LIFE HISTORY ADAPTATIONS OF MAYFLIES TO AN UNSTABLE REACH OF WILSON CREEK, MANITOBA, CANADA

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ABSTRACT

Mayfly life histories were investigated as part of a study into substrate stability/discharge relationships and aquatic insects in Wilson Creek, Manitoba, Canada. Mayfly densities were greatly reduced in the most unstable, shale-paved reach, following spates. Several species were abundant during prolonged periods of low flow and were able to complete their life cycle. Life history adaptations of several species were examined with respect to frequency, intensity and predictability of spates in Wilson Creek.

INTRODUCTION

The role of disturbance in stream ecology has been overlooked until recently, and may be the dominant determinant in stream ecology (Resh *et al.* 1988). For years researchers have been aware of the impact of floods on aquatic insects, but did little to characterize benthic community habitats with respect to frequency, intensity, and periodicity of these events, perhaps because they were unaware of hydrological techniques for these analyses. Newbury (1984) described simple techniques to characterize hydrological habitats. He described ways to analyze movement of substrates, and suggested that substrate stability may be an important component of aquatic habitats.

Large reductions in benthic invertebrate densities following floods in unstable rivers have been reported in the literature (Gray and Fisher 1981, Sagar 1986, Scrimgeour and Winterbourn 1989). Reduction in aquatic insect diversity has been attributed in part to substrate stability in the Ochre River, Manitoba, Canada (Flannagan and Cobb, 1991).

Adaptations which allow insects to exist in unstable, flood prone streams include life history adaptations such as rapid development, multivoltinism, egg diapause, and effective recolonization mechanisms and behavioral avoidance (Gray 1981, Fisher *et al.* 1982, Scrimgeour and Winterbourn 1989).

In 1986 and 1987 the aquatic insect fauna of Wilson Creek, Manitoba was studied to investigate the influence of substrate stability/discharge relationships on the density and diversity of the insect fauna. These relationships were studied for three reaches of varying substrate stability. This paper examines the life history for several mayfly species which occurred in the most unstable reach of Wilson Creek. The life history strategies are examined with respect to frequency, intensity and predictability of discharge and related substrate movement.

MATERIALS AND METHODS

Study Area:

Wilson Creek, a fourth order stream with a 22km^2 drainage basin, is located in west-central Manitoba (50° 43' N, 99° 33' W) (Fig. 1). It is one of many streams originating on the Manitoba escarpment, a 400 m high bench of Cretaceous shale overlain by glacial till (Newbury 1983). The source is 747 meters above sea level (m.a.s.l.), in Riding Mountain National Park, and Wilson Creek descends steeply to 340 m.a.s.l. over a distance of 6.4km.

Wilson Creek was chosen as a study site for several reasons. It was the site of a 25 year study to investigate the feasibility of flood storage dams and sediment control related to flooding problems in the surrounding agricultural district (Newbury 1983). As part of this study, a continuous gauging station has been maintained, providing a long-term data base of hydrological and meteorological information. Many relationships between hydrological and geological processes have been derived from these data (Newbury 1984).

Three stations were established along the stream for the aquatic insect study (Fig 1). Station W1, situated near the Park boundary, is the most unstable reach and is the focal point of this paper. Descriptions of various attributes of this station are presented in Table 1.

Hydrology:

In order to determine the effect of channel bed material movement on aquatic insects, several hydrological relationships were derived using techniques described in detail by Newbury (1984). The average % slope of reaches was measured with a surveyor's level. The median diameter of bed paving material (mean l x w x h) was measured, ranked and plotted on a cumulative frequency curve. Movement of channel bed paving materials is a result of tractive forces acting upon them, where tractive force (kg/m^2) = mean depth of flow x slope of channel x 1000 (specific weight of water). Thus for a given discharge, the tractive force can be described if the mean depth of water and slope is known. Average depth of flow was measured over a range of discharge at each station in Wilson Creek to gain this relationship. Tractive force is approximately equal to the median diameter (cm) of rounded, non-compacted particles at incipient motion (Lane 1955), while approximately 1/2 the tractive force is required for an equivalent mean diameter of shale to be at incipient motion (Magalhaes and Chau 1983). From these derived relationships the % of the stream bed paving materials at incipient motion for a given discharge were obtained.

Benthic invertebrate sampling:

Aquatic insects were sampled monthly as well as immediately following spates from May to October 1986, and from March to October 1987 using a modified Hess (Waters and Knapp 1961) bottom sampler (area $0.1m^2$) with a 400um mesh net. Samples were preserved in 4% formalin, later sorted and identified to genus and species when possible and stored in 70% ethanol.

Two, $1m^2$ box emergence traps (Flannagan 1978) were sampled Tuesday and Friday from May to September 1986 to assist in species identification and life history patterns. Samples were stored in 70% ethanol and identified to lowest possible taxon.

