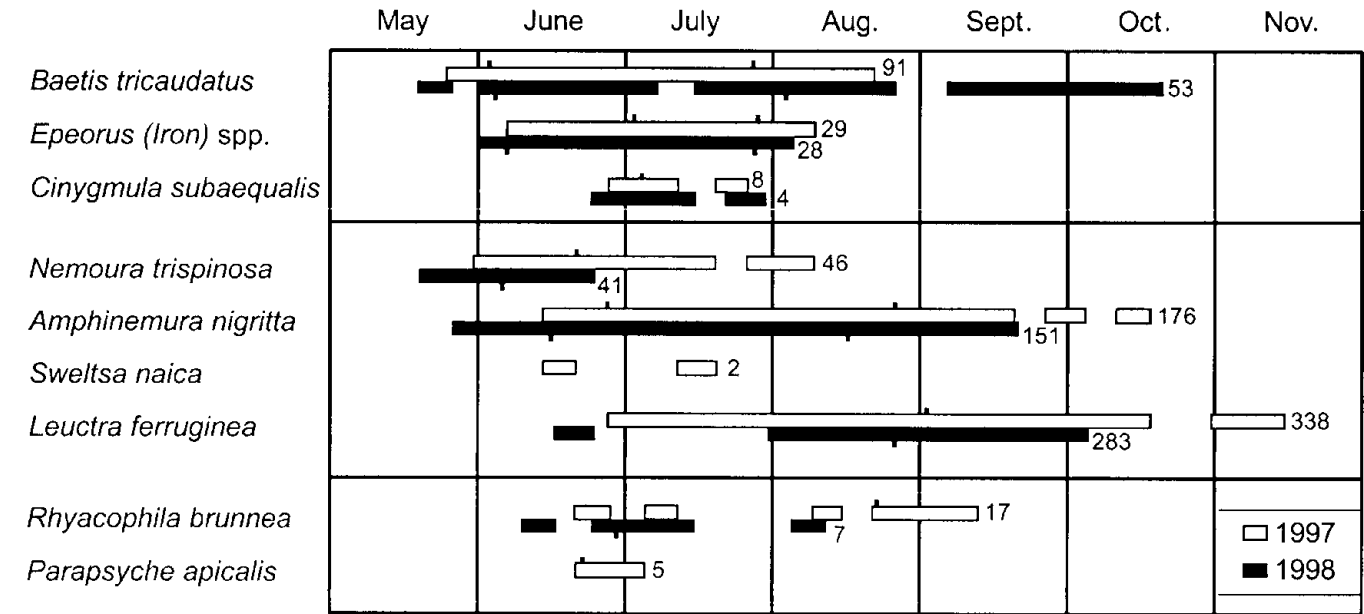
fragilis were identified from late-July and early-August samples. This emergence pattern was similar to that found concurrently in Winter Creek, a nearby stream similar in physical characteristics to Balsam Hollow Brook (Dobrin 2000). Larvae presumed to be *E.* (*I.*) *fragilis* first appeared in early spring, then grew rapidly through the warm summer months (July–August; Fig. 3), to emerge in late summer (August; Fig. 2). Larvae assumed to be *E.* (*I.*) *pleuralis* were first seen in October and December and grew through the winter (Fig. 3), to emerge in early summer (June; Fig. 2). These life cycles matched those previously reported by Minshall (1967) at a small stream in Kentucky and by Mackay (1969) in Quebec.

Plecoptera

Six species of stoneflies were found in Balsam Hollow Brook. Five of these (all except *Paraleuctra sara*; Table 3) were abundant enough in benthic and emergence samples to permit life-cycle analysis. Three of the species had a univoltine cycle, while 2 required 2 years to complete their development.

