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The Growth of *Coenis horaria* (L.), *Leptophlebia vespertina* (L.), and *L. marginata* (L.) (Ephemeroptera).

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(Text-figure 1.)

Introduction.

This investigation was undertaken as a result of preliminary observations on the growth of two kinds of insect nymphs, made in 1933–34. These observations showed that during the winter one of these nymphs grew, while the other showed no growth. The work was therefore continued on a larger scale to see whether these results could be repeated. The earlier results suggested that some insect nymphs ceased growing in the winter.

No previous attempt has been made to measure a large population of wild aquatic nymphs.

Material and Methods.

The results in this paper are based on the length measurements of two nymphs from the order Ephemeroptera, collected from Windermere, in the English Lake District. These nymphs are (1) *Leptophlebia* sp., (2) *Coenis horaria* (L.).

In the case of *Leptophlebia* the nymphs of two species, *L. vespertina* (L.) and *L. marginata* (L.), are present. The nymphs of these two species cannot be distinguished, but they appear to grow at the same rate. The adults emerge about the tenth of May, and emergence is completed within a few days. After this date nymphs of *Leptophlebia* are not to be found until the following October. The approximate length of time between the emergence of the adults and the hatching of the young is twenty weeks.

Coenis is represented by the nymph of one species, *Coenis horaria* (L.). The approximate date of the main emergence is the tenth of June, but a certain amount of emergence is taking place throughout June and July. The approximate length of time between emergence of the adults and hatching of the young is six weeks.

A large number of nymphs was measured, and collections were made as far as conditions allowed every fourteen to twenty days. The investigations extended over a period of ten months. Collections for any particular nymph were always made from the same locality, and the area from which the collections were made lay between the lake edge and a depth of two feet.

The insects were measured with a projection apparatus, the images of the nymphs appearing upon a calibrated screen. The nymphs were arranged in rows on microscope slides, and in order to get a clear image of the nymphs on the screen it was necessary to remove all surplus fluid from the microscope slide with blotting paper. This left the nymphs moist, but did not allow any possibility of the nymphs drying and contracting. Once the nymphs were arranged in rows on the slide it was possible to measure them at the rate of eight a minute, while in one day seven to eight hundred nymphs could be measured.

The nymphs were measured from the free margin of the frons to the base of the caudal cerci. Any measurements including the caudal cerci would be unreliable, because the cerci are frequently lost or damaged during collection. Measurements were made to the nearest quarter of a millimetre, the number of individuals in each size group being recorded by counters dropped into a row of glass tubes. In view of the jointed structure of an insect it was important to know how much the length of the insect was reduced by telescoping of the segments, when it was fixed in 70 per cent. alcohol. The amount of contraction due to fixation was 14 per cent. of the total body-length in the case of *Coenis*, and 15 per cent. in the of *Leptophlebia.*

Obviously when considering questions of growth the food of the animals concerned is important. For this reason the contents of the gut from ten individuals in each collection were examined, the individuals examined representing the various size groups present. The specimens were killed in 70 per cent. alcohol as soon after capture as possible to prevent digestion of the material in the gut.

The Growth Curves.

The data on which these growth curves are based are given in Tables I. and II.

1. *Leptophlebia.* (Table I.)

In view of the fact that both species (*L. vespertina* (L.) and *L. marginata* (L.)) emerge at the same time, and the nymphs hatch approximately at the same

TABLE I.

Date.	Number measured.	Mean length in mm.	Standard deviation.
1..13. 12. 34	108	1·74	·38
2.. 9. 1. 35	520	2·73	·22
3.. 25. 1. 35	631	3·57	·37
4.. 7. 2. 35	676	3·90	·45
5.. 4. 3. 35	538	4·60	·61
6.. 23. 3. 35	573	5·15	·76
7.. 14. 4. 35	297	5·64	·88
8.. 27. 4. 35	429	6·37	·89
9.. 13. 5. 35	53	6·21	·76

Total number measured=3825.

dates, the data for *Leptophlebia* are taken as representing correctly the growth of these two species. Moreover, the frequency curves show no trace of the bimodality which might be expected if the two species showed different growth-rates.

Text-fig. 1 represents the growth curve for *Leptophlebia,* and it will be seen that, although growth is continuous through the winter, there is a slight decrease in the rate of growth after January. Growth increases again after the end of April, just before emergence. After the beginning of emergence there is complete cessation of growth. The drop at the last point of the growth curve in May is probably due to the emergence of the large mature forms. This leaves a residuum of smaller immature nymphs.

