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Aquatic Insect Communities of a Small Stream on Mont St. Hilaire, Quebec

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Weekly sampling of a small woodland stream in Quebec between March 1966 and March 1967 revealed at least 120 species of insects in sand, gravel, stones, leaves, and leaf detritus habitats. Fallen leaves were the primary food source. Characteristic communities of insects were found in each habitat. Widely distributed species were usually more abundant in one of the five habitats than in the others. Some species changed their habitats with age. Congeneric species either occupied different parts of the stream or developed at different times of the year. Linear distributions of insects were determined by the substrate type, by the extent of summer drought and the ability to avoid desiccation, and in some species by upstream flying of adult females. The species composition of each community may be characteristic of small, slow-flowing streams in deciduous forests in eastern Canada.

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Un ruisseau frais et ombragé du Québec fut étudié de mars 1966 à mars 1967. Des échantillonnages hebdomadaires ont démontré qu'il y a au moins 120 espèces d'insectes vivant dans le sable, le gravier, et les détritus de feuilles, et entre les pierres et les feuilles tombées. La chute de feuilles constituait le principal apport de nourriture. Dans chaque habitat on trouvaient des communautés charactéristiques d'insectes bien que quelques espèces se trouvaient dans plus d'un habitat. Certaines espèces changaient d'habitat selon l'âge. Les espèces du même genre n'occupaient pas la même section du ruisseau ou bien se développaient en saisons différentes. La distribution des insectes le long du ruisseau était déterminée par le type de substrat; par le degré d'assèchement durant l'été et l'aptitude à éviter le dessiccation; et dans une certaine mesure par le vol des femelles adultes. Il est possible que dans chacun de ces habitats ces espèces soient la faune typique des ruisseaux lents de forêts caduques de l'est du Canada.

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INTRODUCTION

INCREASING CONCERN over the pollution of streams and rivers has stimulated the search for plant and animal indicators of water quality (Gaufin and Tarzwell, 1956; Hynes, 1960, 1962; Patrick, 1962). But in order to measure the rate and extent of changes in stream conditions, more basic information on species in "natural" waters (Hynes, 1960) must be available. The presence or absence of a single index species is probably not as useful in revealing the condition of the water as the species composition of the stream community as a whole. Although microorganisms may eventually prove to be the most

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specific indicators, present field methods rely on a knowledge of the macrofauna, especially aquatic insects. However, although the number of described insect species is increasing, purely taxonomic studies usually do not include a description of the community from which an animal came, and the records seldom include details of the ecology and seasonal occurrence of the immature stages. The most valuable ecological investigation of stream insects in northeastern North America, that of Sprules (1947) is confined to the summer emergence of adults. No account of stream communities in this area has included all members of winter and summer faunas.

The present study of insect communities in a small woodland stream was undertaken to examine the species compositions in different habitats within the stream, including the distributions of immature stages throughout the year. The ability of many species to tolerate large amounts of allochthonous organic material in the form of autumn-shed leaves may have a bearing on their survival in environments organically polluted by man.

STUDY AREA

Mont St. Hilaire (Fig. 1) is one of the Monteregian Hills, which lie in the plain of the St. Lawrence River valley between Montreal and the Sutton Mountains in southern Quebec. West Creek rises from small springs at an

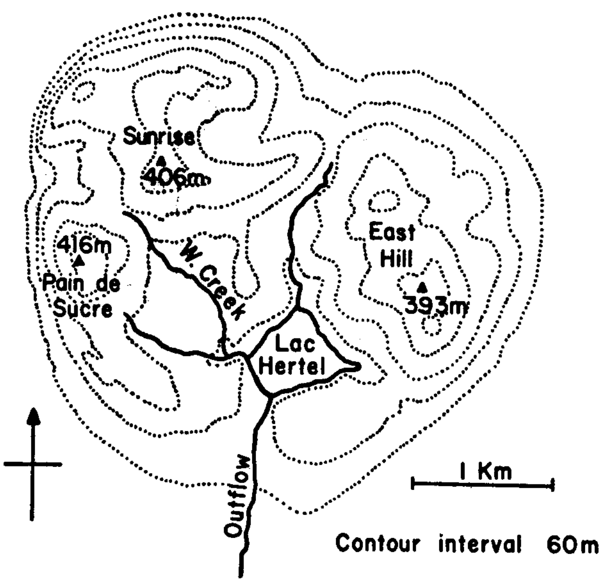

FIG. 1. The principal streams on Mont St. Hilaire, Quebec.

altitude of about 300 m and flows through thick beech–maple forest into Lac Hertel, which lies in the centre of the bowl-shaped mountain.

West Creek is 1.7 km long, but during most summers the upper third is dry. The width of the stream varies from 30 cm to 2 m, though some parts of the lower reaches flood to as much as 4 m during the April thaw. The water is cool and clear. Flow ranges from about 1 liter/sec in autumn after a dry summer to about 130 liters/sec in April.

There are no higher plants growing in the stream; algal growth is sparse and moss is found only on the exposed surfaces of immovable boulders. Leaves from the trees choke the stream during October and November and remain trapped behind fallen branches and stones for more than a year.

Four sampling stations were chosen, each being 60 m long. Station I was 300 m from the source (as established at the beginning of the study in November 1965). Here the width of the stream never exceeded 1.0 m and the water was only 2–5 cm deep over most of the station. The bottom consisted of sand, gravel, and pebbles with occasional boulders embedded in the gravel (substrate types classified according to Cummins (1962)). By July 25, 1966, the upper 40 m at station I were dry, leaving a few patches of damp gravel and leaves. Further downstream were some small isolated pools, 20–30 cm in diameter and 3–8 cm deep, which retained some water throughout the autumn.

Station II was immediately above a small pond that had been dug halfway downstream in 1964. The upper limit of station II coincided with the upper limit of flowing water during summer and autumn of 1966. The stream bed differed from that of station I only in having flat stretches of sand and silt at the lower end. The water seldom exceeded 8 cm in depth.

Station III was immediately below the pond. The upper 7 m of the station was a narrow stretch of gravel and pebbles over which the water flowed swiftly. Beyond, the water flowed sluggishly over sand and silt, 3–12 cm deep and 1–2 m wide. Three small tributaries, two of them temporary, entered the stream at this station. The third, an underground stream of seepage water, precipitated ferric hydroxide where it surfaced, about 2 m from the main stream. The dissolved oxygen concentration at the mouth of the tributary was less than 1 mg/liter.

Station IV was 300 m from where the stream entered Lac Hertel. At this station, the increased gradient of the valley floor allowed the water to flow more rapidly and the bottom consisted of boulders, cobbles, and pebbles resting on gravel with occasional sandy patches. The depth and width of the water were somewhat greater than at the higher stations but varied greatly with the seasons.

Mont St. Hilaire had a warm summer in 1966 and long cold spells in the preceding and following winters (Fig. 2). The mean air temperatures between December and March in 1965/66 and 1966/67 were −6.4 and −8.0 C respectively (P. D. Baird, personal communication).

The water temperature in West Creek ranges from a low of 0 C in January and February to a high of 17–18 C. Between January and March, ice forms at the sides of the stream, often developing into ice bridges on which snow accumulates. During 1966 and 1967 the difference in water temperature between points along the stream was small and stations I and IV reached the same

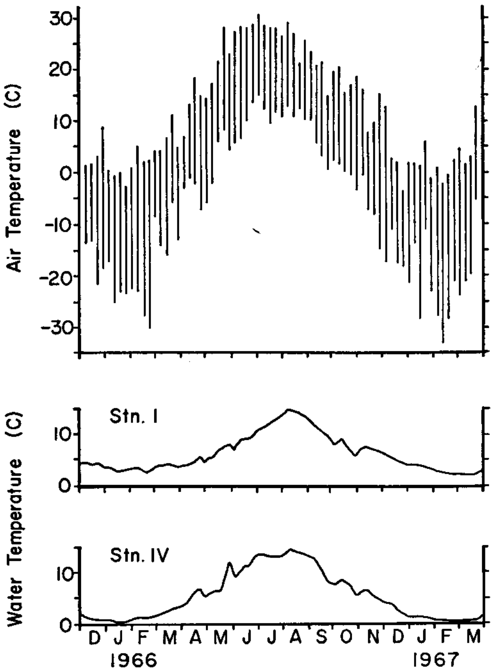

FIG. 2. Weekly records of maximum and minimum air temperatures, and mean water temperatures, in West Creek from December 1965 to March 1967.

maximum, 17.2 C (Table 1), in August 1966. However the water temperatures nearer the source increased more slowly between April and June, decreased more slowly during autumn and remained 1–3 degrees C higher than lower stations during most of the winter (Fig. 2). The greatest weekly range in temperature, 7–8 degrees C, occurred at station IV in May, October, and November. Maximum diurnal variation at station IV was 4.5 degrees C.

Total alkalinity in West Creek and concentration of dissolved salts were low (Table 1) reaching minima at the time of the spring thaw, and maxima at low water in September and October. The minimum *p*H (6.5) at station I was recorded in one of the small summer pools.

The minimum recorded concentration of dissolved oxygen and the lowest saturation level (Table 1) occurred in October, when the volume of water was low and fallen leaves choked the stream. Water samples from several points along the stream during the autumn showed that low oxygen concentrations persisted until late November, when temperatures were low, and increased flow began to thin out the leaves. Values of dissolved oxygen and saturation at all stations were highest between December and April, the levels dropping slightly when ice covered the stream.

A near maximum turbidity of the water at station IV on April 1, 1967, when the snow was melting, was 24 ppm SiO_2. The colour of the water was always less than 3 Pt colour units.

TABLE 1. Physical and chemical analyses of water samples from West Creek between November 1965 and April 1967.

