



Life History and Ecology of *Epeorus pleuralis* (Banks) (Ephemeroptera: Heptageniidae)

Judy N. Minshall

American Midland Naturalist, Vol. 78, No. 2 (Oct., 1967), 369-388.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0031%28196710%2978%3A2%3C369%3ALHAEOE%3E2.0.CO%3B2-%23>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Midland Naturalist is published by The University of Notre Dame. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/notredame.html>.

American Midland Naturalist
©1967 The University of Notre Dame

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

Life History and Ecology of *Epeorus pleuralis* (Banks) (Ephemeroptera: Heptageniidae)¹

JUDY N. MINSHALL

Department of Biology, University of Louisville, Louisville, Kentucky² 40208

ABSTRACT: The life history and ecology of *Epeorus pleuralis* in Morgan's Creek, Kentucky, were studied over a 20-month period beginning February, 1963, and continuing through September, 1964. *E. pleuralis* has a univoltine life cycle. Hatching begins in late September or early October and extends through May, with a peak in January or February. Emergence starts in late February or early March and continues into June, with a peak in late April or early May. Growth proceeds during the winter despite very low temperatures. The nymphs are herbivorous and eat principally allochthonous leaf detritus, with some diatoms.

The nymphs were most abundant in a cascade near the spring source of the stream. Their longitudinal distribution in the stream was largely determined by the interplay of temperature, substrate, and current. They were restricted to cool-water areas and to fast-water habitats, such as riffles and cascades. They were found mainly on loose, rubble substrate.

The seasonal abundance of the nymphs was controlled mainly by factors associated with life-history phenomena. Temperature had some effect on these phenomena but was not the only factor involved, especially in the headwaters, where temperatures were nearly constant.

INTRODUCTION

There have been few detailed life-history studies of species of Ephemeroptera in North America. Notable exceptions include those by Hunt (1953), Fremling (1960), and Britt (1962). In the present paper the life history of *Epeorus pleuralis* (Banks) is described in detail for the first time, and the seasonal and longitudinal distribution and abundance of the nymphs in Morgan's Creek, Kentucky, are examined in the light of pertinent environmental data. The data were obtained between 1 February 1963 and 26 September 1964, in connection with a study of the dynamics of the benthic community of the stream.

E. pleuralis is the only abundant heptageniid mayfly in Morgan's Creek. It is the largest obligate herbivore in the stream and thus one of the most important primary consumers. In terms of the whole benthic community *E. pleuralis* was the eighth most abundant species and the second most common ephemeropteran taken. Seven other species of mayflies occur in the mainstream. In order of abundance they are: *Baetis amplus* Traver, *B. herodes* Burks, *B. phoebus* McD., *Centroptilum rufostrigatum* McD., *Paraleptophlebia moerens* McD.,

¹ Contribution number 94 from the Department of Biology, University of Louisville. Based on a thesis submitted to the graduate faculty of the University of Louisville, in partial fulfillment of the degree of Master of Science.

² Present address: Department of Biology, Idaho State University, Pocatello, Idaho 83201.

Pseudocloeon carolina Banks, and *Stenonema interpunctatum* (Say). Ide (1935a) has given notes on the post-embryological development of *E. pleuralis* nymphs, and discussions on the effect of temperature on growth and on distribution of the nymphs have been given by Maxwell and Benson (1963) and Ide (1935b), respectively.

Acknowledgments.—The present study was made possible by a grant from the National Science Foundation in the form of an NSF Cooperative Graduate Fellowship. I wish to thank Dr. Louis A. Krumholz, chairman of my graduate committee, for his help and advice during the study. Dr. T. T. Macan read the manuscript in its final stages and made many helpful suggestions. Dr. Lewis Berner identified the mayflies in Morgan's Creek, and his assistance is gratefully acknowledged. Especially I would like to acknowledge my husband, Dr. G. Wayne Minshall, for the help he has given throughout the study and for much of the supplementary data used in this paper.

DESCRIPTION OF THE STUDY AREA

Morgan's Creek is a small, spring-fed, stony stream in Otter Creek Park, Meade Co., Kentucky. The stream originates in Morgan's Cave and flows approximately 0.8 mile (1335 m) to empty into the Ohio River. Eight permanent stations were established along the stream, with Station I at the spring source and Station VIII at the mouth. Station II lies 25 m downstream from the source, Station III about 325 m further on, and Stations IV, V, VI, and VII, 470, 750, 860, and 1150 m from the source, respectively.

The basic habitat in the stream is the rubble-riffle complex. About 73% of the area in the stream consists of this type. Five of the stations are in riffle areas; of the remainder, Station II is a cascade with a steep (45°) gradient, Station V, a pool, and Station VIII, a sandy reach. The substrate at Station I is a bedrock slab, covered with scattered bits of rubble. At Station II the substrate consists of a series of rocky ledges overlain with large boulders and rubble. At the other stations (except Station VIII) the rubble substrate predominates; there is some deposition of silt in the pool at Station V, and mud from floodwaters of the Ohio River adds to the substrate at Stations VII and VIII.

From the source to just below Station III, and from a little below Station VI to just above the mouth, there is a thick growth of riparian vegetation. The banks along the stream from Station IV to below Station VI have been cleared of vegetation. Morgan's Creek is relatively cool (Fig. 1); at Station I the temperature is fairly constant all year. Temperatures at Station II, though not shown, closely paralleled those at Station I; only twice were temperatures recorded that varied more than 2 C from those at Station I. On 14 December 1963, the temperature was 10.8 C at Station I and 7.5 C at Station II. One week later the temperatures recorded were 9.8 and 6.5 C, respectively. For all practical purposes the range in temperatures at Station II was 10-14 C; only four of 50 readings were outside this range and all were less than 10 C. At the remaining six stations temperatures varied

