The distribution, life cycle and production of *Leptophlebia vespertina* (L.) (Ephemeroptera) in a lowland lake

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Abstract

Oak Mere, the water body studied, is a moderately productive base-poor lowland lake. It has zones of submerged marginal vegetation growing on sand at the south-west end and on peat at the north-east end. The distributions of *L. vespertina* and other macroinvertebrates are described in relation to these two distinct areas. Laboratory experiments on behaviour and survival are described in an attempt to explain the patterns of distribution. The seasonal distribution, variations in population density, spatial distribution variance in relation to mean density, life cycle, length-weight relationship, growth and biomass of *L. vespertina* are then described during two years at the sandy south-west end. The data are used to estimate annual production. Distribution, life cycle, growth and production are compared with populations in water bodies of lower conductivity in the British Isles and Scandinavia.

Introduction

Leptophlebia vespertina (L.) is widely distributed in the Palaearctic region. It has been studied especially in Scandinavia, Poland and the British Isles producing a total of eight separate accounts of the life cycle (Clifford, 1982). Although found in rivers, it normally occurs in lentic habitats situated in mountain areas. Thus it is associated with waters which contain low concentrations of dissolved solids, are frequently of low base status and may be described as unproductive or oligotrophic. In contrast, the present study was undertaken in a lake in a lowland glacial drift plain in Cheshire, England. The lake, Oak Mere, is one of a group of approximately 60 ranging in area from 1–70 ha distributed below 120 m O.D. in intensively cultivated agricultural land. The majority of these lakes contain base-rich alkaline waters with abundant dissolved solids and hence are productive or eutrophic (Reynolds, 1979; Savage & Pratt, 1976). The typical ephemeropteran species are *Cloeon dipterum* (L.) and *Caenis horaria* (L.); *L. vespertina* has been recorded from only three of these lakes.

Thus Oak Mere provides an opportunity for a study of *L. vespertina* at the probable limit of its range in relation to eutrophic conditions. The aim was to describe the distribution, life cycle and production of *L. vespertina* within Oak Mere in relation to abiotic and biotic environmental factors. The field data are supported by laboratory experiments on habitat choice and survival in relation to predation. The results are then compared with data on populations from oligotrophic lakes (Brittain, 1972, 1974, 1978; Kjellberg, 1972, 1973; Macan, 1965, 1975, 1977a, 1977b; Moon, 1939).

It should be noted that the term 'distribution' is used to describe different population densities in relation to different environmental conditions while 'spatial distribution' is used to describe the spatial relationships of individuals within populations.

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Methods

Collection of field data

Collections of macroinvertebrates (except Chironomidae) were made at five stations along the edge of the lake. Each station comprised a square with 50 m sides; one side formed by the edge of the lake (Fig. 1). Each station was divided into a number of zones parallel with the shore according to the zonation of plants and/or substrata. The zonation varied both spatially and temporarily and hence full details are given in the description of the habitat. Initially, ten standard samples were taken from each zone at every station on each visit. During the later part of the study attention was confined to station 1 (collection dates are shown in the relevant text figures; the gaps during each winter were caused by ice cover).

A standard sample was based on a standard net sweep. A narrow D-shaped net of 0.5 mm mesh and 20 cm wide was pushed a distance of 25 cm just below the substratum; thus sampling 0.05 m^2. During the initial stages a 12.7 cm diameter core sampler was used to check the net samples. There were no significant differences in the mean numbers of *L. vespertina* but fewer specimens were caught of some taxa. This method caused damage to the substratum and was abandoned. Emergence data were obtained from floating traps. Each trap covered 0.05 m^2 and comprised a box-shaped wooden frame with a celluloid acetate top and nylon mesh sides.

The numbers of each species or taxon were counted, arithmetic means calculated and 95% confidence limits estimated from log-transformed data (Elliott, 1977). On each collecting date, a random sample of nymphs from each zone of station 1 was measured live to the nearest 0.1 mm from the front of the head to the back of the last abdominal segment. The entire sample was dried at 105 °C for four hours and weighed to the nearest 0.1 mg. Mean lengths (±95% confidence limits) and mean dry weights were then calculated.

The distribution of macrophytes was surveyed in 1977 and 1979. The survey was based on line transects at right angles to the shore placed at 10 m intervals within stations and at 100 m intervals for the remainder of the lake. Samples of substratum from each zone of each station and surface water samples were taken on six occasions. The percentage organic matter of the substrata; conductivity, pH and major ions of water samples were estimated (for methods, see Savage, 1981). Water temperatures were recorded with maximum-minimum and integrating thermometers.

Laboratory experiments

Specimens of *L. vespertina* were collected in March 1979 and maintained in the laboratory above a sand substratum containing plants of *Littorella uniflora* (L.) Aschers. in water from Oak Mere. Two experiments were performed; a series on survival in relation to predation and a series on environmental choice.

Survival experiments were performed in enamel dishes 20 cm long, 15 cm wide and 6 cm deep. The bottom of each dish was covered with a layer of washed Oak Mere sand 1 cm deep into which were anchored 9 leaves of *L. uniflora.* Fifty nymphs of *L. vespertina* were placed in each of five dishes; one dish was left as a control and five specimens of *Polycelis nigra* (Müller) were placed in the second dish. Then five specimens of *Asellus meridianus* Racovitza, *Coenagrion puella* (L.) nymphs, and *Rhantus exoletus* (Forster) larvae were placed in each of the remaining dishes respectively. The numbers of surviving *L. vespertina* were counted daily for five days. A total of five replicates was used. The Coefficient of Mortality (Z) was derived from the equation:

$$Z = \frac{-(\mathrm{Log_e}N_2 - \mathrm{Log_e}N_1)}{t_2 - t_1} \qquad (1)$$

where N_1 and N_2 are initial and final population densities and t_1 and t_2 initial and final times. This equation (1) is also used for field data.