	Station I		Station IV	
	Min	Max	Min	Max
Temp (*C*)	0	17.2	0	17.2
*p*H	6.5	7.6	7.1	7.4
Alkalinity (*mg* $CaCO_3$*/liter*)	7.0	15.0	16.2	35.0
Conductivity (*μmhos at 25 C*)	80	114	88	137
Dissolved oxygen (*mg/liter*)	5.7	12.2	7.8	13.4
% saturation oxygen	48.5	95.5	66.0	100.0

METHODS

The stream insects were studied from November 1965 until March 1967, but a regular sampling programme was not begun until March 1966. Monthly samples of the fauna were collected at each station. To observe changes in the stream as a whole at frequent intervals, station I was sampled in the last week of each month, stations II and III on 1 day near the middle of the month, and station IV during the 1st week of the month. In Tables 2–4, showing linear distributions of species, the total number collected of each species was corrected to a total per 30 samples per station so that relative abundances at each station are shown.

The stations were each divided into 12 substations 5 m long. To avoid denuding the subtrate in any one area and to ensure that each sample was of the undisturbed fauna, a different substation was sampled each month. Within the substation, samples were taken from all habitat types that lay on a diagonal transect. The habitat types sampled were sand, gravel, stones (cobbles and pebbles), leaves, and detritus. The term detritus was given to finely divided leaf material lying on pool bottoms, or near the stream margins. The leaf habitat consisted of fallen beech, maple, and other hardwood leaves that were loosely piled in slow flowing areas, or were trapped behind stones or fallen branches. During sampling, mixed substrates, such as leaves with stones or stones with sand, were purposely avoided; but silt concealed between leaves or stones was inevitably collected in many samples. Two to five samples were taken per station per month, depending on the number of habitat types encountered per transect. Conditions allowing the accumulation of detritus prevailed mainly in the late summer, so that samples of detritus were collected only from June to October in 1966, and in January and March in 1967. Sand at stations II, III, and IV was also sampled irregularly because sandy areas were not found in all transects. No quantitative samples were taken from sand at station I.

A Hess sampler enclosing 0.07 m^2 was used on sand and gravel, the substrate being disturbed to a depth of about 10 cm. Where the stream bed was uneven, an open half-cylinder was worked into the bottom more easily and placed on the downstream side of stones or twigs with the lateral wings of the frame curved round them. A semicircular brass rod was clipped on the half-cylinder to mark the anterior border of the area to be sampled (0.07 m^2). Both samplers were covered with Nitex net having a mesh size of 452 μ (16 threads/cm).

The importance of the mesh size used for collecting-nets and sieves has been emphasized by Jonasson (1955), Macan (1958), Hynes (1961), and Maitland (1966). A net of 16 threads/cm was chosen as being fine enough to retain all but the smallest insects, yet allowing the ubiquitous silt and leaf detritus that would clog a finer net to be washed away.

All animals and materials retained by the net were transferred to pint-sized plastic pots after rough sorting to remove large carnivores. The pots were anchored in the stream to maintain the organisms at normal water temperature while other samples were collected. The time taken to transport the organisms from the stream to a cool laboratory (12 C) was 1–1½ hours. The insects

TABLE 2. Linear distributions of Ephemeroptera, Plecoptera, and Trichoptera in West Creek between March 1966 and March 1967 on basis of numbers of specimens per 30 samples (the numbers of samples taken are given in parentheses). +, <10 specimens; ++, 10–100; +++, 101–200; ++++, >200.

Species	Station I (32)	Station II (30)	Station III (28)	Station IV (50)
Ephemeroptera				
Siphlonurus sp.	+		+	
Ameletus "C"	++	+++	++++	++
Ameletus "B"	++	+++	+	++
Paraleptophlebia sp.	++	++	++++	++
Ameletus "A"		++		+++
Ephemerella funeralis McDunnough		+	++	++
E. dorothea Needham		+	+	++
Iron sp.		+		++
Heptagenia sp.				++
Plecoptera				
Ostrocerca albidipennis Walker	++++	++++	++++	
Leuctra spp.[a]	++	++	++	++
Alloperla onkos Ricker	++	+++	++	++
Soyedina vallicularia Wu	+	++	++	++
Isoperla similis (Hagen)	+	+	++	++
Allocapnia nivicola (Fitch)		++++	++	++
Amphinemura wui Claassen		++	+	++
Isoperla holochlora (Klapalek)			+	++
Allonarcys proteus Newman				++
Trichoptera				
Pseudostenophylax uniformis (Betten)	++	+		
Lepidostoma "C"	+++	+		
Neophylax aniqua Ross	++	++		
Ironoquia lyrata (Ross)	+	+	+	
Rhyacophila vibox Milne	++	+++	++	++
Lepidostoma "B"	++++	++++	++	++++
Lepidostoma "A"	++	++	++	+
Pycnopsyche gentilis (McLachlan)	+	++	++	++
Parapsyche apicalis (Banks)	+	++	++	+++
Pycnopsyche luculenta (Betten)		++	++	++
Polycentropus sp.		++	++	+
Rhyacophila minora Banks		++	+	++
Psilotreta sp.		+	+++	+
Molanna blenda Sibley		+	++	+
Pycnopsyche scabripennis (Rambur)		+	+	++
Phylocentropus sp.			++	
Oligostomis pardalis Walker			+	
Glossosoma sp.			+	++
Neophylax ornatus Banks				+
Wormaldia sp.				++
Neophylax nacatus Denning				+++

[a]*Leuctra tenella* Provancher and *L. truncata* Claassen.

TABLE 3. Linear distributions of Coleoptera, Neuroptera, and Diptera (excluding Chironomidae) in West Creek between March 1966 and March 1967 on basis of numbers of specimens per 30 samples (the numbers of samples taken are given in parentheses). +, <10 specimens; ++, 10–100; +++, 101–200; ++++, >200.

	Station			
Species	I (32)	II (30)	III (28)	IV (50)
Coleoptera				
Cymbiodonta blanchardi Horn	++	+	++	+
Agabus ambiguus (Say)	+	+	++	+
Helichus striatus LeConte	+		+	+
Hydrobius melaenum Germar		+	++	+
Promoresia sp.				++
Neuroptera				
Sialis sp.		++	++	+
Diptera				
Tipulidae[a]				
Pedicia albivitta Walker	++	+		
Dicranota sp.	+++	+++	++	++
Molophilus hirtipennis (O.S.)	+	+++	++	+
Tipula fraterna Loew	+	++	++	+
Hexatoma spinosa (Loew)	+	++	+	+
Tricyphona sp.	+	+	+	
Ormosia sp.		++	++	
Tipula strepens Loew		+		
Pilaris sp.		+	+	
Tipula abdominalis (Say)		++	++	+
Geranomyia sp.		+	+	+
Pseudolimnophila sp.		+		+
Limnophila sp.		++	++	++
Tipula "A"				++
Ptychopteridae				
Ptychoptera quadrifasciata Say		+	++	
Bittacomorpha clavipes (Fabricius)			++	
Simuliidae				
Twinnia tibblesi Stone and Jamnback	++++			
Simulium aureum (Fries)	+	+		
S. latipes (Meigen)	++	+	++	+
Prosimulium mixtum Syme and Davis	++++	++++	++++	++++
Cnephia mutata (Malloch)	++	+++	+++	++
Simulium tuberosum (Lundström)		+		+
Dixidae				
Dixa modesta Johannsen	++	+	+	++
Psychodidae				
Pericoma sp.	+			+
Ceratopogonidae				
Bezzia sp.	+	+++	+++	++
Empidae				
Roederiodes sp.	+	++	++	++
Hemerodromia sp.	+			+

[a]Ten other tipulid species were identified to tribe only.

TABLE 4. Linear distributions of Chironomidae (Diptera) in West Creek between March 1966 and March 1967 on basis of numbers of specimens per 30 samples (the numbers of samples taken are given in parentheses). +, <10 specimens; ++, 10–100; +++, 101–200; ++++, >200.

Species	Station I (32)	Station II (30)	Station III (28)	Station IV (50)
Tanypodinae				
Conchapelopia sp.	+++	+++	++	++
Zavrelimyia sp.	++			++
Trissopelopia sp.	+	+++	++++	+
Psectrotanypus sp.		++	+	++
Macropelopia sp.		++	++	+
Paramerina sp.		+	+	
Natarsia sp.			+	
Nilotanypus sp.				+
Chironominae				
Constempellina sp.	+			
Tripodura sp.	+			
Micropsectra spp.	++++	++++	++++	+++
Tanytarsus sp.	++	++	++	+++
Polypedilum (s.s.) sp.			++	
Chironomus (s.s.) sp.			+	
Orthocladiinae				
Parochlus kieffeii (Garrett)	++++	+		
Sympotthastia fulva (Johannsen)	+++	+		
Pseudodiamesa pertinax (Garrett)	++++	+	++	
Diamesa spp.[a]	+++	++	+	++
Prodiamesa sp.	++	+	++	
Rheocricotopus sp.	++++	++	+	+
Heterotrissocladius sp.	+++	+++	++	+
Brillia sera Roback	++++	++	++	++
Diplocladius sp.	++	++	+	+
Nanocladius "C"	+++		+	++
Nanocladius "A"	++	+		++
Trissocladius sp.			+	+
Nanocladius "B"				+
Chaetocladius sp.				+
Cardiocladius sp.				+
Corynoneura group[b]	++	++	++	++
Metriocnemus group[c]	+++	++++	++	++

[a]Includes *D. nivoriunda* (Fitch).
[b]Includes *C. taris* Roback and *Thienemanniella* sp.
[c]Includes *Parametriocnemus* sp., *Paraphaenocladius* sp., and *Pseudorthocladius* sp.

were kept alive as long as possible because the presence of leaf detritus made sorting by flotation impossible. Whole leaves were rinsed and removed individually from the containers and other materials were washed many times in cold water, which was poured off through a net identical with those used in the field. Insects were removed by hand until no more were visible; then a few drops of concentrated formalin were added to the water in the sorting basin, causing any remaining concealed specimens to wriggle violently. Subsequent microscopic examination of samples of the remaining bottom materials showed that in most instances less than 1% of the organisms were overlooked. During June, July, and August, all sediments were checked microscopically to remove chironomid larvae.