Life cycles of species which occurred in sufficient numbers were analyzed by measuring total body length (front of head to base of cerci) of at least 30 specimens when possible from station W1. Where only a few specimens were available for life history analysis, specimens from nearby stations were incorporated.

Life cycles were classified by voltinism, and growth was described as slow or fast for each generation (Clifford 1982). No attempt was made, within this scheme, to categorize overwintering of nymphal or egg stages.

RESULTS

Mean water depth was correlated with discharge (Table 1). Since discharge was continuously monitored, it was possible to calculate mean depth of flow for flood peaks prior to each sample time. Tractive force, was then calculated from the mean water depth. The % of stream bed material in motion at each sample period was derived from the cumulative frequency of measured particles, using the relationship between tractive force and mean diameter of shale particles at incipient motion.

Total mayfly density was negatively correlated with % bed material at incipient motion (Fig. 2). The exponential relationship was :

log density = 2.605-0.479 arcsin sqrt %/ bed material
at incipient motion,
$r= -0.9102$,
$n=20$, $p< 0.001$.

Samples collected one day prior and 2 days post spate in both June and September allowed an estimate of the % reduction of insects resulting from these spates. The June spate resulted in a 94% reduction in density of mayflies, while the September spate resulted in an 85% reduction (Table 2).

Seven species of Ephemeroptera were collected in sufficient numbers to construct life history information (Table 3). Five of the seven species had univoltine life cycles, while the life cycles of the remaining two species appeared to be multivoltine. *Pseudocloeon turbidum* (Fig. 3), and *Nixe (Akkarion) simplicioides* (Fig.4), of the species with univoltine life cycles, had fast seasonal growth. Both species first appeared in May as small nymphs (<2.0mm) and developed rapidly until first emergence in late June for *P. turbidum* and mid-July for *N.(A). simplicioides*. The three remaining species with univoltine life cycles had slow seasonal cycles. *Ephemerella* nr. *inermis* first appeared in late August as small nymphs (< 2.0mm), and they emerged in late June (Fig. 5). The other two species, *Ameletus* sp. (Fig. 6) and *Leptophlebia* sp. first appeared as small nymphs in late July, and were last collected in April. One female of *Ameletus* sp. was collected from the emergence traps in late May.

Baetis tricaudatus (Fig. 7) and *B. flavistriga* had multivoltine life cycles. There were two distinct emergence peaks, one from mid-June to mid-July and a smaller one from early August to early September. An overwintering generation of *B. tricaudatus* hatched in late Sept., grew through the winter, matured by late May and emerged in early June. A second generation appeared as tiny nymphs in late July, matured rapidly and emerged by late August and early September.

DISCUSSION

Total density of mayflies in this reach of Wilson Creek was negatively correlated to the degree of movement of the shale particles paving the stream bed (Fig.2), which was a function of the water depth (i.e. discharge). When the historical flow data (Environment Canada 1965-1986) was examined, a spring snow melt-related discharge of 2.7 m^3/s or greater, during which at least 75% of the bed paving material would be in motion, occurred in 2 out of 3 years (Table 2). The regularity with which this snow melt related flow or a greater one occurred in late April/early May is considered highly predictable. During a summer spate (June 1986) only 12% of the bed paving material was at incipient motion, but this resulted in a 94% reduction in Ephemeroptera density. Historically, an equal or greater rainfall-related discharge occurred during the summer months in less than 27% of the years and was much less predictable. This discharge occurred on average 3.7 times over an entire season. Slightly less, but still significantly disruptive, was a Sept. 1986 discharge in which 8% of the stream bed paving material was at incipient motion, which resulted in an 85% decrease in standing stock. This intensity of discharge was related to a combination of fall storms and the seasonal reduction of water uptake by vegetation in the drainage basin. On average this magnitude of discharge occurred historically 5.6 times a year.

In this reach of Wilson Creek, the life cycle of four of the seven species, *P. turbidum* and *N.(A). simplicioides* of the univoltine group, and *B. tricaudatus* and *B. flavistriga* of the multivoltine group, all exhibited fast seasonal growth. The latter two species exhibited fast seasonal summer growth (late July-early Sept.), and slow seasonal winter growth (Sept.-June), a life cycle most commonly reported for these species (Clifford 1982, Rader and Ward 1987). Ciborowski and Clifford (1984) reported a third generation which hatched in June and emerged in July for *B. tricaudatus*. A third generation of this species from Wilson Creek is not ruled out. By sampling monthly, a cohort may have been missed. Also, the June and July spates may have sufficiently disrupted this cohort so as to make it indistinguishable in the length frequency histograms.