Null hypothesis choice experiments were performed in 10 cm diameter, 2 cm deep glass dishes. Two contrasting environments were provided in each half of a given dish and a control dish, containing a single environment, was placed 25 cm distant. Both dishes were placed on a matt black background. Each pair of experiments was performed at a series of nine light intensities ranging from 50–5000 lux (the lowest was omitted in some experiments as the nymphs could not be seen). A light source was placed vertically above each dish and light intensities were controlled by adjusting the

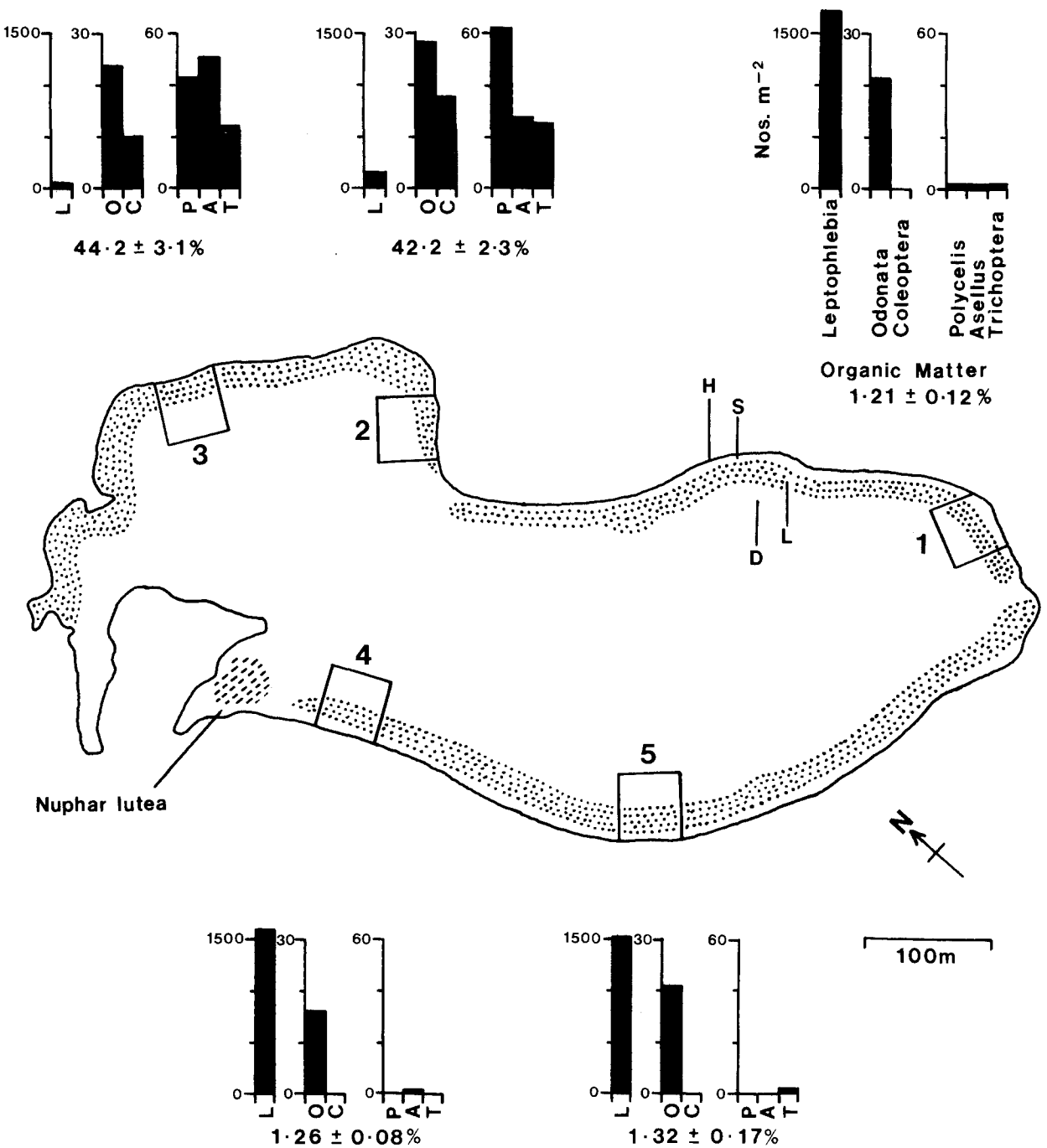


Fig. 1. The distribution of macrophytes, major macroinvertebrate taxa and percentage organic matter of the substrata in the *Littorella* zone (L) at five stations (1 – 5) in Oak Mere. Spearman rank correlation coefficients: for *L. vespertina* and % organic matter $r_S - 0.75$, p 0.01, df 19; for *L. vespertina* and remaining macroinvertebrate taxa except Odonata $r_S - 0.68$, p 0.01, df 19. Data from collections on 14 March, 16 May, 26 October and 9 December 1978. Key to zones: H, *Hydrocotyle;* S, sand; L, *Littorella;* D, deeper water devoid of macrophytes.

distances of the sources, checking with light meters placed adjacent to the dishes. The remainder of the laboratory was in total darkness. It was noted that nymphs tended to show periods of 2–3 h high activity followed by 2–3 h low activity. Thus experiments were started at 4 h intervals throughout a given 24 h period. The diel behaviour described by Solem (1973) was not readily apparent under experimental conditions. Details of the environmental choices provided are given in Fig. 12. Ten nymphs were introduced into an experimental dish and then into the adjacent control dish. They were left undisturbed for 1 h. Then the number of nymphs in one half of each dish was noted on 20 occasions at 2 min. intervals at each light intensity. The Chi-squared test was then applied and results expressed as percentage occurring in one half of a dish over 20 replicates.