All specimens except blackfly larvae were placed temporarily in 5% formalin to preserve the natural colour patterns as an aid to identification. Blackfly larvae were killed and preserved in 95% ethanol. After the insects had been identified, measured, and counted, they were preserved in 70% ethanol. Subsequently, representative specimens of the age-classes of each species were weighed so that the biomass could be calculated for each habitat and for the stream as a whole (Mackay and Kalff, 1969).

The most reliable measurement used to group immature insects into age-classes was the width of the head (including compound eyes). The length of the lateral border of the mesonotum was also measured on nymphs of Ephemeroptera and Plecoptera. Measurement of length alone was unreliable in most instances because of shrinking or telescoping of the abdomen. Length was used as the distinguishing character for the dipterous families Tipulidae, Ceratopogonidae, and Empidae as the head capsules in these groups were incomplete or inverted, or too narrow for changes in size to be measured accurately. However, in all immature insects increase in length during the year gave a good indication of growth rate, and changes in total length were more gradual than changes in head width and mesonotum length. Therefore approximate total lengths are included in the figures showing larval life histories.

The average monthly abundance of common insects in each of the five habitats was based on samples from four stations (with the exception of sand at station I). The species considered as common were those whose numbers exceeded $50/m^2$ during at least 1 month; thus common species having only a short aquatic season were not excluded. The arbitrary value chosen to distinguish common from occasional species proved satisfactory in that all species that were collected consistently in small numbers fell into the common category.

SAND FAUNA

Common species of insects living in or on sand (Fig. 3) were members of the Trichoptera (2 spp.) and Diptera (17 spp.). Larvae of the caddisfly *Psilotreta* sp. were taken from the surface of bare sand, usually from midstream areas. A few collections contained nymphs of Ephemeroptera and Plecoptera, most of which were more common in other habitats. However, the mayfly *Siphlonurus* sp. was found only swimming in open water above bare sand. *Molanna blenda* (Trichoptera) was another occasional member of the sand fauna, but was rarely collected from bare sand; most specimens were found in areas where thick piles of leaves had been removed before the sand below was disturbed.

The most numerous larvae covered by sand were Tipulidae; this family was also represented by the most common species (7). Other common Diptera were Ptychopteridae (2 spp.), Chironomidae (6 spp.), Ceratopogonidae (1 sp.), and Empidae (1 sp.)

The average monthly abundance of the common sand fauna species (Fig. 3) shows that October and February have similar features. The data for October 1966 are the results of a single sample of sand from the mouth of the nearly deoxygenated tributary at station III. The sand was mixed with ferric hydroxide and was ochrous in colour. Three sand samples were collected in February 1967, including another ochrous sample taken immediately downstream of the tributary. All species common only in October and February were members of the ochrous sand fauna.

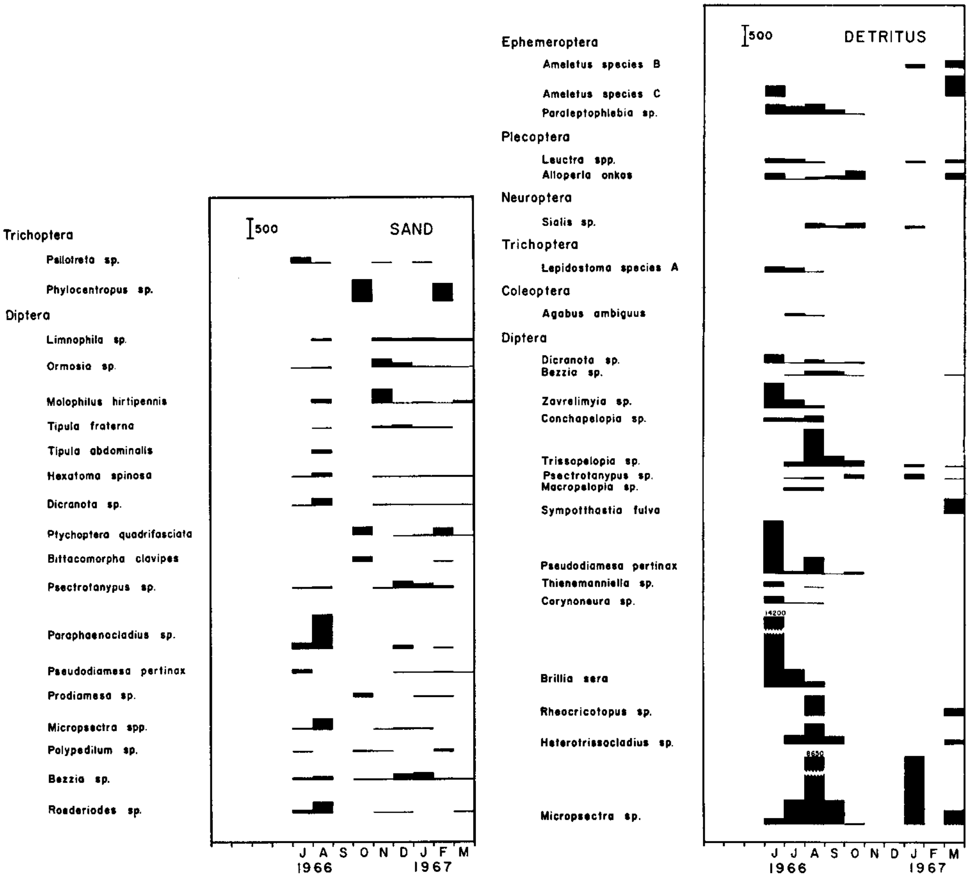

FIG. 3. The average numbers/m² per month of common insects in the sand habitat, West Creek, between July 1966 and March 1967, and in the detritus habitat between June and October 1966 and in January and March 1967.

Phylocentropus sp. larvae built their partially buried sand tube systems near the stream margins, and appeared to tolerate very low concentrations of dissolved oxygen.

None of the sand fauna species were collected regularly enough to provide reliable life history information.

DETRITUS FAUNA

Samples of detritus were taken from areas of slow-flowing water where detritus lay over sand, or occasionally over gravel. The detritus fauna, like some members of the sand fauna, was often found in poorly oxygenated water; between July and October the dissolved oxygen concentration was sometimes reduced to less than 50% of saturation (Table 1). The detritus fauna also resembled the sand fauna in that most of the 23 common species were Diptera (Fig. 3). However, in detritus the Chironomidae was the predominant family and species of *Micropsectra* were abundant at all seasons. The fauna included species in five other insect orders, but only *Paraleptophlebia* sp. (Ephemeroptera) and *Sialis* sp. (Neuroptera) were more common in detritus than in other habitats.

The data for June 1966 are the results of a single sample at station I, and the high numbers of *Brillia sera* and *Pseudodiamesa pertinax* were peculiar to this station. The results for July and August are based on samples from all stations and therefore are representative of West Creek as a whole.

GRAVEL FAUNA

Insect species diversity was notably greater in the gravel habitat than in sand; 27 species were common in gravel, representing five orders (Fig. 4). Some species such as *Cymbiodonta blanchardi* and *Promoresia* sp. (Coleoptera), and *Trissocladius* (Chironomidae) were apparently confined to the gravel habitat. Most of the remaining common species were found in other habitats also, either having a broad range in habitat preference or spending only part of their larval development in gravel.

Species appearing to have a broad range in substrate preference include the three species of *Ameletus* (Ephemeroptera) which were common in all habitats except sand, where they were found occasionally. *Alloperla onkos* (Plecoptera) was also common in all habitats except sand. Blackfly larvae, common in gravel, stones, and leaf habitats, were very abundant in gravel during winter and early spring. Between January and April, gravel areas at stations II and III immediately below the pond appeared black owing to large numbers of *Prosimulium mixtum* and *Cnephia mutata* larvae.

The three congeneric species of Ephemeroptera did not develop simultaneously, so that any overlap in seasonal occurrence of the species rarely involved nymphs of the same size (Fig. 5). *Ameletus* A hatched in August and grew continuously during the winter to emerge as the adult in March and April. *Ameletus* B nymphs first appeared during October or November, grew very slowly until January, and developed rapidly between February and April to emerge in May and June. The third species, *Ameletus* C, hatched in March and completed its development in 5 months.

Species that are members of the gravel fauna for a limited period include the stoneflies *Ostrocerca albidipennis*, *Isoperla similis*, and *Allocapnia nivicola*. Each of these species was common in gravel (Fig. 4) during months when the nymphs were small (Fig. 6–8). Young larvae of *Parapsyche apicalis*, collected between July and November (Fig. 9) were common on gravel during this period although previous records of the species have not noted this (Flint, 1961). Young larvae of the tipulid *Dicronota* sp. were also found in gravel but later instars were taken mainly from leaves trapped in small waterfalls.

