

Life history patterns of insects in an intermittent and a permanent stream

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Abstract. Samples were taken in an intermittent stream (dries only at some locations) and a permanent stream in a single watershed in Tompkins County, New York, over a 3-yr period to compare the life history patterns of specialist species (occurring primarily in intermittent streams), facultative species (occurring in both permanent and intermittent streams) and permanent-stream species (occurring primarily in permanent habitats). We also tested the hypothesis that to avoid the dry period, populations of species grow and develop faster and emerge earlier in the intermittent than in the permanent stream. Specialist species emerged by mid-June, whereas permanent-stream species had late summer emergences. Although two of the three specialist species (*Amphinemura delosa* and *Ameletus ludens*) had drought-resistant eggs, the third (*Paracornia opis*) had immediately hatching eggs. Nymphs of this last species survived the dry period either in the hyporheic zone or in riffles that did not dry. Only one of two facultative species and one specialist species showed greater size and/or advanced development in sites that dried compared with populations in permanent sites; however, these differences occurred only in early spring and had disappeared long before the stream dried. Thus, populations of the same species emerged at the same time from the intermittent and permanent streams. At any one time, individuals of specialist and permanent-stream species were usually larger and/or more developed in the stream or at sites where they were most abundant. Although each specialist species had life history patterns enabling it to survive drought, these patterns were not unique to the intermittent-stream fauna. In addition, species without those characteristics were also present in the stream, and species with populations in both permanent and intermittent streams did not show site-specific variation in life history patterns consistent with drought-avoidance in intermittent streams.

Key words: life history patterns, intermittent streams, stream insects, insect growth, insect development.

The drying of a stream results in elimination of much of the habitat for the macroinvertebrates that live there. If some aquatic invertebrate species are unable to survive drought, one might expect to find very different macroinvertebrate communities in temporary and permanent streams. Previous studies have shown that although some species may be specific to temporary streams, others are facultative, living in both temporary and permanent habitats (Knight and Gaufin 1967, Mackay 1969, Williams and Hynes 1977, Wright et al. 1984). Delucchi (1988a) showed that although invertebrate community structure in temporary streams (entire bed dries), intermittent streams (only parts dry) and permanent streams differs immediately after a period of drying and rewetting, all stream invertebrate communities in a single watershed are surprisingly similar just

before the dry season, after streams have been flowing for a maximum amount of time. Boulton and Suter (1986) also found that the fauna of two temporary streams in Victoria, Australia, was similar to nearby permanent streams. Thus, the invertebrate fauna of temporary streams, at least in some regions, may not be as unique as has been suggested previously (Williams and Hynes 1977).

Invertebrates in temporary habitats can use one of two strategies for survival of the dry period. First, the aquatic stage can migrate from the temporary habitat to a permanent habitat, such as adjacent permanent pools or riffles, or to the hyporheic zone. Although aquatic invertebrates are known to recolonize reflooded temporary habitats from these refuges (Williams 1977, McArthur and Barnes 1985), little work has been done to show that invertebrates actually move into these refuges as streams dry. In fact, a previous study showed that migration patterns of aquatic stages may result in concen-

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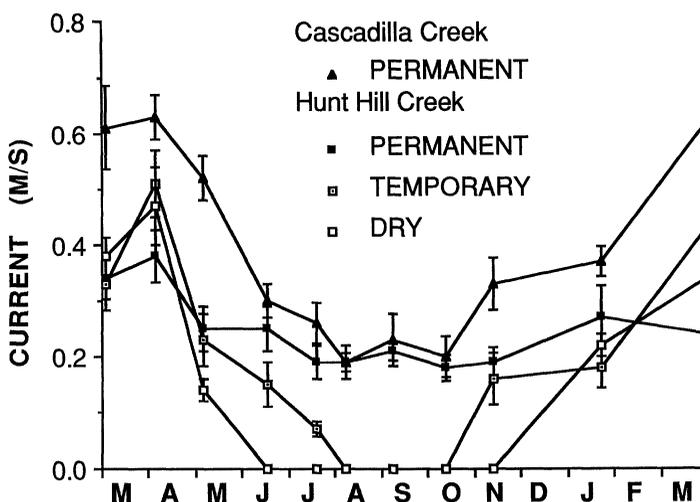


FIG. 1. Average current (m/s \pm 1 SE, $n = 8$) at each of four riffle types from March 1985 to March 1986.

tration of invertebrates in riffles as they dry (Delucchi 1989). Second, temporary stream invertebrates can have a drought-resistant life history stage, such as a terrestrial adult or a drought-resistant egg, larva, or pupa. The drying of a stream may eliminate species that have not emigrated or are in non-resistant life stages. Thus, natural selection should favor species with life history patterns enabling them to avoid drought, which could lead to a unique set of species characteristic of temporary habitats.

Alternatively, the same species may occur in both habitats but show different life history patterns in permanent and temporary streams. For example, temporary stream populations should grow faster and emerge earlier to survive the dry period as adults or drought-resistant eggs. Such intraspecific differences may be due to the existence of separate gene pools or to physiological responses to differences in environmental factors between the temporary and permanent streams. Sweeney et al. (1986) have shown that it is possible for a species to have genetic differentiation between populations within a drainage basin; however, it is unknown how common this phenomenon may be. On the other hand, physiological responses of aquatic insects to environmental factors are well documented. For example, insects generally grow faster at higher temperatures within a non-lethal range (Sweeney 1984), and growth rate may be higher at lower flow because less energy is

expended to maintain position in the stream (Kovalak 1978, Statzner et al. 1988).