Pseudocloeon spp. are reported as having bivoltine life cycles (Clifford 1982), however *P. turbidum* in this stream was clearly univoltine. Rapid development following spring peak discharge appeared to be an advantageous life history adaptation, as *P. turbidum* constituted nearly 50% of total mayfly density for the two years of the study (Table 3).

The remaining three species have slow seasonal life cycles. *Ameletus* sp. and *Leptophlebia* sp. both completed growth before spring peak discharge. *Leptophlebia* sp. has been reported to commence emergence in mid-May at a slightly higher latitude (Clifford *et al.* 1979). These two species may have emerged at the onset of or just after the spring peak discharge in Wilson Creek, the former situation would seem to satisfy life history requirements to extreme flow events. Further research will be required to elucidate the emergence phenology of these two species. *Ephemerella* nr. *inermis*, the third species with slow seasonal univoltinism was present at all times of the study period. Although its abundance was reduced by spates, the species recovered rapidly, and subsequently completed its development. This genus has been reported as being one of the most abundant mayfly species in stream drift (Ciborowski and Clifford 1983, Armitage 1977), and as such has the potential to recolonize this reach of Wilson Creek rapidly from upstream stable reaches.

No attempt was made to characterize egg development time. Brittain (1982) cautioned that absence of small nymphs from samples does not necessarily mean egg diapause, as tiny nymphs may be deep in the substrates. Humpesch (1981) confirmed this possibility with a lab study of life histories of a Heptageniidae species. Mesh size also has been shown to alter the interpretation of life cycles, where small (<2mm) nymphs can be missed using large mesh samplers (Suter and Bishop 1980).

With these cautions in mind, several species in Wilson Creek appeared to have extended periods before egg hatch. For example it appeared that *P. turbidum* spent up to 9 months in the egg stage, because no nymphs were collected during these months in over 50 samples during two seasons, while small nymphs of other species were adequately sampled. Clifford (1982) reported that about 25 % of all mayfly life cycles have long periods of egg dormancy in winter. He suggested that the adaptive significance of this strategy may be related to harsh winter conditions, allocation of food resources, or avoidance of predation. In station W1 of Wilson Creek, it appears that the adaptive significance of egg diapause favors survival under the current flow regimes.

From the life history analyses of the seven mayfly species occurring at this unstable reach of Wilson Creek, it is evident that at least four of the species have life cycle adaptations which favor survival in an environment where substrates are disturbed in a predictable fashion in the spring and fall, while not so predictably during the summer. While such a strategy was not evident for the remaining three species, behavioral and life history adaptations may account for their presence in this reach of stream. Substrate stability as determined by frequency, duration, intensity and predictability of discharge should be an important component in any ecological investigation.

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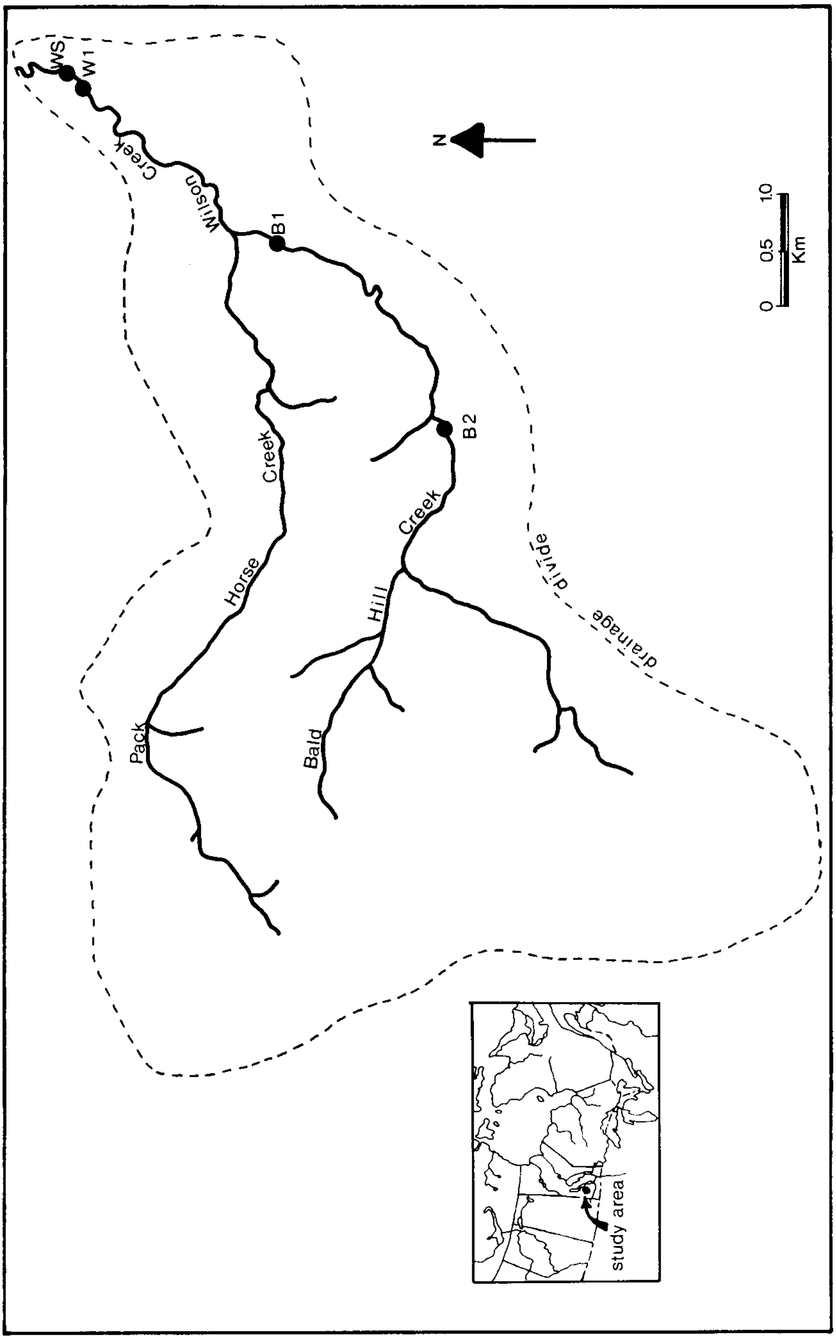