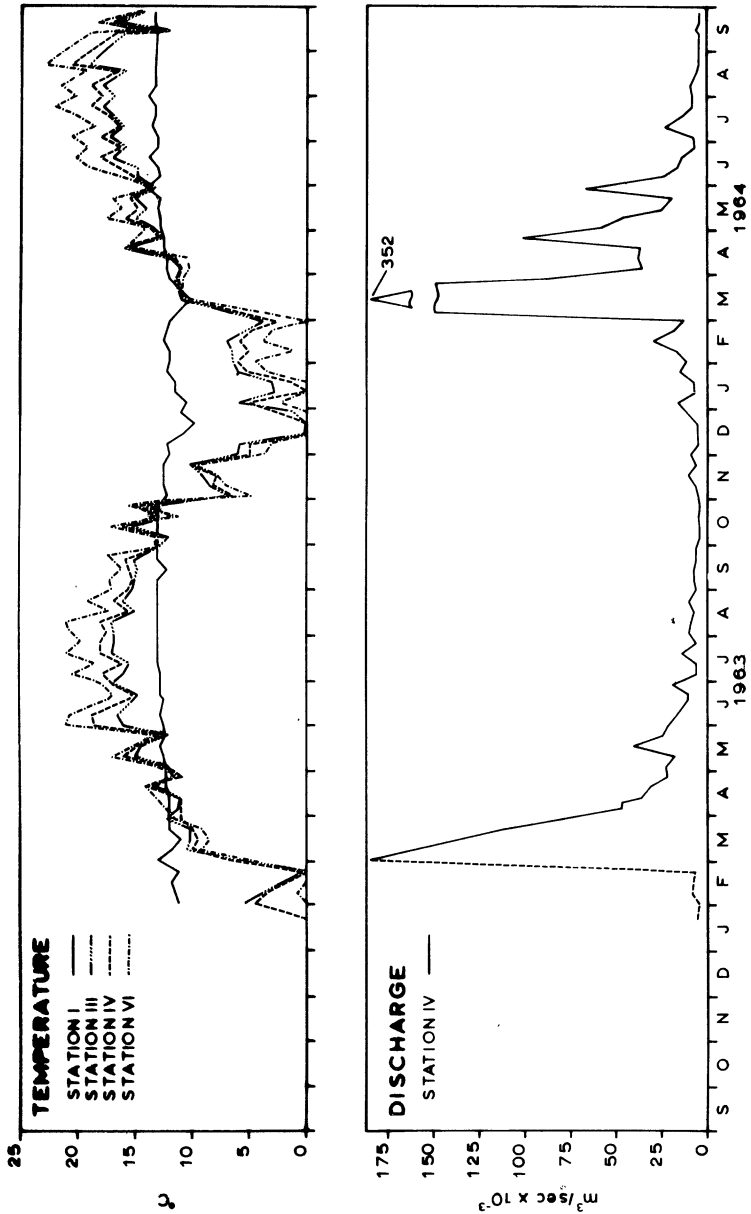


Fig. 1.—Variations in temperature at Stations I, III, IV, and VI, and discharge at Station IV, during the study period.

from zero to highs between 19 (Station III) and 23 C (Station VI).

The modal discharge, measured at Station IV, was 0.007 m³/sec (range 0.005 to 0.35 m³/sec) (Fig. 1). The best estimates of current velocity at the spring source and at each riffle station during modal flow are: 19 (I), 20 (III), 26 (IV), 27 (VI), and 35 (VII) cm/sec. During periods of modal discharge the average stream width is about 1.7 m and the average depth 5 cm. The oxygen content of the water issuing out of the cave is about 10 mg/l and is high throughout the creek, even at Station V, where the lowest oxygen concentration recorded was 8.9 mg/l.

METHODS

Nymphs of *E. pleuralis* were obtained from composite samples of the benthic community in Morgan's Creek. Regular biweekly sampling was begun 1 February 1963, and standard samples were taken at each of the eight stations through 1 February 1964. Thereafter, regular sampling at Stations II, V, and VIII was discontinued because samples from those areas were not strictly comparable with those from the riffle areas and added little to the overall study of the stream. Regular sampling at the five remaining stations continued through 26 September 1964.

A standardized netting technique of 5-minute duration (Hynes, 1961 and personal communication; see also G. W. Minshall, 1965) was used for these samples. A coarse-mesh net (8 threads/cm) was used on 1 February 1963; for all other samples a fine-mesh net (24 threads/cm) was used. The area covered in the 5-minute sample was nearly the same for Stations I, III, IV, V, and VI. The area covered at Station II was only about one-tenth as large, whereas that at Stations VII and VIII was slightly more than twice as large.

Qualitative samples were taken at frequent intervals to check the adequacy of the standard samples and to give additional insight into changes in the fauna as they took place. After regular sampling was discontinued at Stations II, V, and VIII, qualitative sampling continued, especially at Station II. Subimago and adult *E. pleuralis* were collected with an insect net or picked from bushes and other resting places, or were obtained by rearing mature nymphs in the laboratory. The nymphs were maintained in cool (8-14 C), well-aerated water.

Measurements of body length, exclusive of head and cerci, were made on preserved specimens. Measurements were made to the nearest 0.5 mm on a 1-mm grid under 14X magnification. Sex of mature nymphs was determined on the basis of genitalia. The genital forceps are well developed on mature male nymphs of *E. pleuralis* and usually are visible on immature males 6.0 mm long or larger.

Five nymphs in each month from February through June 1963 were used for gut analyses. The anterior two-thirds of each gut was removed intact, and the contents extruded onto a slide and dispersed in the mounting medium (Turttox CMC-10). The entire slide was scanned (400X magnification), and then representative fields were counted. Three hundred items were counted in all but two cases,

when 280 and 290 items were counted. Individual clumps of detrital material, individual diatom frustules, and individual mineral particles were counted as separate items.

Egg counts were made on each of 10 mature nymphs, between 7.5 and 12.5 mm in body length. The egg packets were extracted from the body cavity by dissection. The individual eggs were then separated from the packets, suspended in 5% formalin, stirred, and allowed to settle in a counting chamber. Seventeen of the 49 1-cm squares of the chamber were chosen at random, and the eggs in those squares were counted under 14X magnification. From those counts an estimate of the total number of eggs was derived. For five of the nymphs, counts of all 49 squares were made to check the accuracy of the estimates. In all cases the estimate was within 10% of the total by actual count.

Eggs used for artificial insemination were obtained by dissection of female imagoes. Sperm were extruded from adult males by crushing the genitalia and were then stirred together with the eggs. Water from Morgan's Creek was used as the culture medium. Fertilized eggs from each of four pairs of adults were kept in separate containers under refrigeration (8-14 C). Measurements were made of 10 of the eggs with an ocular micrometer at 100X magnification.