Earlier emergence is not always the result of higher growth rate; in some cases individuals that develop faster emerge earlier but at a smaller size. Thus, rates of growth and development may be controlled by different environmental variables or have different responses to the same variables (Butler 1984). Sweeney and Vannote (1978) have shown that at sub-optimal temperatures insects tend to emerge as adults at a smaller size. Thus, one might observe differences in rates of development but not growth between populations of temporary and permanent stream insects.

This study had two main purposes: first, to determine whether life history patterns of intermittent stream species enabled them to successfully avoid drought, while those of permanent stream species were more variable. The second purpose was to determine if species occurring in both types of streams grew and developed faster and emerged earlier in an intermittent stream than in a permanent stream, resulting in avoidance of the dry period in the intermittent stream.

Methods

Samples were taken in two streams in a single watershed in Tompkins County, New York during 1983–1986. Ringwood Branch of Cascadilla

TABLE 1. Size and developmental categories used for insect nymphs in this study. Size measurements refer to head capsule widths, with the maximum size of each category approximately double the size of the next smallest category. Developmental criteria modified from Clifford et al. (1979).

Category	Range in mm or Definition
	Size
1	0-0.089
2	0.09-0.183
3	0.184-0.369
4	0.37-0.759
5	0.76-1.49
6	1.5-2.9
7	3.0-5.9
	Development
I	No wing pads
II	Wing pads shorter than wide
III	Wing pads longer than wide
IV	Wing pads darkened

Creek is a second order stream that is permanent along its entire length. Hunt Hill Creek is a first order intermittent stream that dries each year over at least one half of its length. Riffles on this latter stream begin drying in June with the maximum extent of drying occurring in late August to mid-September. Both streams have substrates primarily of gravel and cobble with particles ranging from silt to boulders. Cascadilla Creek is larger, having annual non-storm discharges ranging between 0.01 and 0.13 m³/s, while Hunt Hill Creek discharges range from 0 to 0.07 m³/s. We sampled one permanent riffle (P_C) on Cascadilla Creek and three types of riffles on Hunt Hill Creek classified by length of dry period: (1) two permanent (P_H), (2) two temporary (T_H), dry for less than three months and (3) one dry (D_H), dry for about five months. Figure 1 illustrates the 1985-1986 differences in flow regime among the four riffle types.

We sampled sites on both streams at 2-4-wk intervals from June 1983 to March 1986 except for 4-mo periods during the winters of 1983-1984 and 1984-1985. Maximum-minimum thermometers were placed at one of each type of site in April 1984, then checked and reset at each sampling date until March 1986.

Five (1983-1984) or eight (1985-1986) Surber samples (mesh 355 μm) were taken at randomly selected positions at each site on each date. Samples were placed in a pan of water; stones and

TABLE 2. Dates and sites of Surber samples used for analyzing life histories.

Date	Cascadilla Creek		Hunt Hill Creek	
	Per- manent (P _C)	Per- manent (P _H)	Tem- porary (T _H)	Dry (D _H)
1983				
June (early)	X			X
August				
Early		X		
Late	X			
September	X	X		
October	X			
November				
Early	X	X		
Mid	X	X		
1984				
June ^a				
Early	X	X	X	X
Late	X	X	X	X
July				
Mid	X	X	X	
Late	X	X	X	
August				
Early	X			
Late	X	X	X	
1985				
March ^a	X	X	X	X
April	X	X		
July ^a (mid)	X	X	X	

^a Dates used for size and development analysis.

large detritus were rinsed and removed. The remaining detritus and invertebrates were strained through an aquarium net and preserved in 70% ethanol. The aquarium net had an irregular knitted mesh, the largest openings of which were triangular with a base of 610 μm and a height of 430 μm. However, the majority of the openings had dimensions of less than 355 μm. Samples were sorted under a dissecting microscope at 10× magnification. Invertebrates were identified and classified into seven size categories, each having a maximum head capsule width approximately double the next smaller category (Table 1). Hemimetabolous insects were categorized by developmental stage after Clifford et al. (1979) (Table 1). Samples that contained over 300 invertebrates were subsampled using a method modified from Wrona et

TABLE 3. Individuals in each size category at each site on the dates used for between-site size comparisons. Site abbreviations as in Table 2; size categories as in Table 1.