Fig. 1. Map of Wilson Creek showing 1986-87 aquatic insect study sample stations.

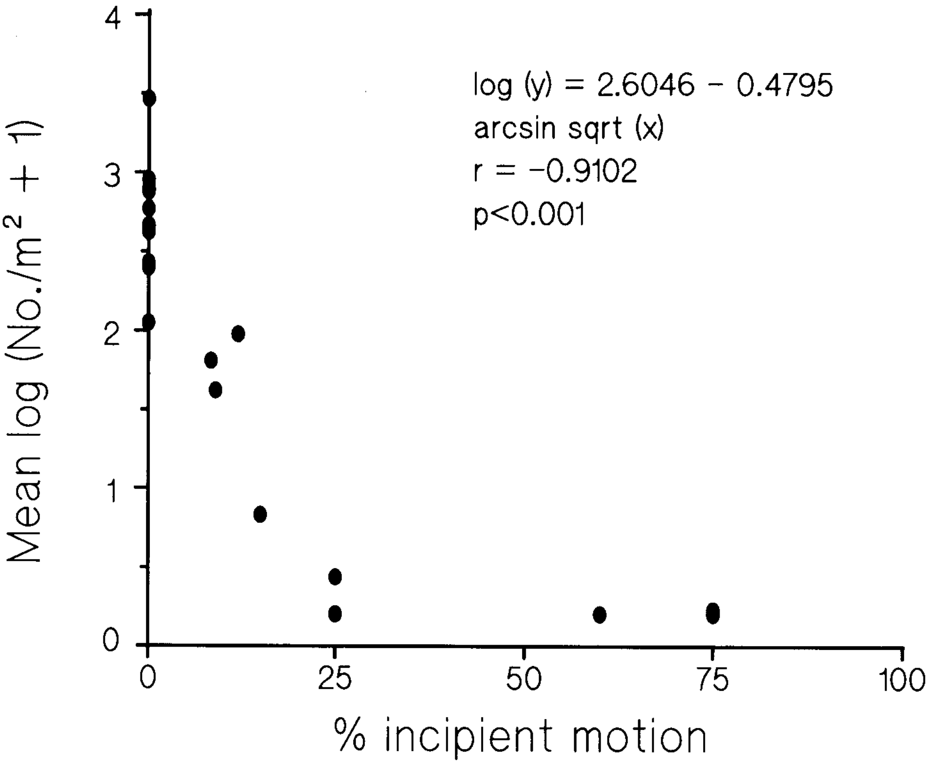

Fig. 2. The relationship between % of stream bed paving material at incipient motion and density of mayflies at station W1 Wilson Creek.

