The life histories of some Plecoptera and Ephemeroptera in a southern Ontario stream

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Received May 15, 1970

COLEMAN, M. J., and H. B. N. HYNES. 1970. The life histories of some Plecoptera and Ephemeroptera in a southern Ontario stream. Can. J. Zool. **48**: 1333–1339.

The life cycles of 4 species of stonefly and 11 of mayfly are described, based upon the flight season of the adults and measurements of nymphs collected at all seasons from the Speed River. It is shown that they fit into all but one of the categories of life cycle that have been described for stream insects in Europe, and that where more than one species of the same genus coexist there is usually a marked difference in the timing of their life histories.

Introduction

During a study of the benthic fauna of a reach of the Speed River, Wellington County, Ontario, sufficient specimens of the young stages of several species of Ephemeroptera and Plecoptera were obtained throughout the year to demonstrate the main features of their life histories. Although there have been some recent studies on this continent (e.g. Hartland-Rowe 1964; G. W. Minshall 1967, 1968; J. N. Minshall 1967; Clifford 1969, 1970) such information is in short supply for North American species. This is in considerable contrast to the situation in Europe (e.g. Pleskot 1958, 1961; Hynes 1961; Landa 1968), and the information is needed for a fuller understanding of stream ecology.

Most of the species were identified as nymphs, using the publications of Ricker (in Edmondson 1963), Burks (1953), and Allen and Edmunds (1963*a*, *b*, *c*), and the identifications were confirmed by breeding out or collecting adults. One species of *Baetis* could not be certainly identified, and we failed to obtain a male adult of one species of *Stenonema*. Only those species are included here for which we obtained sufficient data to be fairly certain of the pattern of the life cycle.

The Stream

The reach studied is a stony run about 6 m wide and 20 cm deep at modal flow, about 3 km from the stream source at 80°13′18″ W, 43°45′40″ N, and flowing through rough agricultural land. The substratum consists of stones, coarse gravel, and sand, and the area is a marginal habitat for brook trout (*Salvelinus fontinalis* (Mitchill)).

During the study the stream was frozen over from mid-December to mid-April, with the water at or near 0 °C. After the thaw the temperature, recorded by a maximum–minimum thermometer enclosed in a tile drain on the stream bed, rose steeply to a maximum of 29.5 °C (minimum 17.5°) in July, having reached a maximum of 17 °C in early May. After July it fell as steeply to a maximum of only 4 °C in November, at the end of which month anchor ice was formed. The pH ranged from 7.5 to 8.7 and the oxygen content was always near saturation. Further details of the locality are given by Bishop and Hynes (1969).

Methods

The benthic samples were of two kinds. One type was collected every month from December 1965 to December 1966, with the pot sampler described by Coleman and Hynes (1970). This essentially encloses a cylinder of substratum 25.5 cm in diameter and 30.5 cm deep which had been open to colonization for at least 2 months, and usually much longer, before lifting. It was possible to obtain such samples even when there was a thick cover of ice, and samplers were lifted every month from December 1965 through December 1966. The other samples were kick samples (Hynes 1961) obtained every 2 weeks when the water was open. In both, the mesh size used was fine enough to retain the smallest specimens, although this fact probably resulted in some underrepresentation of larger specimens in the kick samples. Macan (1958) has shown that actively swimming large mayfly nymphs tend to evade a fine-meshed net.

Samples were preserved in formalin in the field, or merely allowed to freeze during the winter. The insects were washed out of the gravel, and then floated from the debris with saturated calcium chloride solution (Hynes 1961). All specimens longer than 5 mm were picked out from the flotsam, the rest of which was divided into four equal portions by the method of Hynes (1961). The lengths of all specimens in one portion, and all the larger individuals, were measured to the nearest millimeter. From the results the mean size of each species at each sampling date was calculated, due allowance being made for the fact that only one-quarter of the smaller specimens had been measured.