Larvae of the chironomids *Sympotthastia fulva* and *P. pertinax* (Diamesini) were sometimes collected in large numbers from gravel, but only when this was mixed with organic detritus. The association between these two species and detritus is emphasized by their abundance in the pure detritus habitat

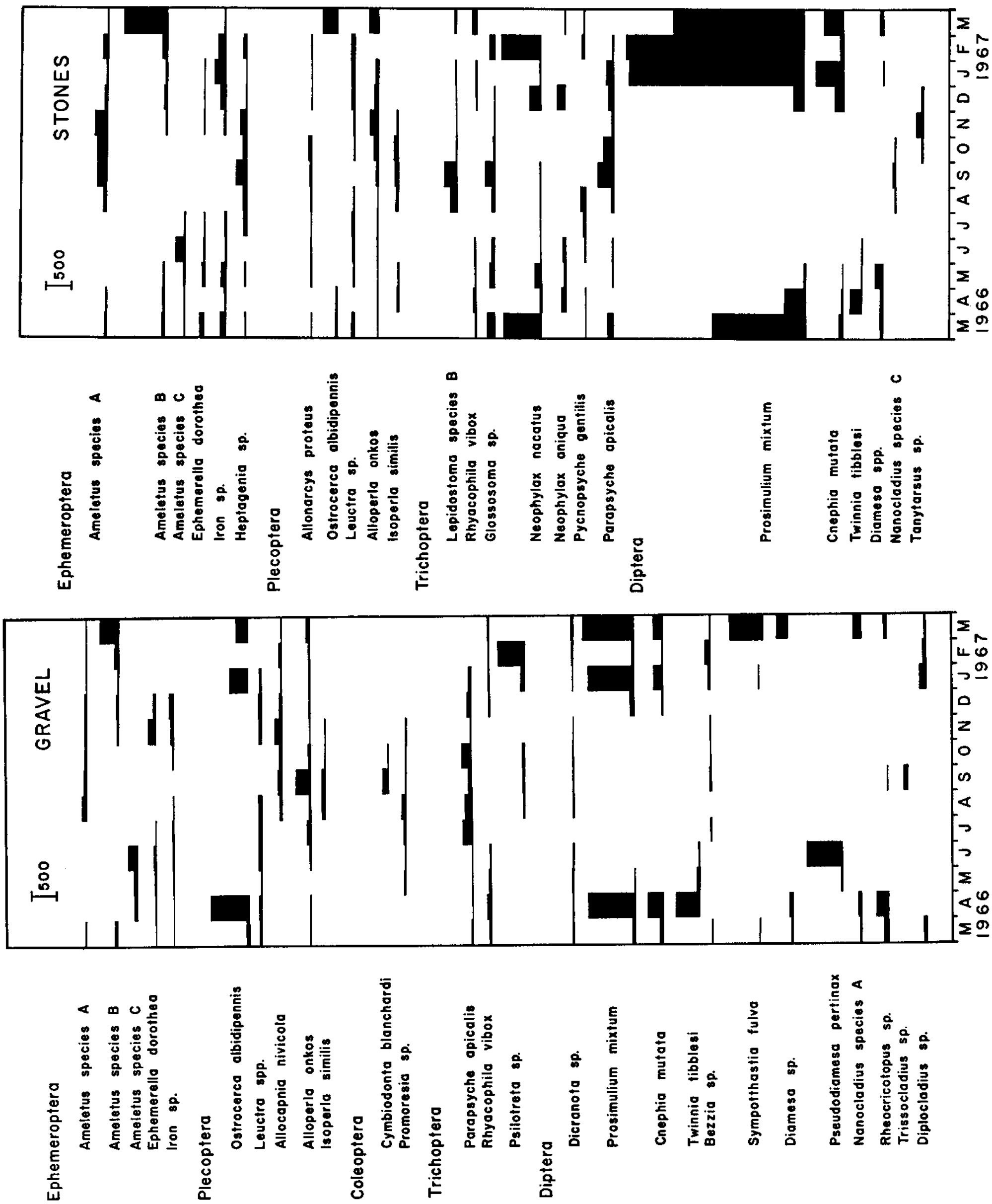

FIG. 4. The average numbers/m² per month of common insects in the gravel habitat and in the stone habitat, West Creek, between March 1966 and March 1967.

(Fig. 3). In both detritus and gravel the two species were clearly separated temporally. Larvae of *S. fulva* were collected between January and March, adults between February and April; larvae of *P. pertinax* were collected from May through August, pupae and adults during September and October.

When station I was dry between July and October 1966, samples of damp gravel below the surface of the stream bed revealed larvae of many species,

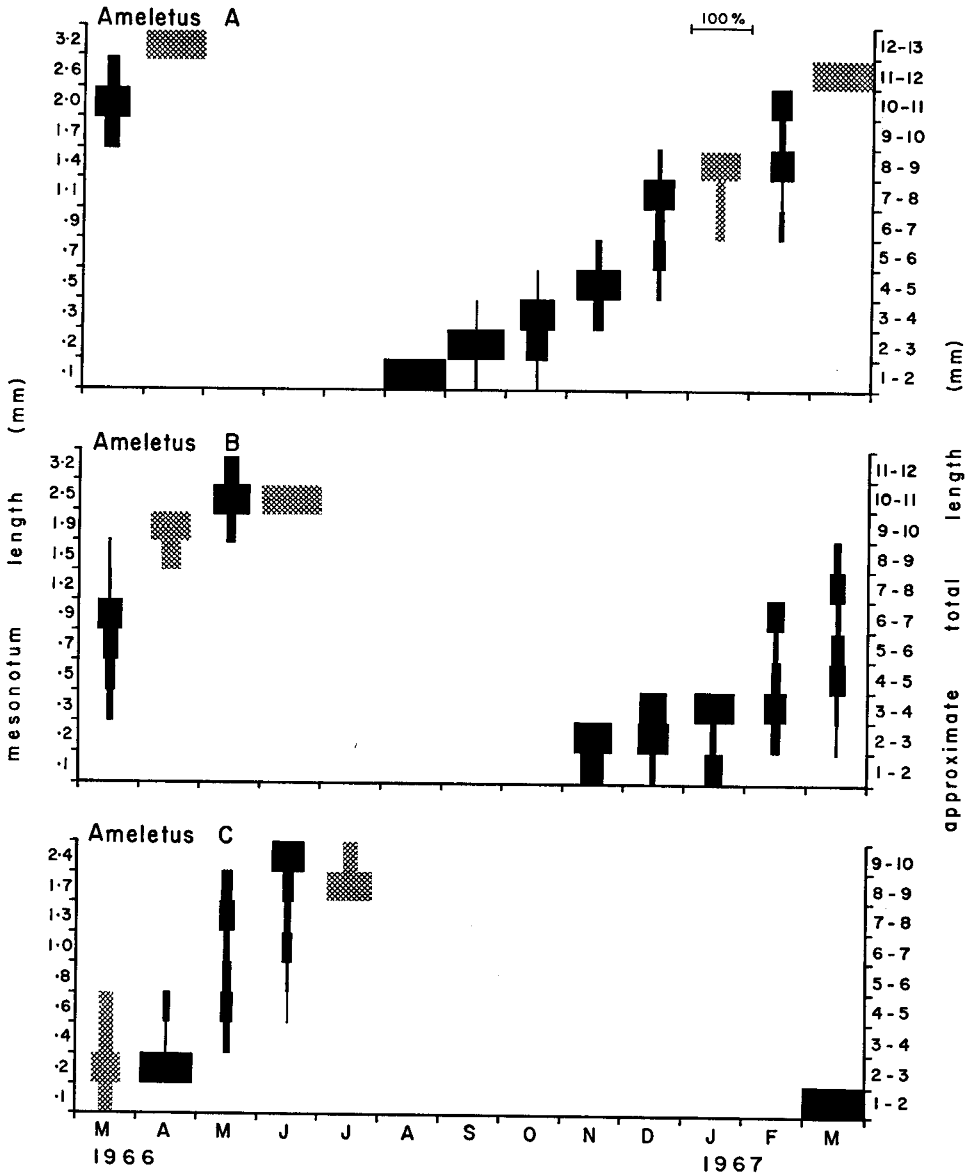

FIG. 5. Growth of nymphs of three species of *Ameletus* (mayflies), West Creek, 1966–67. (Each histogram shows percentage of total specimens per month having size indicated. Cross-hatched histograms based on <10 specimens/month.)

including the caddisflies *Pseudostenophylax uniformis* and *Lepidostoma* "C," wich must have burrowed into the substrate as the water receded. Other species collected from damp grazel and sand at this station included *Pseudorthocladius* sp., *Paraphaenocladius* sp., and *Brillia sera* (Chironomidae); and young larvae of *Molophilus hirsutipennis* and *Dicranota* sp. (Tipulidae).

