A STUDY OF THE LIFE CYCLES AND GROWTH-RATES OF FOUR SPECIES OF MAYFLIES.

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The life history of few mayflies is completely known, although numerous records have appeared, mainly from anglers, of the emergence dates of the imagines.

Rawlinson (1939) found that there were two broods of *Ecdyonurus venosus* (Fab.) a year, and also found a marked seasonal difference in the growth-rate. Moon (1938) estimated the growth-rate of two species of *Leptophlebia* and of *Caenis horaria* (L.), and showed that there is a single brood each year of all three species.

Method.

This investigation was carried out on *Ecdyonurus torrentis* Kimmins, *Heptagenia lateralis* (Curtis), *Rithrogena semicolorata* (Curtis), and *Baetis rhodani* (Pictet) from Wayoh Stream near Bolton, Lancashire. The life cycles were determined by measuring a series of nymphs each month, and also by collecting imagines as they emerged.

Collections were made by holding a net in the stream, upturning stones or otherwise disturbing the bottom on the upstream side, and allowing any animals present to be washed into the net. Collecting was carried on for a period of ten minutes in each of the various types of habitat present. No constant number of nymphs was collected using this method, but it was thought to be the best means of obtaining random collections.

The nymphs were measured on microscope slides, care being taken to prevent their drying as this caused contraction. Measurements were taken from the anterior edge of the clypeus to the base of the caudal cerci and were made to the nearest millimetre. All nymphs above two millimetres in length were measured : nymphs below two millimetres could not be identified with any certainty and they were difficult to separate from the rubble collected in the net.

Ecdyonurus torrentis Kimmins.

The percentage of nymphs of *Ecdyonurus torrentis* in each length class, measured from September, 1949, to June, 1951, is shown in fig. 1.

In September, 1949, the highest percentage of nymphs occurred in the 7 mm. class, 40 per cent. of the nymphs being in that class. Only 25 per cent. were in the 6 mm. class and nymphs in the 4 and 5 mm. classes were comparatively rare ; 24 per cent. and 28 per cent. were present in the 3 and 2 mm. classes respectively. This indicates that two main groups were present, and it is possible to trace these through the subsequent records, month by month, until March, 1950. The group of larger nymphs then disappeared ; it seemed likely that this was due to emergence, an interpretation which was confirmed by the presence of adults. At the same time a high percentage of nymphs less than

5 mm. in length made their appearance. Since nymphs of this size had been absent since January, 1950, it would appear that they had been produced from newly laid eggs, and this is confirmed by the fact that adults are present at this time.

In April, 1950, there were still two size groups of nymphs present; 14, 9 and 7 per cent. were present in the 2, 3 and 4 mm. classes respectively; no nymphs were obtained in the 5, 6 and 7 mm. classes; the rest measured between 8 and 15 mm., with the greatest numbers in the 8, 9, and 10 mm. classes. The group of larger nymphs can be traced as those nymphs which formed the smaller

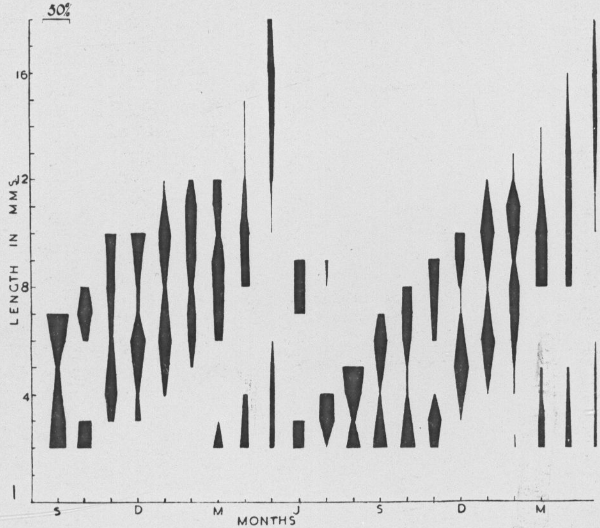

FIG. 1.—The monthly percentage of nymphs of *Ecdyonurus torrentis* Kimmins contained in each millimetre length class.

size group from September to March. In May these larger nymphs disappeared, and again it seems probable that this was due to emergence. Imagines were collected and an increase to 22 per cent. in the 2 and 3 mm. classes in June, as compared with 8 per cent. and 7 per cent. in the previous month, implies a new batch of nymphs.