Weekly temperature measurements were made near the water-streambed interface; the representativeness of the values was checked by comparison with those from maximum-minimum recording thermometers buried in the stream bottom at Stations I, IV, and VII. Velocity of the stream at Station IV was determined weekly by the cork-float method; these measurements were used to estimate discharge by the Embury technique (Welch, 1948). Descriptions of the physical and chemical methods used in the Morgan's Creek study, and the results of the study, will be presented in a subsequent publication by G. W. Minshall.

RESULTS

NYMPHS

Distribution.—*E. pleuralis* nymphs were restricted to the headwaters and upper middle sections of Morgan's Creek (Table 1). The

TABLE 1.—Total number of *E. pleuralis* nymphs of each size group (mm) taken in 5-minute samples at each station from 1 February 1963 through 26 September 1964. No nymphs were taken at Stations V or VIII

Station	1.0- 1.5	2.0- 3.5	4.0- 5.5	6.0- 7.5	8.0- 9.5	≥ 10.0	Total
I	8	35	26	39	15	7	130
II*	190	385	316	130	26	5	1052
III	36	184	187	191	141	51	790
IV	13	80	93	104	69	35	394
VI	3	12	17	21	25	10	88
VII	3	7	1	0	0	0	11
Total	253	703	640	485	276	108	2465

* No samples were taken at Station II after 1 February 1964.

total number taken at Station II for the entire study period was greater than for any other station, even though no standard samples were taken there after 1 February 1964. The nymphs were relatively scarce or absent from the lower stretches, particularly below Station IV. None were taken at Station VIII or in the pool at Station V, though some were present in the riffle area just below the pool. All 11 nymphs taken at Station VII were collected in February 1963. Floodwaters from the Ohio River covered the area around Station VII the first week in March 1963 and remained until mid-April. No nymphs were taken there afterwards. Nymphs were absent from standard samples at Station VI in 1964, though an occasional specimen was taken in qualitative samples there. Observations made since the conclusion of the study showed that large numbers of *Epeorus* nymphs had reinvaded the area by the spring of 1965.

Nymphs were taken in standard samples from December through July (Fig. 2). In general, the numbers increased to a peak in March or April, remained relatively high through part of May, and declined rapidly after the first of June. A spate in early March 1963 (Fig. 1) was accompanied by a marked decrease in numbers of nymphs. A more severe flood occurred in March 1964, but there was no noticeable decrease in numbers of nymphs, largely because just prior to the flood nymphs were not abundant at any station where standard samples were being taken. The current during the 1964 flood (as observed on 14 March) was sufficiently strong to move small boulders and caused considerable disruption of the substrate, especially at Station II. However, despite the torrent pouring over the rocky ledges there, nymphs of all sizes were present and relatively abundant. During the spate no nymphs were taken at Station I, as the substrate was scoured to bedrock. Destruction of the habitat, rather than high discharge *per se*, appears to be primarily responsible for the decline in numbers. The nymphs are able to remain in very swift water so long as there is some shelter available, but they may be killed by the grinding action of the shifting substrate (see also Sprules, 1947).

The nymphs were found primarily on rubble substrate, though a few were taken in leaf packets. The stones on which the nymphs occurred were of various sizes, but nearly all were relatively smooth and flat. Newly hatched nymphs and other small specimens often were taken from stones approximately 10 x 15 cm, and mature nymphs usually occurred on larger rocks. It was possible, however, to find many rocks occupied by both small and large nymphs. The nymphs were found almost exclusively on the undersurfaces of the rocks and seldom occurred on rocks embedded in the stream bottom or on unaltered bedrock. They were further restricted to fast waters in the cascade and riffles and seldom were found in the slow, quiet parts of the stream.

Development.—Data on the life history and development of *E. pleuralis* are given in Fig. 2. Information from qualitative samples

has been used to supplement the data shown in the figure. Newly hatched nymphs obtained from artificially inseminated eggs were approximately 0.4 mm long. No first instar nymphs were taken in collections from the creek; the smallest nymphs taken were about 0.5 mm long and were in approximately the sixth or seventh stadium (see Ide, 1935a). Nymphs smaller than 1.0 mm were included with

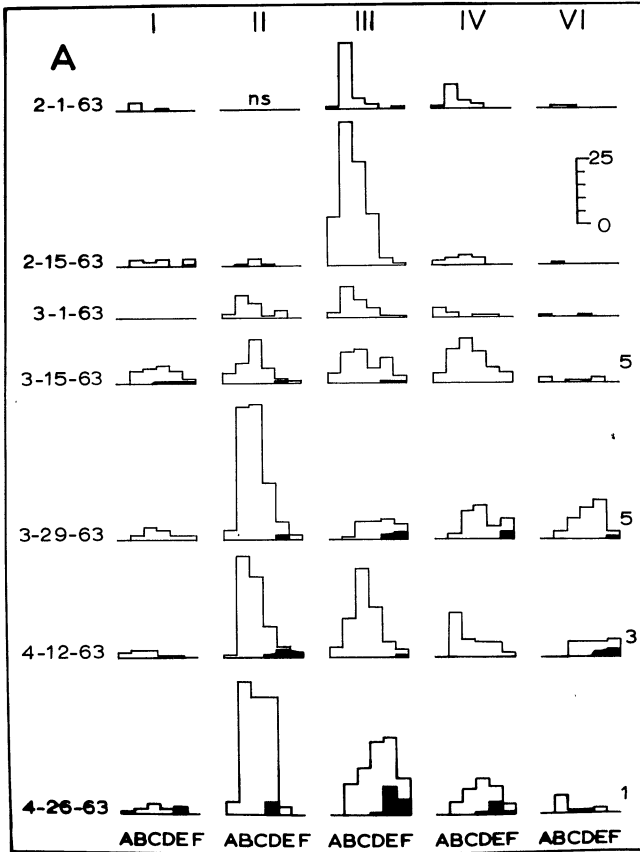


Fig. 2.—Size distribution of *E. pleuralis* nymphs taken in 5-minute samples. No samples were taken at Station II after 1 February 1964, and nymphs were scarce at Station I and absent at Station VI in collections after that date. NS indicates no sample taken. Shaded portions of histograms indicate size and number of mature nymphs taken. Numbers to the right of the histograms refer to numbers of adults and subimagos taken on that date. Adults and subimagos persisted until late May in 1963; though not shown, two were taken on 31 May that year. A = recruits; B = 2.0-3.5 mm; C = 4.0-5.5 mm; D = 6.0-7.5 mm; E = 8.0-9.5 mm; F \geq 10.0 mm. A.—February through April, 1963.