Paracapnia angulata Hanson (Capniidae) is a winter stonefly species. It is commonly found in cold, spring-fed streams (Harper and Hynes 1972), but may also be found in small to large rivers and in littoral areas of lakes (Harper et al. 1991). This species was univoltine in Balsam Hollow Brook (Fig. 4). The first recruits to the population were noted in late June and July and small nymphs were abundant in benthic samples in July and August. Emergence apparently began prior to the April 9 sampling period, before emergence traps were set up in May; however, some large nymphs were still found in the stream in April 1998, and emerging adults were hand-collected on the banks at this time. A similar life-cycle pattern has been reported by Harper and Hynes (1972)

in southern Ontario and by Grubbs and Cummins (1996) at an Appalachian stream in Pennsylvania. Hilsenhoff et al. (1972) reported this species as very common in a Wisconsin stream, with an emergence period from early April to early May. Giberson and Garnett (1996) recorded emergence in May in a stream in northern New Brunswick.

Leuctra ferruginea (Walker) (Leuctridae) is a ubiquitous species found in streams of various sizes (Harper 1973b). At Balsam Hollow Brook, *L. ferruginea* was one of the most common stonefly species. Two cohorts were present on most sampling dates, and examination of the frequency histograms (Fig. 4) shows that larvae need 2 years to complete one life cycle, a pattern similar to that reported in small streams in southern Ontario by Harper (1973b). New recruits may occur as early as mid-December, and small larvae were common in samples in April and May, suggesting an extended egg hatch during the winter. Emergence also showed an extended pattern, ranging from June through October and November. Giberson and Garnett (1996) recorded emergence of this species in late August in New Brunswick.

Amphinemura nigritta (Provancher) (Nemouridae) was common both years at Balsam Hollow Brook, and was clearly univoltine (Fig. 4), with extended summer emergence (Fig. 2). The first recruits were noted at the end of October, and larvae grew slowly through the winter, then rapidly from April to May in 1998. The larval part of the cycle is similar to that reported from previous life-history studies on this species from streams in southern Ontario and Pennsylvania (Harper 1973b; Grubbs and Cummins 1996).

Nemoura trispinosa Claassen (Nemouridae) was also univoltine (Fig. 4), but the emergence period was more restricted to the early part of the summer than that of *A. nigritta* (Fig. 2). Overwintering larvae began to emerge in late May and small nymphs were seen between July and December,

