Limnological Features of a Northern Brown-water Stream, with Special Reference to the Life Histories of the Aquatic Insects

Hugh F. Clifford

American Midland Naturalist, Vol. 82, No. 2 (Oct., 1969), 578-597.

Stable URL:
http://links.jstor.org/sici?sici=0003-0031%28196910%2982%3A2%3C578%3ALFOANB%3E2.0.CO%3B2-6

Limnological Features of a Northern Brown-water Stream, with Special Reference to the Life Histories of the Aquatic Insects

HUGH F. CLIFFORD
Department of Zoology, University of Alberta, Edmonton, Alberta, Canada

ABSTRACT: Aquatic invertebrates of a northern brown-water stream of west central Alberta, the Bigoray River, were studied for 2 years. The stream drains extensive muskeg terrain, but the *p*H of the water is always on the alkaline side; water temperatures are near 0 C for 6 months of the year, and the stream is completely ice-covered for 5 months; there is progressively less flow during the winter months. During dry winters, water freezes into the substrate, causing considerable mortality to riffle-inhabiting insects. The stream supports a large and diverse mayfly (Ephemeroptera) fauna, *Leptophlebia cupida* (Say) and *Baetis tricaudatus* Dodds accounting for over 50% of the total yearly fauna by numbers and also volume biomass. Life history data are presented for 11 aquatic invertebrates. Compared to faunas of other streams, the Bigoray River has the following pertinent features: (1) a fauna with a restricted emergence period; (2) a short period (5 months) of seasonal succession and a long period (7 months) when the fauna changes very little; (3) various seasonal growth patterns exhibited by individual species, but the fauna as a whole growing most intensely in autumn; (4) a relatively large number of temporary (or summer) mayfly species; and (5) a winter species fauna having extensive delayed hatching.

INTRODUCTION

There are many slowly moving streams, usually termed muskeg or brown-water streams, draining extensive regions of subarctic and arctic Canada. A unifying feature of these streams, varying in size from small trickles to large rivers, is the dark color of the water. The brown water color is due to organic substances, usually humic or fluvic acid, brought into the water in colloidal form from poorly drained, often muskeg, terrain. Brown-water streams of northern muskeg regions have received little attention from biologists. With the exception of economically important biting flies (Hocking, 1960, reviews these studies), and a summer study of adult insects from a brown-water stream of Ontario (Sprules, 1947), the invertebrates of brown-water streams have been almost completely neglected. And there are no ecological observations of the streams' faunas during the long and extremely cold winters.

From April, 1965, through June, 1968, I have been studying the aquatic invertebrates and gathering routine physical and chemical data from a brown-water stream of west central Alberta, the Bigoray River. Ultimately it is hoped this information will help to fit these northern streams into the broad lotic system spectrum. The immediate goal was to gain a perspective of the stream's invertebrate fauna in regards to the faunas of streams from other climatic regions. I used a life history approach, working out the life cycles of the abundant species and documenting relative changes in their numbers and biomasses throughout the year. European workers (*e.g.*, Macan, 1957a & b; Hynes, 1961; Pleskot, 1961) have successfully utilized this approach, but it has not been applied extensively in North America.

DESCRIPTION OF STUDY AREA

The Bigoray River (Fig. 1A & B), part of the Athabasca River system and Arctic Ocean drainage, is located 100 mi W of Edmonton, Alberta, on the dry continental side of the Cordillera. The climate of this region is subarctic by the Koeppen classification. Geologically the region is one of Cretaceous and Cenozoic sedimentary rock. The flora is typical of muskeg regions of the boreal forest, major vegetation being black spruce *Picea mariana* (Mill.); tamaracks *Larix laricina* (DuRoi); and a number of willows *Salix* spp. Poplars *Populus tremuloides* Michx. and *P. balsamifera* L. are common on higher ground and burned-over areas. According to Waksman (1938) the muskeg (organic terrain) drained by the Bigoray River would be classified as or close to lowland peatland, forming from decomposed sedge and reed-like plants and characterized by water of low acidity; in contrast, a high moor peatland forms from *Sphagnum,* and its water has a high acidity.

There is little gradient on the Bigoray River's North Fork, and the stream meanders in its lower reaches. The stream bed consists mainly of mud, silt and small gravel particles. Diatoms are seldom

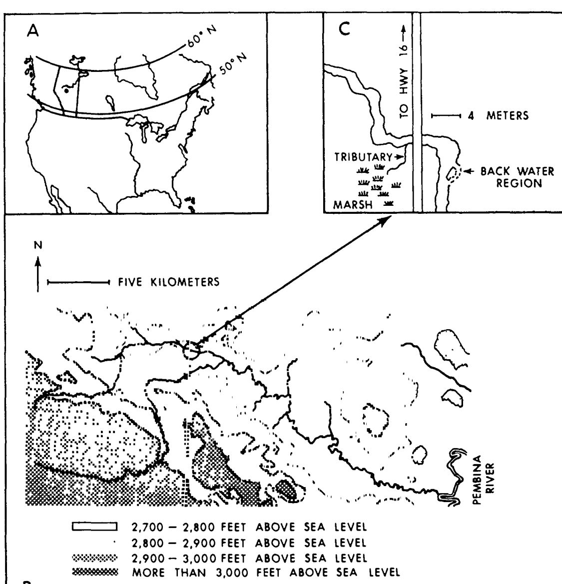

Fig. 1.—Latitudinal (A), topographical (B) and sampling site (C) maps of Bigoray River, Alberta.

found in the stream, but large growths of filamentous algae, mainly *Microspora Loefgrenii* (Nordst.), occur during late summer. There are few fish except during the spring run of white suckers *Catostomus commersonii* (Lacepede), coming from the Pembina River. Burbot *Lota lota* (L.), grayling *Thymallus arcticus* (Pallas) and northern pike *Esox lucius* L. are present but are rare.

The stream was completely ice-covered for 5 months of the year and water temperatures were near 0 C for about 6 months of the year (Fig. 2). Air temperatures frequently drop to —30 or —40 C in winter, but the complete and rapid freeze-over in late autumn furnishes insulation from these temperatures; there is very little supercooling of the water and hence very little anchor ice. Water temperatures, as determined with a 30-day recording thermometer, rose rapidly in late spring and approached 20 C during the summer; but daily fluctuations were small, 3 C being the largest observed during the study. Although the stream drains extensive muskeg terrain, the *p*H of the water was above 7.0; and, although during the ice-free season the water was dark brown, the stream became very clear in late winter. Dissolved oxygen content remained high, even in late winter. The Bigoray River is at maximum discharge shortly after the ice goes out in spring, when the snow is melting. Water levels drop considerably in late winter before the spring break-up. At the sampling site, discharge was seldom over 1 m^3/sec (35 cfs), and flow was reduced to 0.06 or 0.08 m^3/sec (2 or 3 cfs) in late winter 1967.