2. *Coenis horaria* (L.) (Table II.)

The growth curve of *Coenis* is in strong contrast to that of *Leptophlebia*. *Coenis* shows no growth in the winter between December and the end of March. Actually during the winter there may be a slight decrease in the size of the nymph. In April there is renewed growth up to the third week of July, when the main period of emergence for *Coenis* comes to an end. By the end of July a new generation of small nymphs is growing up, as the eggs laid by the adults in the previous weeks begin to hatch. By September there is evidence that the growth curve for this new generation is decreasing in steepness. This decrease in steepness probably represents the beginning of the winter cessation of growth.

TABLE II.

Date.	Number measured.	Mean length in mm.	Standard deviation.
1..15. 12. 34	650	2·49	·14
2.. 8. 1. 35	285	2·56	·38
3.. 25. 1. 35	384	2·26	·26
4.. 9. 2. 35	338	2·36	·11
5.. 6. 3. 35	489	2·32	·17
6.. 29. 3. 35	329	2·31	·39
7.. 13. 4. 35	282	2·88	·46
8.. 27. 4. 35	243	2·74	·44
9.. 14. 5. 35	337	3·36	·61
10.. 30. 5. 35	473	3·81	·64
11.. 14. 6. 35	107	4·08	·65
12.. 16. 7. 35	19	4·30	·89
13.. 31. 7. 35	25	1·47	·81
14.. 15. 8. 35	169	1·78	·46
15.. 26. 8. 35	179	1·87	·43
16.. 12. 9. 35	575	2·01	—

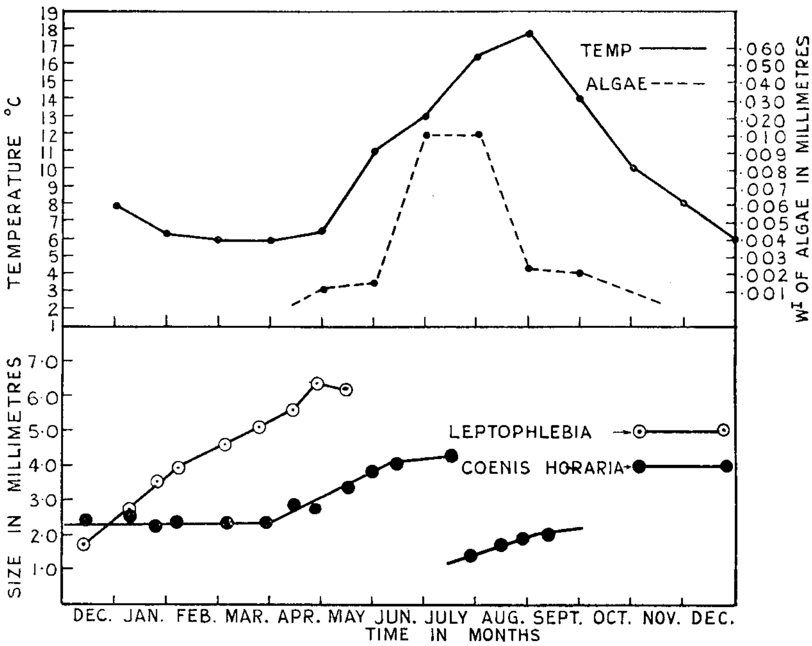
Total number measured = 4884.

Discussion.

The results show that the growths of *Coenis* and *Leptophlebia* are in sharp contrast. *Leptophlebia* grows throughout the winter, while *Coenis* shows no growth in the winter. Two explanations may be offered for the difference in the growth curves of these two species. In the first place the differences may arise as a result of peculiarities of the metabolism in these two insects. For example, Calvert (1929) found that the nymph of *Nannothermis bella* (Uhler) showed no growth in winter, although kept at room-temperature and provided with an excess of food. This may represent a cessation of growth due to an inherent periodicity in the metabolism quite independent of external factors such as food or temperature. In the case of *Coenis* and *Leptophlebia* the evidence available suggests that the differences in the growth curves are not due to such peculiarities of metabolism.