The expression of growth

Growth of Ephemeroptera nymphs is exponential (Humpesch, 1979, 1981, 1983) and therefore may be expressed by the equation:

$$W_t = W_o\, e^{bt} \qquad (2)$$

Converting to logarithms:

$$\mathrm{Log}_e W_t = \mathrm{Log}_e W_o + bt \qquad (3)$$

where W_o is initial dry body weight (mg) and W_t is final dry body weight (mg). For the expression of growth in relation to temperature, in the section on life cycle, t is time (days) between successive samples and b is the relative growth rate (mg mg^{-1} d^{-1}): it is expressed as Mean Specific Growth Rate = b(100) (% increase dry body weight d^{-1}). For estimates of production t between successive samples is taken as 1: hence b is the relative growth rate between samples (mg mg^{-1}) and equals G in the production equation:

$$P = G\bar{B} \qquad (4)$$

Details of other mathematical methods are given in the relevant section of the text.

Results

The habitat

Oak Mere (Grid Ref. SJ 575677) lies at an altitude of 72 m O.D. in the Cheshire-Shropshire Plain, England. It is unique among the principal meres of the region owing to its low base status. The remaining meres are rich in calcium and bicarbonate ions; a typical example, Hatch Mere (SJ 553722) is given for comparison in Table 1. Further data are available in Reynolds (1979) and Savage (1982). However, phytoplankton production is similar to the remaining meres (Reynolds, 1978; Swale, 1968).

In 1977 the surface area was 18.4 ha and the maximum depth 5.7 m. By 1981, owing to a rise in water level, the surface area had increased to 19.2 ha and the maximum depth to 6.0 m.

The mere substratum was divisible into two distinct regions; a peaty north-east part and a sandy south-west part. In 1977 the submerged vegetation, in water up to 0.4 m deep, consisted almost exclusively of a pure sward of *L. uniflora* some 15 m wide (designated L). It was contiguous with the shore at the north-east end but separated by 2–5 m sand (S) elsewhere. In addition, there was a small area of *Nuphar lutea* (L.) Sm. (Fig. 1). The remaining marginal vegetation was above water level except for a few clumps of *Typha latifolia* L., *Carex rostrata* Stokes, *Eleocharis palustris* (L.) R.Br., Roem. & Schult. and *Juncus effusus* L. There followed a slow rise in water level. By March 1979 it reached the marginal zone and by May extended onto it some 4 m (H). The level then remained sta-

Table 1. The pH, conductivity (μS cm^{-1} at 25 °C) and concentrations (m–equiv. l^{-1}) of major ions in Oak Mere (means ±95% confidence limits, df 5) and, for comparison, a more typical northwest Midlands site, Hatch Mere (sampled 14 October 1980).

Lake	Oak Mere	Hatch Mere
pH	4.7 ± 0.14	7.0
Conductivity	157 ±25	490
Ca^{2+}	0.45 ± 0.07	2.23
Mg^{2+}	0.30 ± 0.07	1.61
Na^{+}	0.43 ± 0.08	0.57
K^{+}	0.08 ± 0.02	0.13
HCO_3^-	0.07 ± 0.02	2.12
SO_4^{2-}	0.54 ± 0.23	1.43
Cl^-	0.72 ± 0.08	1.22

ble, apart from a temporary rise in April 1980, until July 1980 when a further rise commenced. The commonest plants in this new marginal zone were *Hydrocotyle vulgaris* L., *Juncus bulbosus* L., *J. effusus, C. rostrata* and *E. palustris* overlying a carpet of bryophytes composed principally of *Sphagnum auriculatum* Schimp. and *Drepanocladus fluitans* (Hedw.) Warnst. Initially, the five stations were divisible into 2 or 3 zones. There were 2 zones at stations 2 and 3; *Littorella* (L) and deeper water devoid of plants (D). There were 3 zones at stations 1, 4 and 5; sand (S), *Littorella* (L) and deeper water (D). Later, the *Hydrocotyle* zone (H) was flooded and there was an additional zone at every station (Fig. 1).

The only species of fish recorded was *Perca fluviatilis* L.

The distribution of L. vespertina *and other macroinvertebrates in relation to environmental factors*

Sixty-five taxa of macroinvertebrates were recorded from Oak Mere (Table 2). Initially, the

Table 2. The macroinvertebrates recorded from Oak Mere.

Coelenterata
- Hydrozoa
  - *Hydra* spp.