METHODS

The stream was sampled regularly for 18 months at one location (Fig. 1C). During the ice-free season, from late April through October, samples were taken at slightly less than monthly intervals; in winter, samples were taken every other month. During the summer it was usually possible to visit the streams at least every other week for spot collections and observations. On each sampling date, except in winter, about 1 hour was spent collecting adult insects from the surface drift, by sweeping the vegetation, and collecting insects on-the-wing.

Stream invertebrates were collected with a long-handled dip net having a round aperture and a net size of 16 meshes/cm. This net size, although quite fine, does not retain a representative sample of very small specimens, *i.e.*, animals smaller than 2.0 mm. When compared to a net of 100 meshes/cm, I estimated the numerical loss of hemimetabolous insects from the 16 meshes/cm net as follows: nymphs less than 1.0 mm, 90%; 1.0 to 1.5 mm, 75%; 1.6 to 2.0 mm, 45%. Maitland (1966a) estimates that a 16 meshes/cm net does retain 99% of the biomass. For each sampling date during the ice-free season, 20 to 25 minutes were spent sampling about 40 m of the main stream, collecting from pools, riffles, the edge of the stream and in the center of the channel. This material was treated as one sample, the main stream sample. The same procedure was used in winter but, because of the thick ice, sampling was less extensive and was restricted to one pool and one riffle.

Two additional areas were also regularly sampled. One was a stretch of the stream called the backwater region, which is disconnected from the main stream except during above average flow. The backwater region, although reduced to one pool in late summer and autumn, never went completely dry during the ice-free seasons. In winter the water froze into the substrate of this region. The second area sampled was an intermittent tributary, flowing during the ice-free season of 1966, but which went dry in July, 1967, and remained dry

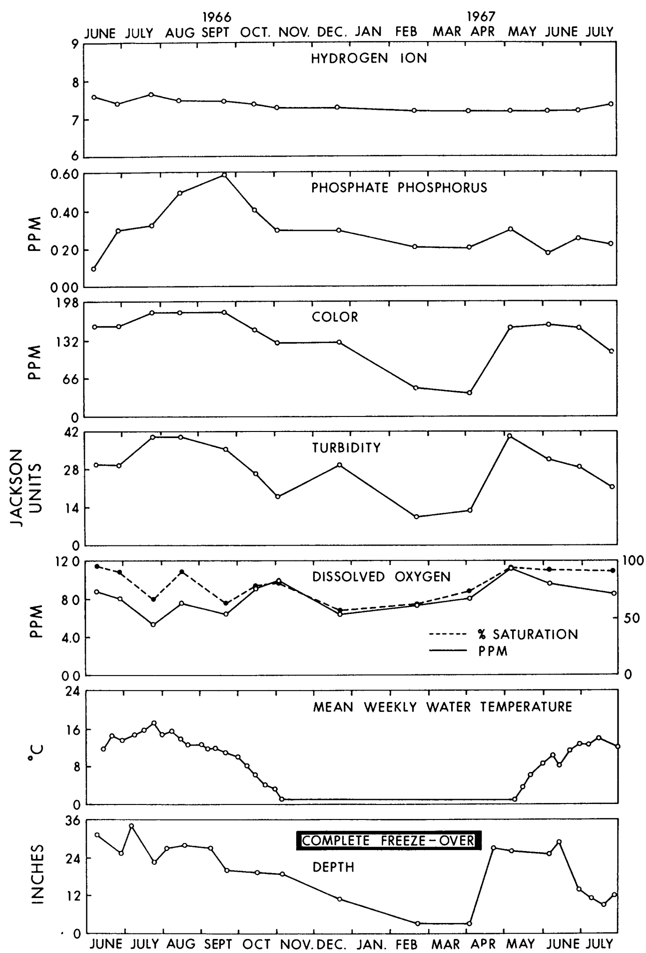

Fig. 2.—Physical and chemical features of Bigoray River, 1966 and 1967.

until the following spring. There is no water in the intermittent tributary during the winter months.

Samples from the three areas were analyzed separately. Animals were identified and counted, mayfly nymphs were separated into males and females, and all animals were measured to the nearest 0.5 mm excluding cerci. Total volume biomass for each species was determined by water displacement for each sampling date. Since length measurements do not in all cases give an accurate picture of the invertebrate's progress through its life cycle, the more abundant species, which were mayflies, were also grouped into arbitrarily chosen stages. This was done mainly in respect to the length of the wing pads and the appearance of the wing pads. However, except for presenting the last nymphal stage (tan wing pads) in the life history graphs, this aspect of the study is not considered in this report.

FAUNA AS A WHOLE

Considering its northern location, the stream supports a large and diverse mayfly fauna (Table 1). Of 124 adult *Leptophlebia* only three were *L. nebulosa,* the remainder being *L. cupida.* I called all the nymphs *L. cupida.* Only three stonefly species were found in this brown-water stream. There is a diverse trichopteran fauna, but with the exception of Hydropsychidae there are few individuals. Larvae of

TABLE 1.—Species list of aquatic invertebrates[a] from Bigoray River and the total number for each species (or higher taxon) collected during the study period 17 May 1966 to 24 August 1967

	Total No.		Total No.
Ephemeroptera		Plecoptera	
Leptophlebia cupida (Say)	5580	*Nemoura cinctipes* Banks	1121
Leptophlebia nebulosa (Walker)	....	*Capnia* sp.	7
Baetis tricaudatus Dodds	4011	*Taeniopteryx nivalis* (Fitch)	5
Callibaetis coloradensis Banks	1326	Trichoptera	
Siphlonurus alternatus (Say)	265	*Hydropsyche slossonae* Banks	....
Cloeon sp.	168	*Hydropsyche recurvata*	....
Paraleptophlebia debilis (Walker)	149	Total *Hydropsyche*	1225
Caenis simulans McD.	23	*Cheumatopsyche analis* (Banks)	1100
Tricorythodes minutus Traver	17	*Limnephilus infernalis* (Banks)	....
Stenonema sp.	14	*Limnephilus canadensis* Banks	....
Ephemerella Subg. *Serratella* Edmunds	5	*Limnephilus perpusillus* Walker	....
Heptagenia sp.	4	*Limnephilus minusculus* (Banks)	....
Ephemerella Subg. *Attenuatella* Edmunds	1	*Grammotaulius interrogatimis* Zett.	....
Ephemera simulans Walker	1		
Hexagenia limbata (Serville)	1		

Hydropsyche slossonae and *H. recurvata* shorter than 6.0 mm could not be separated to species; of those 6.0 mm or longer, 80% were *H. slossonae*. Chironomids were not counted because the 16 meshes/cm net retained only the larger specimens. Beetles are not yet identified; poriferans, ectoprocts and turbellarians were not found, not even when using special collecting methods. These three groups are apparently absent from the stream.