In June 19 per cent. and 22 per cent. of the nymphs were in the 2 and 3 mm. classes, and 18, 19, and 19 per cent. in the 7, 8, and 9 mm. classes respectively. The 7, 8, and 9 mm. nymphs can be traced back to the small April nymphs. In July the group of larger nymphs disappeared and adults were collected; in August the percentage of 2 mm. nymphs rose to 26 per cent. as compared with 1 per cent. in July. Again it is probable that the larger nymphs had emerged in July, and newly laid eggs had produced the increased number of small nymphs present in August.

In August, 1950, two sizes of nymphs, similar to the two size groups which were first observed in September, 1949, were collected ; 26 per cent. of the nymphs were in the 2 mm. class and 4 per cent. in the 3 mm., 30 per cent. and 40 per cent. being in the 4 and 5 mm. classes. These two groups can be traced through the months until March, 1951, when again the group of larger nymphs disappeared, and a group of nymphs less that 5 mm. in length reappeared.

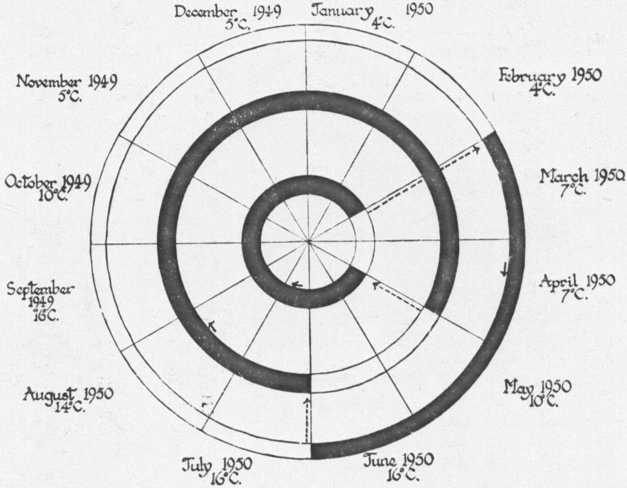

FIG. 2.—A diagram of the seasonal life cycle of *Ecdyonurus torrentis* Kimmins. The arrows indicate the hatching of successive broods.

The length classes showed the same two groupings in April, 1951, as had appeared in April, 1950. Again in May the group of larger nymphs disappeared and an increased percentage of small nymphs occurred in June, implying a new hatch of nymphs following an emergence of the imagines.

Measurements were discontinued in June, 1951, after having been obtained over a period of twenty-one months. From the results it appears that three broods of *E. torrentis* occurred in Wayoh stream throughout the course of the year, the nymphs of two different broods being present at any one time. The three broods fall approximately into the periods March–July, July–May, and May–March (fig. 2). How far overlapping between the broods occurs, due to individual differences in growth rate, cannot be estimated. It appears likely that this may occur to some extent.

The average growth per month within each size group can be calculated from the measurements of the lengths of the nymphs. A graph of the calculated average growth-rate is given in fig. 3. The growth-rate of the summer or March–July brood was greatest in June when the average growth was 3·3 mm. The rate dropped in the second month, May, from 2·7 to 2·0 mm., and again in July to 0·7 mm. The July–May brood showed a slower rate than the March–July brood. From August, 1949, to April, 1950, the rate varied between 0·1 and 1·2 mm. per month, and then prior to emergence

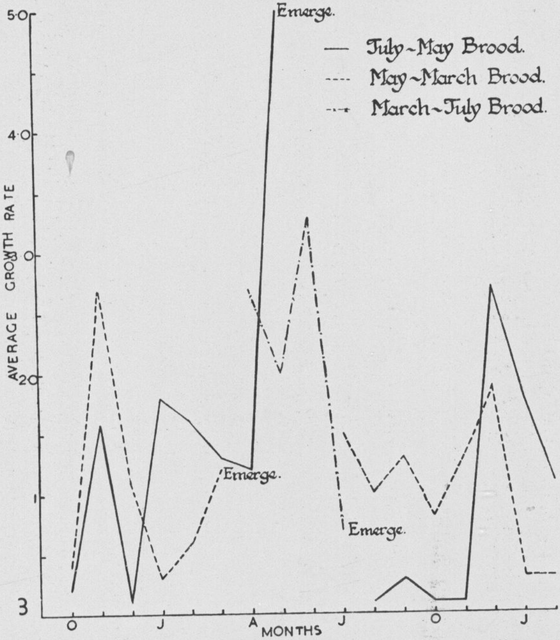

Fig. 3.—The average monthly growth-rate of the nymphs of *Ecdyonurus torrentis* Kimmins.