In the figures the vertical line shows the size range at each sampling time, and the mean sizes are joined by growth lines. The number beside "total" is the number of specimens actually measured, and the horizontal line above the graph, where present, denotes the period when the adults were to be found near the stream.

The Species

Plecoptera

Allocapnia pygmaea (Burmeister) was common, and was the only species of the genus present. Figure 1 shows the size distribution of the nymphs during the year, and demonstrates a simple univoltine cycle. Mature nymphs occurred from mid-February and a few specimens emerged in March through small holes in the ice. The ice began to break up on 15 April, 1966, and thousands of adults emerged on that day, by crawling up onto the ice blocks.

Mating occurred very soon, and it was apparent that males could detect females within a radius of about 15 cm. Apart from deflections caused by sexual attraction, the adults walked steadily away from the water on the snow and maintained a course that was almost at right angles to the stream. Some were followed for at least 75 m. This march away from the stream resembles that reported for *Capnia atra* in northern Sweden by Thomas (1966), but we were not able to confirm his observation that after some distance the adults turn in an upstream direction.

In 1967 the emergence was less concentrated in time and we again checked the mass movement, on March 7 on a clear sunny afternoon, by marking the passage of several individuals across the level surface of the snow and measuring the general direction of each with a compass. The stream at the point of measurement flows towards about 35° west of south (compass bearing 221°) and the bearing of the sun changed from 231° to 260° during our observations. Twenty specimens on the left bank were walking on bearings ranging from 290° to 335° (mean 314.5 $\pm$ 2.87) and 15 on the right bank from 115° to 165° (mean 142.7 $\pm$ 4.66), i.e. at about 90° away from the stream course. Only one specimen was not moving in this general direction, and it was walking on the ice over the stream, but three specimens were found near to the stream which were heading in the wrong direction, as if they were on the opposite bank (bearings 310°, 130°, and 135°). We could not observe any change in direction as the sun moved westwards, but it is likely that we had insufficient measurements to detect this. It seems highly probable that the march was related to the sun on the otherwise featureless expanse of snow.

Adults brought into the laboratory and kept at 10 °C fed readily on algae and lichen on bark, and eggs were laid from 4 to 5 weeks after emergence. This is similar to the findings of Brinck (1949) and Khoo (1968) for European species of *Capnia*. Each female produced one batch of eggs and died within a few days of laying. The eggs began to hatch after 21 days at 10 °C, and continued to do so for 3 days. We did not find any evidence of the ovoviviparity that has been reported for this species in Indiana by Clifford (1966).

In the stream newly hatched nymphs 0.5 mm long first appeared in the collections of early June, and by the end of that month nymphs were taken which were in a condition similar to that described by Khoo (1968) as the diapausing stage of the fourth or fifth instar of *Capnia bifrons* of Europe. The nymphs had become white and opaque with fatty globules, the terminal segments of the cerci were elongate and without the terminal whorl of bristles, and many were in the characteristic flexed position with antennae and cerci crossed as illustrated by Khoo. This is therefore the second record of a true nymphal diapause in the Capniidae, indeed in the Plecoptera, and we have since confirmed that it also occurs in *Allocapnia vivipara* Claassen, diapausing nymphs of which we have dug from the dry but damp substratum of a small temporary stream near Sunfish Lake, Waterloo County, Ontario. We have shown elsewhere (Coleman and Hynes 1970) that most of the diapausing nymphs of *A. pygmaea* were deep in the gravel, more than 7 cm down.

In the Speed River some nymphs were still active in August, but most had entered diapause, and all were in the 1- and 2-mm size groups. In November they all again became active; more specimens were taken, and they grew rapidly through the winter despite the zero temperature of the water. As we found some active specimens right through the summer it is not clear from our results whether all specimens go into diapause or whether some enter it late and others emerge early. Neither is it clear what is the controlling factor. Khoo (1968) has, however, suggested that both temperature and daylength are involved in its inception in *C. bifrons*, and that shortening days may end it. It is difficult though to understand how the last can affect nymphs buried deep in the gravel.