The fauna is a mixture of plains and cordilleran species, *e.g.*, *L. cupida*, *Siphlonurus alternatus*, *Taeniopteryx nivalis*, *Hydropsyche slossonae* and *H. recurvata* belong to the former group; *Baetis tricaudatus*, *Callibaetis coloradensis* and *Nemoura cinctipes* belong to the latter group.

TABLE 1.—(continued)

	Total No.
Asynarchus lapponicus (Zett.)	....
Philarctus quaeris Milne	....
Glyphotaelius hostilis Hagen	....
Total Limnephilidae	203
Polycentropus cinereus Hagen	73
Eobrachycentrus sp.	4
Ptilostomis sp.	3
Oecetis sp.	3
Hemiptera	
Callicorixa audeni Hungfd.	....
Sigara conocephala (Hungfd.)	....
Sigara decoratella (Hungfd.)	....
Total Corixidae	304
Notonecta irrorata Uhler	3
Gerris pingreenis Dr. and Hott.	1
Gerris remigis Say	5
Megaloptera	
Sialis cornuta Ross	32
Anisoptera	
Aeschna subarctica Walker	5
Somatochlora walshii Scudder	2
Diptera	
Simulium venustum Say	....
Simulium vittatum Zett.	....
Simulium verecondum S. & J.	....
Prosimulium sp.	....
Total Simuliidae	1020
Dicranota montana Alex.	257
Tipula sp.	14
Chrysops sp.	1
Chironomidae	NC
Coleoptera	480
Amphipoda	
Gammarus lacustris Sars	365
Hyallela azteca (Saussure)	200
Gastropoda	
Gyraulus parvus Say	....
Aplexa hypnorum L.	....
Physa heterostropha (Say)	....
Lymnaea humilis Say	....
Lymnaea sp.	....
Total Gastropoda	51
Pelecypoda	
Sphaeriidae	114
Hirudinea	
Glossiphonia complanata (L.)	45
Helobdella stagnalis (L.)	10
Haemopis marmorata (Say)	1
Oligochaeta	NC

[a] All aquatic insects are immatures with the exception of Hemiptera and Coleoptera, which include both immatures and adults.

NC = Not counted.

Excluding chironomid larvae, the fauna is composed of 13 abundant taxa (mainly species), making up 86% of the total yearly fauna by numbers and 84% by volume biomass (Fig. 3). Percentage numbers and percentage biomass differed very little for the same species, exceptions being very small animals, *e.g.,* Simuliidae, and the relatively large limnephilid caddis flies and *Gammarus*. The mayflies *L. cupida* and *B. tricaudatus* were the dominant species, both in numbers and biomass. Together they account for 53% of the total yearly fauna by numbers and 51% by volume biomass.

The community structure changed very little from September to April. *L. cupida* was the dominant invertebrate at this time; and *N. cinctipes,* the Hydropsychidae, and small *B. tricaudatus* were present in considerable numbers. In contrast, the species composition during summer fluctuated considerably from month to month. *B. tricaudatus* was usually the dominant species, but the appearance and emergence of summer mayfly species (*Paraleptophlebia, Cloeon* and *Siphlonurus*) and other species groups, *e.g.,* Simuliidae and *Callibaetis,* caused considerable temporal variation in community structure. One could say for survey purposes that one winter sample would suffice, but monthly samples, at least, would be necessary in summer.

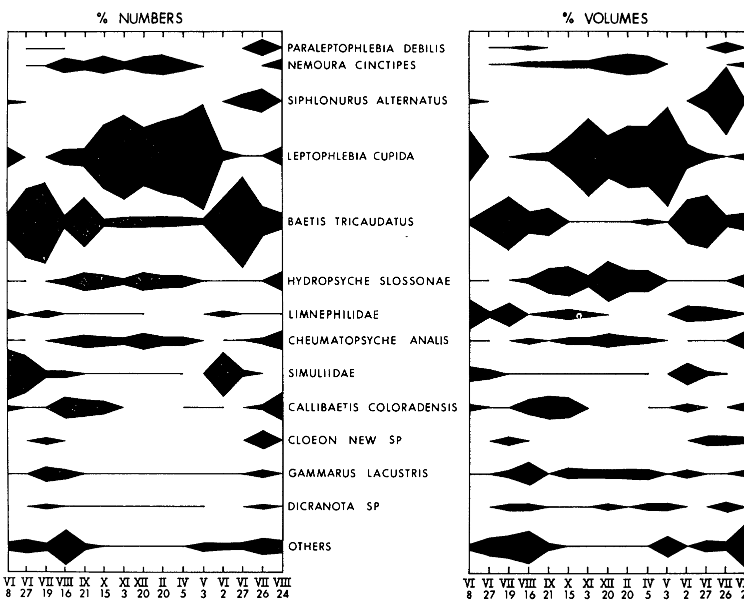

Fig. 3.—Percentage composition in numbers and volume biomass of invertebrates found in Bigoray River during 1966 and 1967. Width of the spindle is proportional to the number or volume of animals on the sampling date.

LIFE HISTORIES

Leptophlebia cupida

L. cupida, formerly *Blasturus cupidus* Say, is usually considered an eastern North American mayfly, but it is probably widely distributed east of the Cordillera. It has been reported south to Arkansas (Peters and Warren, 1966) and I have taken specimens as far north as the Great Slave Lake region. Although several workers, *e.g.,* Morgan (1913), Traver (1925) and Spieth (1938), made ecological observations or carried out morphological studies of *L. cupida,* knowledge of its life history is limited to general observations and emergence records.