Fig. 3. Size-frequency distributions of 4 species of mayflies at Balsam Hollow Brook from June 1997 to May 1998, showing life cycles. *N* is the number of larvae collected per sampling date. *Epeorus* (*Iron*) spp. are *E.* (*I.*) *fragilis* and *E.* (*I.*) *pleuralis*, which could not be separated as larvae. Arrows indicate size (body length) classes not abundant enough to be visible bars in the histograms.
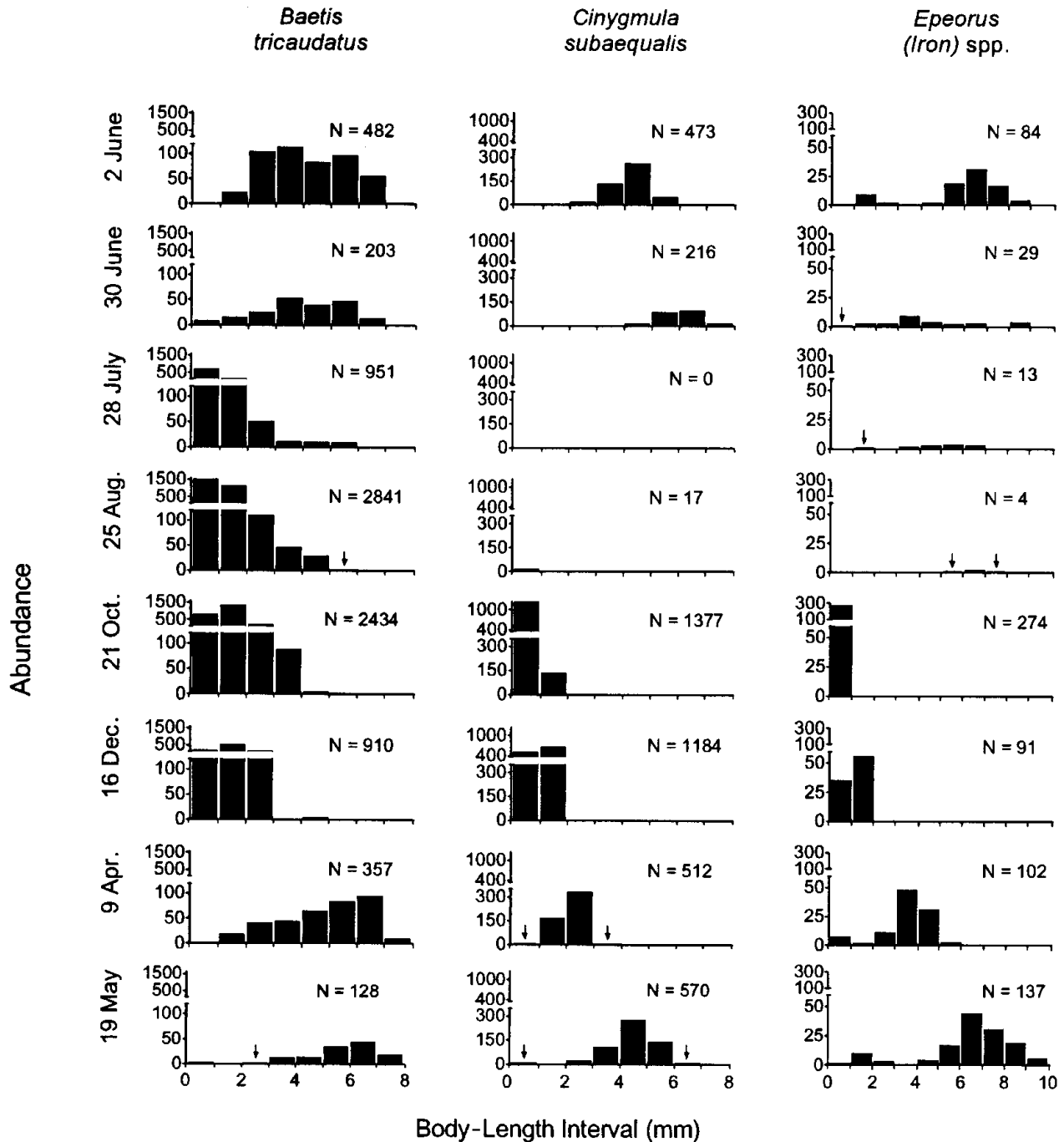
indicating an extended hatching period. The univoltine cycle of this species at Balsam Hollow Brook is similar to that reported from southern Ontario by Harper (1973*b*).

Sweltsa naica (Provancher) (Chloroperlidae) has not been well studied, but *Sweltsa onkos* had a 1- to 2-year cycle in southern Quebec and Ontario streams (Mackay 1969; Harper 1973*a*) and *Sweltsa mediana* was semivoltine in Tennessee (Cushman et al. 1977). At Balsam Hollow Brook, *S. naica* was not very abundant, but the presence of two cohorts in the winter samples suggests a semivoltine life cycle. New re-

cruits probably enter the population in the fall, then grow slowly, to emerge in early to midsummer of their second year (Figs. 2, 4). *Sweltsa naica* emerged in June and July in a stream in northern New Brunswick (Giberson and Garnett 1996).

Trichoptera

There were 2 common species of caddisflies at Balsam Hollow Brook (*P. apicalis* and *R. brunnea*). Nine other species of caddisflies were collected, mainly from emergence

