Freshwat. Biol. 1972, Volume 2, pages 271–277

The life cycles of *Leptophlebia vespertina* (L.) and *L. marginata* (L.) (Ephemeroptera) in Llyn Dinas, North Wales

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Manuscript accepted 18 June 1972

Summary

Data is presented on the life cycles of *Leptophlebia vespertina* (L.) and *L. marginata* (L.) in Llyn Dinas, an oligotrophic North Wales lake. Both species are univoltine and growth continues throughout the winter although somewhat retarded. Except during July and August there is a clear size separation of the two species, *L. marginata* being larger and emerging earlier. The egg incubation period was determined directly from laboratory studies. The results are discussed in relation to previous research in the English Lake District.

Introduction

The first studies on the life cycle of *Leptophlebia vespertina* (L.) and *L. marginata* (L.) were made by Moon (1938) on the population inhabiting Lake Windermere in the English Lake District. However, owing to taxonomic difficulties he was unable to separate the nymphs of the two species. He assumed that they both grew at the same steady rate throughout the winter with the adults emerging around 10 May. After emergence, he was unable to find any nymphs until the following October, so he deduced that the eggs took approximately 20 weeks to hatch.

Kimmins (1954) in his key to the British adult Ephemeroptera recorded the emergence period of *L. marginata* as from April to mid-June and for *L. vespertina* from April through until August.

In studies on the biology of Hodson's Tarn in the English Lake District, Macan (1965) obtained some interesting information on these two *Leptophlebia* species. In 1956 Macan, identifying the adults to species, found that the main emergence of *L. marginata* was nearly a month earlier than that of *L. vespertina*. By sampling monthly during 1957, he deduced that hatching of the eggs had started by the end of July; but, from the number of very small nymphs he found it did not reach a peak before September. There was some growth through the winter and an increase in the rate of growth during the spring. The adults emerged from mid-April to late June with a peak in the second half of May. In these studies in 1957/58 the two species were not separated.

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In a small trout loch in Perthshire, Scotland, Morgan & Waddell (1961) gave the emergence period of *L. vespertina* as from the end of May until the middle of July There are only a few records of the flight period outside the British Isles. Grimeland (1966) recorded the presence of *L. marginata* adults during June and July in the Agdene region of Norway, while Thomas (1969) in his study in Austria obtained adults of *L. marginata* during late April and early May.

Methods

(1) *Habitat*

The life cycles of *Leptophlebia vespertina* and *L. marginata* were studied in a North Wales lake, Llyn Dinas, situated at an altitude of 53·5 m in the Gwynant valley (map reference SH 615495). Llyn Dinas lies in the heart of Snowdonia, an area of mountain and moorland terrain which reaches elevations of over 1000 m. The lake covers an area of approximately 311,000 m^2 and has a maximum depth of 9·1 m. An average calcium level of 2·0 ppm reflects the oligotrophic nature of this habitat. The shores of Llyn Dinas are mainly rocky, grading into a mud substratum at a depth of about 1 m. In this transition zone areas of rooted vegetation, predominantly *Littorella uniflora* (L.), are present. The two species considered here were found both among the stones and in areas of vegetation. A detailed account of the physical, chemical and biological features of Llyn Dinas was given in Brittain (1971).

(2) *Sampling methods*

The populations of *L. vespertina* and *L. marginata* in Llyn Dinas were sampled at least once a month, for a 2-year period, during which the species passed through their complete life cycles twice. Samples were taken along the north-west shore of Llyn Dinas using mainly hand net (16 meshes/cm) collections, but these were supplemented by some collecting under stones. Fifty nymphs of *L. vespertina* were collected on each sampling occasion, except during the summer months when the nymphs were very small, and therefore difficult to find. Nymphs of *L. marginata* were found much less frequently in samples, and only between ten and twenty nymphs were usually collected.

The samples were brought back to the laboratory, where the nymphs were measured live. The parameter of body length, used by previous workers, was the one selected as most useful. Body length was measured, to the nearest 0·03 mm, from the tip of the head to the base of the cerci. Eggs of both species were reared in the laboratory at field temperatures.

Results

Field results from Llyn Dinas demonstrated that both *Leptophlebia marginata* and *L. vespertina* had a 1-year life cycle, with *L. marginata* being larger at a given time and emerging earlier. The two life cycles are shown in Fig. 1. The mean body-length values of each sample collection are plotted for both species. The figures for the first and second instars are taken from laboratory studies (Brittain, 1971) as very few nymphs less than 1·0 mm were found in the field. Both emergence periods were determined from field collections at Llyn Dinas. The period of egg hatching was deduced using the adult flight period and the time taken for eggs to hatch in the laboratory at field temperatures.