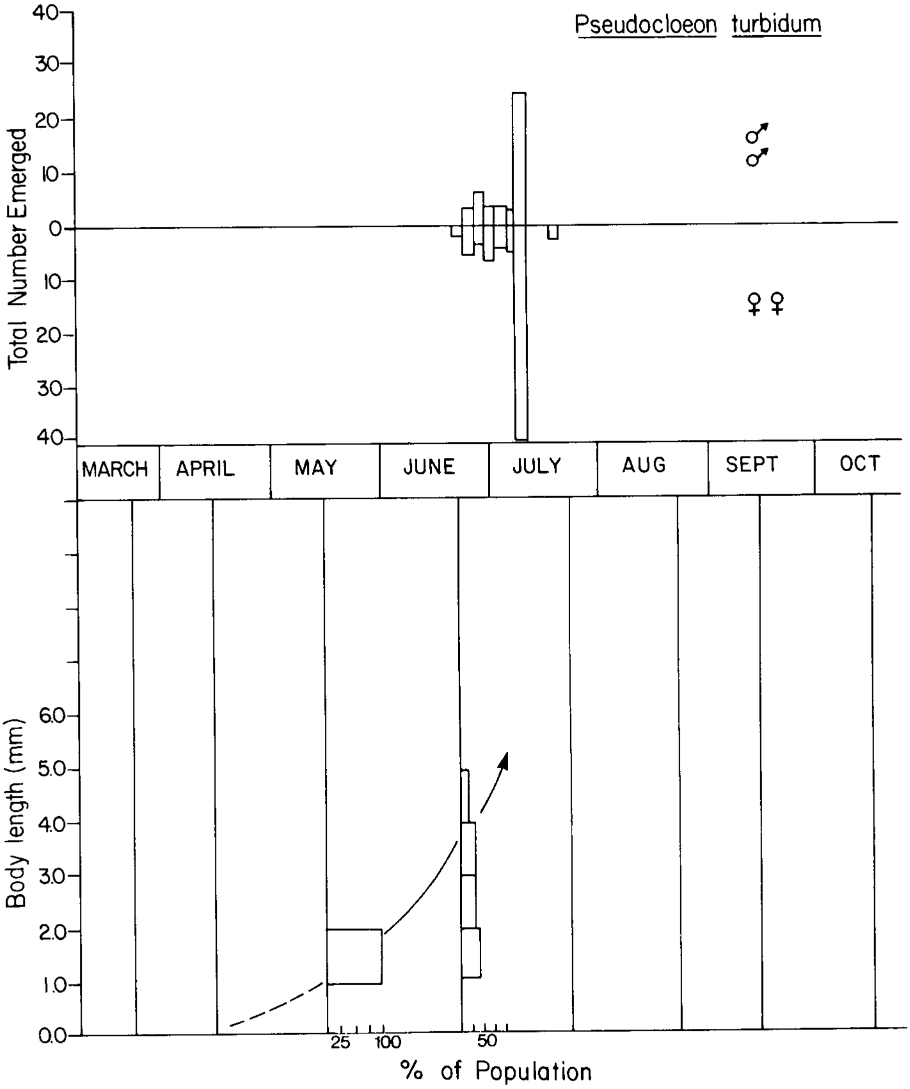

Fig. 3. Life cycle of *Pseudocloeon turbidum* at station W1 Wilson Creek. Upper: adult emergence in 1986, lower: histogram of nymphal growth. Bars represent % of population at a particular body length at sample time.