Platyhelminthes
- Turbellaria
  - Tricladida
    - *Polycelis nigra* (Müller)

Mollusca
- Gastropoda
  - *Lymnaea peregra* (Müller)
  - *Planorbis albus* (Müller)
- Lamellibranchia
  - *Pisidium obtusale* (Lamarck)

Annelida
- Hirudinea
  - *Haemopsis sanguisuga* (L.)
  - *Theromyzon tessulatum* (Müller)

Crustacea
- Malacostraca
  - Isopoda
    - *Asellus meridianus* Racovitza

Arthropoda
- Insecta
  - Ephemeroptera
    - *Leptophlebia vespertina* (L.)
    - *Cloeon dipterum* (L.)
    - *Cloeon simile* Eaton
  - Odonata
    - *Pyrrhosoma nymphula* (Sulzer)
    - *Ischnura elegans* (van der Linden)
    - *Enallagma cyathigerum* (Charpentier)
    - *Coenagrion puella* (L.)
    - *Lestes sponsa* (Hansemann)
    - *Aeshna cyanea* (Muller)
    - *Aeshna grandis* (L.)
    - *Libellula quadrimaculata* L.
    - *Sympetrum danae* (Sulzer)
    - *Sympetrum striolatum* (Charpentier)
  - Plecoptera
    - *Nemoura cinerea* (Retzius)
    - *Perlodes microcephala* (Pictet)
  - Hemiptera
    - *Nepa cinerea* L.
    - *Notonecta glauca* L.
    - *Corixa punctata* (Illinger)
    - *Hesperocorixa linnei* (Fieber)
    - *Sigara dorsalis* (Leach)
    - *Sigara falleni* (Fieber)
    - *Sigara scotti* (Fieber)
    - *Sigara semistriata* (Fieber)
  - Trichoptera
    - *Holocentropus stagnalis* (Albarda)*
    - *Cyrnus flavidus* McLachlan*
    - *Phryganea* spp. larvae
    - *Phryganea striata* (L.)*
    - *Agrypnia pagetana* Curtis*
    - *Limnephilus griseus* (L.)*
    - *Limnephilus politus* McLachlan*
    - Leptoceridae spp. larvae
    - *Mystacides longicornis* (L.)*
    - *Triaenodes bicolor* (Curtis)*
    - *Oecetis lacustris* (Pictet)*
    - *Molanna* spp. larvae
    - *Molanna angustata* Curtis*
  - Coleoptera
    - *Haliplus fluviatilis* Aubé
    - *Haliplus ruficollis* (Degeer)
    - *Hygrobia hermanni* (Fabricius)
    - *Noterus crassicornis* (Muller)
    - Dytiscidae spp. larvae
    - *Laccophilus minutus* (L.)
    - *Hygrotus inaequalis* (Fabricius)
    - *Hydroporus erythrocephalus* (L.)
    - *Hydroporus palustris* (L.)
    - *Hydroporus striola* (Gyllenhal)
    - *Potamonectes assimilis* (Paykull)
    - *Agabus sturmi* (Gyllenhal)
    - *Ilybius fenestratus* (Fabricius)
    - *Ilybius fuliginosus* (Fabricius)
    - *Ilybius subaeneus* (Erichson
    - *Rhantus exsoletus* (Forster)
    - *Colymbetes fuscus* (L.)
    - *Helochares lividus* (Forster)
    - *Enochrus affinis* (Thunberg)
    - *Enochrus testaceus* (Fabricius)
    - *Oulimneus tuberculatus* (Muller)
  - Diptera
    - Chironomidae spp. larvae

* Trichoptera adults identified from trapped specimens.

majority were present only in the *Littorella* zone (L). Only six taxa may be described as generally common: *L. vespertina, P. nigra, A. meridianus,* Odonata, Trichoptera and Coleoptera larvae (Fig. 1). The communities at the five stations were divisible into two distinct groups. Stations 1, 4 and 5, situated on sand, were characterised by large populations of *L. vespertina* and smaller numbers of Odonata. Stations 2 and 3, on peat, contained all six taxa but the numbers of *L. vespertina* were low. This division into two types of communities was associated with equally distinct differences in the organic matter content of the substrata (Fig. 1).

The flooding of the *Hydrocotyle* zone (H) in 1979 permitted further comparisons at Station 1. The same six taxa were common except for *A. meridianus* (Fig. 2). All were virtually absent from the sand zone (S; % organic matter 0.28 ± 0.20, 95% confidence limits, df 19) and the deeper zone (D; 0.31 ± 0.27). Coleoptera (70% *R. exsoletus* larvae and adults) were restricted to the *Hydrocotyle* zone (H; 7.90 ± 3.40). Trichoptera larvae (70% Leptoceridae spp.) and *P. nigra* also reached significantly higher densities in the *Hydrocotyle* zone (H), compared with the *Littorella* zone (L; 1.20 ± 0.09), especially towards the end of the sampling period. *L. vespertina* and Odonata larvae were common in both zones. Thus, the differences within Station 1 confirm those found between stations.

Product-moment regression analysis of the entire data showed closest agreement when percentage organic matter was treated as a logarithmic function. In Fig. 3 data from substrata with an organic matter content below 1.2% (i.e. the zones where few specimens of all taxa were caught) have been omitted from the analysis and are shown only as a visual indication. This procedure makes little difference to those taxa showing a positive correlation (*P. nigra,* Coleoptera and Trichoptera) or no correlation (Odonata). However, it enables one to appreciate that *L. vespertina* would show a positive correlation with organic matter (r 0.99, $p < 0.001$) up to 1.2% and the negative correlation demonstrated thereafter. Thus, 1,2% organic matter provides optimum conditions for *L. vespertina* in Oak Mere. It occurs in the *Littorella* zones (L) at stations 1, 4 and 5. These conclusions are supported by Spearman's rank analysis (Fig. 3).