In the Bigoray River, there is one generation a year (Fig. 4). Small nymphs first appeared in the main stream in August, 1966, in riffle regions. They grew rapidly throughout autumn, and many appeared fully grown when the stream froze over in November. There was little growth at least for the larger specimens in winter; however, delayed hatching continued through December. There are approximately five months of continuous, delayed hatching for *L. cupida* in this northern stream. In early April, 1967, when the stream was very low, the nymphs had congregated in large pools beneath the ice. When the ice started breaking up during the last two weeks

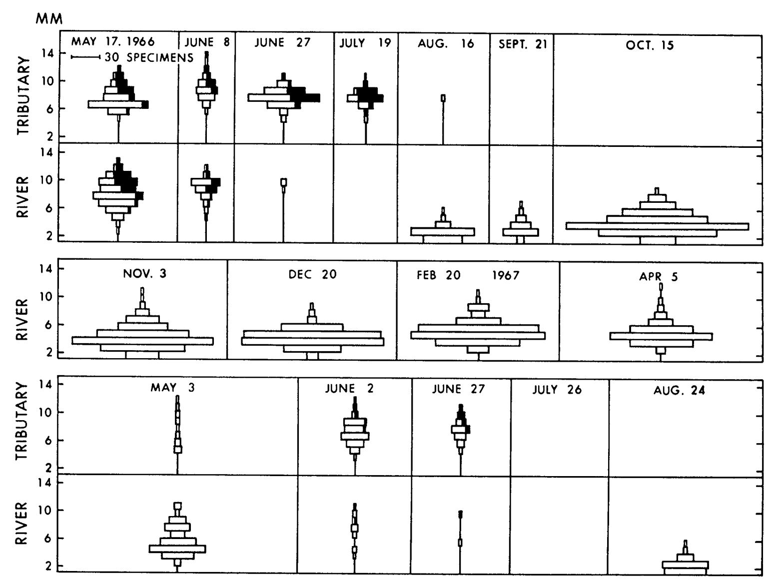

Fig. 4.—Number of *Leptophlebia cupida* in 1-mm size classes, Bigoray River tributary and mainstream, 1966 and 1967. The blackened areas of size classes represent the number of nymphs with tan wing pads, this condition being restricted to the latter part of the last nymphal instar and representing impending emergence. See Table 2 for total number of nymphs per sampling date used in constructing histograms.

of April, 1967, the nymphs moved out of the pools and, by following the shoreline upstream, migrated into the tributaries. Since the tributary in question was dry during the winter, with a frozen stream bed, specimens present here on 3 May represented the vanguard of the migrating nymphs. All sizes of nymphs and equal number of sexes migrate. I observed 71 nymphs moving across a line in 5 minutes. Neave (1930) described a similar migration of *L. cupida* in a Manitoba stream, and Ide (1935) and Lyman (1956) observed migration of related species in other northern waters. Annual migrations have not been reported for *L. cupida* from milder regions.

L. cupida emerged in June, 1967, mainly from the tributary but with a minor emergence from the main stream, not all the nymphs having migrated into tributaries. The species emerged earlier from the main stream than from the tributary, the latter being 4 to 6 C cooler than the main stream; and because the tributary went dry during July, 1967, the emergence period was much shorter in 1967 than 1966. The length of mature, last instar nymphs (*i.e.*, those with tan wing pads) varied considerably, pointing up one of the drawbacks of interpreting life histories entirely from length measurements. This would be especially important in overlapping generations, which was not the case for *L. cupida.*

Baetis tricaudatus

The life history of *Baetis tricaudatus* is difficult to interpret from available data (Fig. 5). Events are clear, however, starting in late autumn and continuing through the winter. There was a large influx of small nymphs in October, 1966; they grew slightly in late autumn and winter, and delayed hatching continued throughout winter. There was an emergence peak in June, scattered emergence throughout the summer, and, as indicated by 1966 data, another emergence peak in September. At this time the *B. tricaudatus* population appeared to be synchronizing, something not evident during the summer months.

Although there was no definitive evidence for a quick summer generation in either 1966 or 1967, *e.g.*, a large influx of small specimens in summer, it is possible the summer sampling intervals were not

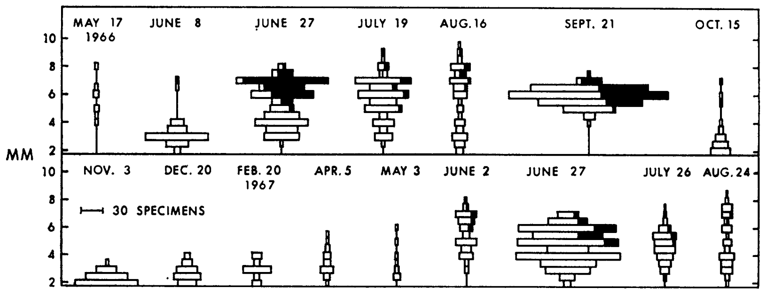

Fig. 5.—Numbers of *Baetis tricaudatus* in 0.5-mm size classes, Bigoray River, 1966 and 1967. See Fig. 4 for explanation.

short enough to catch the rapidly growing nymphs when they were small. The two emergence peaks could be (but are not necessarily) characteristic of bivoltine species; and two and sometimes three generations a year is the usual situation for *Baetis* of more temperate regions. Before one could assign one generation a year for *B. tricaudatus,* and hence a 10-month delayed hatching period, more information is needed for this species.

Sampling dates for this and other species are shown in Table 2.

SUMMER SPECIES

A summer species, following mainly Macan's (1965) definition, is one in which growth, emergence, and reproduction take place during a relatively short time of summer, the remainder of the year being spent in the egg stage or a very small non-growing nymphula stage. The three summer mayflies of the Bigoray River all appeared about the same time each year, and all emerged about the same time (Fig. 6). *Paraleptophlebia debilis* was found in the main stream and the tributary; *Cloeon* sp. was found in the main stream and the backwater region; and *Siphlonurus alternatus* was restricted to the backwater region. Once growth starts, the three species progress uniformly through their univoltine life cycle, there being very little continuous delayed hatching. The nymphs grow very rapidly. In fact to assess accurately the growth rates of the summer species, sampling intervals should be shortened to weekly intervals. Absence of large numbers of small and medium sized specimens is due to sampling at time intervals too far apart to catch the rapidly growing nymphs, and not to errors due to net size. If *B. tricaudatus* nymphs grew as rapidly in summer as the above three species, a quick summer generation would be possible for *Baetis,* large numbers of the small nymphs being absent because of sampling intervals, and the summer generation *in toto* masked by the overlapping winter generation.

P. debilis was the only mayfly with a disparity in the nymphal sex ratio; there were four times as many female as male nymphs.

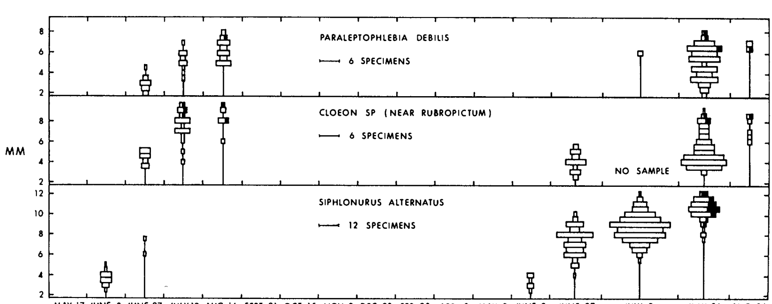

Fig. 6.—Summer species: numbers of *Paraleptophlebia debilis* in 0.5-mm size classes; numbers of *Cloeon* sp. and *Siphlonurus alternatus* in 1-mm size classes, Bigoray River, 1966 and 1967. See Fig. 4 for explanation.