those of the 1.0-mm length group in tabulating the data. Nymphs smaller than 2.0 mm were considered recently hatched and will be referred to as "recruits." Qualitative samples indicated that recruitment begins in late September or early October. The first nymph taken in the autumn of 1963 was a 1.5-mm recruit taken at Station II on 28 September. A 1.0-mm recruit was taken at the same station on 12 October, and four nymphs in the 1.0-2.0-mm size range were taken at Station I on 23 November. Recruits were first taken in standard samples in early December but were not abundant until mid-January. The peak in recruitment apparently occurs in January or February; approximately 50% of the total number of nymphs taken on 18 January and 1 February 1964 were smaller than 2.0 mm. In general, recruits were much more common at Station II than at

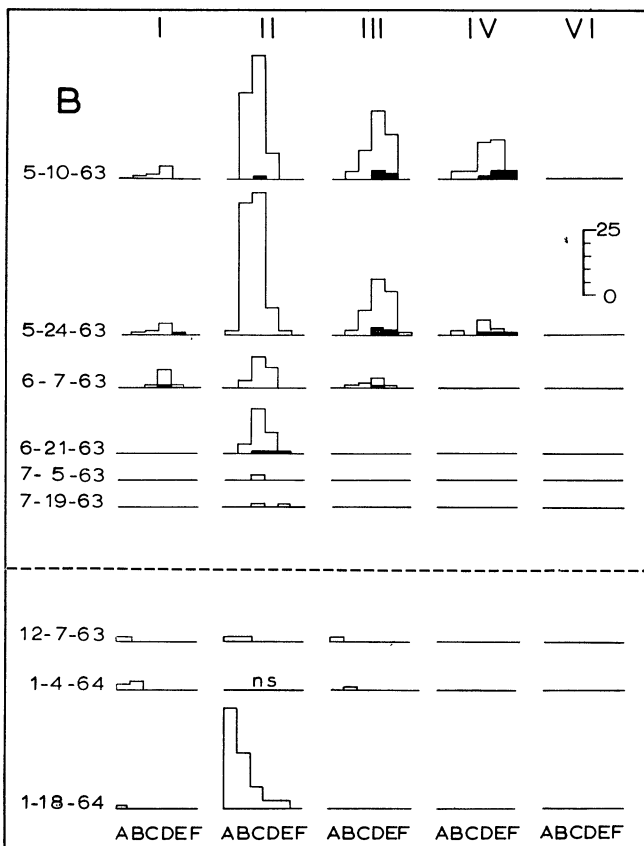


Fig. 2 (cont.). B. — May, 1963, through January, 1964. See legend for Fig. 2A for complete explanation.

any other station (Table 1). Of a total of 245 recruits taken between 1 February 1963 and 1 February 1964, nearly 78% were collected at Station II. Recruits were taken in qualitative samples through the end of May in both 1963 and 1964, but they ceased to be important in the standard samples after the middle of March. The continued presence of small nymphs in the collections indicates an extended hatching period, or delayed growth by the nymphs after hatching, or both. The fact that the emergence period extends over several months suggests that hatching also extends over a long period. On the other hand, some nymphs probably do grow slowly after hatching, while others obviously grow rapidly, as evidenced by the presence of large, mature specimens as early as February. Hunt (1953) found a tremendous range in growth rate of *Hexagenia limbata* (Serville)

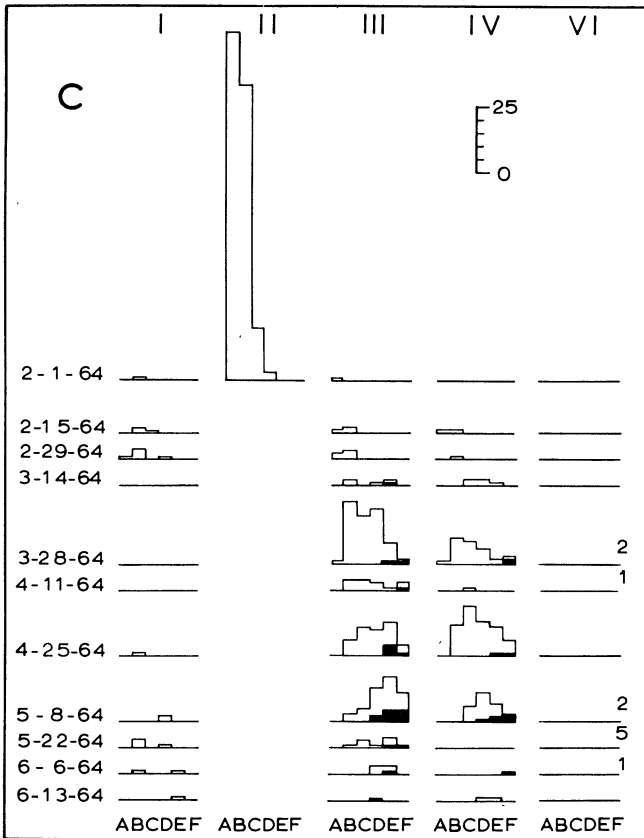


Fig. 2 (cont.). C. — February through June, 1964. See legend for Fig. 2A for complete explanation.

nymphs of the same age, even when they were kept under the same environmental conditions.

Growth rate of the nymphs in Morgan's Creek was not determined, but at least some of the nymphs grow rapidly after hatching. A few large (8.0-9.5 mm) nymphs were taken in mid-January, and mature nymphs were present by mid-February. (In 1963, the first mature nymph was collected on 15 February; in 1964, the first one was taken in a qualitative sample on 22 February.) Growth evidently occurs during the winter, even at Stations III and IV, when temperatures often are quite low (Fig. 1).

Maxwell and Benson (1963) and Benson (personal communication) found that *E. pleuralis* nymphs in West Virginia grew steadily during the winter months; the most spectacular growth occurred during the lowest winter temperatures. The greatest growth rate in one group of the nymphs occurred during a 2-week period in March, when the temperature ranged from 0 to 3.3 C.