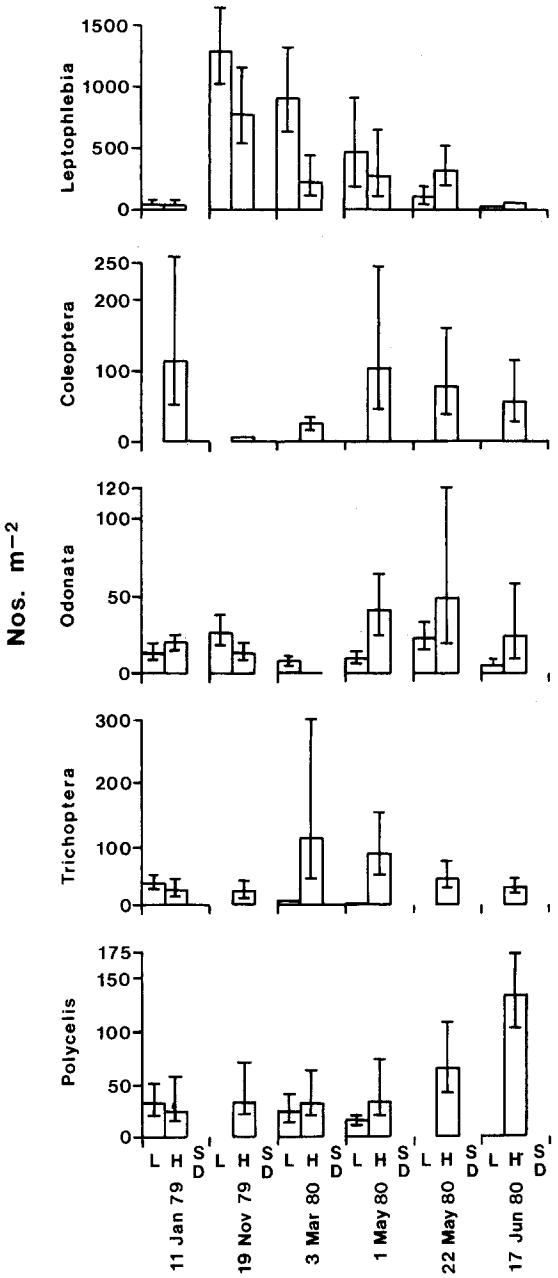


Fig. 2. The distribution of major macroinvertebrate taxa (Nos. $m^{-2} \pm 95\%$ confidence limits; the latter are only marginally different from the means when omitted) in the *Hydrocotyle* (H), sand (S), *Littorella* (L) and deeper water (D) zones of station 1 on the dates indicated. Note that the spatial order of zones has been changed to allow easier comparisons and S and D conflated because so few specimens were caught.

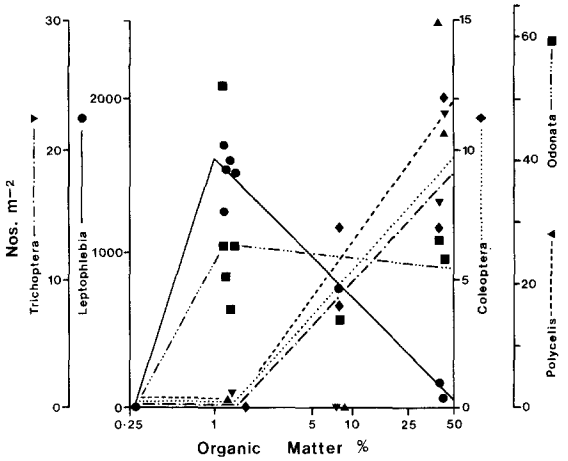


Fig. 3. The distribution of major macroinvertebrate taxa (Nos. m^{-2}) in relation to percentage organic matter of the substrata. The section of the graph <1.2% organic matter is a visual presentation only. Product-moment regression equations: *L. vespertina,*
$Y = 1608.0 - 397.4\ Log_eX$, r −0.98, $p < 0.001$; *P. nigra,*
$Y = 13.76\ Log_eX - 4.99$, r 0.90, $p < 0.001$; Coleoptera,
$Y = 2.63\ Log_eX - 0.64$, r 0.95, $p < 0.001$; Trichoptera,
$Y = 5.04\ Log_eX - 1.73$, r 0.90, $p < 0.001$; Odonata,
$Y = 26.5 - 1.04\ Log_eX$, r −0.14 p not significant.
For each taxon except Odonata $p < 0.05$ from Spearman rank correlation coefficient (r_s). df 7.

The life cycle and distribution of L. vespertina *at Station 1*

L. vespertina had a univoltine annual life cycle in Oak Mere with rapid growth in autumn and spring and slower growth during winter. The only possible deviation from this pattern was indicated by the presence of a few large nymphs on 15 August and 19 September 1979 which must have developed from eggs laid in 1978 (Figs 4 & 5).

From September 1977 until March 1979 nymphs were present only in the *Littorella* zone (L). However, the marginal *Hydrocotyle* zone (H) was then flooded. Nymphs were first recorded in this newly created zone in May 1979 and then on all subsequent occasions until August 1980 (Figs 4 & 5). Thus, the 1977–78 generation (details omitted) developed only in, and emerged from, the *Littorella* zone (L); the 1978–79 generation commenced development in the *Littorella* zone (L) but was recorded in the *Hydrocotyle* zone (H) also from May 1979 while the 1979–80 generation developed continuously in both zones (Figs 4 & 5).