The simplest explanation of the contrast in growth between *Coenis* and *Leptophlebia* is that the differences are due to external factors Two factors have been considered, temperature and food. There is a certain amount of evidence concerning the influence of temperature on the growth of aquatic insects. Balfour Browne (1909) found that certain Zygopterid (Odonata) nymphs developed twice as rapidly if kept during the winter in incubators at summer temperatures. At winter temperatures the nymphs were inactive. Classen (1931) quotes Samal, who states that during the winter *Perla abdominalis* (Burm.) showed reduced activity and ecdysed less frequently. In the present case it is noticeable that renewal of growth in *Coenis* takes place at the end of March, when the lake temperature is rising (text-fig. 1). At the first sight

Text-figure 1.



differences in the two growth curves might be explained by supposing that *Coenis* cannot grow at winter temperatures, while *Leptophlebia* can do so. There is a slight increase in the rate of growth of *Leptophlebia* at the end of March which may be due to rising temperatures.

On the other hand, there is evidence that the differences in growth may be due to seasonal variations in the quality of the food. Both *Coenis* and *Leptophlebia* feed on a detritus composed of the remains of higher plants, diatoms and fragments of filamentous littoral algæ. During the winter there is a reduction in the amount of littoral algæ found in the detritus, but at the end of March there is a great increase in algal growth. The detritus is enriched by the broken filaments of these algæ, and large quantities of filamentous algæ are found in the gut of *Coenis*. This abundance of littoral algæ in the gut of *Coenis* coincides with the renewal of growth, suggesting that *Coenis* can only grow if the detritus is enriched by broken filaments of littoral algæ. Algal fragments occur in the gut of *Leptophlebia* at the end of March. The supply of algal food and not temperature may be responsible for the slightly increased growth-rate of *Leptophlebia* during April.

Without experimental work it is impossible to decide whether temperature or food is responsible for the differences in the growth of these two nymphs. The probability is that both factors are important. Temperature affecting *Coenis* directly by its acceleration or retardation of metabolism, indirectly by influencing the food supply. The rising temperature at the end of March brings about the spring circulation of the lake water. The redistribution of salts brought about by this circulation, and the increased sunlight, results in an increase in algal growth (Pearsall, 1930 ; Godward, 1937). The fragments of filamentous littoral algæ enrich the detritus for *Coenis* to renew its growth.

Coenis and *Leptophlebia* collected on and after the end of March all contained great quantities of yellow fat globules. These fat globules probably represented the greatly swollen fat bodies. The fact that the appearance of this fatty substance coincides with the appearance of the algæ suggests a connection between the two. Possibly the additional food represented by the algæ made it possible for the nymphs to lay up a food reserve in the form of fat.

Available evidence suggests that the growth-rate of *Coenis* is high after hatching but gradually decreases. The same decrease of initial growth-rate is mentioned in the work of Lubbock (1863–5) on *Chloen dimidiatum* (Lubbock), Gros (1923) on *Ecdyonurus forcipula* (Pict), and Durken (1923) on *Ephemerella ignita* (Poda). Figures given by Needham, Traver, and Hsu (1935) for the growth in length of *Stenonema interpunctatum* (Say), *Heptagenia hebe* (McDunnough), and *Iron humeralis* (Morgan) all show a slowing down of the initial growth-rate. Followed in the later instars by an increase in growth-rate. In the case of *Coenis* the decrease of growth-rate is probably correlated with the autumn decline in temperature and algal growth.

There is one important stage which the growth curves do not show, namely, the growth from the time of hatching till the nymphs have reached a length of 1·5 millimetres. In spite of careful collecting and sorting it was impossible to find many nymphs smaller than 1·5 mm.

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Summary.

1. The results obtained from the measurements of the growth in length of three Ephemeropteran nymphs are described. The nymphs were *Coenis horaria* (L.), *Leptophlebia vespertina* (L.), and *L. marginata* (L.).

2. The measurements were made with a projection apparatus.

3. The growth curves show that in winter *Coenis* does not grow, while in *Leptophlebia* growth continues.

4. The factors responsible for this difference in growth appear to be food and temperature. Both *Leptophlebia* and *Coenis* are detritus feeders, but *Coenis* evidently requires a detritus enriched by the fragments of filamentous littoral algæ.

5. The renewal of growth in *Coenis* coincides with the increased growth of littoral algæ and rise of temperature in spring. At this time the gut contents of *Coenis* contains large quantities of filamentous algæ.

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