Species	Size Category	March 1985				June 1984				July 1985		
		P _C	P _H	T _H	D _H	P _C	P _H	T _H	D _H	P _C	P _H	T _H
<i>Tricorythodes</i> sp.	3					19				199		
	4					11				774		
	5					0				291		
<i>Baetis flavistriga</i>	3					33	0	0	0	88	1	0
	4					39	1	0	4	165	2	0
	5					0	0	0	0	4	0	0
<i>Baetis tricaudatus</i>	2	0	0	0	4	0	0	0	0	0	0	0
	3	213	107	157	226	92	29	4	9	142	9	0
	4	794	191	237	517	280	11	0	13	459	11	1
	5	61	31	35	57	42	8	0	1	8	2	0
<i>Diphetero hageni</i>	3	35	111	84	188	1	0	0	1	107	29	19
	4	17	15	27	23	0	11	4	2	34	14	0
	5	0	0	0	0	0	1	0	0	0	0	0
<i>Cinygmula subaequalis</i>	3	31	38	38	34	0	0	0	0			
	4	679	682	923	341	0	0	1	0			
	5	31	31	27	4	13	6	23	22			
	6	0	0	0	0	8	13	14	8			
<i>Amphinemura delosa</i>	2	0	8	0	11	0	0	0	0	0	0	0
	3	89	689	483	1233	0	6	1	0	0	0	0
	4	19	345	172	268	0	12	3	2	0	1	1
	5	0	0	0	0	0	20	6	6	0	1	0
<i>Paracapnia opis</i>	2	0	0	0	0	0	0	0	4	0	0	0
	3	0	0	0	0	0	24	57	0	23	553	360
	4	0	19	15	4	0	0	0	0	0	0	0
	5	9	165	100	138	0	0	0	0	0	0	0
<i>Ameletus ludens</i>	2	0	0	0	0	0	0	0	0	0	1	0
	3	8	4	23	61	0	0	0	0	0	0	0
	4	0	7	42	199	0	0	0	3	0	0	0
	5	0	23	31	155	0	5	2	5	0	0	0

al. (1982), with $\frac{1}{4}$ of the sample counted and identified.

Approximately one third of the Surber samples were analyzed for this study (Table 2). When riffles were sampled more than once during any month, different times of the month (early, middle, and late) were considered separate time periods. Three time periods were chosen for examining size and developmental stage differences between sites (Table 2). The first was March 1985, when all sites had been flowing continuously for at least four months; the second was June 1984, less than one month before the normal time of drying for the dry site; the third was July 1985, when the temporary site was beginning to dry.

Since a complete set of samples was not analyzed for any one year or site (Table 2), between-species comparisons of life history timing were made by combining the number of individuals from all sites sampled during a time period from each of the three years (1983–1985). Although the relative abundance of developmental stages varied between sites and years for univoltine species, the presence or absence of stages did not; thus, the development of generalized life history phenologies for the region was not affected by combining data from different years and sites.

Differences between riffles in the size and development of individuals of each species were determined using the Kruskal-Wallis test and

TABLE 4. Individuals in each developmental category at each site on the dates used for between-site development comparisons. Site abbreviations as in Table 2; developmental categories as in Table 1.

Species	Develop- mental Cate- gory	March 1985				June 1984				July 1985		
		P _C	P _H	T _H	D _H	P _C	P _H	T _H	D _H	P _C	P _H	T _H
<i>Tricorythodes</i> sp.	I					30				387		
	II					0				647		
	III					0				230		
<i>Baetis flavistriga</i>	I					41	0	0	0	92	1	0
	II					25	1	0	4	161	2	0
	III					6	0	0	0	4	0	0
<i>Baetis tricaudatus</i>	I	151	103	111	157	34	21	4	6	111	8	1
	II	906	226	318	647	318	19	0	15	486	13	0
	III	11	0	0	0	54	8	0	2	12	0	0
	IV	0	0	0	0	8	0	0	0	0	1	0
<i>Diphetero hageni</i>	I	16	92	61	100	1	0	0	1	34	21	12
	II	36	34	50	111	0	5	3	2	103	19	7
	III	0	0	0	0	0	7	1	0	4	3	0
<i>Cinygmula subaequalis</i>	I	446	529	540	172	0	0	1	0			
	II	295	222	448	207	0	0	4	3			
	III	0	0	0	0	20	16	27	26			
	IV	0	0	0	0	1	3	6	1			
<i>Amphinemura delosa</i>	I	108	1042	655	1508	0	12	4	0	0	1	0
	II	0	0	0	4	0	13	1	2	0	0	0
	III	0	0	0	0	0	12	4	6	0	1	1
	IV	0	0	0	0	0	1	1	0	0	0	0
<i>Paracapnia opis</i>	I	0	0	0	0	0	24	57	4	23	553	360
	II	0	0	0	0	0	0	0	0	0	0	0
	III	9	184	115	142	0	0	0	0	0	0	0
<i>Ameletus ludens</i>	I	0	11	50	157	0	0	0	1	0	1	0
	II	8	15	34	237	0	2	1	6	0	0	0
	III	0	8	12	21	0	3	1	1	0	0	0

multiple comparison procedure for contingency tables (Conover 1980). Number of individuals in 5 (1984) or 8 (1985) Surber samples was used rather than calculated densities (Tables 3 and 4). Alpha levels for the multiple comparisons were adjusted by dividing the alpha level ($p = 0.05$) by the number of pairwise comparisons.