in May the rate rose suddenly to 5·0 mm. per month. The May–March brood had a rate intermediate between 0·3 and 1·2 mm. per month, except in November, 1949, when it increased to 2·7 mm. per month. From July, 1950, to February, 1951, the rate was fairly uniform, varying from 1·0 to 1·5 except in December, 1950, when the rate increased to 1·9 mm. per month.

Comparison of the growth-rate with the temperature of the stream shows an increase in growth in November in the July–May and May–March broods, when the temperature dropped from 10° C. to 5° C. The growth of the March–July brood increased from 2·0 to 3·3 mm. per month when the temperature rose above 10° C. Growth-rate of the July–May brood increased from an average of 0·8 to 4·3 mm. per month from March to May when the temperature rose above 6° C.; that of the May–March brood dropped from November to February, when the temperature was below 6° C., and rose to an average of 1·1 mm. per month when it was above 6° C.

These changes in growth-rate suggest a correlation between growth and temperature in the spring, but there appear to be other factors controlling growth in the autumn.

Nymphs of the July–May brood kept in the laboratory at room temperatures which were higher than those of the stream, emerged at the same time as the

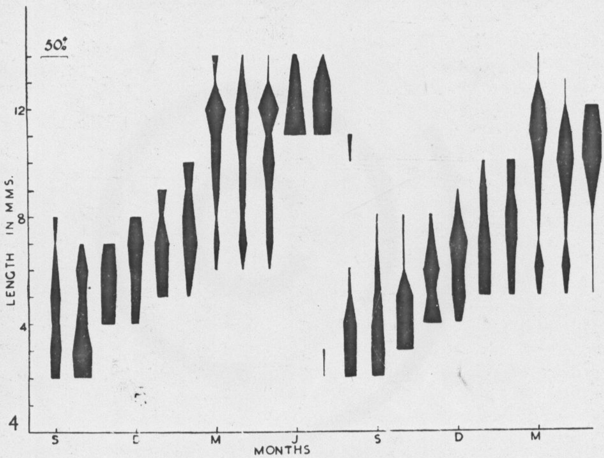

Fig. 4.—The monthly percentage of nymphs of *Rithrogena semicolorata* (Curtis) contained in each millimetre length class.

May–March brood nymphs kept under the same conditions. It is possible that, if the temperature rose early in the year, the July–May brood might emerge with the May–March brood, or conversely if it rose late in the year, the May–March brood might emerge with the July–May brood. It therefore seems likely that the number of broods per year is in part dependant on seasonal factors, and interbreeding between the three broods is probably not prevented by a well-marked time barrier.

Rithrogena semicolorata (Curtis).

The percentage of nymphs of *Rithrogena semicolorata* in each length class, measured from September, 1949, to June, 1951, is shown in fig. 4.

In September, 1949, the highest percentage of nymphs was in the 3 mm. class, 21 per cent. being present. Between 13 per cent. and 18 per cent. were in each of the 2, 4, 5 and 6 mm. classes. In October, 1949, 36 per cent. were still in the 2 mm. class, but the percentage in both the 4 and 6 mm. classes had increased to 21 per cent. This gradual increase in size with a range over five or six millimetre classes can be followed month by month till March, when the variation in size increased to cover nine classes, the greatest percentage being in the 12 mm. class. This wide variation is apparent till May, but gradually the numbers become more concentrated, 70 per cent. being in the 10, 11 and 12 mm. classes. In June the variation only covered four classes, and of these only 6 per cent. were in the largest 14 mm. class. In July, 1950, 5 per cent. of the nymphs appear in the 2 and 3 mm. classes, and since no nymphs of this size have been present since October, 1949, it is probable that these small