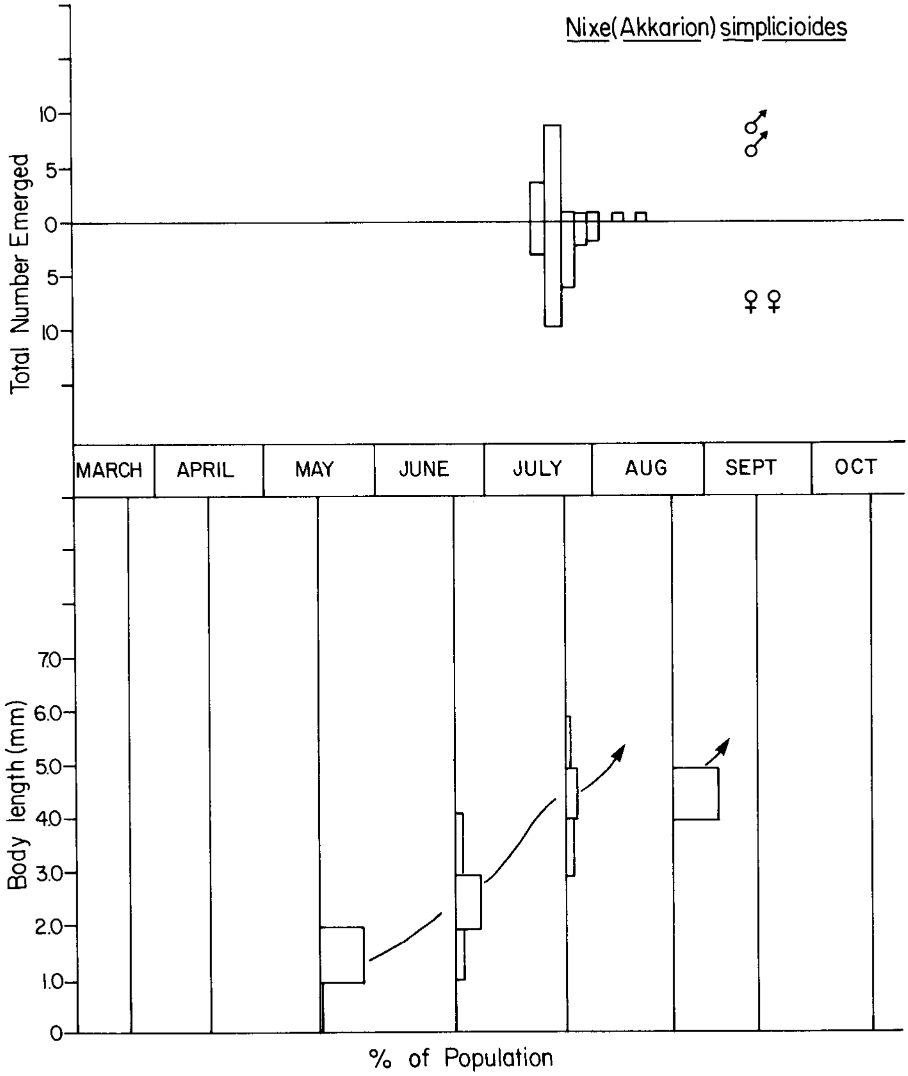

Fig. 4. Life cycle of *Nixe (Akkarion) simplicioides* at station W1 Wilson Creek. Explanation of figure as in Fig. 3.

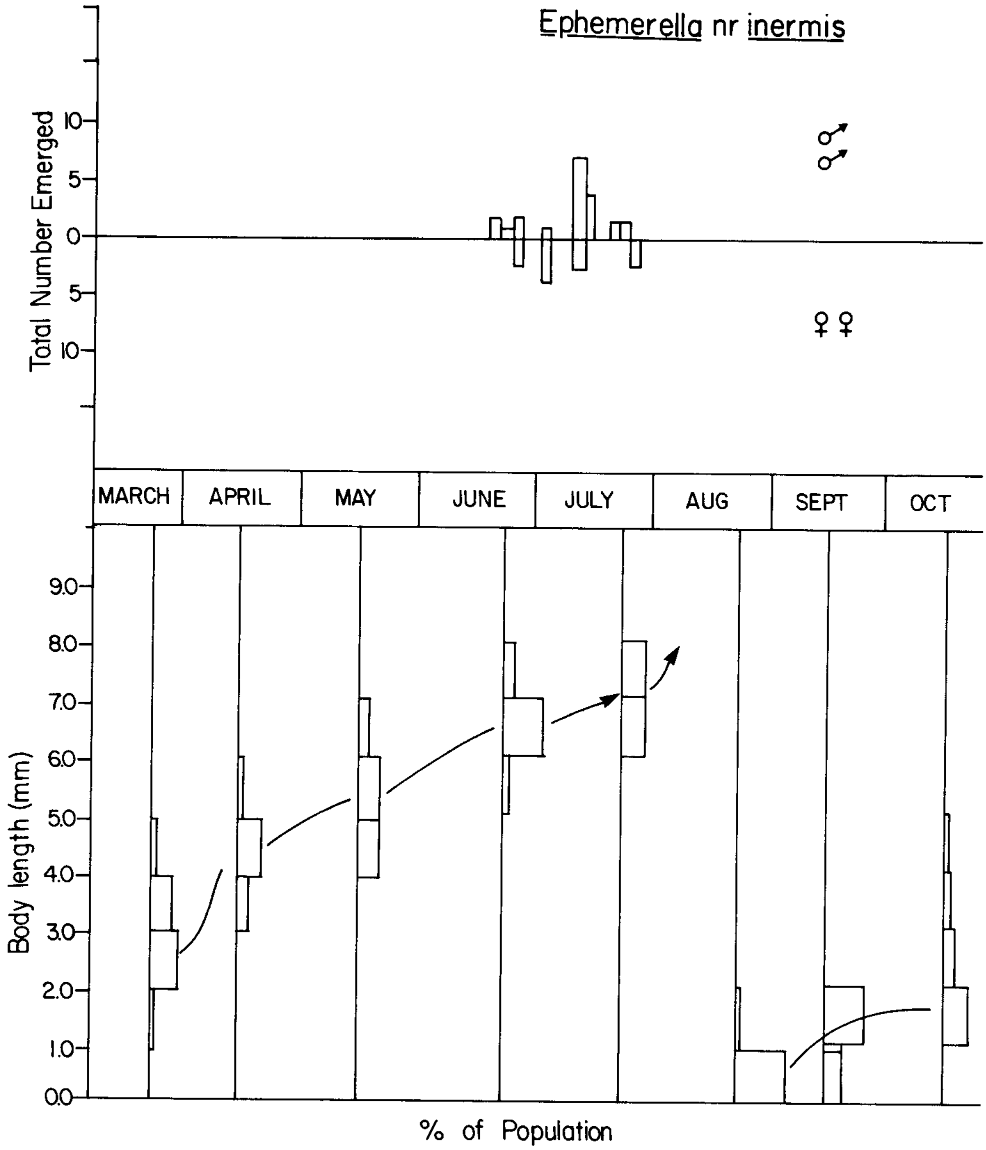

Fig. 5. Life cycle of *Ephemerella* nr. *inermis* at station W1 Wilson Creek. Explanation of figure as in Fig. 3.