Results

The Cascadilla Creek site had significantly higher maximum temperatures than the permanent or the temporary site on Hunt Hill Creek (Wilcoxon test: $p < 0.0001$, $n = 28$; $p < 0.004$, $n = 18$; respectively) (Fig. 2A), but the maximum temperatures did not differ between permanent

and temporary sites on Hunt Hill Creek (Wilcoxon test: $p = 0.263$, $n = 17$). The permanent site on Cascadilla Creek and the temporary Hunt Hill Creek site had significantly colder minimum temperatures than did the permanent site on Hunt Hill Creek (Wilcoxon test: $p < 0.001$, $n = 28$; $p < 0.001$, $n = 21$, respectively), but were not different from each other (Wilcoxon test: $p > 0.45$, $n = 22$) (Fig. 2B). The median difference for all significant differences was 1.0°C. Thus, temperature regimes were site specific and not related to riffle permanence.

Between-species comparisons

Comparisons of life history patterns were made among eight species that were identifiable as early instars and abundant ($>250/m^2$)

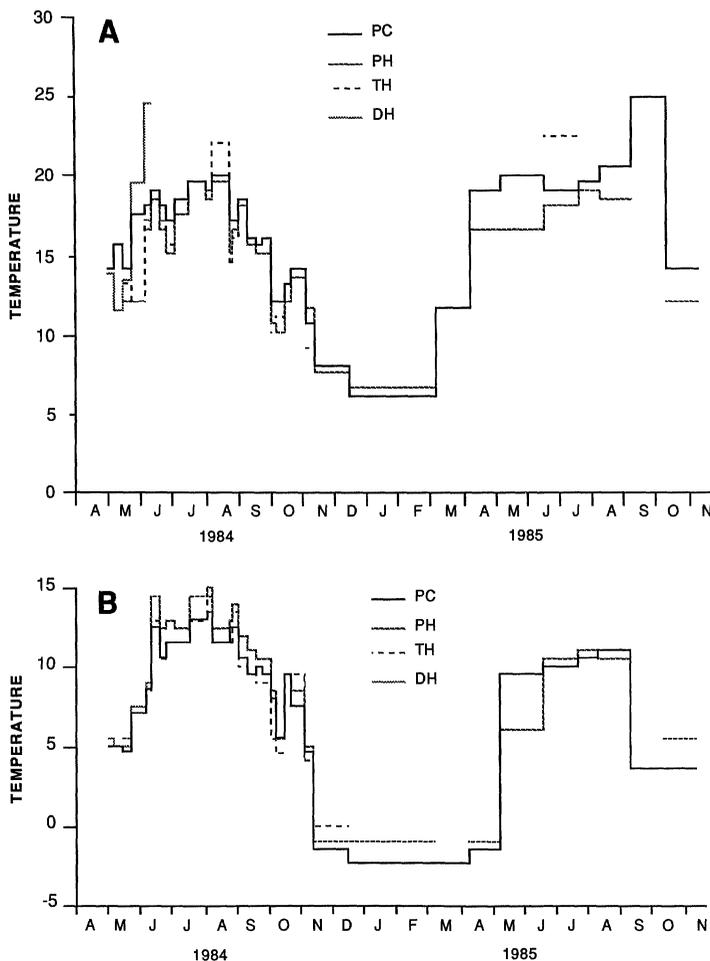


FIG. 2. Maximum (A) and minimum (B) temperatures ($^{\circ}\text{C}$) at each of four riffle types from April 1984 to November 1985. Site abbreviations as in Table 2.

in at least one study riffle. Species were placed in categories according to differences in relative abundance in the two streams (Table 5) (sign test on average densities for each date in each stream). Two mayfly (Baetidae) species (*Baetis tricaudatus* Dodds and *Baetis flavistriga* McDunnough) were significantly more abundant in Cascadilla Creek ($p = 0.0004$, $n = 12$; $p = 0.0156$, $n = 7$, respectively). A third mayfly, *Tricorythodes* sp. (Tricorythidae), was absent from Hunt Hill Creek. These three species were termed permanent stream species. Three species (the mayfly *Ameletus ludens* Needham [Siphonuridae] and the stoneflies *Paracapnia opis* (Newman) [Capniidae] and *Amphinemura delosa* Ricker [Nemouridae]) were significantly more abundant in Hunt Hill Creek ($p = 0.0078$, $n =$

8; $p = 0.0004$, $n = 12$; $p = 0.0156$, $n = 7$, respectively) and were categorized as specialist species. Two mayfly species (*Dipheter hageni* (Eaton) [Baetidae] and *Cinygmula subaequalis* (Banks) [Heptageniidae]) were equally abundant in both streams ($p = 0.3876$, $n = 12$; $p = 0.625$, $n = 4$) and were termed facultative species. Voucher specimens of these eight species have been deposited in the Cornell University Insect Collection, Lot No. 1163. The following descriptions are given in order from highest to lowest ratio of relative abundance in permanent: intermittent streams.

Permanent-stream species.—*Tricorythodes* sp. occurred only in Cascadilla Creek (Table 5). Several nymphs in stages I and II were found in October and November of 1983; however, no

TABLE 5. Range of densities (No./m²) for each species at each riffle type. Average density is given below the range. Only dates on which the species occurred at at least one site were used in calculations.