The length of mature *E. pleuralis* nymphs in Morgan's Creek varies considerably (range 5.0-13.0 mm; see Fig. 2). At each station full-grown nymphs tended to attain the greatest mean length in February or March; those taken later were progressively smaller through May or June. Nymphs 10.0 mm or larger, including both mature and immature specimens, were scarce in May and absent in June, 1963; only two nymphs of that size were taken in the standard samples after May, 1964. During any one month mature nymphs were, on the average, smallest at Station II and increasingly larger downstream. Those at Station I were only slightly smaller than mature nymphs at Station III. These trends were the same for mature nymphs of both sexes.

There was a noticeable difference in the maximum size attained by male and female nymphs. Of 170 mature nymphs examined, 85 were males and 85 females. The mean lengths were 7.8 and 9.7 mm, respectively. The largest male nymph was 9.5 mm long, whereas the largest female measured 13.0 mm.

Food.—The results of the gut analyses (Table 2) indicate that, in general, *E. pleuralis* nymphs eat whatever plant material is available. Mineral particles and detritus were present in all the guts, and

TABLE 2.—Relative abundance of the major components in the gut samples of *E. pleuralis* nymphs taken from Morgan's Creek, February through June, 1963. Five nymphs from each month were analyzed

Month	Total items counted	Mineral particles	Detritus*	Diatoms
February	1500	580	844	76
March	1500	812	634	54
April	1500	750	535	215
May	1490	936	407	147
June	1480	1029	441	10

* Chiefly from allochthonous leaf material.

diatoms in all but one. Filamentous algae were rarely taken, and no recognizable animal remains were found in the guts. Mineral particles were the dominant component in 18 of the 25 gut samples. The nymphs may ingest the particles for the attached microorganisms, or the mineral particles may represent extraneous material ingested along with the actual food.

Detritus was the main food of *E. pleuralis*. The importance of detritus in the trophic economy of Morgan's Creek has been treated in detail elsewhere (G. W. Minshall, 1967). Detritus in Morgan's Creek is derived almost entirely from allochthonous leaf material. Unfortunately, no gut samples were made for *Epeorus* nymphs collected during the autumn and early winter, when accumulation of allochthonous leaf material was at a peak. Detritus was the dominant component in the guts of all five nymphs collected in February. Increased discharge in the stream in early March washed out much of the accumulated leaf material. Possibly this decrease in amount of detritus resulted in the subsequent decrease in importance of this item in the gut samples.

Diatoms were most abundant in the gut samples of nymphs collected during April, at which time thick diatom mats covered the rocks in the stream. Samples of aufwuchs taken from February through May 1963 showed that the algal cell count was greatest in April (G. W. Minshall, personal communication). Chapman and Demory (1963) found that *Epeorus* sp. nymphs from Oregon fed principally on diatoms and other algae in the spring and early summer and on detritus the rest of the year. Brown (1961) also found seasonal differences in food habits of mayfly nymphs, associated with differences in abundance of the available foods.

Samples of gut contents of *Epeorus* nymphs of various sizes (2.5-11.0 mm) were taken to determine whether any difference in food habits existed between small and large nymphs (see Brown, 1961). No relationship was found between size of the nymph and the dominant food item in the gut. A table containing the complete results of the gut analyses of the individual nymphs is available in an unpublished thesis (J. N. Minshall, 1964).

WINGED STAGES

Emergence of the subimago from the nymphal skin occurs underwater in *E. pleuralis*. Ecdysed nymphal skins of specimens reared in the laboratory often were found attached to some object about 2 to 5 cm below the water surface. On several occasions nymphs in the process of emergence were found on the lower surfaces of rocks in the creek (see also Ide, 1930:228).

The exact beginning and end of the emergence period of *E. pleuralis* in Morgan's Creek are unknown. In 1963, adults and subimagoes were collected from mid-March through late May, and mature nymphs were taken from mid-February through late June (Fig. 2). In 1964, a mature nymph reared in the laboratory emerged on 24 February.

The last adult taken that year was collected on 6 June. The emergence period (based on the presence of mature nymphs) was slightly shorter at the downstream stations than at the source. Mature nymphs were collected in February at Stations I (in 1963) and II (1964) but were not taken at Stations III or IV before mid-March. Mature nymphs disappeared 1-3 weeks earlier at Stations III and IV than at Station II.

All observations on the duration of the subimago stage of *E. pleuralis* were made on specimens maintained in the laboratory at a temperature (8-14 C) somewhat lower than the prevailing air temperatures at the creek (see G. W. Minshall, 1965). The length of the subimago stage under laboratory conditions was 2 to 2½ days. Lyman (1944) showed that in *Stenonema femoratum* (Say) (Heptageniidae) the duration of the subimago stage increases with decrease in temperature. Hence, under natural conditions the subimago stage for *E. pleuralis* may be somewhat less than 2-2½ days.

Of 66 mature nymphs reared in the laboratory, 25 died in the subimago stage; another 17 did not completely shed their subimago skins. This incomplete ecdysis would make successful mating practically impossible, as the skins remained attached to the wings or tails. Thus, only 24 (or about 36%) transformed into adults capable of reproducing. During artificial rearing, the danger of excessive moisture or dryness may be greater than under natural conditions; but in the field, predation and other hazards probably offset this, so that the percentage of mayflies that successfully transform to adults may be even less than the 36% found under laboratory conditions.

Twenty-eight of the 33 adults and subimagos collected at the creek were taken in the vicinity of Stations I and II. Although mature nymphs were abundant at Station III and common at Station IV, the winged forms rarely were taken there. Perhaps the subimagos or adults fly upstream soon after emerging (see Müller, 1954; Roos, 1957). Other explanations for their scarcity at Stations III and IV are possible, however. Stations III and IV usually were sampled sometime between 11:00 AM and 1:00 PM, whereas Stations I and II were visited during the late afternoon. Subimagos and adults of *E. pleuralis* seem to be more active during the later parts of the day; during the morning and early afternoon they probably take shelter in the vegetation around the creek.

There was some seasonal variation in average size of adults and subimagos. The largest specimens occurred in the early part of the emergence season. The mean lengths of those taken between late February and mid-April were 8.4 and 9.3 mm for the males and females, respectively. The peak in emergence apparently occurred in late April or early May. During that time the mayflies typically were smaller. (Mean lengths were 7.8 and 8.8 mm for males and females, respectively.) These results generally agree with those of Ide (1935b) for *E. pleuralis* in Ontario, except that there was no increase in average size at the end of the emergence period as noted by him.