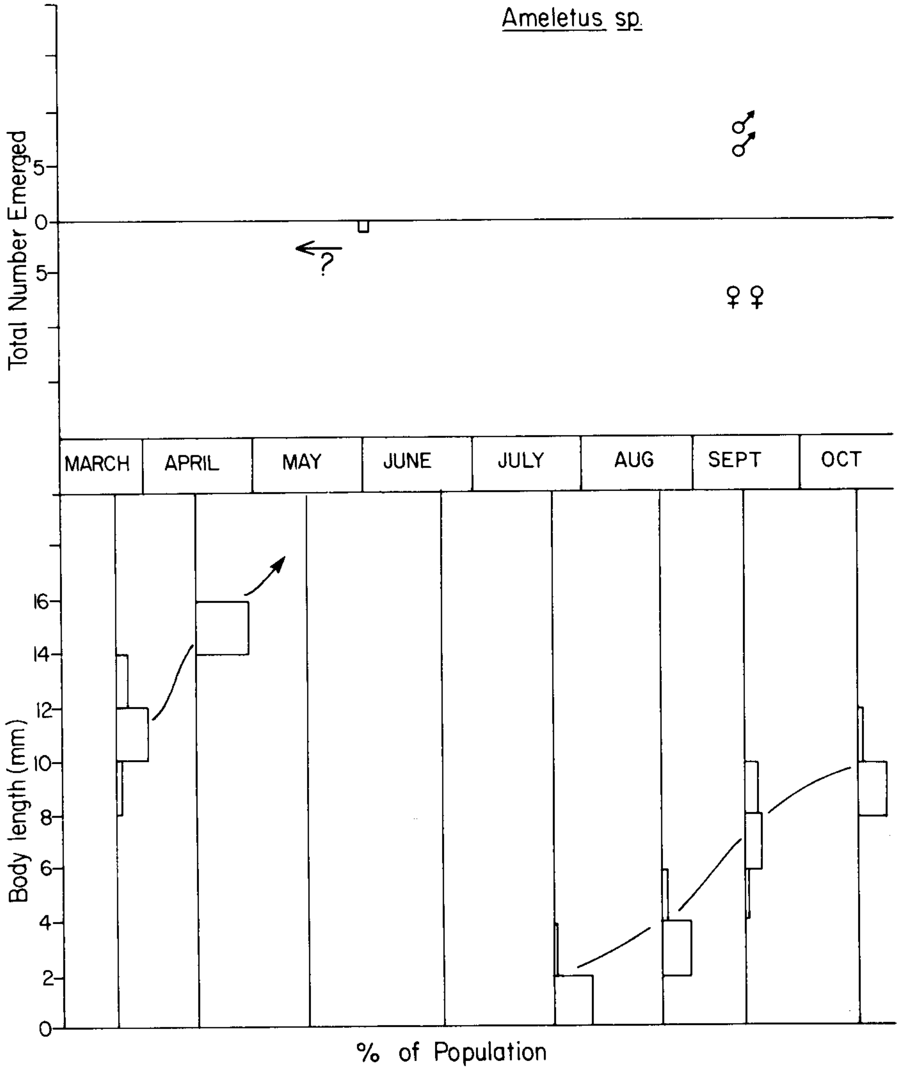

Fig. 6. Life cycle of *Ameletus* sp. at station W1 Wilson Creek. Explanation of figure as in Fig. 3.