Species	Site			
	P _C	P _H	T _H	D _H
<i>Tricorythodes</i> sp.	8-1757 314	0	0	0
<i>Baetis flavistriga</i>	16-1737 773	0-134 29	0-29 8	0-96 35
<i>Baetis tricaudatus</i>	8-1459 423	0-564 142	4-580 92	43-1118 303
<i>Dipheter hageni</i>	0-280 74	2-319 97	9-275 123	4-293 84
<i>Cinygmula subaequalis</i>	33-1097 552	41-1038 640	82-1373 728	46-516 210
<i>Amphinemura delosa</i>	0-175 58	0-1730 449	0-905 138	18-2103 561
<i>Paracapnia opis</i>	0-74 22	0-769 196	2-501 186	7-197 58
<i>Ameletus ludens</i>	0-33 8	1-103 39	0-133 34	18-578 163

nymphs were found in March or April 1985, or early June 1983 and 1984. Nymphs in stage I were present in late June of 1984. Although nymphs in stage IV were not collected, nymphs in stage III were collected only in July and August, becoming more abundant, then disappearing in September, indicating a univoltine life cycle with August emergence (Fig. 3).

Baetis flavistriga was abundant in Cascadilla Creek (Table 5) but uncommon in Hunt Hill Creek. No nymphs were found in September-November of 1983 and March-April 1985. Nymphs in stages I-III were present in June of 1983 and 1984, indicating rapid growth of nymphs between April and June. Nymphs in stage IV were found in July and August (Fig. 3), indicating a late summer emergence similar to that of *Tricorythodes* sp. The large numbers of stage I-III nymphs present in August 1985 suggest that *B. flavistriga* may have a second generation in late summer or an extended emergence period. These data do not enable a distinction to be made between alternative explanations.

Although *B. tricaudatus* was occasionally abundant in Hunt Hill Creek (Table 5), it was always more abundant in Cascadilla Creek.

Nymphs in stages I-III were collected throughout the year. Nymphs in stage IV were found from early June to mid-July, suggesting an extended emergence or two generations per year (Fig. 3).

Facultative species.—*Dipheter hageni* was abundant in both streams (Table 5). With the exception of one nymph in stage III found in September, only nymphs in stages I and II were found from September to April. Nymphs in stage III were present beginning in June (Fig. 3). Nymphs in stage III were absent in late June in 1984. Since nymphs in stage IV were found in August, *D. hageni* appears to be bivoltine with emergences in June and August followed by immediate hatching and slow growth during the fall and winter.

Cinygmula subaequalis was also abundant in both streams (Table 5). Nymphs were collected only during three sampling periods: March, April, and early June (Fig. 3). Nymphs in stages I and II were collected in March and April, and mostly stage III and IV nymphs were collected in early June. These data indicate that *C. subaequalis* is univoltine with early June emergence.

Specialist species.—*Amphinemura delosa* was more abundant in Hunt Hill Creek than in Cas-