No observations were made of the mating activity of *E. pleuralis* at Morgan's Creek, but one observation was made at Falling Springs in Froman Hol, about a mile west of Morgan's Creek. Falling Springs, a small, spring-fed stream, is similar to Morgan's Creek in size, stream flow, and other general characteristics. The mating was observed about 5:00 PM on 15 May 1964, in an open, sunny area. No actual "swarm" was observed, and only about three pairs were seen. The mayflies were approximately 6 m above the ground, flying about in a zigzag fashion and then pairing by colliding in mid-air. It was impossible to discern much about the actual mating procedure. In the family Heptageniidae the nuptial flight commonly occurs at twilight (Needham *et al.*, 1935).

Oviposition by *E. pleuralis* was observed at Morgan's Creek on 29 March and 5 April 1963. In both cases the female flew low over the stream toward the rocky ledges at Station II and struck the water at intervals, presumably washing eggs off the tip of her abdomen each time. This is the common method of oviposition in Heptageniidae (Leonard and Leonard, 1962).

EGGS

Comparison of the dates of earliest emergence (late February or early March) and earliest hatching (late September or early October) of *E. pleuralis* in Morgan's Creek suggests an egg stage of about 7 months. The interval between the peak emergence and the 'peak in hatching would allow for a 9- or 10-month egg stage. Eggs artificially inseminated on 9 May 1964 and kept at 8-14 C began hatching on or shortly before 23 June 1964, indicating that under certain conditions the egg stage may last only about 6 weeks.

Mature eggs of *E. pleuralis* are ellipsoid and measure 85-90 by 135-155 μ . The surface of the egg is plain, without appendages or sculpturing. The eggs are cream-colored and, when fertilized, adhere to solid objects (such as the bottoms of the containers used in the artificial insemination experiment).

Egg counts of mature nymphs indicate that the number of eggs per female ranges from slightly less than 2000 to a little more than 6000. The average for the 10 estimated counts was 4260; for the five total counts it was 4300. However, the number of eggs carried by an average-sized mature nymph may be closer to 3000-3500. The mean size of the nymphs used for the egg counts was 10.0 mm, which is slightly larger than the average size for mature female *E. pleuralis* nymphs. A 9.5-mm nymph examined contained 3037 eggs. In a few of the mature nymphs some of the eggs were of subnormal size, indicating that further development of the eggs occurs before adulthood is reached. Thus, the number of eggs present in the mature nymph may be somewhat less than the number deposited by the adult. The number of eggs produced generally increased with increasing size of the nymphs within the 7.5-10.5-mm range. After reaching a peak with the 10.5-mm nymph, the number of eggs decreased with increasing

size of the individual. Too few counts were made to determine whether or not this apparent decline is real.

COMPARISON OF 1963 AND 1964 COLLECTIONS

Comparison of the data in Fig. 2 shows clearly the variation in abundance and distribution of the nymphs during the two years. Nymphs were much more numerous in collections the first year. During the period of February through June the numbers taken in standard samples were: Station I - 103, 20; III - 575, 213; IV - 262, 132; and VI - 88, 0 in 1963 and 1964, respectively. Qualitative samples taken at Station II in 1964 showed that the nymphs were abundant there, probably even more so than in 1963. Thus, while the longitudinal distribution of the nymphs was more restricted in 1964, the overall abundance possibly was greater.

Qualitative samples were especially useful in comparing life-history data for the two years. In general, the life history varied little from year to year. In both years hatching began in autumn, and recruits were present through the end of May, though not abundant after March. The peak in hatching may have occurred earlier the first year. No large group of recruits was taken during the winter of 1962-63, as was taken on 18 January or 1 February 1964. Four nymphs taken (with a coarse-mesh net) 23 November 1962 ranged in length from 2.0-4.5 mm. In 1963-64, no nymphs larger than 2.5 mm were taken until January.

The emergence period, based on the presence of mature nymphs, extended from February through June, with a peak in late April or early May. The disappearance of the nymphs from the stream in early summer was somewhat different in the two years. In 1963, it was more gradual, occurring first at Station VI, then at Station IV, at I and III, and finally at Station II. That year nymphs were not taken at Station IV after late May. In 1964, however, nymphs were taken there through mid-June, *i.e.*, as late as at Station III. At Station II, five nymphs were taken in summer collections after June in 1963: four in standard samples in July and one in a qualitative sample in early August. The following year no nymphs were taken in any sample after June. The last nymphs were taken at Station II in late June, only a week after the last specimens were taken at Stations I, III and IV.

The large numbers taken at Station III in February 1963 (Fig. 2) are unusual, especially since very few nymphs were collected at Station II then. Possibly a spate in December 1962 or January 1963 washed many nymphs downstream from Station II to Station III. Or Station III may have offered a better location for ovipositing and hatching in 1962 than in 1963. The unusually small samples taken at Stations III and IV on 11 April 1964 resulted from the presence of thick mats of diatoms on the stones in the stream. The diatoms clogged the net during sampling, so that few benthic invertebrates of any kind were retained in the net.

DISCUSSION

FACTORS AFFECTING DISTRIBUTION AND ABUNDANCE

Longitudinal.—Station II, and the area immediately surrounding it, evidently offers the most suitable conditions for *E. pleuralis* nymphs in Morgan's Creek, since they were taken in greatest numbers there. In attempting to define the environmental factors affecting the distribution and abundance of the nymphs, it seems appropriate to describe in greater detail the habitat at Station II and to indicate how conditions varied at the other stations.

As a cascade, Station II represents a unique habitat in the stream. The substrate consists of piles of large, loose rubble and boulders, overlying rocky ledges. The water cascades over the rocks and trickles between them, thus providing many well-protected areas where there is a constant flow of water. Temperatures at Station II are cool and rather constant all year. Dissolved oxygen concentrations generally are at saturation and, because of the near-constant temperatures, fluctuate little. The stream near the source lies in a narrow, wooded ravine and consequently is well protected from the influence of the terrestrial weather throughout the year. The terrestrial environment at Station II may be characterized as cool, humid, and windless.

Differences in substrate at the various stations have been discussed earlier. The rubble at Stations III, IV, and VI differs from that at Station II in that it is smaller and mixed with varying quantities of sand and gravel. The bottom becomes increasingly compacted downstream from Station III. Nymphs of *E. pleuralis* were taken almost exclusively from the undersurfaces of stones. Thus, the loose rubble at Station II seems to provide a better habitat than the more compacted rubble downstream. Percival and Whitehead (1929) found nymphs of *Rhithrogena* abundant on loose stones but absent from fixed stones, under which they could not seek shelter.