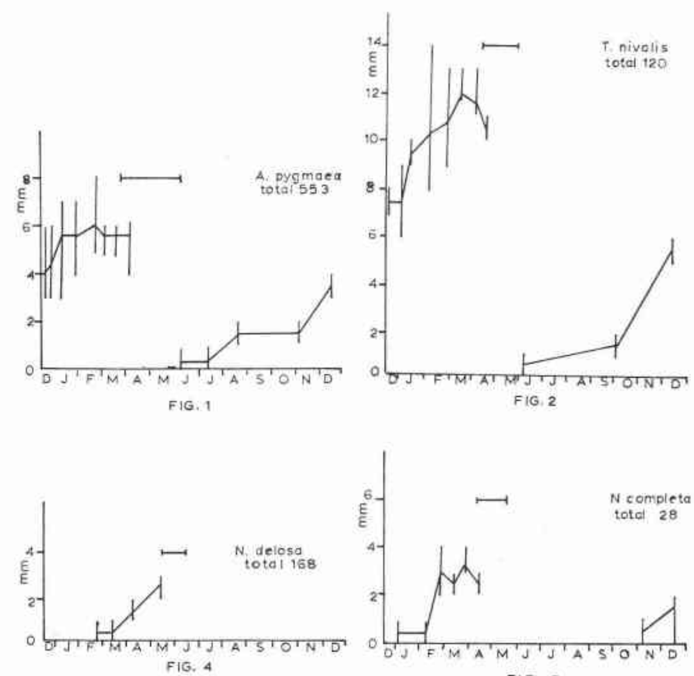
Taeniopteryx nivalis (Fitch) was also fairly common and the sizes of the nymphs collected are shown in Fig. 2. There the capture of one laggard specimen in April has caused the mean-size curve to dip at the end; this is, of course, spurious.

Here also the figure demonstrates a simple univoltine cycle with little growth during the warm months and steady growth through the winter.

Most of the adults emerged at about the same time as *A. pygmaea*, with, similarly, a few early specimens, but they did not march away from the stream. They mated soon after emergence and presumably laid eggs fairly soon. We obtained, however, no evidence on this point, but young nymphs were first found about a month after the main emergence. There was no direct evidence of diapause in this species, but the nymphs were unaccountably absent during the summer. It seems probable that during this season they were living away from the center of the stream where the samples were collected.

Nemoura completa (Walker) probably began to emerge early in April as adults occurred from the second week of that month until mid-May. It was scarce in our samples as it is mostly confined to the edge of the stream, but our data indicate rapid growth during the coldest part of the year (Fig. 3). We did not find small specimens before early November, which may indicate a long egg diapause or merely the scarcity of the species in our samples. Undoubtedly though, little growth occurs before the temperature has fallen to very low levels.

Nemoura (*Amphinemura*) *delosa* (Ricker) was a more abundant species but was found in the stream for a much briefer period. Adults occurred from mid-May to mid-June but no newly hatched nymphs were taken until late February. Most of the growth of this small species



FIGS. 1–4. The life cycles of four stonefly species. The vertical lines at each sampling time show the size range in millimeters of the specimens; the mean sizes are joined by oblique lines, and the horizontal line at the top denotes the period when adults were present. The total number is the number of specimens measured.

occurred during April and early May as the water warmed up (Fig. 4). G. W. Minshall (1967) gives data indicating a similar cycle in Morgan's Creek, Kentucky, and as neither he nor we found specimens before February it seems probable that this species has a long incubation period. It is interesting also that these two *Nemoura* species, although occurring together, grow at different times, as has been reported for several pairs of species in Europe.