TABLE 2.—Number of animals per sampling date of species appearing in Figures 4 through 7

	1966									1967						
	17 May	8 Jun.	27 Jun.	19 Jul.	16 Aug.	21 Sep.	15 Oct.	3 Nov.	20 Dec.	20 Feb.	5 Apr.	3 May	2 Jun.	27 Jun.	26 Jul.	24 Aug.
Leptophlebia cupida	609	239	243	117	181	107	859	654	610	630	411	326	170	85	0	155
Baetis tricaudatus	12	180	632	408	216	679	76	180	123	90	50	16	174	871	170	140
Paraleptophlebia debilis	0	0	12	12	27	0	0	0	0	0	0	0	0	0	91	4
Siphlonurus alternatus	0	26	2	0	0	0	0	0	0	0	0	0	9	122	104	0
Callibaetis coloradensis	..	22	6	19	280	230	188	14	0	0	1	3	8	0	29	255
Cloeon sp.	0	0	13	24	8	0	0	0	0	0	0	0	0	24	92	7
Nemoura cinctipes	..	0	1	2	142	117	215	144	187	159	60	0	0	0	6	88
Cheumatopsyche analis	..	4	0	0	63	179	149	110	193	93	54	0	2	8	25	156
Hydropsyche spp.	..	0	0	0	75	226	191	113	240	119	59	0	8	0	14	148
Gammarus lacustris	..	11	24	44	88	14	18	18	9	13	16	2	6	2	22	13
Dicranota montana	..	0	7	21	30	8	21	33	34	9	10	10	0	3	42	2

Although *Leptophlebia cupida* had a sex ratio near unity, large female nymphs were about 2 mm longer than their male counterparts, a situation similar to what Minshall (1967) found for *Epeorus pleuralis* (Banks). In part, this will account for the large size range of *L. cupida* nymphs with tan wing pads. However, other mayfly species also exhibited considerable variation in the size of nymphs with tan wing pads, and there was little difference in the size of male and female nymphs of these species.

WINTER SPECIES

The remaining abundant species overwinter as fairly large nymphs or larvae and, as is also true of *L. cupida* and *B. tricaudatus,* are considered winter species. The stonefly *Nemoura cinctipes* was the first aquatic insect to emerge in spring, when the ice started breaking up in late April, 1967 (Fig. 7). Actually some nymphs had transformed to the adult stage by 5 April, 1967, when the stream was still completely ice-covered. Adults were found clinging to the undersurface of the ice cover in air spaces between the ice and water. Sailer (1950) found a similar phenomenon in an Alaskan stream for *N. columbiana* Claassen, the nymphs of this species not only transforming to adults under the ice, but mating and probably ovipositing beneath the ice as well. *N. cinctipes* in the Bigoray River has a well defined univoltine life cycle. There was very little continuous delayed hatching and the nymphs grew throughout the winter. *Nemoura* is one of the few insects of this northern stream for which growth rates could be plotted accurately from mean size data.

Callibaetis coloradensis makes up a large part of the standing crop in summer; but this mayfly is not restricted to river habitats, the nymphs also being found in oxbows, sloughs and ponds of the region. There is one generation a year, and the species overwinters as large non-growing nymphs in the main stream. Most specimens shown in

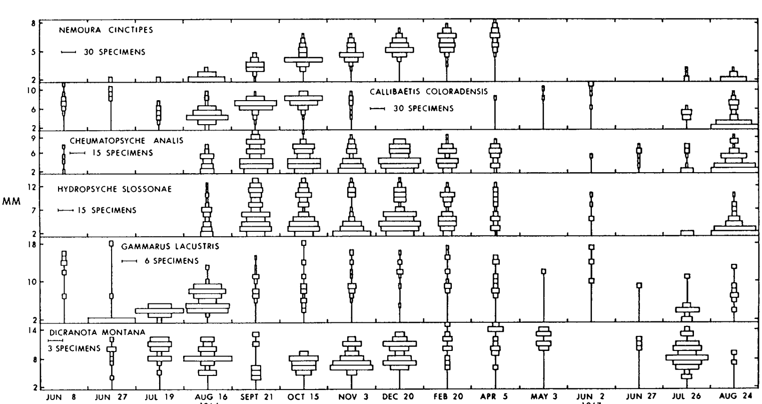

Fig. 7.—Winter species: numbers of *Nemoura cinctipes* in 0.5-mm size classes; numbers of other winter species in 1-mm size classes, Bigoray River, 1966 and 1967. See Fig. 4 for explanation.

Fig. 7 (the backwater region and main river samples were combined for this species only) came from the backwater region. Of course, all macroinvertebrates of this region perish in winter, when the water freezes solidly into the substrate. Most of the new generation in the river came from *Callibaetis* adults emerging in late spring from nearby ponds and then ovipositing in the river, especially in the backwater region.

Net-spinning caddis flies *Cheumatopsyche analis* (Banks) and *Hydropsyche* spp. (mainly *H. slossonae*) pupate in May and emerge in early June, with scattered emergence throughout the summer. There were large size ranges when the new generations appeared in August of both years—a rather difficult thing to explain. It seems likely that all the net-spinning caddis fly larvae go into a prepupal aestivation in the spring, and this takes place quite deep in the substrate. Most of the aestivating larvae will shortly pupate and emerge; but some will not pupate, and these will return to the stream as active larvae. This suggestion is based on removing to a laboratory water system, rocks to which were attached the pebbled retreats of the hydropsychids. Some of the larvae within the retreats eventually pupated, while some left the retreats and again became active larvae.

The amphipod *Gammarus lacustris* has an annual cycle. Females produced one brood in June and then died; the new generation grew rapidly in late summer and autumn and overwintered as large non-growing animals. In contrast the tipulid larva *Dicranota montana,* a predaceous species, grew throughout the winter.