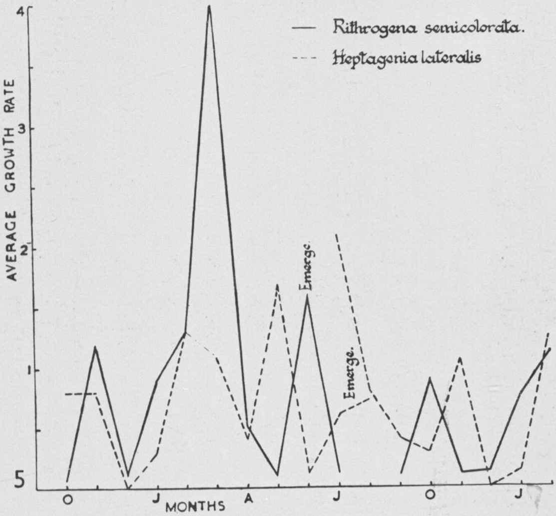

Fig. 5.—The average monthly growth-rate of the nymphs of *Rithrogena semicolorata* (Curtis) and *Heptagenia lateralis* (Curtis).

nymphs came from newly hatched eggs. In August all the nymphs above 11 mm. disappeared and the greatest numbers were in the 2, 3 and 4 mm. classes. These two facts together point to emergence having taken place in June and July. Adults were also collected at this time. By September, 1950, all the nymphs above 8 mm. had disappeared, so that it may be supposed no more adults emerged after that time.

The average growth per month has been calculated from the length measurements, and a graph of the calculated average rate is given in fig. 5.

The growth-rate is fairly uniform throughout the year, varying between 0·1 and 1·2 mm. per month, except in March, when it increased to 4·0 mm. per month as the temperature increased from 4° to 7° C., and in June when it increased to 1·6 mm. per month as the temperature rose from 10° to 16° C. There are similar rises in temperature at other times of the year, but these do not appear to have the same effect as the increases in March. This suggests that a temperature level of about 6° C. is required for active growth. A similar condition appeared to exist for *E. torrentis*.

From these results it is concluded that *R. semicolorata* has a univoltine life cycle, but that emergence may be spread over some months and the time of emergence depends, at least in part, on seasonal factors.

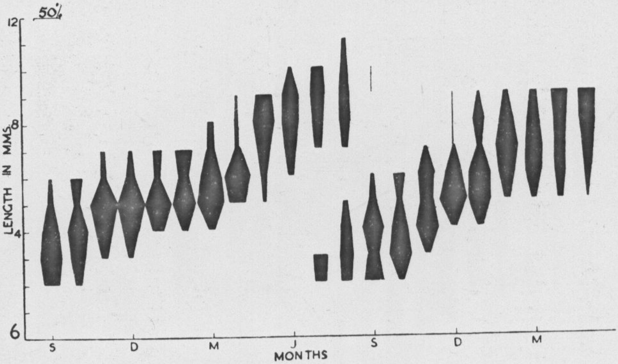

Fig. 6.—The monthly percentage of nymphs of *Heptagenia lateralis* (Curtis) contained in each millimetre length class.

Heptagenia lateralis (Curtis).

Measurements of the nymphal lengths between September, 1949, and June, 1951, appear in fig. 6.

In September, 1949, nearly all the nymphs were in the 2, 3 and 4 mm. classes, with 3 per cent. and 4 per cent. in the 5 and 6 mm. classes. In October, 1949, 30 per cent. and 38 per cent. were in the 3 and 4 mm. classes and 5 per cent. were in the 7 mm. class. This gradual movement into the larger classes is followed each month to June, 1950, with a variation within each month of four or five millimetres. In July 34 per cent. of the nymphs were in the 2 and 3 mm. classes, and, as no nymphs of this size had been present since October, 1949, it is probable that these were newly hatched. At the same time the percentage of nymphs in the larger classes fell, and this, together with the fact that adults were collected, suggests that emergence was taking place. A few large nymphs were present until September, when only 4 per cent. were in the 9 and 10 mm. classes, while the number in the small classes increased, 78 per cent. being in the 2, 3 and 4 mm. classes.

The growth-rates calculated from these measurements are given in fig. 5. Growth varies from 0·3 to 1·7 mm. per month throughout the year, and shows no obvious relation to the temperature fluctuations of the stream.

The life cycle of *H. lateralis* is apparently univoltine, emergence taking place in this stream in June, July and August. The life cycle does not seem to be as closely inter-related to the temperature as it does in *E. torrentis* and *R. semicolorata*.

Baetis rhodani (Pictet).

The measurements of the nymphs of *B. rhodani* captured each month from September, 1949, to February, 1951, are given in fig. 7.