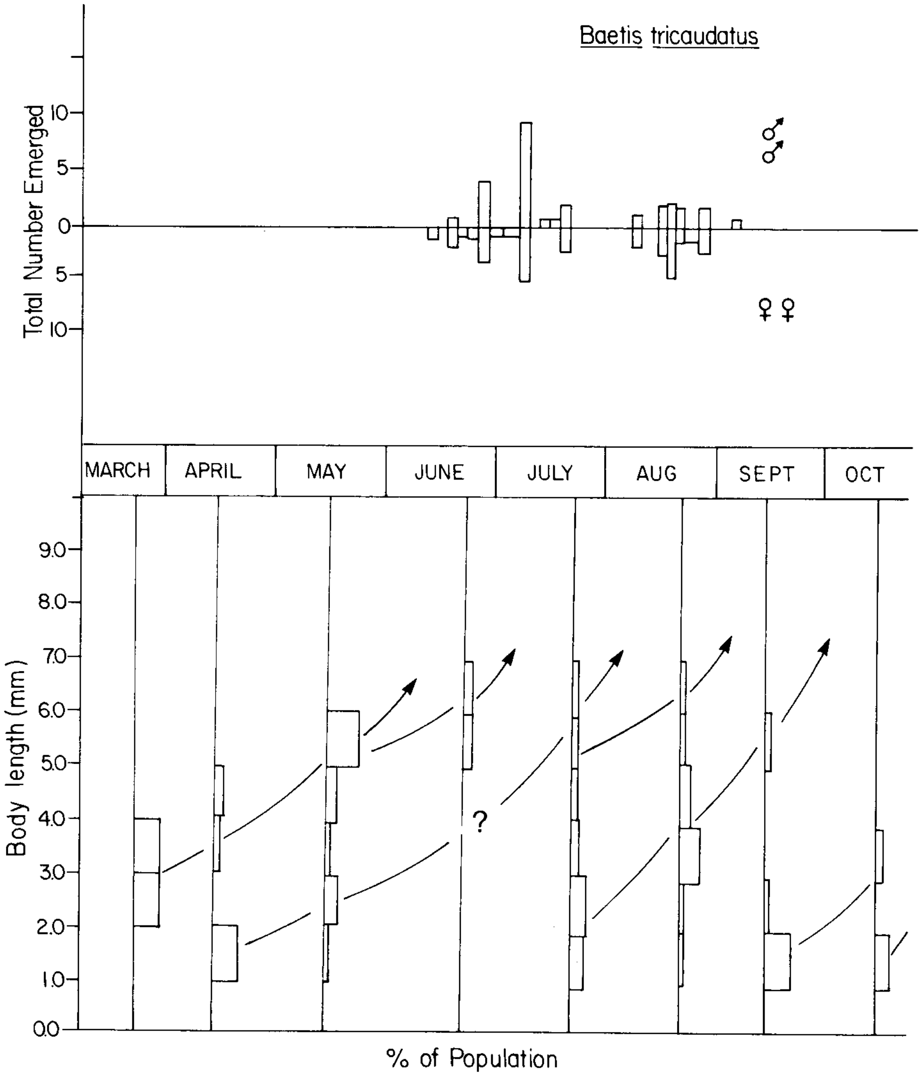

Fig. 7. Life cycle of *Baetis tricaudatus* at station W1 Wilson Creek. Explanation of figure as in Fig. 3.

Table 1. Physical and hydrological characteristics of station W1 Wilson Creek, with relationships used to estimate substrate stability.

DRAINAGE AREA (km^2):	22.1
SLOPE (%):	1.0
MEDIAN CHANNEL PAVING MATERIAL (cm):	4.0
BANKFULL CONDITIONS	
WIDTH (m):	4.3
DEPTH (m):	0.35
DISCHARGE (m^3/s):	2.7
TRACTIVE FORCE (kg/m^2):	3.5

RELATIONSHIPS TO ESTIMATE SUBSTRATE STABILITY:

MEAN WATER DEPTH = .10476 + .0450 DISCHARGE

$r = 0.9151, n = 12, p < 0.001$

ARCSIN SQRT % CHANNEL PAVING MATERIAL = -6.734 + 16.834 TRACTIVE FORCE

$r = 0.9706, n = 12, p < 0.001$

Table 2. Analysis of Wilson Creek 1986 peak discharge and comparison with historical (1965-85) flow data.

	SPRING	SUMMER	FALL
1986			
DISCHARGE (m^3/s)	2.7	.3341	.0623
% BED PAVING MATERIAL AT INCIPIENT MOTION	75	12	8
% REDUCTION MAYFLIES (1d pre, 2d post spate)	N/A	94	85
HISTORICAL			
% > DISCHARGE (ANNUAL)	67	27	80
% > DISCHARGE (DAILY)	0.8	18	53
PERIODICITY	1	3.7	5.6
PREDICTABILITY	HIGH	LOW	HIGH

Table 3. Species list, relative abundance and life history strategies of selected mayflies at station W1 of Wilson Creek.

LIFE CYCLE		TAXON	ABUNDANCE (%)
A. Univoltine			
	1. Fast seasonal:	*Pseudocloeon turbidum* McDunnough	46
		Nixe (*Akkarion*) *simplicioides* (McD)	11
	2. Slow seasonal:	*Ephemerella* nr. *inermis* Eaton	26
		Ameletus sp.	2
		Leptophlebia sp.	7
B. Multivoltine		*Baetis tricaudatus* Dodds	5
		B.flavistriga McD	3