WINTER FLOW AND MORTALITY OF INSECTS

Additional data collected during winter and spring of 1967-1968 indicate that many riffle-inhabiting invertebrates perish when surface ice freezes into extensive regions of the stream's bed. During autumn and early winter of 1965-1966 and 1966-1967 the region received near normal precipitation, but the same seasons of 1967-1968 were very dry (Table 3); and by late winter, water had frozen into the substrate completely across shallow riffle regions. At this time flow in riffle regions was restricted to subsurface layers. Large insects restricted to riffle regions experienced considerable mortality, *e.g., Baetis* and *Nemoura* (Table 4). Adult *Nemoura* were not found during spring,

TABLE 3.—Average seasonal air temperatures and total seasonal precipitation for Bigoray River region,[1] 1965-1968

	Summer & autumn			Winter[2]	
	°C	mm		°C	mm
1 Jul. 1965- 1 Nov. 1965	11	329	2 Nov. 1965-10 Apr. 1966	–8	135
1 Jul. 1966-10 Nov. 1966	9	347	11 Nov. 1966-18 Apr. 1967	–8	106
1 Jul. 1967-14 Nov. 1967	11	180	15 Nov. 1967-20 Apr. 1968	–7	90

[1] Data from Edson, Alberta, Weather Station.
[2] Calculated from estimated complete freeze-over to start of break-up.

1968, the species apparently being eliminated in this section of the river. In contrast small *Baetis* nymphs hatching from overwintering eggs appeared again in early June, 1968, pointing up the adaptative value of delayed hatching.

Severity of ice conditions in winter depends chiefly, and this cannot be overemphasized, on precipitation prior to the freeze-up in late autumn and, then, during early winter. Meteorological conditions of mid and late winter have no effect on stream flow, because the stream by this time is completely isolated by a thick ice cover. If there is little precipitation in autumn, the stream enters the long winter at lower than normal flow, with the surface ice perilously close to the substrate. In early winter the lack of an insulating snow cover combined with continuously low air temperatures result in the muskeg's water freezing to depths much greater than would be the case if a thick snow layer covered the terrain; consequently the stream's water level is further reduced. Surface ice becomes progressively thicker and extends out from the banks into the substrate; and, as indicated above, in exceptionally dry years, water freezes into the substrate in all regions except deep riffles and pools.

DISCUSSION

The use of life cycles to compare faunas of different streams entails some sort of classification scheme. Macan (1965) classifies cycles into three major groups: (1) development of one generation taking longer than one year, (2) more than one generation in one year, (3) one generation in one year, a category that is further divided into summer species (*i.e.*, eggs hatch and development is completed in summer, and the species overwinters as adults or in an egg stage) and winter species (*i.e.*, overwintering as larvae and then disappearing or becoming scarce at some time in summer). For mayfles and stoneflies, Hartland-Rowe (1964) recognized, in addition to summer species, two types of winter species based on growth characteristics: (1) hatching in late

TABLE 4.—Number of animals collected from the main stream, Bigoray River, during the spring months, 1967 and 1968

	1967		1968	
	5 Apr	3 May	4 Apr	16 May
Species	No.	No.	No.	No.
Leptophlebia cupida	411	326	25	26
*Baetis tricaudatus**	50	16	0	0
*Nemoura cinctipes**	60	0	1	0
Hydropsyche spp.*	59	0	0	7
*Cheumatopsyche analis**	54	0	0	3
Gammarus lacustris	16	2	0	0
Hyalella azteca	3	7	0	4
*Dicranota montana**	10	10	0	0
Caenis simulans	0	0	1	10
Others	9	35	4	13

* Riffle-inhabiting species.

summer and some growth in autumn, no growth in winter but growth resuming again in spring with development completed in summer; (2) egg laying and hatching in spring, growth through summer, autumn, and more slowly in winter, more rapid growth and emergence in spring.

In the Bigoray River, and confining remarks to groups for which there are adequate data, all species except *Baetis tricaudatus* have one generation a year. Compared to other streams, the fauna of this northern stream has the following pertinent features:

1) *The fauna has a restricted emergence period.* Except for two species, emergence is confined to a period from late May through August, with about 80% of all emergence taking place during June and July. *Baetis* continues to emerge in September, and *Nemoura* emerges when the ice breaks up in late April. The short period involves emergence shifts at both ends of the ice-free season, *i.e.*, species normally emerging in early spring, *e.g.*, *Leptophlebia cupida*, emerge in late spring and summer; and species emerging in autumn, *e.g.*, *Paraleptophlebia debilis*, emerge in summer. The short emergence period is in contrast to what happens in streams where winters are shorter and milder and even to high altitudinal streams remaining open in winter because of a steep gradient. Hynes (1961), for a Welsh mountain stream, and Sheldon and Jewett (1966), for a high altitudinal stream of California, found adult stoneflies present during every month of the year. Kraft (1964) reported adult mayflies in every month except January for a coastal Oregon stream, and Peters and Warren (1966) found adult mayflies in every month except December and January in northern Arkansas, a region where winters are mild but nevertheless occur. For northern regions adult mayflies have been reported as late as October in Michigan (Leonard and Leonard, 1962) and southern Ontario (Ide, 1935).

Several workers noted emergence taking place at a smaller size as the species' emergence period progresses. This size disparity was found not only between the two generations of bivoltine species (the rapid generation is composed of smaller mature animals), *e.g.*, Rawlinson (1939) and Pleskot (1961), but within one generation a year species as well, *e.g.*, Gledhill (1959), Brown (1961), and Khoo (1964). In the Bigoray River, with the exception of *L. cupida*, these seasonal size differences were not very pronounced. For other mayfly species, the nymphs transforming into subimagos were as large late in the emergence period as at the beginning of the period. This is probably associated with the short period of seasonal succession, *e.g.*, the nymphs, because of the short "open" season, are not exposed to extensive fluctuations in water temperatures and day lengths (for 5 months of the year the stream's fauna lives in total darkness).

2) *There is a short period of seasonal succession, and consequently a long period when the fauna changes very little.* Based on disappearance of species because of emergence and appearance of species from the hatching of eggs, there were about 5 months when seasonal

succession occurred (Table 5). This is a much shorter period than found in most streams, *e.g.,* Hynes (1961), Clifford (1966) and Egglishaw and MacKay (1967), but similar to the periodicity reported by Pleskot (1961) for an Austrian stream. An outstanding feature of this northern stream is the 7-month period when the species composition does not change. Species present in October are also found in April. Some species grow throughout the winter, growth stops or is greatly retarded for others; but no additional species appear from the hatching of eggs, and there is no emergence.

3) *Growth patterns of species are variable, but the fauna as a whole grows more intensely in autumn.* The type of growth exhibited by mayflies and stoneflies of the Bigoray River can also be found for different species from other regions: *e.g., Leptophlebia cupida* has a growth pattern similar to Macan's (1957b) *Heptagenia lateralis* (Curtis); seasonal growth of *Nemoura cinctipes* resembles that of Maitland's (1966b) *Amphinemura sulcicollis* (Stephens); the summer mayflies correspond to Maitland's (1965) *Ephemerella ignita* (Poda).