Examination of the growth curves in Fig. 1 shows that the nymphs of *L. vespertina* grew steadily during the summer, autumn and early winter. During the coldest months

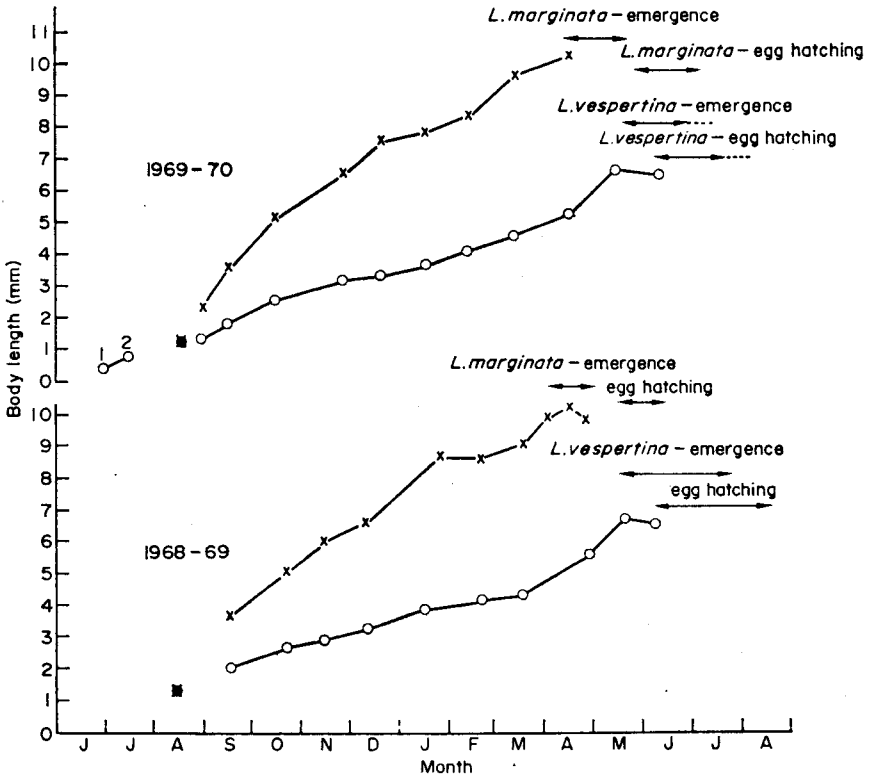

Fig. 1. Life cycles of *Leptophlebia vespertina* and *L. marginata* in Llyn Dinas. Instars 1 and 2 are taken from laboratory data (Brittain, 1971). ×——×, *L. marginata*; ○——○, *L. vespertina*; ⊠ *Leptophlebia* spp.

of January and February, there was an indication, especially in 1968/69, that growth was somewhat retarded at low temperatures. As the temperature rose, so the growth rate increased until at the end of May emergence had begun. Once emergence had started, the mean size of the population fell owing to the loss of the larger, more mature, nymphs. Emergence, which began around 20 May, reached a peak early in June and continued rather sporadically until the latter half of July.

Leptophlebia marginata showed a similar growth pattern. Again growth continued at a steady rate, but more rapidly than for *L. vespertina*, until January. The cold conditions, either directly or indirectly, affected the growth rate of *L. marginata* more than that of *L. vespertina*. After this period of low temperatures, there was a short interval of rapid growth before the start of emergence. The flight period of *L. marginata* at Llyn Dinas extended from early April until the middle of May.

The growth curves for the two species in Fig. 1 show the mean values for each monthly sample. In order to show the range of size within the population and to demonstrate the size-separation of the two species the size-distribution of each sample is plotted in histogram form in Fig. 2. Each sample is divided into 0·5 mm size categories: 0–0·5 mm, 0·5–1·0 mm, etc. The width of each size group represents the number of individuals found in that particular group. In August it was not possible to separate the two species, but thereafter there is a clear separation. The upper histogram