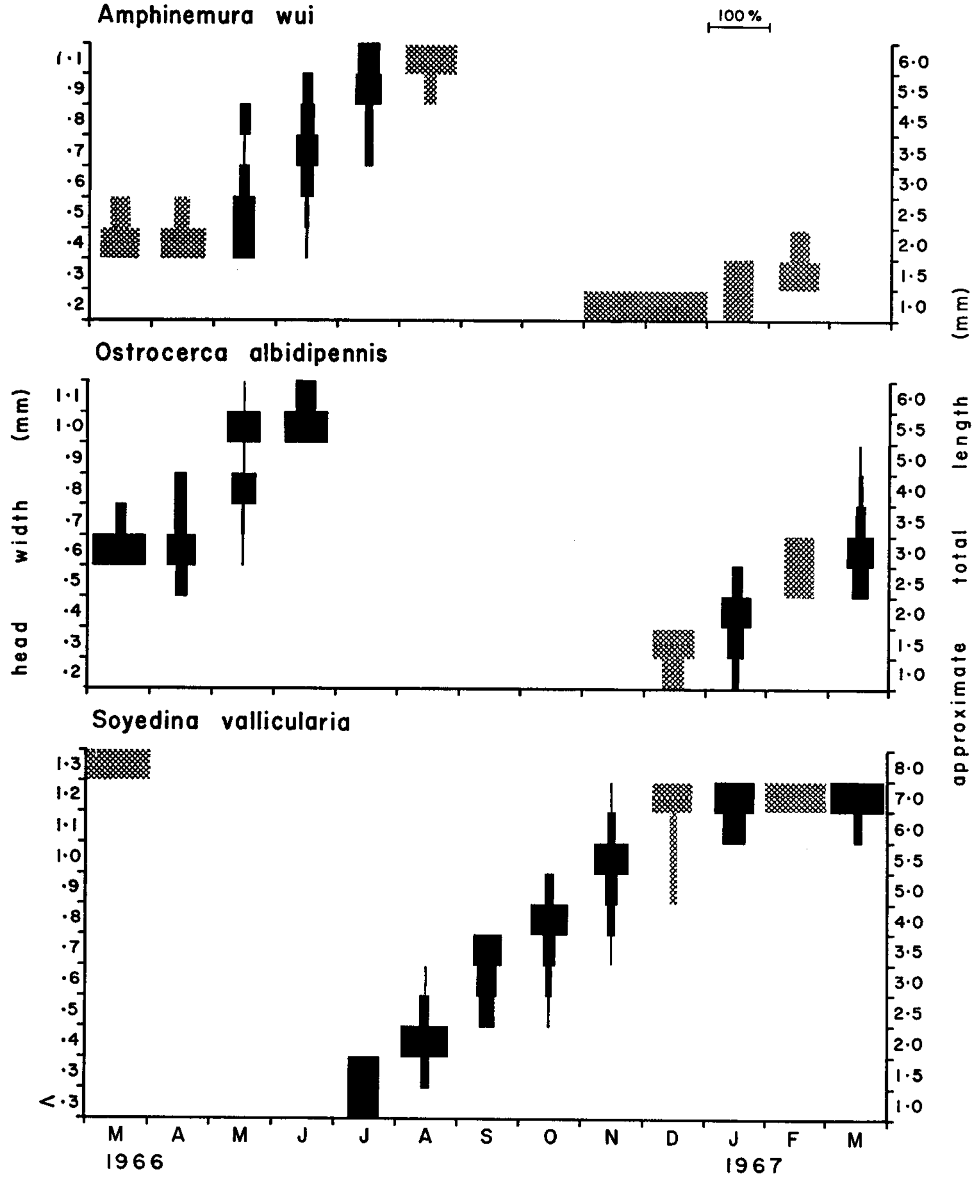

FIG. 6. Growth of nymphs of the nemourid stoneflies *Amphinemura wui*, *Ostrocerca albidipennis*, and *Soyedina vallicularia*, West Creek, 1966–67. (Each histogram shows percentage of total specimens per month having size indicated. Cross-hatched histograms based on <10 specimens/month.)

STONE FAUNA

The number of common species in the stone fauna (Fig. 4) was slightly less than that in gravel, but included insect larvae found only on the surfaces of stones. These were the mayfly *Heptagenia* sp., and the caddisflies *Glossosoma* sp., *Neophylax nacatus*, and *N. aniqua*. A third species of *Neophylax*, *N. ornatus*,

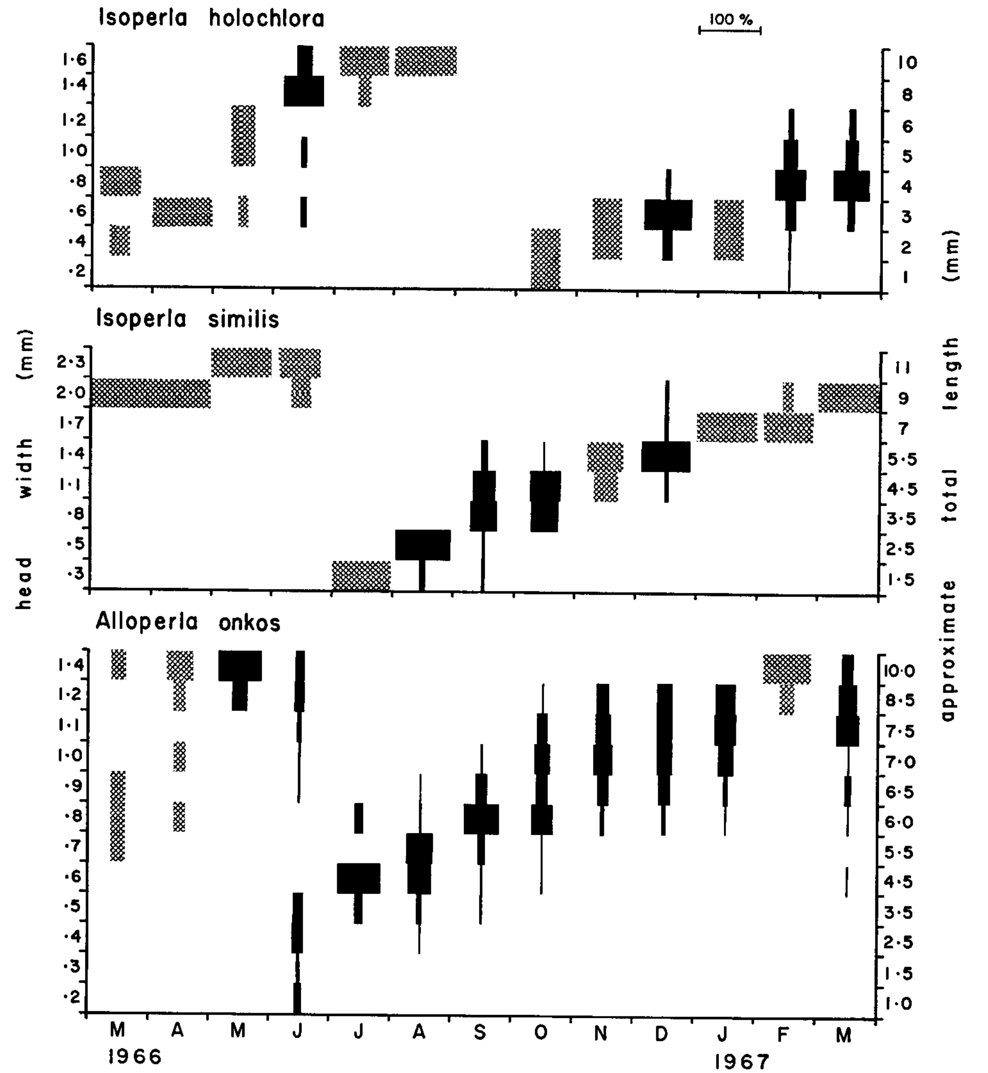

FIG. 7. Growth of nymphs of the stoneflies *Isoperla holochlora*, *I. similis*, and *Alloperla onkos*, West Creek, 1966–67. (Each histogram shows percentage of total specimens per month having size indicated. Cross-hatched histograms based on <10 specimens/month.)

was collected occasionally. *Neophylax nacatus* was the commonest of the three species.

The Ephemeroptera in general, and especially *Ameletus* species A and B, were more abundant among stones than they were in other habitats. *Heptagenia* sp. and *Iron* sp. nymphs were found clinging to the lateral and ventral surfaces of stones. The Plecoptera common on stones included the large *Allonarcys proteus* which has a 2–3 year life cycle (Fig. 10). Most of the *A. proteus* nymphs in the stone fauna were in their late 2nd or 3rd year of

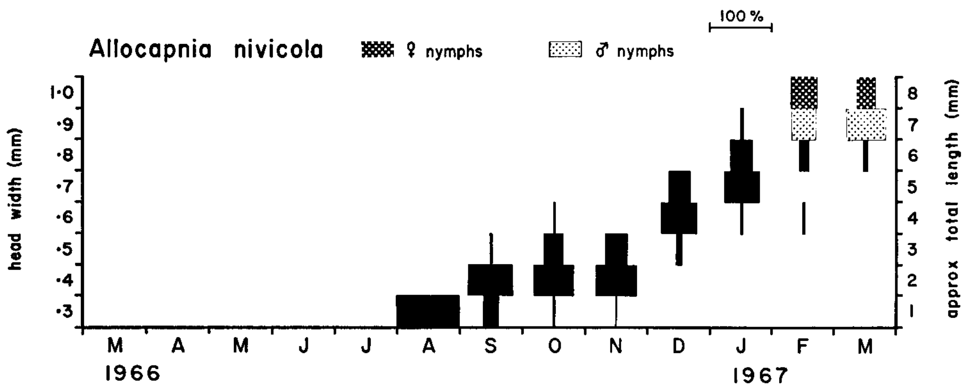

FIG. 8. Growth and sexual dimorphism in nymphs of *Allocapnia nivicola*, West Creek, 1966–67. (Each histogram shows percentage of total specimens per month having size indicated.)

growth, for the earlier instars were usually in the leaf habitat. Several caddisfly species, including *Rhyacophila vibox* and *Pycnopsyche gentilis*, moved into the stones during their terminal larval instar and pupated on the ventral surfaces of stones. Larvae of *P. apicalis*, mainly medium and large sizes, were collected from stones throughout the year, the long hatching period in gravel allowing recruitment into the stone fauna from August through March.

The Simuliidae were the most numerous insect larvae in winter and spring; they clung to the upper surfaces of stones, usually on the downstream edges. *Prosimulium mixtum* and *C. mutata* were the predominant larvae during winter, being followed in smaller numbers in spring by *Twinnia tibblesi* (Fig. 11).

Young larvae of the caddisfly *N. nacatus* were first collected in December (Fig. 9); they grew during winter and spring until all were at the prepupal stage by the end of June. Pupae were found up to September but adults were not collected. *Neophylax aniqua* appeared to have a similar life history, but, as described below, it was not found in the same parts of West Creek as *N. nacatus*. *Neophylax ornatus* differed in its life cycle, as young larvae were collected in August, mature larvae in December.

The majority of larvae of the caddisfly *P. apicalis* appeared to complete their development in one year (Fig. 9). But although no terminal-instar larvae were collected in August 1966, their appearance in September suggests that some individuals may spend a second winter in the stream before emerging as adults.