Several workers studying mayflies and stoneflies in milder regions, *e.g.,* Egglishaw and MacKay (1967) and Elliott (1967), found the nymphs, regardless of size, growing very little when low water temperatures set in during winter. Svensson (1966) reported retardation of growth in autumn and a quiescent period in winter for all species of stoneflies of a northern Swedish stream. In the Bigoray River certain species do stop growing in winter, *e.g., Callibaetis,* but others, such as *Nemoura* and *Dicranota,* grow throughout the long winter. *Leptophlebia, Baetis* and the Hydropsychidae, when they reach a certain size, grow very slowly if at all in winter; but their precise growth patterns are masked by delayed hatching and the resulting winter growth of the newly hatched animals. Excluding summer species, the fauna as a whole grows most intensely in autumn; mainly because this is when the new generation of the dominant species—*Leptophlebia, Callibaetis, Nemoura,* the hydropsychids, etc.—are growing rapidly.

TABLE 5.—Seasonal changes in species composition[1] of Bigoray River fauna, 1966-1967

Sampling period	Species change[2] No.	Sampling period	Species change No.
17 May 1966-27 Jun.	5	20 Dec.-20 Feb. 1967	0
27 Jun.-19 Jul.	4	20 Feb.- 5 Apr.	0
19 Jul.-16 Aug.	1	5 Apr.- 3 May	6
16 Aug.-21 Sep.	4	3 May- 2 Jun.	5
21 Sep.-15 Oct.	0	2 Jun.-27 Jun.	2
15 Oct.- 4 Nov.	0	27 Jun.-26 Jul.	3
4 Nov.-20 Dec.	0	26 Jul.-24 Aug.	1

[1] Based on 13 species for which sufficient life cycle data were available.

[2] Numbers are the sum of species appearing and species disappearing from one sampling date to the next.

4) *There is a relatively large number of summer (or temporary) mayfly species.* Pleskot (1962) describes species appearing in streams for only a short period each year as temporary species. This seems to be a more appropriate term than summer species since it does not seasonally restrict such life cycles. Compared to other streams of North America, the three temporary species of the Bigoray River (which are true summer species) constitute a large number. Scattered reports of other temporary species include the following for North America: *Ameletus ludens* Needham (Clemens, 1922); *Parameletus columbiae* McD., (Edmunds, 1957); and *Heptagenia* prob. *maculipennis* Walsh (Clifford, 1966). For northern streams Robertson (unpublished) found *Tricorythodes minutus* Needham to be a temporary species in east-central Alberta, and Hartland-Rowe (1964) reported two temporary species, *Epeorus longimanus* (Eaton) and *Ephemerella lapidula* McD. for a mountain stream of southern Alberta. The list should be greatly enlarged when life histories of North American mayflies are better known. Of the above species, *Ameletus* and *Heptagenia* were found in streams drying up in the summer, and the remaining species were from northern or high altitudinal streams. Berner (1950) in a comprehensive study of Florida mayflies found few seasonal species and none that could be considered a temporary species.

Of the three temporary species of the Bigoray River, *Cloeon* sp. is probably a hitherto unreported species, and nothing is known of its life cycle in other regions. I know of no other complete life history study of *Siphlonurus alternatus;* but Burks (1953) mentions *Siphlonurus* eggs being deposited in spring and not hatching until the

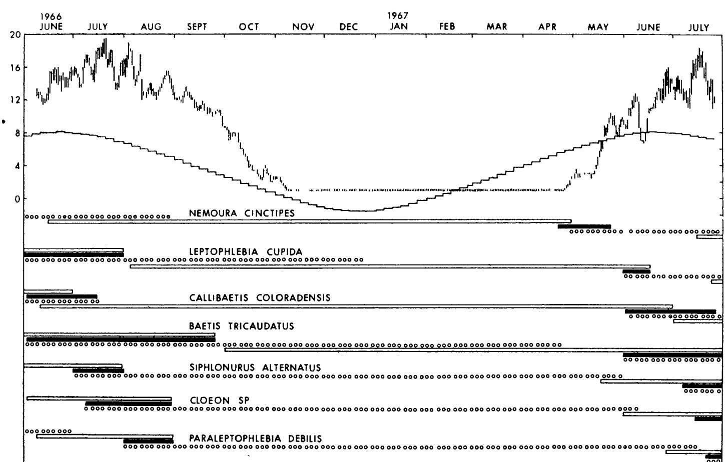

Fig. 8.—Daily maximum-minimum water temperatures, day-lengths as calculated from sunrise-sunset data, and generalized life histories of the hemimetabolous insects of Bigoray River, 1966 and 1967.

following spring, indicating a temporary cycle for some species in North America. In the Bigoray River *S. alternatus* is restricted to the backwater region. The water of this region freezes solidly into the substrate during winter; and the species' resting stage, probably an egg state, is subject to conditions analogous to those of temporary species reported from summer-dry streams. The temporary cycle would appear to be an adaptation to a rather obvious adverse physical environment.

The third summer species, *Paraleptophlebia debilis*, presents a different picture. It is not unvaryingly a temporary species throughout its range. Ide (1935) found *P. debilis* nymphs (the new generation) in October, and Gordon (1933) suggests that in the Ithaca, New York, region it has three generations in two years, *i.e.*, 6-month, 9-month, and 9-month cycles. In the Bigoray River, *P. debilis* is a summer species. The temperature regime offers little as a basis for explaining the temporary cycle (Fig. 8). The species oviposits in August; water temperatures are still quite high at this time, but the new generation does not develop, nor does it appear with the onset of warm temperatures in early summer of the following year. Adaptive value of *P. debilis*' temporary cycle is to be found in its periodicity in respect to *Leptophlebia cupida*, a closely related mayfly and the dominant macroinvertebrate of the river. *P. debilis* appears, grows, and emerges during the short period when *L. cupida* nymphs are absent or very small. Both species are detritus feeders, and both are found in the same type habitat. It is in respect to competition and not the physical environment that we might find the significance of the temporary cycle of *P. debilis* in the Bigoray River.

Acknowledgments.—I am indebted to the following persons for taxonomic assistance: Dr. O. M. Abedelmur, Ministry of Health, Khartoum, Sudan, Africa (Simuliidae); Dr. R. G. H. Cormack, University of Alberta (Flora); Dr. G. F. Edmunds, Jr., University of Utah (Ephemeroptera); Mr. M. E. Pinsent, University of Alberta (Gastropoda); Dr. W. E. Ricker, Fisheries Research Board of Canada, Nanaimo, British Columbia (Plecoptera); Mr. D. Rosenberg, University of Alberta (Corixidae); Drs. G. B. Wiggins and T. Yamamoto, Royal Ontario Museum, University of Toronto, and Mr. A. P. Nimmo, University of Alberta (Trichoptera). Miss Teresa Delane, University of Alberta, did much of the field and laboratory work during the first summer of the program. This study was supported by a grant from the National Research Council of Canada.