Fig. 4. Size-frequency distributions of 5 species of stoneflies at Balsam Hollow Brook from June 1997 to May 1998, showing life cycles. *N* is the number of larvae collected per sampling date. Arrows indicate size (body length) classes not abundant enough to appear as visible bars in the histograms.
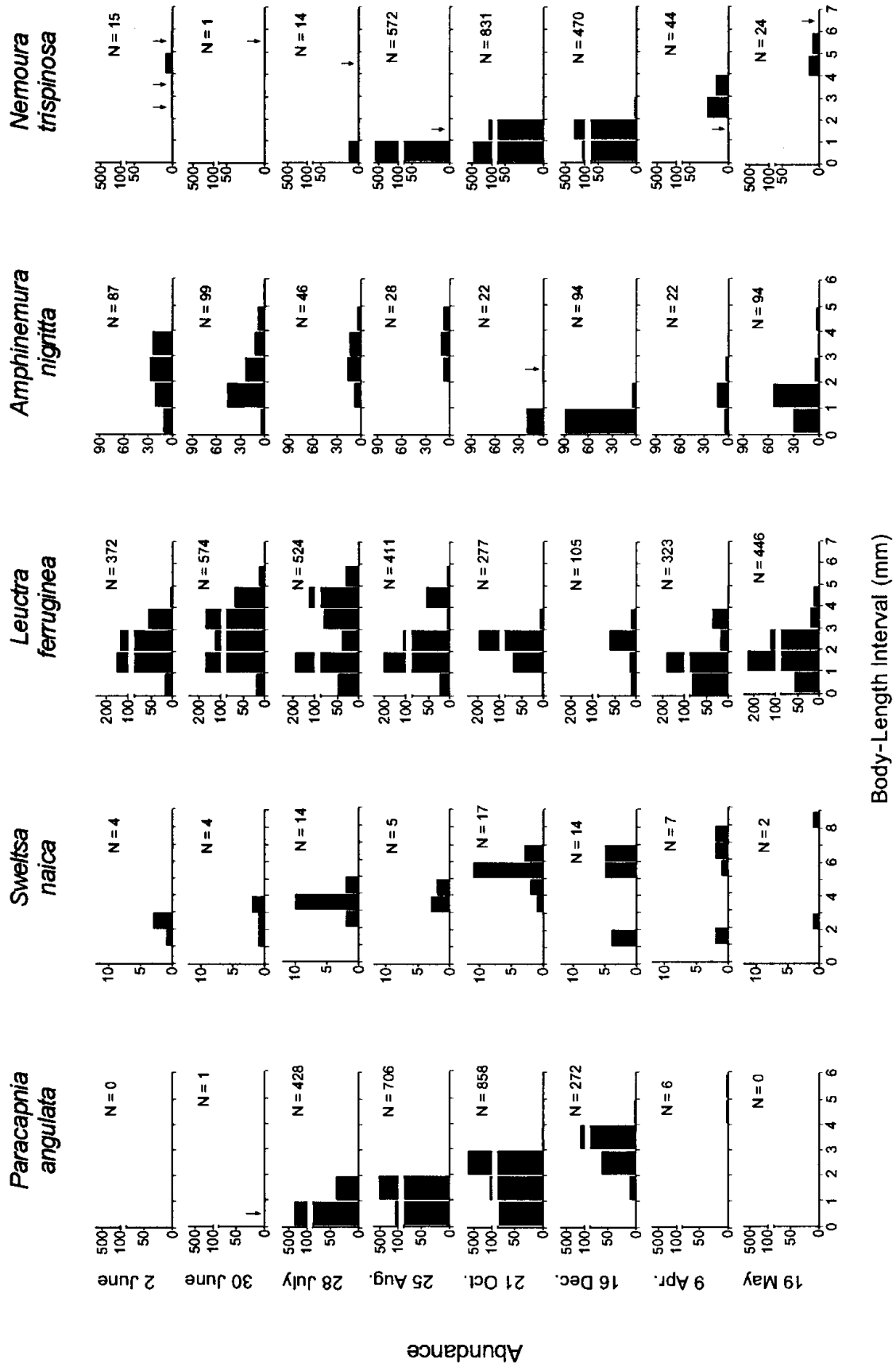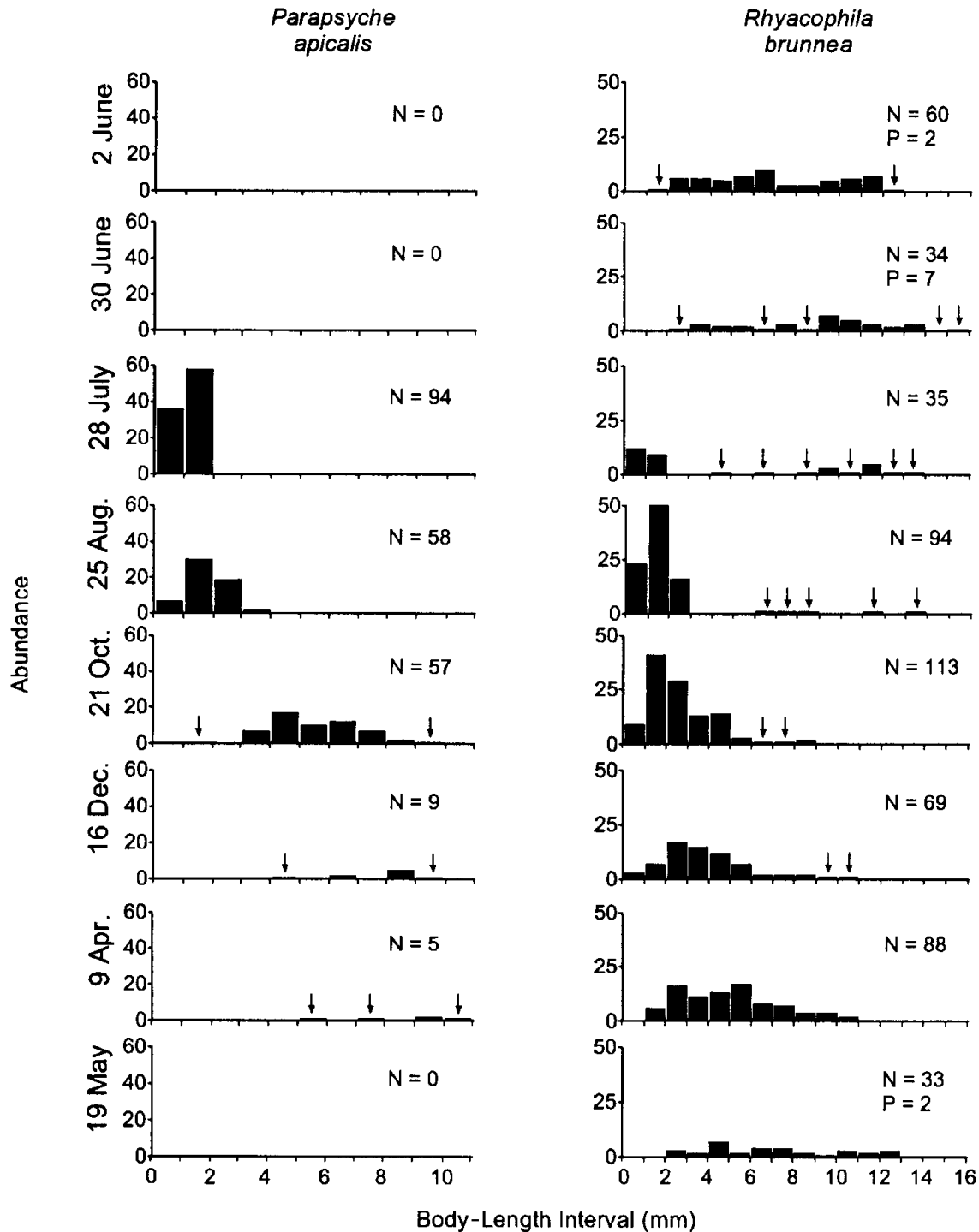
Fig. 5. Size-frequency distributions of 2 species of caddisflies at Balsam Hollow Brook from June 1997 to May 1998, showing life cycles. *N* is the number of larvae collected per sampling date and *P* is the number of pupae collected. Arrows indicate the presence of size (body length) classes not abundant enough to appear as visible bars in the histograms.