The bedrock substrate at Station I is much less suitable for *E. pleuralis* than the rubble area at Station II. *Iron* and *Ironopsis* (Heptageniidae) in Wyoming show a similar habitat preference (Armitage, 1961). The slight depressions and crevices in the bedrock offer little shelter for any but the smallest nymphs. Most of the nymphs at Station I probably were restricted to scattered bits of rubble. Only 10 nymphs were taken there in 1964 after the March floods scoured the area to bedrock, as opposed to 88 during the same period (mid-March through June) in 1963.

The mud and silt substrate at Stations VII and VIII undoubtedly was partially responsible for the absence of nymphs at those stations. Certain other members of the Heptageniidae are known to be unable to survive in areas where the substrate consists of mud or silt (Lyman, 1943).

Very slow current velocities seem to be unfavorable for *E. pleuralis* nymphs. None was taken in the pool at Station V, and qualitative collections showed that they seldom occurred in local slow-water stretches elsewhere in the stream. The nymphs may be unable

to obtain enough oxygen in these slow-water habitats (see Wingfield, 1939). During rearing experiments four nymphs kept in a refrigerated but unaerated container died within 5 days. (Two died within 2 days; the smallest nymph survived longest.) Some of the nymphs kept in water aerated by a bubbler apparatus survived as long as 3 weeks. The agitation of the water by the bubbler, simulating current, may have been more important than the aeration *per se* (see Ambühl, 1959).

Downstream from Station II the creek is less influenced by the spring source and more affected by the terrestrial environment. Temperatures fluctuate more widely; this becomes increasingly so downstream to Station VI (Fig. 1). Maximum temperatures reached at Stations VII and VIII are slightly less than at Station VI.

E. pleuralis is a cool-water species. Geographically it is found mainly in the areas of eastern Canada and northern United States. Where it occurs in more southerly regions, it is restricted to relatively cool environments, such as mountain streams and spring-fed brooks (Banks, 1910; McDunnough, 1925; Ide, 1930, 1935b; Spieth, 1938; Pugh, 1956; Maxwell and Benson, 1963).

In winter and early spring, the principal growing period for *E. pleuralis*, Morgan's Creek generally is cool throughout, and the temperatures are low enough at all stations for the nymphs to survive. Later, however, the downstream stations warm rapidly. In late spring 1963 the nymphs disappeared first at Station VI, then IV, III, and finally Station II, *i.e.*, in the order in which the stations warmed up. (The nymphs disappeared earlier at Station I than at Station II, despite the very similar temperature regimes in the two areas. However, since the substrate generally was unsuitable at the source and the nymphs were never abundant there, Station I does not fit into the same pattern as the other stations discussed.) The early disappearance of the nymphs from the lower stations does not necessarily mean that they have been killed; it might result from emergence or emigration. The disappearance of the nymphs from Station VI in 1963 was not entirely due to emergence, since on the last date they were taken there, only one of the 11 nymphs collected was mature, and eight were less than 6.0 mm long (Fig. 2). Likewise three-fourths of the nymphs taken at Station IV in the last collection in 1963 were immature. There was no detectable increase in the upstream populations, thus showing no recruitment by immigration from the downstream stations.

As discussed earlier, disappearance of the nymphs from the lower stations was less gradual in 1964, possibly because late May and early June were cooler that year than in 1963 (Fig. 1). By mid-June, however, the temperatures at Stations III and IV were above 17 C, and no nymphs were taken at either station thereafter.

The longitudinal distribution of the nymphs in the stream seems to be determined primarily by the interplay of temperature, substrate, and current. These factors are most suitable at Station II. Recruits

and other small nymphs were most abundant at that station (Table 1), suggesting that most hatching occurs there. However, mature nymphs and other large specimens were taken most frequently downstream (Fig. 2). It may be that as more and more nymphs hatch at Station II and the population becomes more dense, increased competition for food and space leads to dispersal of the nymphs to other areas of the stream. In areas where the nymphal populations are smaller than at Station II, the nymphs tend to attain a greater length at maturity. The nymphs may disperse from Station II to the downstream stations early in the nymphal stage, or later, when they are mature or nearly so. In the latter case the larger size of the nymphs downstream may be explained by assuming that the largest nymphs tend to disperse farthest. Downstream "drift" was not examined in the present study; however, it is obvious that: (1) not all mature nymphs drift downstream, since qualitative samples showed they were especially numerous just below Station II; and (2) mature nymphs are not the only ones that drift, since small, immature nymphs were also commonly taken downstream.

If dispersal occurs early in the nymphal stage, the larger size of the nymphs in areas other than Station II must reflect some environmental factor that enhances growth. Decreased competition in these areas with smaller populations seems the best explanation. Temperature can be ruled out, because mature nymphs were, on the average, always larger downstream than at Station II, whether the lower stations were cooler or warmer than the source. Similarly, mature nymphs at Station I were larger than at Station II, although temperatures varied little between the two stations.

Emergence of subimagoes presumably occurs frequently in the downstream areas (especially Station III), because mature nymphs were abundant there. However, since recruits were relatively scarce downstream, it appears that successful oviposition occurs less often there than at Station II. Lack of riparian vegetation between Stations IV and VI reduces the amount of shelter there, so that subimagoes and adults that remain in that area are likely to perish from overheating or desiccation. Another danger at the lower stations is of predation by fish during oviposition; no fishes are present above Station III. Some subimagoes and adults that emerge at the downstream stations probably fly upstream to cooler, more shaded areas (see Müller, 1954; Roos, 1957). The winged stages of *E. pleuralis* were always most abundant near the headwaters.

Seasonal.—The factors that control the seasonal abundance of the nymphs are primarily those associated with life-history phenomena. In general, no nymphs are present during the summer, when the insects are in the egg stage. Young nymphs first appear in September, and recruitment builds up to a peak in January or February. The peak in the total nymphal population occurs later, owing to the accumulative recruitment. Emergence begins in March, resulting in losses

to the nymphal population. Hatching essentially is over by late April and May, and losses from mortality and emergence become pronounced then. By June nearly all nymphs are gone.