REFERENCES

BERNER, L. 1950. The mayflies of Florida. Univ. of Florida Press, Gainesville. 267 p.

BROWN, D. S. 1961. The life cycle of *Chloeon dipterum* L. (Ephemeroptera, Baetidae). *Entomologist*, **94**:114-120.

BURKS, B. C. 1953. The mayflies or Ephemeroptera of Illinois. *Bull. Illinois Natur. Hist. Surv.*, **26**:1-216.

CLEMENS, W. A. 1922. A parthenogenetic mayfly (*Ameletus ludens* Needham). *Canad. Entomol.*, **56**:77-78.

CLIFFORD, H. F. 1966. The ecology of invertebrates in an intermittent stream. *Invest. Indiana Lakes and Streams,* **7**:57-98.

EDMUNDS, G. F., JR. 1957. On the life history of *Parameletus columbiae* McDunnough (Ephemeroptera). *Utah Acad. Sci., Proc.,* **34**:25-27.

EGGLISHAW, H. J. AND D. W. MACKAY. 1967. A survey of the bottom fauna in the Scottish Highlands. Part III. Seasonal changes in the fauna of three streams. *Hydrobiologia,* **30**:305-334.

ELLIOTT, J. M. 1967. The life histories and drifting of the Plecoptera and Ephemeroptera in a Dartmoor stream. *J. Anim. Ecol.,* **36**:343-362.

GLEDHILL, T. 1959. The life history of *Ameletus inopinatus* (Siphlonuridae, Ephemeroptera). *Hydrobiologia,* **14**:85-90.

GORDON, E. 1933. Notes on the ephemerid genus *Leptophlebia. Brooklyn Entomol. Soc. Bull.,* **28**:116-134.

HARTLAND-ROWE, R. 1964. Factors influencing the life histories of some stream insects of Alberta. *Verhandl. int. Verein. Limnol.,* **15**:917-925.

HOCKING, B. 1960. Northern biting flies. *Annu. Rev. Entomol.,* **5**:135-152.

HYNES, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.,* **57**:344-388.

IDE, F. P. 1935. The effect of temperature on the distribution of the mayfly fauna of a stream. *Univ. Toronto Stud., Biol. Ser.,* No. 39. *Publ. Ontario Fish Res. Lab.,* **50**:3-76.

KHOO, S. G. 1964. Studies of the biology of *Capnia bifrons* (Newman) and notes on the diapause in the nymphs of this species. Verh. 3, Int. Symp. uber Plecopteren. Limnol. Schrif. 34/35:23-31.

KRAFT, G. F. 1964. Seasonal occurrence and distribution of aquatic insects in Berry Creek. Ph.D. thesis, Oregon State Univ., Corvallis. (Libr. Congr. Card No. 64-7423). 122 p. Univ. Microfilms, Ann Arbor, Mich.

LEONARD, J. W. AND F. A. LEONARD. 1962. Mayflies of Michigan trout streams. *Cranbrook Inst. Sci., Bull.,* No. 43. 139 p.

LYMAN, F. E. 1956. Environmental factors affecting distribution of mayfly nymphs in Douglas Lake, Michigan. *Ecology,* **37**:568-576.

MACAN, T. T. 1957a. The Ephemeroptera of a stony stream. *J. Anim. Ecol.,* **26**:317-342.

———. 1957b. The life histories and migrations of the Ephemeroptera in a stony stream. *Trans Soc. British Entomol.,* **12**:129-156.

———. 1965. The fauna in the vegetation of a moorland fishpond. *Arch. Hydrobiol.,* **61**:273-310.

MAITLAND, P. S. 1965. The distribution, life cycle, and predators of *Ephemerella ignita* (Poda) in the River Endrick, Scotland. *Oikos,* **16**:48-57.

———. 1966a. Studies on Loch Lomond. II. The fauna of the River Endrick. Blackie and Son Limited, Glasgow. 194 p.

———. 1966b. The distribution, life cycle, and predators of *Amphinemura sulcicollis* (Stephens) (Plecoptera) in the River Endrick, Scotland. *Entomologist,* **99**:72-81.

MORGAN, A. H. 1913. A contribution to the biology of mayflies. *Ann. Entomol. Soc. Amer.,* **6**:371-413.

MINSHALL, J. N. 1967. Life history and ecology of *Epeorus pleuralis* (Banks) (Ephemeroptera: Heptageniidae). *Amer. Midl. Natur.,* **78**:369-388.

NEAVE, F. 1930. Migratory habits of the mayfly *Blasturus cupidus* Say. *Ecology,* **11**:568-576.

PETERS, W. L. AND L. O. WARREN. 1966. Seasonal distribution of adult Ephemeroptera in northwestern Arkansas. *J. Kansas Entomol. Soc.,* **39**:396-401.

PLESKOT, G. 1961. Die Periodizität der Ephemeropteren Fauna einiger osterreichischer Fliessgewasser. *Verhandl. int. Ver. Limnol.,* **14**:410-416.

———. 1962. Beobachtungen über Diapausen in der Entwicklung der Ephemeropteren. *Verhandl. XI int. Kongr. Entomol.,* **3**:363-366.

RAWLINSON, R. 1939. Studies on the life history and breeding of *Ecdyonurus venosus. Proc. Zool. Soc. London, Ser. B.,* **109**:377-450.

SAILER, R. I. 1950. A thermophobic insect. *Science,* **112**:743.

SHELDON, A. L. AND S. JEWETT. 1966. Stonefly emergence in a Sierra Nevada stream. *Pan-Pacific Entomol.,* **43**:1-8.

SPIETH, H. T. 1938. Studies on the biology of the Ephemeroptera. I. Coloration and its relation to seasonal emergence. *Canad. Entomol.,* **70**: 210-218.

SPRULES, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. *Univ. Toronto Stud., Biol. Ser.,* No. 56; *Publ. Ontario Fish Res. Lab.,* **69**:1-81.

SVENSSON, P. 1966. Growth of nymphs of stream living stoneflies (Plecoptera) in northern Sweden. *Oikos,* **17**:197-206.

TRAVER, J. R. 1925. Observation of the ecology of the mayfly *Blasturus cupidus. Canad. Entomol.,* **57**:211-218.

WAKSMAN, S. A. 1938. Humus: Origin, chemical composition and importance in nature. Williams and Wilkins Co., Baltimore. 526 p.

SUBMITTED 22 AUGUST 1968 ACCEPTED 23 SEPTEMBER 1968