Ephemeroptera

Leptophlebia cupida (Say) was abundant in the stream, and adults were on the wing from early May until early July. Young nymphs were first found in mid-July, and apparently newly hatched specimens occurred until mid-September. Growth was slow at first, but became rapid from mid-September to January. The nymphs reached maximum size by mid-February and most emerged in May (Fig. 5).

The early-emerging specimens were larger than the later emerging ones, a phenomenon which has also been noted in European species, and the eggs apparently take $3\frac{1}{2}$ to 4 months to develop. This is a shorter period than the 6 months required by the European *L. marginata* (Pleskot 1953).

It will be noted in Fig. 3 that the samples contained no nymphal specimens in May, the month of maximum emergence. This is because after the spring thaw the nymphs migrated in large numbers into flood pools in swampy areas along the banks and remained there for about three weeks. This active migration into flooded areas has been reported for this species in northern areas (Neave 1930; Clifford 1970) and has also been noted in a European species of the genus (Pleskot 1953). It presumably has the advantage of bringing the nymphs into water which warms up rapidly, but it is not a habit which was shared by other species in the fauna. This shows that the movement is an active one and is not merely the result of washout onto the flooded areas. Our results are in close agreement with the recently reported study by Clifford (1970) of this species in Alberta except that the cycle begins and ends 1 month earlier in our more southern locality.

Paraleptophlebia mollis (Eaton) was also common. Adults began to emerge in mid-May and were taken throughout the summer until the middle of August. The main emergence peak occurred in June with a smaller one at the end of July.

It was not possible to be certain of the identity of very small nymphs of this genus that were taken during the summer, and both *P. moerens* (see below) and *P. adoptiva* (McDunnough) occur in the stream. However, by August small nymphs of *P. mollis* were definitely recognizable, and presumably at least some of the very small ones taken in June and July belonged to this species. The nymphs grew slowly from August till October and then not at all during the cold season (Fig. 6). After the thaw, however, they grew very rapidly to maximum size in mid-May and, as with some other species, the size at maturity tended to decrease as the emergence season progressed.

Paraleptophlebia moerens McDunnough, although closely related to *P. mollis*, has a different life cycle, and provides another example of a coexisting species pair with differing growth patterns. The adults began to emerge soon after the thaw and the total flight period lasted only 6 weeks, from the end of April to mid June. The first small definitely identifiable nymphs were taken in October. This may indicate a long incubation period or it may be that some of the small nymphs collected earlier belonged to this species. We cannot be sure about this, especially as G. W. Minshall (1968) reports data on this species indicating that its life cycle in Kentucky resembles that found by us for *P. mollis*.

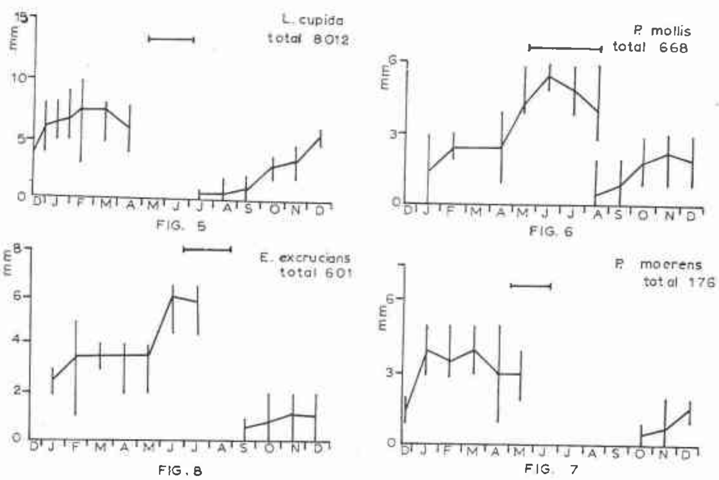
Growth was slow until November and was then rapid during the cold period with maximum size being attained in January under the ice (Fig. 7). As with *P. mollis* and *N. delosa*, later emerging specimens tended to be smaller.