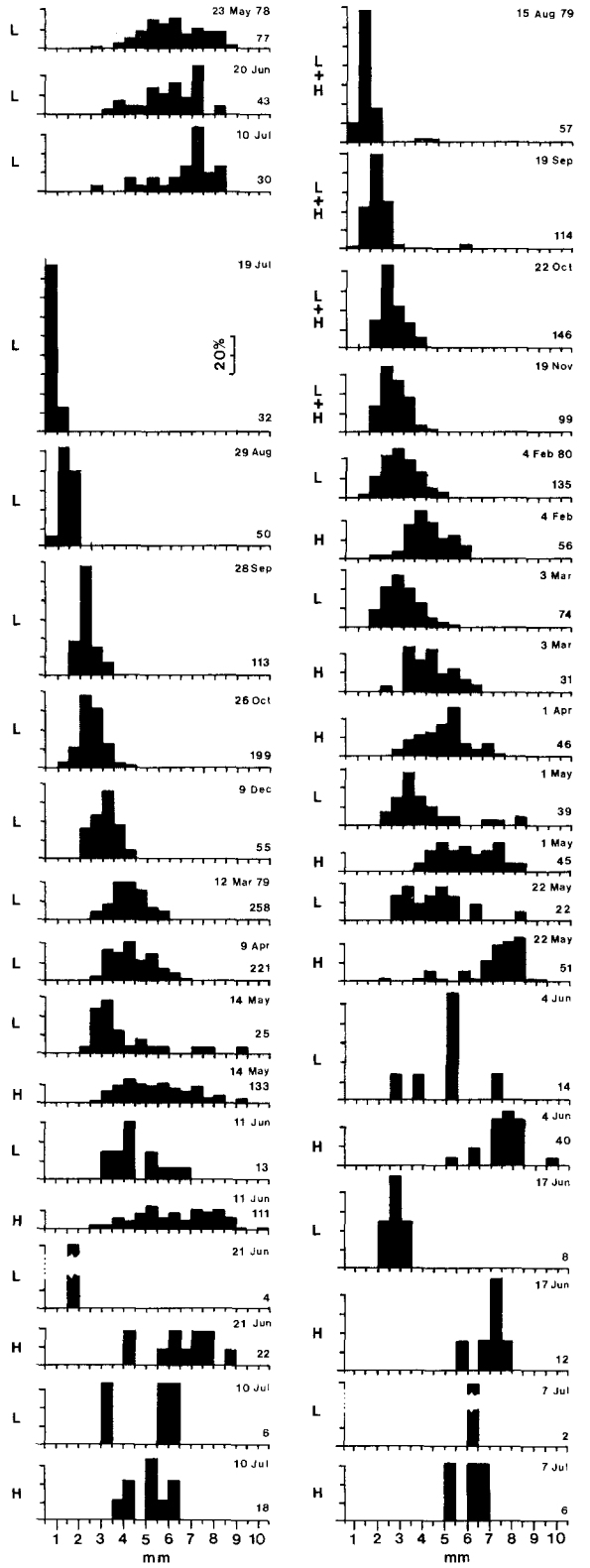


Fig. 4. Size structure histograms of nymphs of *L. vespertina* in the *Littorella* (L) and *Hydrocotyle* (H) zones at station 1 in Oak Mere. Sample sizes and dates are indicated.

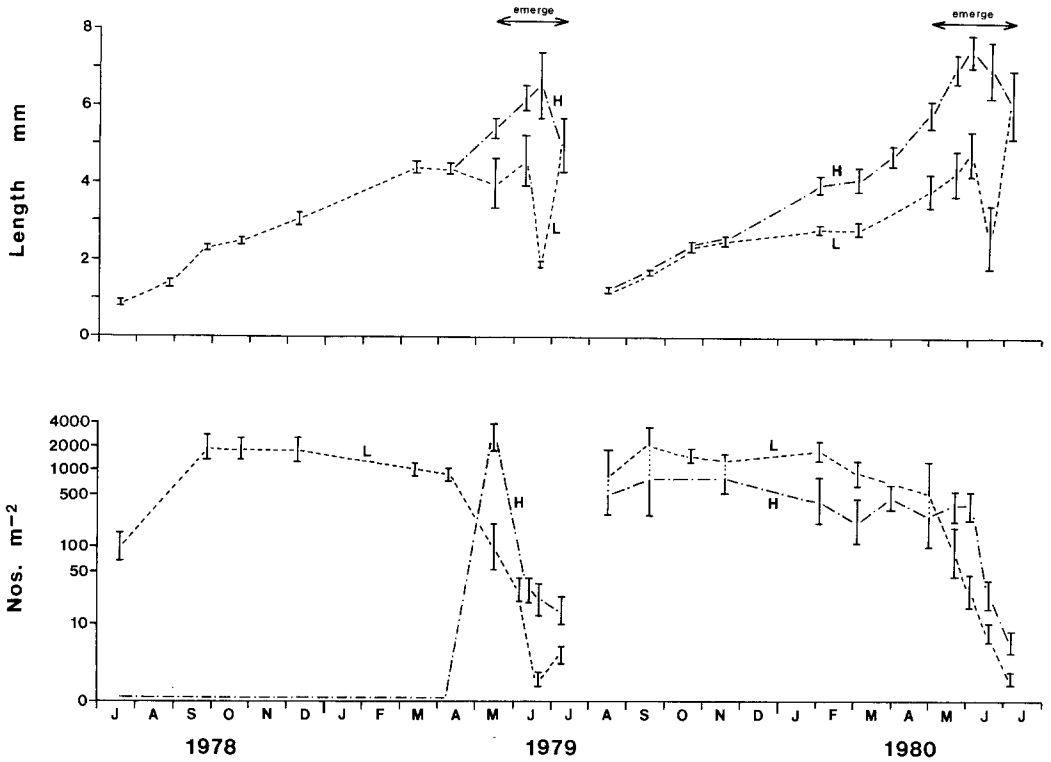


Fig. 5. The population densities (Nos. m^{-2}) and mean lengths (mm) (±95% confidence limits) of nymphs of *L. vespertina* in the *Littorella* (L) and *Hydrocotyle* (H) zones at station 1 in Oak Mere.