traps (Fig. 2), but these were extremely rare and most could not be identified as larvae.

Parapsyche apicalis (Banks) (Hydropsychidae) is a net-spinning caddisfly commonly found in small, spring-fed streams (Flint 1961; Ross and Wallace 1983). *Parapsyche apicalis* was clearly univoltine in Balsam Hollow Brook (Fig. 5). Emergence occurred in early to midsummer (Fig. 2), and recruits were first seen in late July (Fig. 5). Flint (1961)

reported an extended emergence period for this species in Massachusetts, from May to early October. Larvae grew rapidly during the summer and fall, then overwintered in a variety of size classes. This pattern was similar to that reported by Mackay (1969) in Quebec.

Rhyacophila brunnea Banks (Rhyacophilidae) larvae in Balsam Hollow Brook apparently needed 2 years to complete their life cycle. A range of size classes was collected

on most sampling dates, but two clear cohorts were present on several dates (Fig. 5). Recruitment began in midsummer, and larvae grew slowly; pupation and emergence began in the spring – early summer of their second year. Both recruitment and emergence were extended, occurring over several months. Smith (1968) reported that this species (listed as *Rhyacophila acropedes* Banks) overwinters as third- or fourth-instar larvae in New England and Labrador, with pupation occurring from late May to June and emergence from late July to early August.

Life-history and temperature patterns

Williams and Hogg (1988) and Wallace and Anderson (1996) suggested that the life cycles of at least some aquatic insects in springs should be less synchronous than the life cycles of those in nearby non-spring habitats, owing to a lack of temperature cues to synchronize development. For example, *Lepidostoma unicolor* (Banks) (Trichoptera: Lepidostomatidae) in a spring-fed river in Oregon showed more variation in larval size and an extended emergence period compared with *L. unicolor* in a runoff stream with greater temperature fluctuation (Grafius and Anderson 1980). Similarly, in Idaho and Utah, the mayfly *Tricorythodes minutus* Traver (Ephemeroptera: Leptohyphidae) was able to complete more generations per year in streams (3 generations) than in cold springs (2 generations) (Newell and Minshall 1978).

In Balsam Hollow Brook, the life cycles of over half of the common species (*B. tricaudatus, L. ferruginea, A. nigritta, N. trispinosa, P. apicalis*, and *R. brunnea*) were asynchronous, with considerable variation in larval size distributions, extended egg hatches, and (or) extended emergence periods. Several researchers have found higher proportions of asynchronous taxa in springs than in non-spring habitats. Singh et al. (1984) found that one-third of stonefly species in a spring in southern Ontario had asynchronous emergence periods, and Williams and Hogg (1988) found that 50% of stonefly and caddisfly species in their spring were asynchronous. These values are much higher than those in non-spring habitats (12% of total stonefly species in a first-order Pennsylvania stream (Masteller 1983) and 18% of total mayfly and stonefly species in a mountain stream in North Carolina (Huryn and Wallace 2000)). However, most of these species also showed similar asynchronous life cycles in non-spring habitats, as detailed in the previous section, indicating that the asynchrony is not related to the stable thermal conditions in the cold-spring habitat. In contrast, *A. nigritta*, which showed extended emergence in Balsam Hollow Brook, has been reported to exhibit relatively synchronous emergence in other locations (May to June–July in a first-order stream in northwestern Pennsylvania (Masteller 1983) and late May to mid-June in southern Ontario (Harper and Hynes 1972)). *Rhyacophila brunnea* may also have a different life cycle in the cold spring than that reported from a runoff stream; Smith (1968) indicated that the species is univoltine in Labrador and New England streams, compared with an apparently 2-year cycle in Balsam Hollow Brook, which is a cold spring. Some variations in life-cycle timing were also reported for the synchronous species found in Balsam Hollow Brook. For example, *P. angulata* grew faster in summer and reached mature size sooner in both Balsam Hollow Brook and a constant-temperature Ontario cold spring

(temperatures <13°C; Harper and Hynes 1972) than in a Quebec lake outlet (where summer water temperatures reached 25°C; Harper et al. 1991).

We conclude that despite a pattern consisting of a high proportion of taxa with asynchronous life cycles, there is little or no evidence that the EPT taxa have altered their life-cycle strategies from synchronous to non-synchronous development in the thermally stable Balsam Hollow Brook. However, the large proportion of species with asynchronous development in the cold spring compared with non-spring habitats suggests that thermal patterns do have an effect on species composition in these habitats, possibly by favouring taxa that already possess asynchronous development. Since species that live in cold springs must also be able to complete their development at low summer temperatures, it is possible that the high population asynchrony is simply a result of the life-history patterns of the species which can colonize and survive in these habitats.

Acknowledgements

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