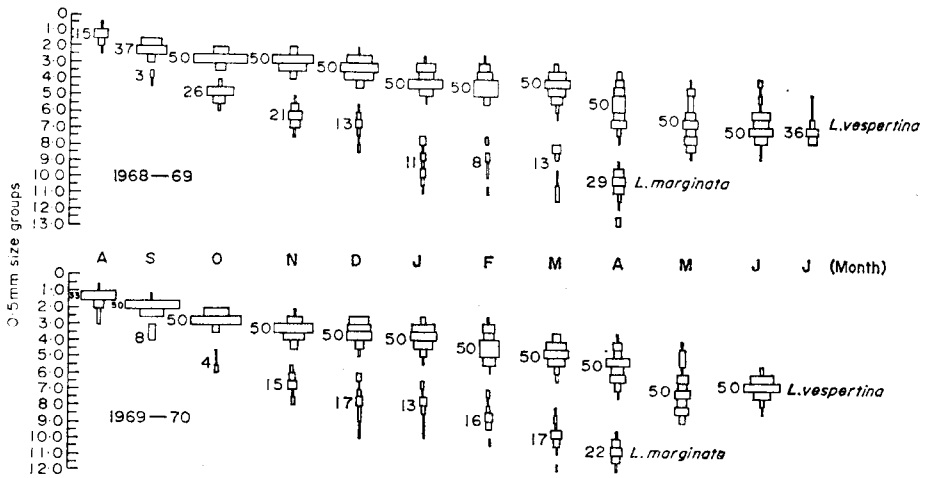

Fig. 2. Size-structure histograms of *Leptophlebia* species in Llyn Dinas. Numbers in each sample are indicated.

of each pair relates to *L. vespertina*, while the lower histogram represents the *L. marginata* population.

Discussion

The results substantiate the findings of Moon (1938) and Macan (1965) that both *Leptophlebia vespertina* and *L. marginata* are univoltine species. The nymphs in Moon's study were killed in 70% alcohol before being measured and so a shrinkage factor must be taken into account. Moon gives a figure of 15% for this, but does not indicate whether his results are adjusted to a 'live length', or not. Therefore in Fig. 3 two growth

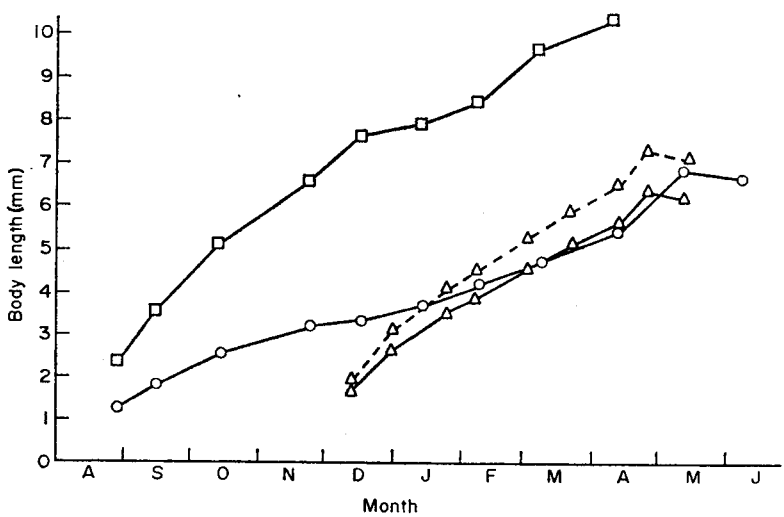

Fig. 3. Growth curves of *Leptophlebia* species in Llyn Dinas and Lake Windermere. □——□, *L. marginata*, Llyn Dinas, 1969–70; ○——○, *L. vespertina*, Llyn Dinas, 1969–70; △——△, *Leptophlebia* spp., Lake Windermere (Moon, 1938); △– – –△, *Leptophlebia* spp., Lake Windermere (Moon, 1938), adjusted for shrinkage.

curves are given; one is Moon's original curve and the other is one where 15% has been added to each mean length value.

In Llyn Dinas the separation of the two life cycles is particularly well seen in the size-structure histograms (Fig. 2). After August *L. marginata* was always larger in size than *L. vespertina*. Emergence, as Macan (1965) had found, occurred first in *L. marginata*. Although *L. marginata* emerged earlier, its eggs took longer to hatch. This may be due, at least in part, to the lower temperatures earlier in the summer. This causes considerable overlap in the hatching periods of the two species. Therefore during July and August nymphs of both species are similar in size. This period is also the time of maximum primary production which presumably lessens the intensity of any inter-specific competition for food. As the primary production falls, so the difference between the mean sizes of the two populations widens.

The data, given in Fig. 1, for the periods of egg hatching have been derived from the observed flight period in the field and the incubation of eggs in the laboratory at field temperatures. Both Moon and Macan obtained their dates for the hatching of the eggs from the time at which they first found nymphs in the field. In Llyn Dinas, nymphs were not found until mid-August, but laboratory studies had shown that hatching could have been occurring since the end of May in the case of *L. marginata* and since early in June for *L. vespertina*. Clearly, the absence of nymphs in field collections is not necessarily indicative of real absence, merely that the sampling technique used is not suitable to detect the very small nymphs (cf. Jónasson, 1955). Nymphs were obtained in August only by detailed examination of bottom material under the binocular microscope.