Although there is some doubt about the possible coexistence of very small specimens of this species and *P. mollis* it is clear that their periods of active growth are quite different. *P. mollis* grows in cool water and *P. moerens* when the temperature is at or near zero.

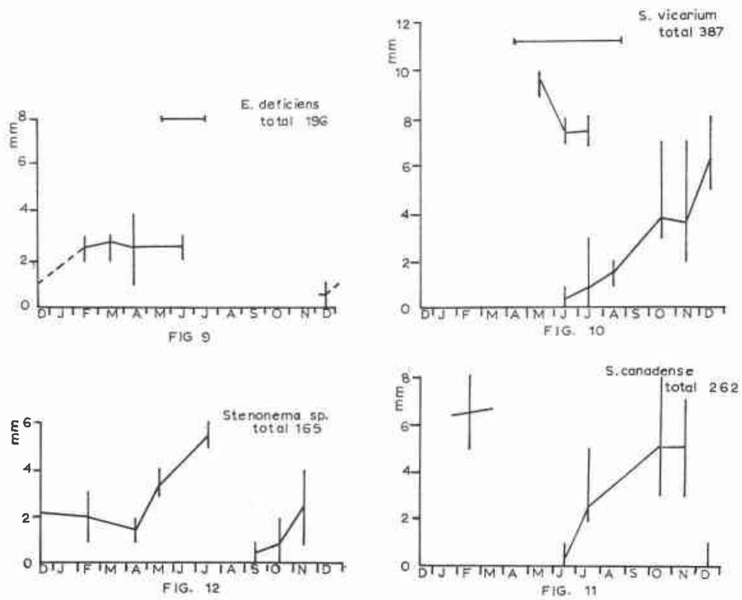
Ephemerella excrucians Walsh was on the wing throughout July and August, and, as newly hatched nymphs were taken in September, it seems that the incubation period can be fairly short. However, small nymphs were taken until December, so either there is little growth in the fall or hatching is prolonged (Fig. 8). Our data indicate slow growth until February, through the cold months, followed by a 3-months static period and then by rapid growth from mid-May to mid-June. This is difficult to correlate with the pattern of temperature change, but we had sufficient specimens to be fairly sure of the general trend in growth rate.

Ephemerella deficiens Morgan showed a peak emergence in mid-May but some adults could still be found until mid-July. The occurrence of nymphs in our samples was irregular, possibly because they do not occur mainly in midstream where most of our samples were taken. It seems, however, that this species may have a long egg-diapause and hatch and grow only during the coldest season (Fig. 9).

Ephemerella minimella McDunnough was scarce and was present in the stream for a very short period and no adults were collected. Despite



FIGS. 5–8. The life cycles of four mayfly species. Arranged as in Figs. 1–4.



FIGS. 9–12. The life cycles of four mayfly species. Arranged as in Figs. 1–4.

this, however, the life cycle appears to be fairly clear from our data. Nymphs first appeared in mid-January at a length of 0.5 mm; by mid-February they were 1.5 mm long and by mid-March 2.5 mm long. None was found in April. It seems then that, like the European *E. ignita*, this species has a long egg diapause and then grows very rapidly to emerge within 3 months. Unlike *E. ignita*, however, which is a summer species (Pleskot 1958; Hynes 1961), it grows in very cold water.

Stenonema vicarium (Walker) was on the wing from April until August, but very small specimens were taken only in June and July. The nymphs then grew steadily until December (Fig. 10), after which they disappeared from our samples. Possibly they move to the banks during the very cold weather, but they reappeared in the samples in early May, and indications are that growth had continued during their absence. Also, as with several other species, the size of the mature nymphs fell as the emergence season progressed. This then appears to be a species whose eggs hatch soon and which grows steadily throughout the year.