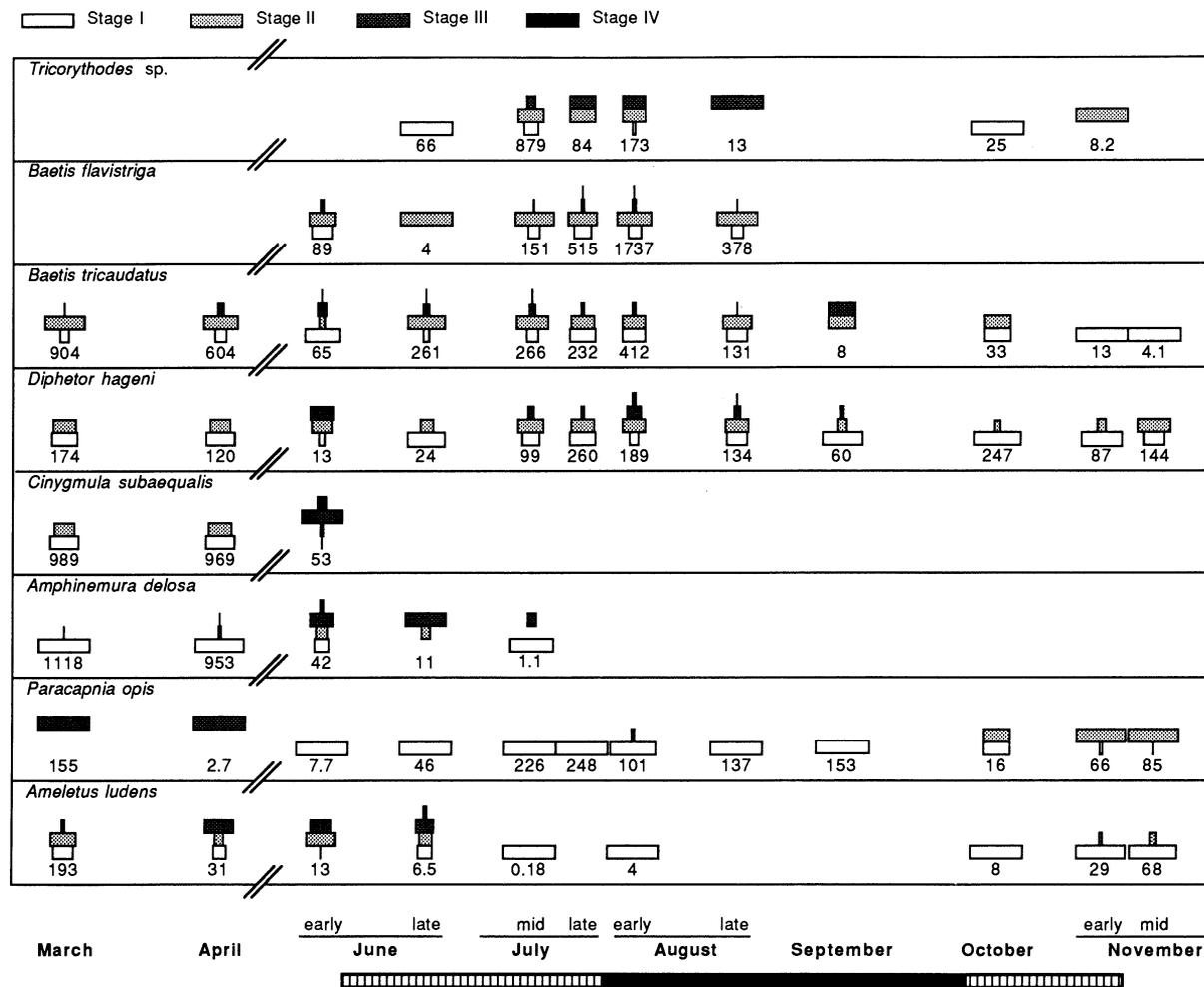


FIG. 3. Relative abundance of the four nymphal development stages during 12 time periods for each of the eight species studied. Data from three years and four riffle types were combined; see Table 2 for number of years and riffles used for each time period. Length of bars shown in figure legend represent 100%. Numbers represent average density (No./m²) for each time period. Stage I = no wing pads; Stage II = wing pads shorter than wide; Stage III = wing pads longer than wide; Stage IV = wing pads darkened. The bar at the bottom of the figures represents the time periods when the temporary (hatched bar) and dry (solid bar) sites on Hunt Hill Creek were dry in 1985.

cadilla Creek (Table 5). No nymphs were found between late July and November. Nymphs in stages I and II were present in March and nymphs in stages I–III were present in April. Nymphs in stage IV were found only in June (Fig. 3). Only a few smaller nymphs were present in July. Thus, *A. delosa* has a univoltine life cycle with emergence in June.

Paracapnia opis densities were higher in Hunt Hill Creek than in Cascadilla Creek (Table 5). Nymphs in stage I are present from June to November, indicating that eggs probably hatch soon after oviposition, and that nymphal growth is slow during the spring and summer. Nymphs grow to size category 3 (0.184–0.369 mm head width) by July but not to developmental stage II until November. Although no nymphs in stage IV were collected during the study, the decline in the number of nymphs in stage III between March and April (Fig. 3) suggests that emergence occurs mainly in March.

Ameletus ludens was also more abundant in Hunt Hill Creek than in Cascadilla Creek (Table 5). Nymphs in stage I were found only sporadically between July and October (one during each month, July, August and October), but increased in abundance in November. Nymphs in stage III were found from March through June. The only nymph in stage IV collected during the study was found in late June (Fig. 3). Thus, *A. ludens* had a June emergence as did most other specialist and facultative species.

Within-species comparisons of size and development

No comparisons of *Tricorythodes* sp. size or development were made between permanent and temporary riffles because it was only present in Cascadilla Creek. Of the remaining seven species, five had significant differences in sizes and/or development between permanent and temporary riffles in March, two in June and none in July (Table 6).

Baetis tricaudatus was the only species to show significant differences between permanent and temporary riffles in both size and development. It was also the only species to show differences in more than one sampling period and the only permanent-stream species to show any between-riffle differences. In both March and June, *B. tricaudatus* nymphs were larger and in later

instars in Cascadilla Creek than in Hunt Hill Creek.

Both of the facultative species (*D. hageni* and *C. subaequalis*) showed no size differences between sites, but in March had slowest development at the permanent site on Hunt Hill Creek compared with other sites. In contrast, all the specialist species showed no development differences, but in March (*A. delosa* and *A. ludens*) or June (*P. opis*) were largest at the permanent site on Hunt Hill Creek compared with all other sites (Table 6).

Discussion

Comparisons with other studies

The life histories found in this study were generally consistent with those described in other studies. For example, Bergman and Hilsenhoff (1978) were also unable to distinguish whether *B. flavistriga* (as *B. phoebus*) had two generations or an extended emergence period in Wisconsin. Clifford (1982) and Unzicker and Carlson (1982) reported that *Cinygmula* species were univoltine as we found in this study. In addition, Clemens (1922) reported that *A. ludens* was univoltine, hatching in October and emerging in April to mid-June as in this study.

Although there was general agreement with other studies some discrepancies were apparent. *Baetis tricaudatus* has been reported as multivoltine (Murphy 1922 as *B. vagans*, Clifford 1982), which is most probably the case in Cascadilla and Hunt Hill Creeks. However, Murphy (1922) found that *B. tricaudatus* had three generations over a 2-yr period in an Ithaca, New York, stream, with emergences in August during the first year and in May and October during the second year of the cycle. This is not the pattern we observed in Cascadilla and Hunt Hill Creeks, since stage IV nymphs were found only in June (1984) and July (1984–1985) and did not show different emergence periods in different years; i.e., there were nymphs in stage IV in two consecutive Julys.