LEAF FAUNA

In all areas of West Creek, leaves supported the greatest number of species. There were 43 common species in 5 orders, more than half of the species being Diptera (Fig. 12). The commonest larvae in the habitat were those of a small caddisfly, *Lepidostoma* "B," highest numbers/m² being collected in

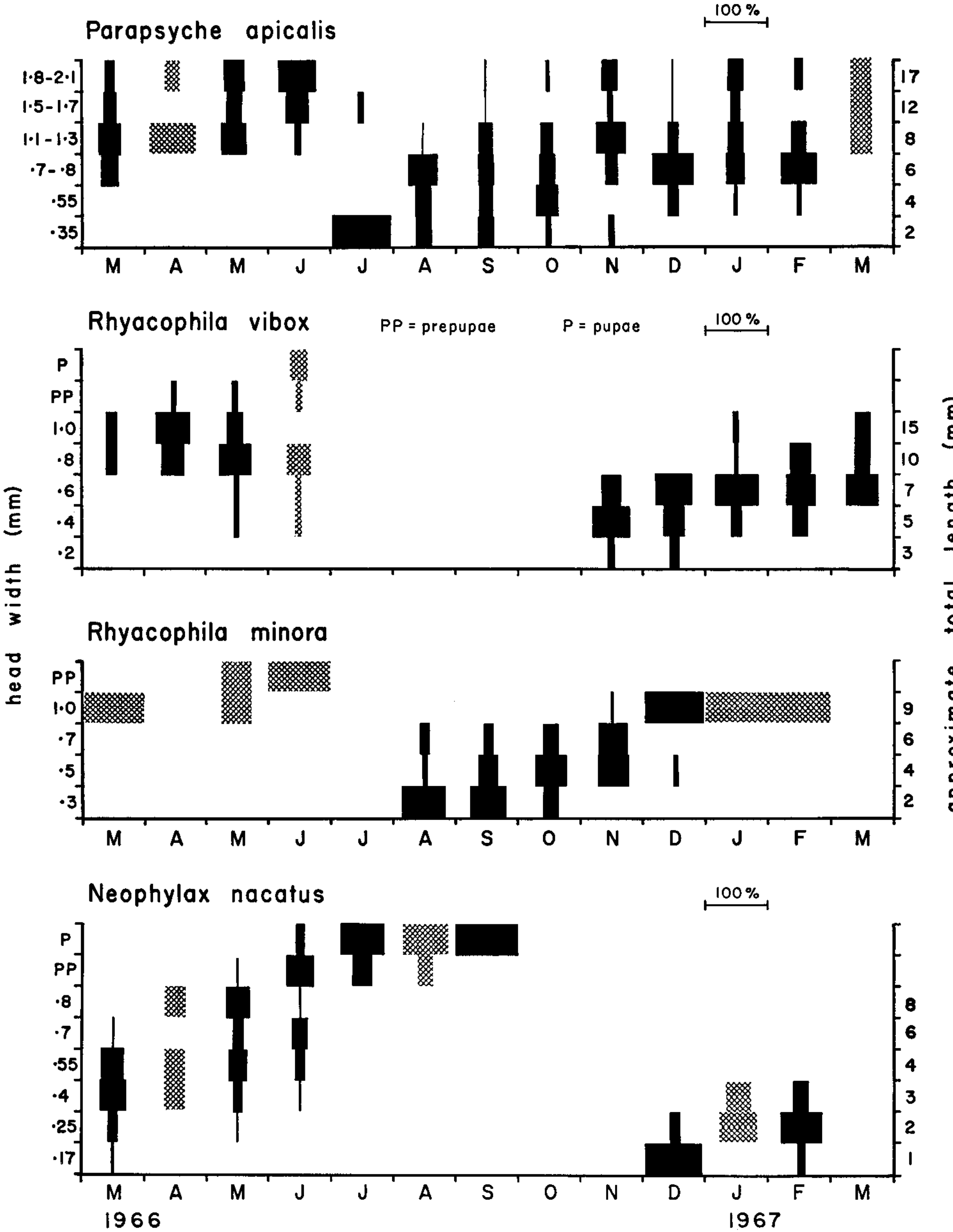

FIG. 9. Growth of immature stages of four species of caddisflies, West Creek, 1966–67. (Each histogram shows percentage of total specimens per month having size indicated. Cross-hatched histograms based on <10 specimens/month.)

September. Nymphs of the plecopteran *O. albidipennis* which were found mainly in gravel during winter, increased in numbers in the leaf habitat in spring. Blackfly larvae were found on leaves caught on branches and stones in the current; *P. mixtum* was the predominant species between December

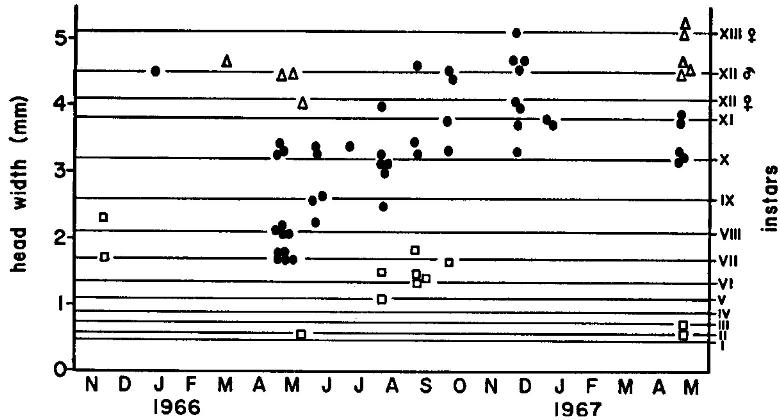

FIG. 10. Head widths of *Allonarcys proteus* nymphs taken from station IV, West Creek, in relation to known instars reared by Holdsworth (1941). □, 1st year of growth; ●, 2nd year; △, 3rd year. Each symbol represents one specimen.

and April. The tipulid *Tipula* "A" and the psychodid *Pericoma* sp. were found in closely packed leaves near the water surface. The mayfly *Paraleptophlebia* sp., the stonefly *A. nivicola*, and the chironomid *Trissopelopia* sp. were in leaves resting loosely in slow-flowing areas. Several chironomid species were abundant for short periods and the numbers of maturing larvae of the tipulid *Dicranota* sp. increased during spring and early summer.

Wherever a genus was represented by more than one species (or subgenera in the case of *Amphinemura*, *Ostrocerca*, and *Soyedina* in the genus *Nemoura*), the species differed in the time of their larval growth periods or in their linear distributions along the stream. In most instances there was a clear temporal succession of species, as shown by the common Ephemeroptera, *Ameletus* species A, B, and C being followed by *Paraleptophlebia* sp. (Fig. 5 and 12).

The nemourid stoneflies *O. albidipennis* and *Soyedina vallicularia* also had different periods of nymphal growth and emergence (Fig. 6). *Soyedina vallicularia* developed continuously from July through December, when the nymph was almost fully grown, then remained about the same size until March when it moulted once or twice before emerging. Young nymphs of *O. albidipennis* appeared in December, grew during the winter and emerged in May and June. A third common nemourid in the leaf habitat, *Amphinemura wui*, resembled *O. albidipennis* in size and in its life cycle (Fig. 6) but was rarely found in the same part of the stream.

Two species of *Isoperla* (stoneflies) occurred in the leaf habitat although *Isoperla holochlora* was collected only occasionally. *Isoperla similis* developed slowly but continuously from July to the following June, whereas small nymphs of *I. holochlora* appeared in October, grew little during autumn and winter, but completed their development rapidly the following summer (Fig. 7).

A similar temporal separation existed between the caddisflies *R. vibox* and *R. minora* (Fig. 9). Young larvae of *R. minora* were first collected at the

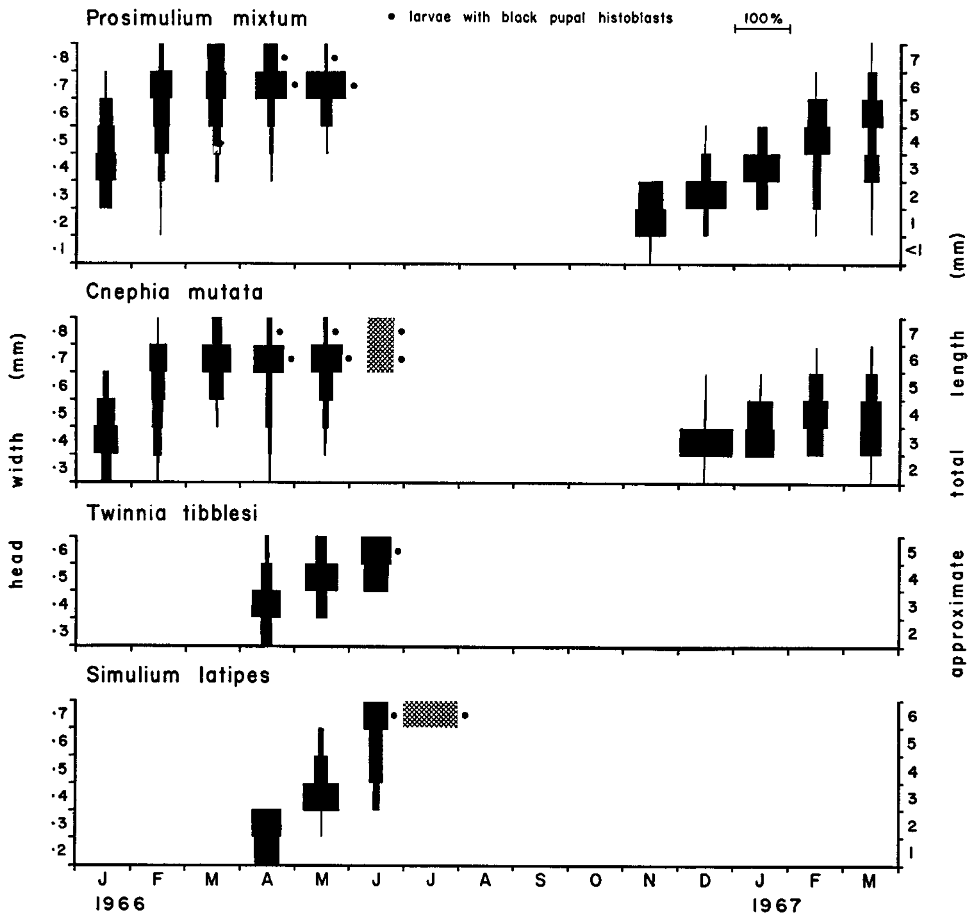

FIG. 11. Growth of larvae of the common Simuliidae, West Creek, 1966–67. (Each histogram shows percentage of total specimens per month having size indicated. Cross-hatched histograms based on <10 specimens/month.)

beginning of August, but initial development was rapid since some larvae had reached the 3rd instar by the end of the month. Subsequent growth was slow. Larvae of *R. vibox* were not found until early November, but they grew during winter and early spring, and most were in the 4th or 5th instar by March. The younger larvae collected in May and June, though attributed to *R. vibox*, may have been those of another species; but none were reared, and older stages were not found in later months.