In September, 1949, 34 per cent. of the nymphs were in the 2, 3 and 4 mm. classes, 19 per cent. in the 6 and 7 mm. classes, and 22 per cent. in the 9 and 10 mm. classes. The remaining 25 per cent. were scattered between these classes and up to the 12 mm. class. It can be seen from this that three groups

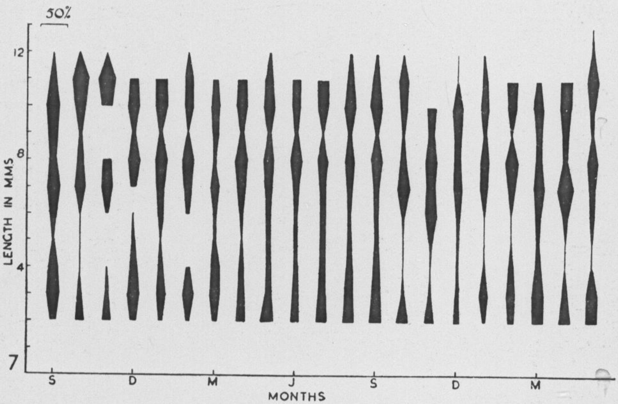

FIG. 7.—The monthly percentage of nymphs of *Baetis rhodani* (Pictet) contained in each millimetre length class.

of nymphs occur. These three groups were present every month till measurements were discontinued, with the greatest concentration of the numbers in the 2–3 mm., 7–8 mm., and 10–11 mm. classes.

Examination of the nymphs showed that there were two size groups of penultimate instar nymphs, one of average length 7 mm., and the other of average length 10 mm.

From the results no indication of the length of the life cycle can be estimated. The presence of the two groups of nymphs ready to emerge, and the presence of all sizes of nymph in all months of the year, makes it impossible to follow the life cycle by measurement alone. Adults were collected in every month of the year except January and February, and the length of the emergence period further complicated any attempt to elucidate the life cycle.

An insufficient number of imagines were collected to show with any certainty whether groupings in size similar to those of the penultimate instar nymphs occurred. It is interesting to note that a similar discontinuous size variation has been found for an Australian species of the same genus, *Baetis baddamsae* Harker (Harker, 1950).

Summary.

1. The results obtained from the measurements of the lengths of four species of mayfly nymphs each month are described. The species were *Ecdyonurus torrentis* Kimmins, *Rithrogena semicolorata* (Curtis), *Heptagenia lateralis* (Curtis), and *Baetis rhodani* (Pictet).

2. *E. torrentis* was found to have a trivoltine life cycle. The growth-rate varies with the temperature.

3. *R. semicolorata* showed a univoltine life cycle with emergence partly dependent on temperature.

4. *H. lateralis* was found to have a univoltine life cycle. Growth does not show a direct relation to the temperature.

5. The life cycle of *B. rhodani* could not be determined by length measurements. Two size groupings of penultimate instar nymphs were found to be present.

References.

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Moon, H. P., 1939, The Growth of *Caenis horaria, Leptophlebia vespertina* and *L. marginata*. *Proc. zool. Soc. Lond.* (A) **108** : 507–512.

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Book Notice.

Caddis. By Norman E. Hickin. 8vo. London (Methuen & Co.), 1952. Pp. x + 50, pls., text illust. Price 9*s*. 6*d*.

This book forms No. 5 of the Field Study Series, the purpose of which is to discuss the problems of the countryside from the intimate angle of the expert but in such a way as to appeal to the general reader, the student, including the older school child, and the teacher.

It is also the first book in English dealing exclusively with the immature stages of Caddis Flies.

The introductory chapter defines the insect and describes special features of its biology, including importance as food for fish and their use in wet and dry fly fishing.

Chapter 2 deals with the life cycle of Caddis and its *Agriotypus* parasite, and Chapter 3 with collecting, rearing and preserving. The morphology of the larva and pupa with keys to the identification of families are dealt with in Chapters 4 and 5.

The final chapter is a guide to research on the biology of Caddis. There are two appendices, one comprising a bibliography of literature on the adult and immature stages and the other a complete list of British Caddis Flies.

The work is very fully illustrated, many of the drawings having previously appeared in the author's series of papers in the Society's *Transactions* and *Proceedings*; there are also four coloured plates.