Generally similar life cycles were found in the 1978–79 and 1979–80 generations. However, certain differences of detail were apparent. A comparison of population densities of the 1978–79 generation shows significant evidence of migration from the *Littorella* (L) to the *Hydrocotyle* zone (H) immediately prior to emergence from the latter. Moreover, the nymphs in the *Hydrocotyle* zone (H) were significantly longer and hence migration was differential in relation to body length. The size-structure distributions were distinctly different from the later stages of the 1977–78 generation (Fig. 4). In the 1979–80 generation there were significant differences in body length between the two zones by February 1980. It is not possible to deduce whether these differences were caused by differential growth or by migration. Population densities were significantly higher in the *Littorella* zone (L) on occasion and there is a suggestion of migration to this zone between November 1979 and February 1980. By May 1980 the evidence strongly suggests that differential migration from the *Littorella* (L) to the *Hydrocotyle* zone (H) is the most probable explanation, as in 1979 (Figs 4 & 5). Again, emergence occurred from only the *Hydrocotyle* zone (H). A single night collection during the emergence period in 1979 suggested that nymphs crossed the intervening sand zone (S) during the hours of darkness.

Nymphal growth and population densities may be considered for the two zones together (m^{-1} shore) by calculation from the separate sets of raw data (m^{-2}). Nymphal body length (L, mm) and dry body weight (W, mg) show a highly significant correlation when analysed by the equation:

$$W = aL^b \tag{5}$$

or logarithmically:

$$\mathrm{Log_e}W = \mathrm{Log_e}a + b\mathrm{Log_e}L \tag{6}$$

where a and b are constants (see also Brittain, 1978 and Smock, 1980). Thus, proportional dry weights

were calculated from proportional mean body lengths (Fig. 6) and used to estimate Mean Specific Growth Rates (% increase dry weight d^{-1}). There was a marked difference in the relationships between growth rate and water temperature in the two generations (Fig. 7). The correlation coefficient (r 0.52, $p<0.1$, df 8) was barely significant for the 1978–79 generation but highly significant (r 0.92, $p<0.001$, df 7) in 1979–80. There was a significant correlation (r 0.65, $p<0.01$, df 16) when the two generations were considered together.

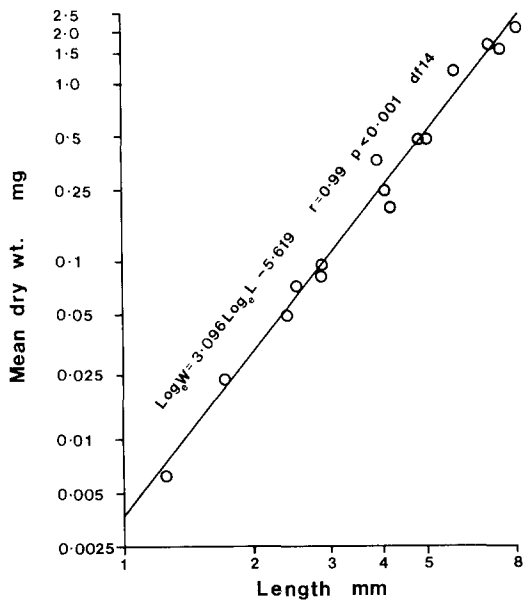


Fig. 6. The relationship between individual dry weight (mg) and length (mm) in nymphs of *L. vespertina* from Oak Mere.

Mean population densities of nymphs (m^{-1} shore) from maxima in September to collections immediately prior to emergence showed significant mortality (Fig. 8). The decreases in population densities fitted linear and exponential regression models equally well. Increase in body length was significantly higher during winter 1978–79 than in 1979–80 and hence dry body weight and growth (Figs 5, 6 & 7). Biomass (B), at a given time, may be expressed by the equation:

$$B = NW \qquad (7)$$

where N is population density (m^{-1} shore) and W is mean dry weight (mg) of an individual nymph. It follows that the marked difference in biomass between the two generations immediately prior to emergence is significant; similarly, the proportional difference in biomass of subimagines (Fig. 8). It is equally probable that the decreases in biomass in March-April 1979 and February 1980 are significant since growth was negligible at those times and the phenomena occurred whether population densities were derived from raw data or regression analysis. Thus biomass was significantly higher in 1978–79 than in 1979–80.

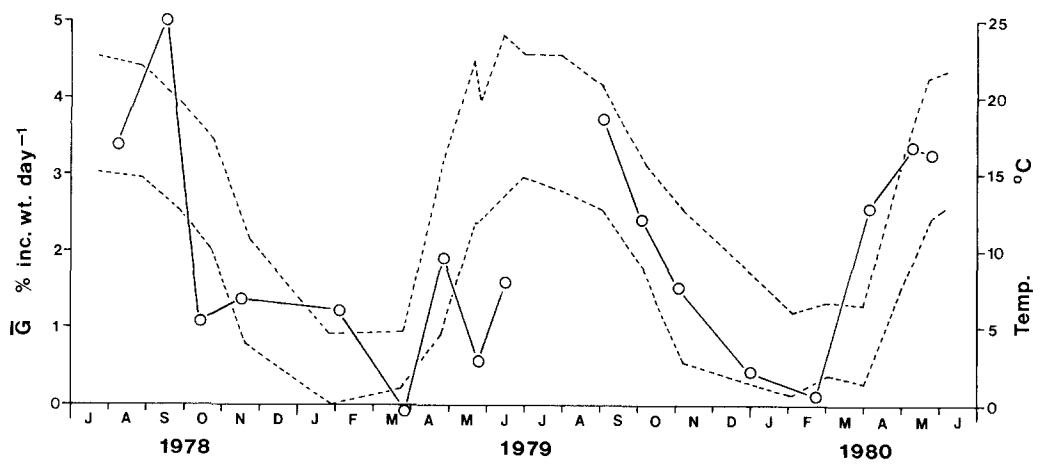


Fig. 7. The Mean Specific Growth Rates, $\bar{G}$ (% increase dry weight d^{-1} between successive combined samples from both the *Littorella* (L) and *Hydrocotyle* (H) zones at station 1), of nymphs of *L. vespertina* from Oak Mere together with maximum and minimum lake temperatures (°C).