The three species of *Lepidostoma* (caddisflies) that occurred in the leaf habitat also showed temporal separation. *Lepidostoma* A larvae appeared to hatch in December (Fig. 13) but little growth took place before March. During the summer months *Lepidostoma* A grew rapidly and emerged in August. Adults of species B and C emerged early in the summer, but, unlike species A, young larvae appeared from the eggs immediately. *Lepidostoma* B larvae

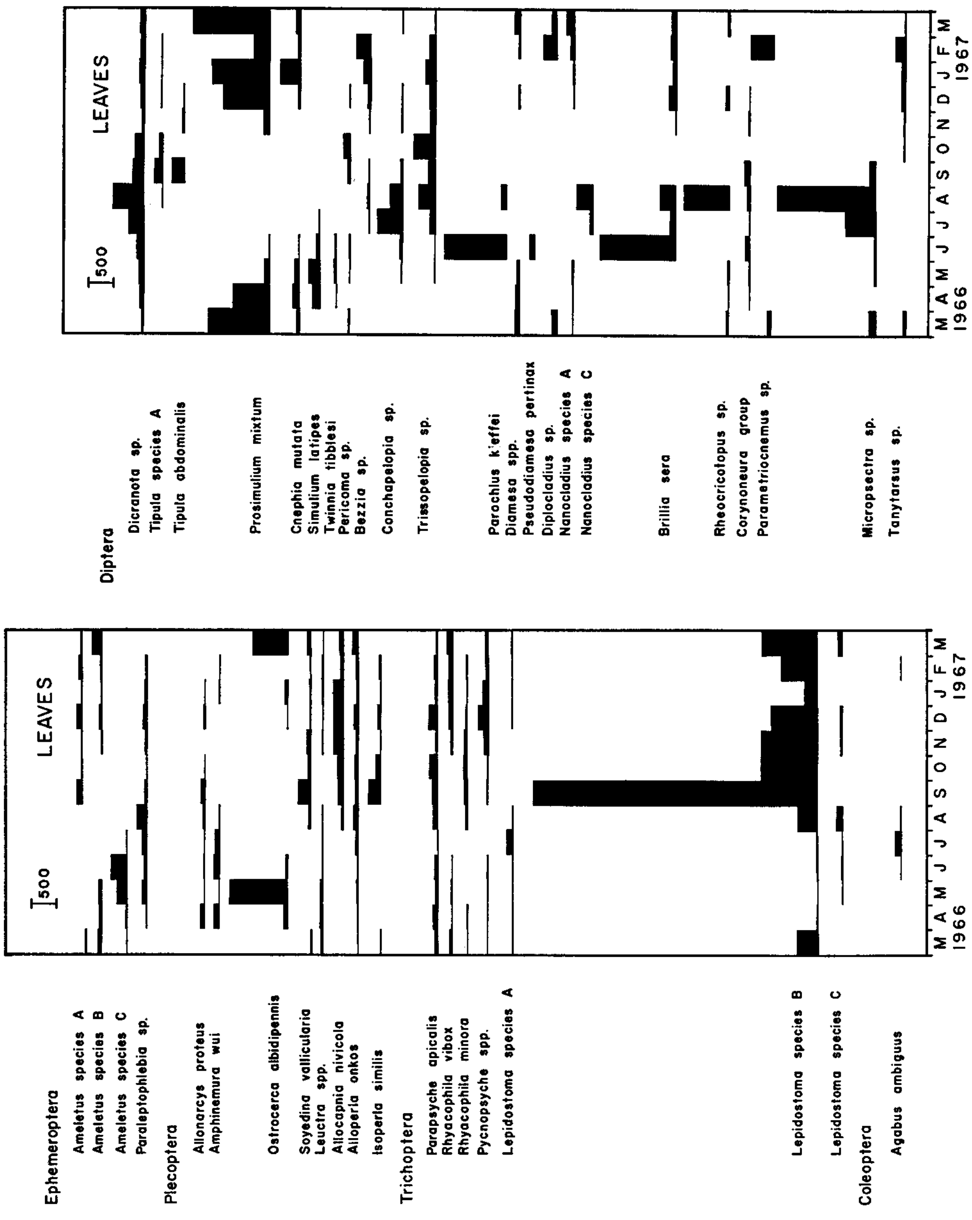

FIG. 12. The average numbers/m² per month of common insects in the leaf habitat, West Creek, between March 1966 and March 1967.

grew steadily throughout the summer and autumn and all were fully grown by the end of the following March. However, the majority of *Lepidostoma* C larvae completed their development in 3 months and remained the same size during the winter. As well as having specific life cycle patterns, the three species differed in their spatial distribution in the leaf habitat. *Lepidostoma*

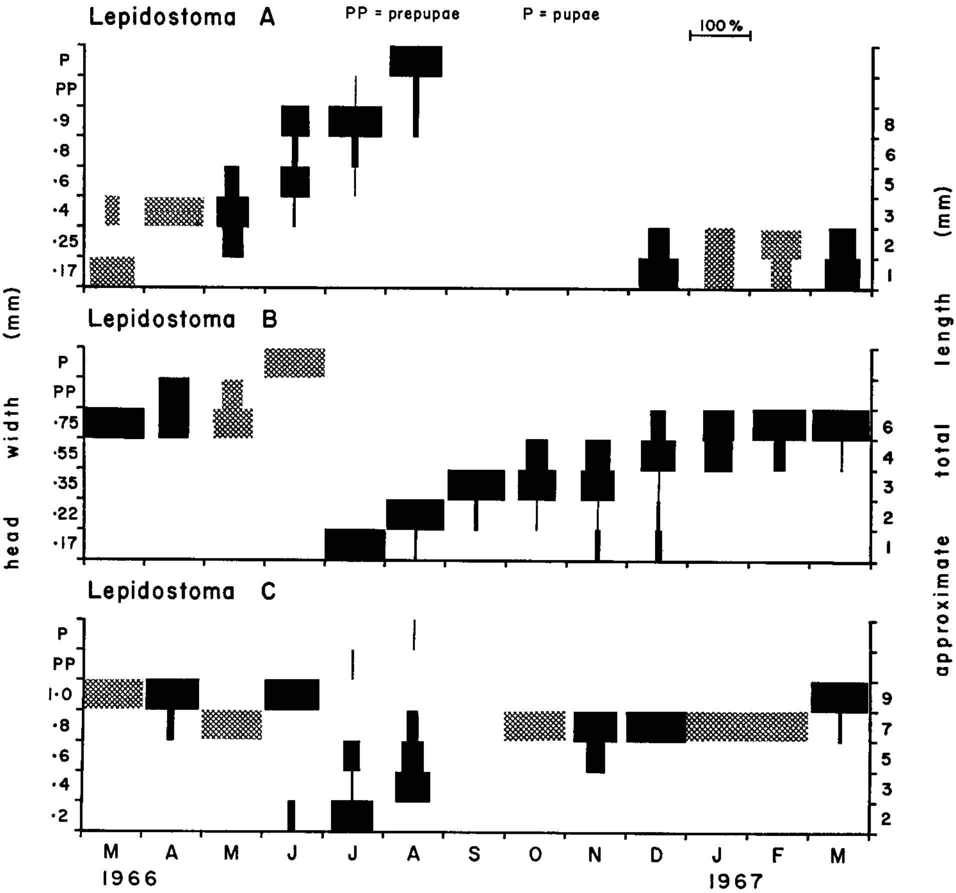

FIG. 13. Growth of larvae of three species of *Lepidostoma* (caddisflies), West Creek, 1966–67. (Each histogram shows percentage of total specimens per month having size indicated. Cross-hatched histograms based on <10 specimens/month.)

A was found mainly on leaves in pools and in slow-moving water, whereas *Lepidostoma* B was most common on leaves trapped on fallen branches in the current but was collected from all types of leaf habitat. *Lepidostoma* C was restricted to leaves near the source of the stream.

The seasonal relationships between species of Diptera were traced in detail only for the Simuliidae, whose larvae could be identified at all stages of development. The succession of species in the leaf habitat was similar to that in the stone habitat, but a second common spring species, *Simulium latipes* (Fig. 11) was present on leaves. Although the remaining common species of Diptera in the leaf habitat (Fig. 12) were less easy to recognise, *Nanocladius* "A" clearly alternated with *Nanocladius* "C," and high numbers of *Conchapelopia* sp. larvae in July were followed by high numbers of *Trissopelopia* sp. in October.

LINEAR DISTRIBUTIONS OF INSECTS

Very few of the insects in West Creek were equally abundant at all four collecting stations. The number of species per station tended to increase from station I to station IV in most insect groups (Tables 2–4).

Eight species of Ephemeroptera (Table 2) were collected at station IV, including *Heptagenia* sp. which was confined to this station, whereas only 4 species were found at station I. *Ameletus* C and *Paraleptophlebia* sp. were the most abundant species at any one station, in both instances at station III.

The number of Plecoptera species (Table 2) increased from 5 or 6 species at station I to 8 or 9 species at station IV. *Allonarcys proteus* was found only at station IV, and *I. holochlora* was found only at stations III and IV. The remaining 8 species of Plecoptera were collected from at least three stations. *Ostrocerca albidipennis* was very abundant at the upper stations but absent from station IV; even at station III, nymphs were found only on one occasion in May in a mass of leaves caught on some twigs just below the pond, and had probably been washed down by high water from station II. However, *A. wui*, resembling *O. albidipennis* in size and life history, was more common at station IV than at the other stations.

Nine species of Trichoptera (Table 2) were collected at station I, of which *P. uniformis*, *Lepidostoma* C, and *N. aniqua* were found only at stations I and II. *Ironoquia lyrata* was collected occasionally at stations I and II, and one specimen was found at station III in the mouth of a temporary tributary. However, *I. lyrata* was not found elsewhere at station III and had probably been washed in from the tributary, where the larvae were common. The remaining five species of Trichoptera collected at station I were more or less evenly distributed along the stream. Station II supported six species more than station I, all six occurring also at stations III and IV. Three more species were collected at station III, of which *Phylocentropus* sp. and *Oligostomis pardalis* were confined to this station. Except for the last two species and *I. lyrata*, all Trichoptera found at station III were found also at station IV. In addition, there were three species peculiar to station IV: *N. nacatus*, *N, ornatus*, and *Wormaldia* sp.