In other respects, besides the hatching period of the eggs, the results of the present study are in agreement with those of Macan. On the other hand, they do not at first sight appear to fit those of Moon on the *Leptophlebia* species in Lake Windermere. There are a number of possible explanations for these discrepancies. Figure 3 suggests that Moon's data do not represent the growth curve of both *Leptophlebia* species but only *L. vespertina*, or at least mainly that of *L. vespertina*. If this is so, and Moon (pers. comm.) agrees that this seems likely, it would explain the absence of any bimodality in his results compared with the obvious size separation in the data from Llyn Dinas (Fig. 2). Because of the taxonomic situation, Moon had to rely on the species determination of adults caught during emergence, assuming that he was sampling the nymphal population of both species. Why then were *L. marginata* nymphs not well represented in his collections? Firstly, *L. marginata* is usually much less common than *L. vespertina*, and secondly, there is the possibility that they occupy different habitats. A survey by Macan & Maudsley (1968, 1969) of the fauna on the stony shores of Lake Windermere suggested that *L. marginata* commonly occurs at greater depths than *L. vespertina*. Moon made his collections in the 0–60 cm zone, whereas in Llyn Dinas collections were made down to 1·25 m.

Assuming that Moon's figures do in fact represent *L. vespertina*, there remains the question of the hatching period of the eggs. Whereas Moon deduced a period of 20 weeks for the eggs to hatch, results from the present study, both in the field and in the laboratory, indicate that eggs of *L. vespertina* hatch in about 3 weeks. A lower temperature in Windermere would lengthen the incubation period, while a higher temperature might cause the eggs to go into a state of diapause in order to survive adverse temperatures. However, when the monthly maxima and minima temperatures for Windermere and Llyn Dinas are compared (Fig. 4), the regimes of both lakes can be

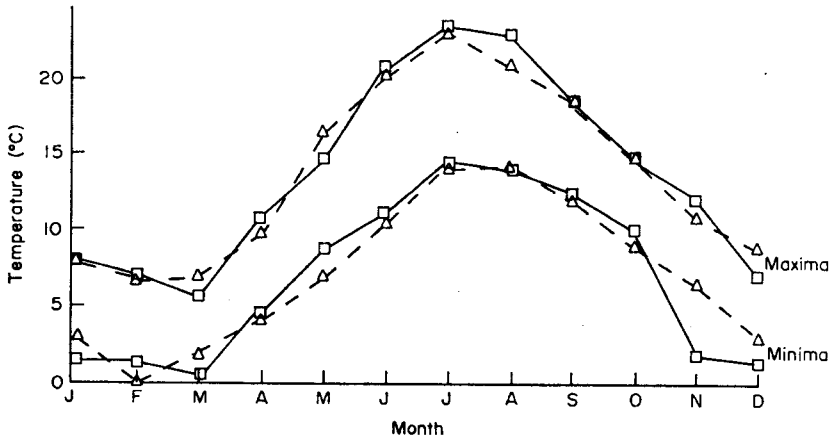

Fig. 4. Monthly maximum and minimum temperatures in Llyn Dinas and Lake Windermere. □——□, Llyn Dinas, 1969; △- - -△, Lake Windermere (Jenkin, 1942).

seen to be remarkably similar. The values for Windermere are taken from Jenkin (1942) and are the mean values for the years 1933–38, which covers the period of Moon's fieldwork. The small mean length of Moon's December sample suggests that hatching occurred at a later stage than in Llyn Dinas. The mean length for Moon's sample on 13 December 1934 was 1·74 mm (2·0 mm adjusted), whereas the mean length in Llyn Dinas on 18 December 1969 was 3·41 mm (Fig. 3). Even if the smaller size groups are under-represented in the Llyn Dinas sample the samples are still very different. Without conducting laboratory studies on the incubation period of eggs from Lake Windermere and carrying out field collections between August and November in Windermere, it is difficult to go any further with this comparison and its explanation. There is the possibility that the life cycle of *L. vespertina* differs in the two habitats in that diapause eggs are found in Windermere (cf. Khoo, 1968).

Acknowledgments

The study was carried out under the supervision of Professor T. B. Reynoldson to whom I am most grateful for advice both during the study and in the preparation of this manuscript. Laboratory facilities were provided by the late Professor F. W. R. Brambell and by Professor J. M. Dodd. The work was carried out during the tenure of a NERC research studentship.

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