Two species had emergence periods slightly different from those reported in previous studies. Bergman and Hilsenhoff (1978) found that *D. hageni* emerged earlier (April and May) in Wisconsin than was found in this study (June). However, they speculated that the specimens from Wisconsin may have belonged to a sibling

TABLE 6. Results of Kruskal-Wallis tests for size and developmental differences between riffles within each species. Only species that had significantly different ($p < 0.05$) sizes and/or development between riffles during a time period are included. Sites are listed from those with the largest (or most developed) individuals to smallest (or least developed). Sites that are not significantly different are connected by a line. N.S., not significant. Site abbreviations as in Table 2.

Date	Taxon	Comparisons							
		Size				Development			
March 1985	<i>Baetis tricaudatus</i>	P _C	D _H	P _H	T _H	P _C	D _H	P _H	T _H
	<i>Diphetero hageni</i>	N.S.				P _C	D _H	T _H	P _H
	<i>Cinygmula subaequalis</i>	N.S.				D _H	T _H	P _C	P _H
	<i>Amphinemura delosa</i>	P _H	T _H	P _C	D _H	N.S.			
	<i>Ameletus ludens</i>	P _H	D _H	T _H	P _C	N.S.			
June 1984	<i>Baetis tricaudatus</i>	P _C	D _H	P _H	T _H	P _C	D _H	P _H	T _H
	<i>Paracapnia opis</i>	P _H	T _H	D _H	N.S.				
July 1985	No significant differences								

species of *D. hageni*, since the population they studied was parthenogenetic, while populations elsewhere have both males and females present. The March emergence of *P. opis* is slightly earlier than has been found for this species in Quebec (Harper and Magnin 1969).

Comparisons between species

Even though six of eight species were significantly more abundant in one or the other stream, all but *Tricorythodes* sp. had populations in both streams. Thus, the intermittent stream did not have a unique fauna. Only one of the eight species studied, *Ameletus ludens*, has been reported as a temporary stream specialist (Clemens 1922). However, Mackay (1969) found this species (*Ameletus "C"*) to be abundant in permanent habitats. Knight and Gauvin (1967) also found species in temporary streams to be mainly facultative. Of the ten Plecoptera species that they collected in temporary streams in Colorado, all were found in at least one other type of stream and most occurred in four of five other categories of stream type, ranging from small stony streams to sluggish rivers. Similarly, in a study of a small stream in Quebec, Mackay (1969) found only three species restricted to an upstream area that dried.

Despite the occurrence of most species in both streams, life history patterns varied between

the species according to their abundances in each stream. The specialist species had univoltine life cycles, with emergence in spring before stream drying (Fig. 3). The three permanent-stream species had emergence periods in mid-to-late summer (during the dry period of the intermittent stream). The facultative species had the most variable life history patterns. One, *C. subaequalis*, had a pattern similar to the specialist species. The other, *D. hageni*, had emergence periods in the summer as did permanent stream species, although there was an indication of some spring emergence. Thus, species that emerged before drying were more successful in the intermittent stream as indicated by higher abundance. These data are consistent with the hypothesis that the lower abundance of summer-emerging species is the result of local population failures due to stream drying. Continued presence of these species in the intermittent stream may be due to repeated recolonization from sites that do not dry. Thus, the abundance, but not the presence or absence of a species, was related to its ability to avoid the dry period.

Although emergence before stream drying is one possible way to sustain populations in intermittent streams, a second alternative is the production of drought-resistant eggs. Five of the eight species studied, representing specialist, facultative and permanent-stream species, were absent from all sites during part of the

year (Fig. 3). One possible explanation for these absences is delayed hatching of eggs. Two of the three specialist species (*A. delosa* and *A. ludens*), absent from samples for long periods coinciding with the dry period in the temporary riffles of Hunt Hill Creek, have been shown to have an egg diapause. Harper (1973) found that eggs of *A. delosa* laid in July and kept in the laboratory under ambient stream conditions did not start hatching until October. Clemens (1922) reported that *A. ludens* lives in temporary streams, emerges in April to mid-June, and when kept in the laboratory has eggs that hatch in October. These observations are consistent with the data from our study, although here, some hatching of *A. ludens* occurred at permanent sites before October (Fig. 3). Thus, two species prevalent in the intermittent stream could have avoided the dry period in egg diapause.

However, two permanent stream species (*Tricorythodes* sp. and *B. flavistriga*) and one facultative species (*C. subaequalis*) were also absent for long periods, part or all of which corresponded to periods of drought (Fig. 3). Although recent studies have shown that delayed hatching in Ephemeroptera may be more common than previously thought (Brittain 1982, Friesen et al. 1979, Giberson and Galloway 1985), this may not be the case for all species with long absences from samples in our study. Newell and Minshall (1978) found that 7.5°C *Tricorythodes minutus* eggs took at least 3 mo to hatch; however, at 12.5–21°C, eggs took <2 mo to hatch. These higher temperatures are more typical of Cascadilla Creek in the fall and would result in hatching of *Tricorythodes* in October. Thus, the virtual absence of this permanent-stream species during fall, winter and early spring may be due to slow growth of early instar nymphs that are missed during sampling due to use of a coarse mesh (355 µm) net rather than to delayed hatching (Suter and Bishop 1980). This may also be true for the facultative species, *C. subaequalis*, which has been found in other studies to overwinter as nymphs (Clifford 1982, Unzicker and Carlson 1982).