To some extent these life-history phenomena are governed by temperature. The timing of the emergence period, for example, seems to depend at least partially on temperature. In Morgan's Creek emergence occurs from late February or early March through late May or early June. In the headwaters of an Ontario stream, where temperatures are colder than at Stations I and II, the emergence period is later, from mid-April to mid-August (Ide, 1935b). As mentioned earlier, the emergence period tends to be shortened at Stations III, IV, and VI, beginning later and ending 1-3 weeks sooner than at the headwaters. Temperature may also influence the beginning of the hatching period. Hatching began at Station II in September, but no tiny nymphs were taken at Stations III or IV until early December. In September, temperatures at the downstream stations are still relatively high, perhaps high enough to prevent hatching. High temperatures apparently do delay hatching, since no tiny nymphs were collected during the summer months.

These results agree with the findings of Ide (1935b). In his stream, emergence started earlier and ended later near the source than at the lower stations. He postulated that the emergence period ended earlier downstream because the temperatures there soon became lethal for any nymphs that had not yet emerged. Only the egg stage could resist the high summer temperatures; nymphs from eggs hatching too early would be killed by the high temperatures in late summer or early fall. Thus, hatching usually started later at the lower stations than at the source, so that emergence also started later.

It is easy to postulate that temperature influences the start of hatching or the beginning and end of emergence in areas like Stations III, IV, and VI, where temperatures are quite variable; but it is difficult to imagine that these phenomena are controlled by temperature in areas near the source. The appearance of the nymphs at Station II in September or October, or their disappearance in early July, cannot be explained on the basis of temperature, because the temperature there is nearly constant all year. Clearly some other factor that varies seasonally, *e.g.*, photoperiod, must also be involved.

REFERENCES

- AMBÜHL, H. 1959. Die Bedeutung der Strömung als ökologischer Faktor. *Schweiz. Z. Hydrol.*, **21**:133-264.
- ARMITAGE, K. B. 1961. Distribution of riffle insects of the Firehole River, Wyoming. *Hydrobiologia*, **17**:152-174.
- BANKS, N. 1910. Notes on our eastern species of the May-fly genus *Heptagenia*. *Canadian Entomol.*, **24**:197-202.
- BRITT, N. W. 1962. Biology of two species of Lake Erie mayflies, *Ephoron album* (Say) and *Ephemera simulans* Walker. *Bull. Ohio Biol. Surv.*, **1**:1-70.

- BROWN, D. S. 1961. The food of the larvae of *Chloëon dipterum* L. and *Baëtis rhodani* (Pictet) (Insecta, Ephemeroptera). *J. Anim. Ecol.*, **30**: 55-75.
- CHAPMAN, D. W. AND R. L. DEMORY. 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. *Ecology*, **44**:140-146.
- FREMLING, C. R. 1960. Biology of a large mayfly, *Hexagenia bilineata* (Say), of the Upper Mississippi River. *Res. Bull. Iowa Agric. Exp. Sta.*, **482**: 842-852.
- HUNT, B. P. 1953. The life history and economic importance of a burrowing mayfly, *Hexagenia limbata*, in southern Michigan lakes. *Bull. Inst. Fish. Res.*, **4**:1-151.
- HYNES, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.*, **57**:344-388.
- IDE, F. P. 1930. Contribution to the biology of Ontario mayflies with descriptions of new species. *Canadian Entomol.*, **62**:204-213, 218-231.
- . 1935a. Post-embryological development of Ephemeroptera (mayflies), external characters only. *Canadian J. Res.*, **12**:433-478.
- . 1935b. The effect of temperature on the distribution of the mayfly fauna of a stream. *Univ. Toronto Stud., Biol. Ser.*, **39**:3-76.
- LEONARD, J. W. AND F. A. LEONARD. 1962. Mayflies of Michigan trout streams. *Cranbrook Inst. Sci. Bull.*, **43**:1-139.
- LYMAN, F. E. 1943. A pre-impoundment bottom-fauna study of Watts Bar Reservoir area (Tennessee). *Trans. Amer. Fish. Soc.*, **72**:52-62.
- . 1944. Effect of temperature on the emergence of mayfly imagoes from the subimago stage. *Entomol. News*, **55**:113-115.
- MAXWELL, G. R. AND A. BENSON. 1963. Wing pad and tergite growth of mayfly nymphs in winter. *Amer. Midl. Natur.*, **69**:224-230.
- MCDUNNOUGH, J. 1925. The Ephemeroptera of Covey Hill, Que. *Trans. Roy. Soc. Canada*, **19**:207-224.
- MINSHALL, G. W. 1965. Community dynamics and economics of a woodland springbrook: Morgan's Creek, Meade County, Kentucky. Unpubl. Doctoral Dissertation. Univ. Louisville, Louisville. 261 p.
- . 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology*, **48**:139-149.
- MINSHALL, J. N. 1964. An ecological life history of *Epeorus pleuralis* (Banks) in Morgan's Creek, Meade County, Kentucky. Unpubl. Master's Thesis. Univ. Louisville, Louisville. 79 p.
- MÜLLER, K. 1954. Investigations on the organic drift in north Swedish streams. *Rept. Inst. Freshw. Res. Drottningholm*, **35**:133-148.
- NEEDHAM, J. G., J. R. TRAVER AND Y. HSU. 1935. The biology of mayflies. Comstock Publishing Co., Ithaca. 759 p.
- PERCIVAL, E. AND H. WHITEHEAD. 1929. A quantitative study of the fauna of some types of stream-bed. *J. Ecol.*, **17**:282-314.
- PUGH, J. E. 1956. Observations on the mayfly fauna of a stream in central Virginia. *Virginia J. Sci.*, **7**:22-28.
- ROOS, T. 1957. Studies on upstream migration in adult stream-dwelling insects. *Rept. Inst. Freshw. Res. Drottningholm*, **38**:167-193.

- SPIETH, H. T. 1938. Taxonomic studies on Ephemera, I: Description of new North American species. *Amer. Mus. Novitates*, No. 1002. 11 p.
- SPRULES, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. *Univ. Toronto Stud., Biol. Ser.*, **56**:1-81.
- WELCH, P. S. 1948. Limnological methods. McGraw-Hill Book Co., New York. 381 p.
- WINGFIELD, C. A. 1939. The function of the gills of mayfly nymphs from different habitats. *J. Exp. Biol.*, **16**:363-373.

SUBMITTED 18 JULY 1966

ACCEPTED 26 SEPTEMBER 1966