Stenonema canadense (Walker) apparently emerged early in the year and over a short period, but no adults were collected in the field. Young nymphs appeared in June and growth was rapid until October. However, the absence of the species from some of our sets of samples and the unexpected occurrence of small nymphs in December present some difficulties in interpretation of our data. Probably though, this species has a long egg-diapause from early spring to midsummer and grows mostly during the warm months.

Stenonema sp. although readily distinguishable as nymphs was not certainly identified because no male specimens were obtained. It apparently began to emerge in mid-July and young nymphs appeared in September and October. Some growth occurred in October and November, and then apparently little until the thaw, after which growth was rapid (Fig. 12).

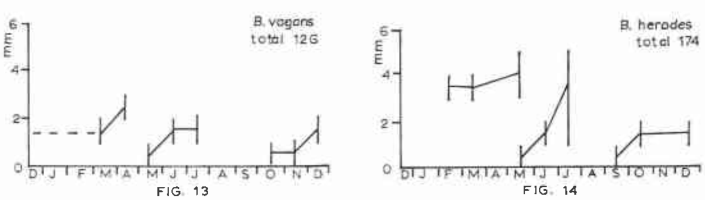
Baetis vagans McDunnough was not common, but our data (Fig. 13) indicate two generations as has also been found in Minnesota (Waters 1966). They also show, as is known for some European species of the genus, e.g. *B. rhodani*, that fully grown nymphs resulting from the overwintering generation are larger than those of the summer generation.

Baetis ? *herodes* was not certainly identified. In many respects it resembles *B. herodes* Burks but detailed differences, particularly in the male genitalia, lead us to suspect that it may be an undescribed species. However, it also displayed a fairly clear bivoltine cycle (Fig. 14) in the Speed River, and, although we took no specimens in January, it appears that, in contrast to *B. vagans*, it grows fairly rapidly during the cold season. The adults of the first generation emerged in late April and early May and those of the second in late July.

Ephemera simulans Walker is not common in the stream except in pool areas which were not sampled. In view, however, of the fact that very small nymphs of the ecologically very similar *E. danica* Müller have proved difficult to find (Pleskot 1961), we should put on record that we found newly hatched nymphs in our pot samples in July. Presumably they live deep in the gravel and so escape collection by conventional means. Our data, although incomplete, indicate a 2-year cycle with rapid growth from July to September, so that by that month the sizes of the two generations overlap. Adults were on the wing in May.

Discussion

Hynes (1961), as a result of his investigation of the insects in a stream in Wales, showed that the life histories of species that do not live for longer than 1 year can be classified as fast or slow, according to whether or not a long egg diapause or an intermediate generation is interposed between the end of a generation and



FIGS. 13 and 14. The life cycles of two *Baetis* species. Arranged as in Figs. 1–4.

the beginning of another occupying the same season. Each type can then be divided into categories F1, F2, F3, and F4 and S1, S2, and S3, etc., according to whether emergence is early, mid-season, or late (March–April, May–June, July–August, August–September in the northern hemisphere). Hartland-Rowe (1964) has confirmed that the same concept can be applied to insect life cycles in a stream in the Albertan Rocky Mountains, and has further shown that the slow cycles which span the winter at a time when the insects are partly grown (S1 and S2) can also be divided into two types. These are the ones in which growth continues during the cold period and those in which it is markedly slowed or stopped by low temperatures.

Applying these ideas to the species considered here we have the following grouping.