A third strategy for surviving drought in intermittent streams is movement by nymphs into the hyporheic zone during the dry period. Previous studies have shown that some invertebrates do move toward the hyporheic zone of Hunt Hill Creek before the dry period (Delucchi 1989) and that small nymphs are found in

the hyporheic zone during the dry period (Delucchi 1988b). This is a possible explanation for the survival of *P. opis* nymphs (Delucchi 1988a, 1988b). However, this is probably not true for *D. hageni* (another species that lacks delayed hatching and is abundant in the intermittent stream), since Delucchi (1988a) showed that Baetidae in the intermittent stream are eliminated by riffle drying.

Comparisons within species

Only *C. subaequalis* and *A. ludens* had growth or development differences between sites that were consistent with the hypothesis that populations of the same species develop earlier in intermittent than permanent streams. In March, *C. subaequalis* was more mature at the dry site and *A. ludens* was larger in the stream susceptible to drying than in the permanent stream. However, these differences disappeared closer to the dry period when differences might be adaptive. Overall, very few differences among size and development of nymphs were found between riffles in June and July, the times when differences would be expected if different populations of the same species show differential emergence resulting in avoidance of drought. In fact, species that did show differences in June (*B. tricaudatus* and *P. opis*) were actually smaller or less developed at sites that dry. Thus, factors other than riffle drying were most probably responsible for the within-species differences in growth and development.

Thermal regime could explain the occurrence of larger and more developed nymphs of *B. tricaudatus*, *D. hageni*, and *C. subaequalis* in the permanent stream than at the permanent site on the intermittent stream. Unexpectedly, the permanent stream was not colder than the intermittent stream but it was more variable, having both significantly higher and lower temperatures, by 1°C each way, than the permanent site on the intermittent stream. Although it has generally been found that insects grow faster at higher temperatures within non-lethal limits (Sweeney 1984), insects grown under variable temperature regimes may grow faster, at the same rate, or slower than those at constant temperatures, depending on the specific conditions (Beck 1983). Pradhan (1945, in Sweeney 1984) has presented a model of the expected growth differences in a constant versus a variable tem-

perature regime with the same mean temperatures. At temperatures below the inflection point of a constant temperature growth curve with a sigmoidal pattern, growth should be increased by thermal variation; at temperatures above the inflection point growth should be decreased by thermal variation. At temperatures below the inflection point, the rate of increase of growth per unit increase in temperature is higher than at temperatures above the inflection point. Thus, in March when stream temperatures were low (0–5°C), one would expect nymphs to be larger and/or more developed in the permanent stream (the stream with more variable temperatures) than at the permanent site in the intermittent stream, as was found for these three species.

Another factor that may affect growth and development is current velocity. Kovalak (1978) hypothesized that nymphs in slow flow regimes should have higher growth rates than those in high flow, because they use less energy to maintain their position in the stream. Flow rate was higher in the permanent stream in the spring (Fig. 1); however, only *A. ludens* was smaller in the permanent stream. Thus, this mechanism can be ruled out as a direct causal agent of differential growth and development for most species in these streams.

However, Kovalak (1978) based his arguments on Cummins's (1972) hypothesis that in areas of preferred habitat (current and substrate) and high food abundance, insects will have reduced maintenance costs, because of reduced locomotion; this results in increased growth rates and higher densities in preferred habitats. It follows, then, that individuals in their preferred habitat should be larger than those in less preferred habitats. If higher densities are an indication of preferred habitat, we would expect species to be larger and/or more developed at sites where they are more abundant. Of the four specialist and permanent-stream species with growth and/or development differences, two species (*B. tricaudatus* and *P. opis*) showed this pattern over all sites (Tables 5 and 6). Although *A. ludens* did not show this pattern within Hunt Hill Creek, it was larger in the stream in which it had higher abundance. However, *A. delosa* did not show this pattern.

In summary, the intermittent stream did not have a unique fauna. Seven of eight species studied occurred in both the permanent and intermittent streams. Species more abundant in

the intermittent stream emerged earlier, by mid-June, whereas species with late summer emergences had lower abundances in the intermittent stream. Although our data suggested that two of the specialist species had drought-resistant eggs, species with immediately hatching eggs (e.g., *P. opis*) were also abundant in the intermittent stream. Nymphs of this species may have survived the dry period in the hyporheic zone or in riffles that did not dry. Repeated colonization following population failure may be responsible for the continued presence in the intermittent stream of species without apparent adaptations to survive stream drying. Even though some species showed larger size and/or faster development in temporary versus permanent sites, most of these differences occurred in March and had disappeared before drying (in June and July). Thus, we found little evidence that stream drying exerted sufficient selection pressure on any facultative species to cause earlier emergence in the intermittent stream than in the permanent stream. Observed variation in growth and development within species is probably due to physiological responses to different temperature regimes or reduced maintenance costs in preferred habitats.

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