Coleoptera, Neuroptera, and Tipulidae (Table 3) were all represented by fewer species at station I than at stations II–IV. Members of the Tipulidae and Ptychopteridae were found chiefly at stations II and III. Exceptions were the leaf-dwelling tipulids: *Pedicia albivitta* mainly at station I, *Tipula* "A" only at station IV, and *Dicranota* sp. at all stations. The Simuliidae (Table 3) were represented by more species at stations I and II than at stations III and IV. *Twinnia tibblesi* was found only at station I, but was abundant there.

Of the Chironomidae (Table 4) only the subfamily Tanypodinae showed a marked downstream increase in the number of species. Station I was characterized by low numbers and few species of Tanypodinae and Chironominae, but had high numbers and many species of Podonominae and Orthocladiinae. At the other stations the Tanypodinae were more diverse and the numbers of Orthocladiinae declined.

DISCUSSION

The species composition of insects in West Creek is influenced considerably by the thick deciduous forest surrounding the stream, and by the climate. Only a small amount of light reaches the stream while the trees are in leaf, and during the winter the stream bottom is shaded by ice bridges and snow. The small amount of incident radiation appears primarily responsible for the near absence of autotrophic plants in West Creek. The food available to herbivores is almost entirely allochthonous organic material in the form of fallen leaves. The feeding habits of the insects were not studied beyond simple observations of behaviour, but information from other sources (Wu, 1923; Frison, 1929; Claassen, 1931; Chapman and Demory, 1963) shows that algal feeders in the stream were few, and that many of the common species feed on leaves or leaf detritus, e.g. *Paraleptophlebia* sp., *Allocapnia nivicola*, *Soyedina vallicularia*, *Allonarcys proteus*, and all species of *Lepidostoma*, *Pycnopsyche*, and the Simuliidae.

The cool water temperatures are maintained by the spring source and by the dense shade provided by the forest in summer. The amount of water that evaporates from the vegetation surrounding West Creek exceeds precipitation during summer (Baird, 1968), and as a result parts of the stream and its tributaries dry up. The drought not only has a direct effect on the fauna, but also allows the stream to be choked with fallen leaves in October when the water volume is lowest.

The distributions of the insect species are probably influenced chiefly by food and temperature; however, the size of the stream is also an important factor, because the smaller the stream, the more it is affected by environmental conditions and by the accumulation of leaves. Ross (1963) has related the distribution of many eastern Nearctic Trichoptera to the influence of deciduous forest, and the majority of the Trichoptera in West Creek are known to be cold water, small stream species (Ross, 1944, 1959; Flint, 1960, 1961, 1962; Wiggins, 1960). The three species of *Ameletus* (Ephemeroptera) in West Creek appear to be restricted to cool water. Neither *Ameletus* A nor *Ameletus* C was found in the Lac Hertel outflow stream (Fig. 1) where water temperatures in August exceeded 22 C, whereas both species occurred in West Creek (17 C) in August. *Ameletus* B, aquatic only during cool months (Fig. 5) was abundant in the outflow stream; since the nymphs complete their development and emerge as adults before the water temperature exceeds 10 C, they are able to avoid high summer temperatures. The Orthocladiinae (Chironomidae) are more characteristic of cool streams than warm streams, so the relatively high numbers of species and individuals in West Creek is in agreement with the generally cool temperatures. However, the abundance of *Pseudodiamesa pertinax* in small summer pools at station I was still surprising, as this species was previously known only from the Arctic and from high mountain streams in Utah and British Columbia (Oliver, 1959). All the Simuliidae of West Creek have been reported previously (Davies et al., 1962) as occurring in small streams, supporting the idea that a small stream has a characteristic fauna.

The various communities within West Creek are probably influenced greatly by the current velocity, which in turn determines substrate type, accumulation of allochthonous organic material, and dissolved oxygen concentration. The fauna of each substrate type (sand, gravel, and stones) is made up of organisms adapted to the particular niche size or surface area offered by the substrate particles, and to the speed of the current over the substrate. The burrowing members of the sand fauna are probably least affected by the size of the stream and accumulations of leaves since light and food materials in the habitat differ little from those for sand in other parts of the stream. However, the ability to tolerate low dissolved oxygen concentrations, as shown by the ochrous sand fauna, is advantageous in a stream that receives a large amount of slow-moving organic material every autumn. *Bittacomorpha clavipes* was confined to the mouth of the deoxygenated tributary at station III, but other species from this special habitat such as *Phylocentropus* sp. and *Ptychoptera quadrifasciata*, and also species in the detritus fauna, may be peculiar to West Creek and similar streams.

The insect community in gravel is the least specialised and includes many species more common in other habitats. However, the interstices of the substrate shelter early stages of Plecoptera, Trichoptera, and Diptera, especially during summer. The gravel presumably forms an important reservoir from which other habitats are stocked, and also protects many species from desiccation during periods of drought. The tendency of young larvae to move from gravel to leaves as they grow suggests that there may be insufficient food in the gravel habitat to support a large population of herbivores.

Stones in West Creek, having only sparse algal growth and no moss on them support fewer algal feeders and more leaf feeders than stony habitats described elsewhere (Sprules, 1947; Scott, 1958; Hynes, 1961). Since the current responsible for the stony substrate tends to flush fallen leaves from the stream bottom, the stones habitat probably suffers the same food shortage as gravel. The temporal separations of congeneric species of *Ameletus* and *Neophylax* (all assumed to be algal feeders) may be interpreted as examples of ecological segregation allowing the most efficient use of limited resources (Grant and Mackay, 1969). On the other hand, the high numbers of Simuliidae in the habitat are able to utilize the drifting organic detritus resulting from disintegration of fallen leaves.

The leaf and detritus faunas are the most important communities since they support the highest numbers of species and individuals per unit area of stream. Accumulations of leaves and detritus in the slow-flowing areas are typical of small streams in thick deciduous forest, yet the rich fauna has not been described before in terms of species associations. The fauna of fallen autumn leaves in October and November gradually changes the following spring to include species able to tolerate warmer temperatures and more detritus. Species living and feeding on entire leaves, e.g. *Lepidostoma* B, become more crowded as the leaves break down, resulting in very high numbers per unit area in September when few whole leaves remain. At this time the dissolved oxygen concentration in shallow pools is near the annual minimum and is further reduced by falling leaves. Yet both leaves and detritus continue to support a high number of species.

The linear distributions of the species (Tables 2–4) partly reflect the linear distributions of habitat types. The species peculiar to station III are members of the sand or detritus faunas typical of the slow-flowing areas at this station. Species confined to stony substrates are most abundant at station IV. However, the distinctive fauna at station I is more likely the result of summer drought, which restricts the species to those that can avoid desiccation. Some larvae, described above, appear to survive while buried in damp gravel. Others, as noted by Hynes (1958) for several species in Wales, have emerged as adults by the time the stream dries up. Either they lay drought-resistant eggs, or they have flight periods long enough to allow females to lay eggs when the stream flows again. The eggs of *Ostrocerca albidipennis* and members of the Simuliidae may tolerate desiccation, since the abundance of larvae (totalling more than $1000/m^2$ in winter) at station I is unlikely to be due to chance, but adults were not observed later than August, when the stream was still dry. The eggs of *Lepidostoma* B may also be drought-resistant because a collection made at station I in November, when the water was just beginning to flow again, revealed many 1st instar larvae. This late hatching, some 4 months after the first appearance of the larvae at other stations (Fig. 13), may have been triggered by contact with water (G. B. Wiggins, personal communication).

The only insect whose distribution might have been affected by a temperature gradient in West Creek was the chironomid *Parochlus kieffeii* which was very abundant at station I in June 1966 when the water temperature was about 5 degrees C lower than at other stations. During the rest of the year the temperature gradient was not marked.

The presence of *Twinnia tibblesi* at station I only is explained by the behaviour of adult females of this species, which always fly to the upstream limit of flowing water before laying their eggs (D. M. Wood, personal communication). It is possible that the similar behaviour noted by Roos (1957) in some Trichoptera may account for the restriction of *Lepidostoma* C, *Pseudostenophylax uniformis*, and *Ironoquia lyrata* to stations I and II, as well as their ability to avoid desiccation.

The insect communities in West Creek together include a remarkably high number of species, their diversity evidently not being in proportion to the size of the stream nor reduced by the large quantity of organic matter. In each of the five habitats studied are many species apparently well adapted to the conditions found in a small cool stream flowing slowly through thick deciduous forest. The diversity of species is enhanced by the temporal or spatial segregation of congeneric species that allows many similarly adapted species to utilize the resources efficiently, yet reduces interspecific competition.

When more insect larvae have been identified to species level, it will be possible to compare the fauna of West Creek with that of similar streams.

If the insect communities described above are indeed characteristic of this type of stream, then the information on their distributions and seasonal occurrences in West Creek may be used in studies on water quality.

ACKNOWLEDGMENTS

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Since this paper went to press, the following species have been identified by Dr. G. B. Wiggins (Trichoptera) and Dr. F. P. Ide (Ephemeroptera).

Lepidostoma "A" as *Lepidostoma griseum* (Banks)

Lepidostoma "B" as *L. ontario* Ross

Lepidostoma "C" as *L. sommermanae* Ross

Psilotreta sp. as *Psilotreta frontalis* Banks

Ameletus "A" as *Ameletus browni* McD.

Ameletus "B" as probably *A. tertius* McD.

Ameletus "C" as *A. ludens* Needham

Heptagenia sp. as *Heptagenia thetis* Traver

Iron sp. as *Epeorus (Iron) pleuralis* (Banks)

Paraleptophlebia sp. as *Paraleptophlebia moerens* (McD.)

R. J. M.