F1 *N. completa*, *E. minimella*, *B. vagans* 1st generation
F2 *N. delosa*, *P. moerens*, *E. deficiens*, *B. ? herodes* 1st generation
F3 *B. vagans* 2nd generation, *B. ? herodes* 2nd generation
S1 *A. pygmaea*, *T. nivalis*, *S. canadense*
S2 *L. cupida*
S3 *P. mollis*, *S. vicarians*, *E. excrucians*

It will be noted that all the known cycles except F4, autumnal fliers, are represented by these 14 species and that among the S1 cycles both winter growers (*A. pygmaea* and *T. nivalis*) and winter non-growers (*S. canadense*) are represented. It can also be seen that in almost all instances closely allied species have cycles of different types. This probably allows them to coexist without intense interspecific competition. The one exception is that the two species of *Baetis* both occupy cycle F3. Multiple occupation of this cycle by *Baetis* species was also observed in Wales (Hynes 1961), and it may represent a peculiar feature of the genus which is perhaps able to avoid competition in some other manner. Or it may occur simply because the period when occupants of this cycle are growing actively is one when few other insects are in a rapid phase of growth.

Acknowledgments

We are grateful to Mr. D. Rowan for access to his land, to Mr. J. Bishop for much help with the field work, and to the National Research Council of Canada whose grant to one of us supported this work.

Allen, R. K., and G. F. Edmunds, Jr. 1963*a*. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). VI. The subgenus *Seratella* in North America. Ann. Entomol. Soc. Amer. **56**: 583–600.

——— 1963*b*. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). VII. The subgenus *Eurylophella*. Can. Entomol. **96**: 597–623.

——— 1963*c*. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). VIII. The subgenus *Ephemerella* in North America. Misc. Publ. Entomol. Soc. Amer. **4**: 244–282.

Bishop, J. E., and H. B. N. Hynes. 1969. Upstream movements of the benthic invertebrates in the Speed River, Ontario. J. Fish. Res. Board Can. **26**: 279–298.

Brinck, P. 1949. Studies on Swedish stoneflies. Opuscula Entomol. Suppl. **11**: 1–250.

Burks, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. Bull. Ill. Natur. Hist. Surv. **26**: 1–216.

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

——— 1969. Limnological features of a northern brown-water stream, with special reference to the life histories of the aquatic insects. Amer. Midland Natur. **82**: 578–597.

——— 1970. Analysis of a northern mayfly (Ephemeroptera) population, with special reference to allometry of size. Can. J. Zool. **48**: 305–316.

Coleman, M. J., and H. B. N. Hynes. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnol. Oceanogr. **15**: 31–40.

Edmondson, W. T. (*Editor*). 1963. Freshwater biology. Ward and Whipple. John Wiley & Sons Inc. p. 1248.

Hartland-Rowe, R. 1964. Factors influencing the life histories of some stream insects in Alberta. Verh. Int. Ver. Theor. Angew. Limnol. **15**: 917–925.

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

Khoo, S. G. 1968. Experimental studies on diapause in stoneflies. I. Nymphs of *Capnia bifrons* (Newman). Proc. Roy. Entomol. Soc. London, A, **43**: 40–48.

Landa, V. 1968. Developmental cycles of Central European Ephemeroptera and their interrelations. Acta Entomol. Bohemoslov, **65**: 276–284.

Macan, T. T. 1958. Methods of sampling the bottom fauna in stony streams. Mitt. Int. Verein. Theor. Angew. Limnol. **8**: 1–21.

Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology, **48**: 139–149.

——— 1968. Community dynamics of the benthic fauna in a woodland springbrook. Hydrobiologia, **32**: 305–339.

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

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

Pleskot, G. 1953. Zur Ökologie der Leptophlebiiden (Ins., Ephemeroptera). Oesterr. Zool. Z. **4**: 45–107.

——— 1958. Die Periodizität einiger Ephemeropteren der Schwechat. Wasser Abwasser, 1958: 1–32.

——— 1961. Die Periodizität der Ephemeropteren-Fauna einiger österreichischer Fliessgewässer. Verh. Int. Ver. Theor. Angew. Limnol. **14**: 410–416.

Thomas, E. 1966. Orientierung der Imagines von *Capnia atra* Morton (Plecoptera). Oikos, **17**: 278–280.

Waters, T. F. 1966. Production rate, population density and drift of a stream invertebrate. Ecology, **47**: 595–604.