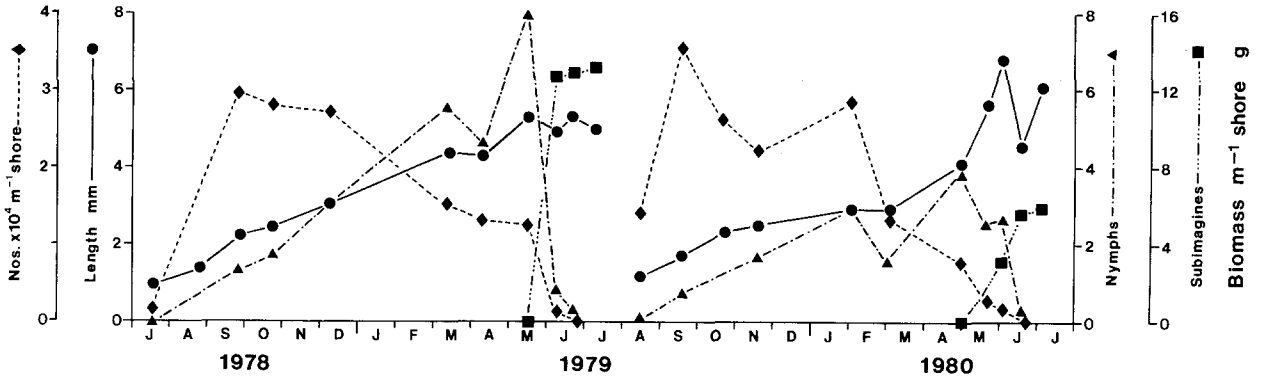


Fig. 8. The population densities (Nos.$\times 10^4$ m^{-1} shore), mean length of combined samples (mm), biomass (g dry weight m^{-1} shore) of nymphs and cumulative biomass (g dry weight m^{-1} shore) of emerged subimagines of *L. vespertina* at station 1 in Oak Mere. The linear and logarithmic regression equations (constants ±95% confidence limits) derived from population density (Nos. m^{-1} shore) in relation to time ($month^{-1}$ from date of autumn maxima to date prior to emergence) and mortality ($Z\ d^{-1}$) for the two generations are:
1978–79, $Y = 30894.6 \pm 1870.1 - 2556.7 \pm 650.0X$, r −0.98, $p < 0.001$, Z −0.0040; $Log_e Y = 10.383 \pm 0.098 - 0.129 \pm 0.034X$, r −0.98, $p < 0.001$, Z −0.0043; 1979–80, $Y = 32661.7 \pm 6127.4 - 3008.2 \pm 2372.6X$, r −0.85, $p < 0.02$, Z −0.0053; $Log_e Y = 10.480 \pm 0.327 - 0.168 \pm 0.127X$, r −0.86, $p < 0.02$, Z −0.0056, df 5.

The spatial distribution of nymphs of L. vespertina *at Station 1*

Recent studies have produced convincing evidence that Taylor's power law (Taylor, 1961) provides a suitable model for expressing the spatial characteristics of density-dependent distributions of organisms (Elliott, 1982; Taylor *et al.*, 1978, 1979).

Taylor's model proposes that spatial variance (s^2) is proportional to a fractional power (b) of mean population density ($\bar{x}$). It is given by the equation:

$$s^2 = a\bar{x}^b \qquad (8)$$

or logarithmically:

$$Log_e s^2 = Log_e a + b Log_e \bar{x} \qquad (9)$$

where both a and b are constants.

Preliminary calculations from the present data showed that there were no significant differences in spatial distribution of nymphs in the *Littorella* (L) and *Hydrocotyle* (H) zones, at different times of the annual cycle or between the two generations. Thus, total data are presented (Fig. 9). The power law provides an excellent fit with the data ($p < 0.001$) and thus demonstrates that spatial dis-

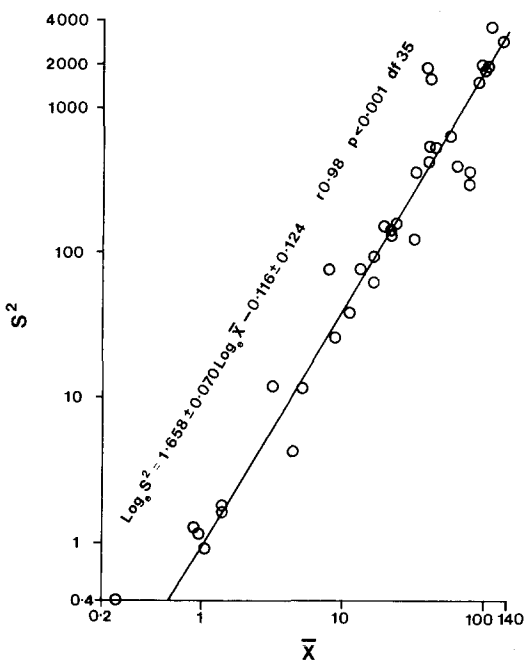


Fig. 9. The relationship between variance (s^2) and mean population density ($\bar{x}$) in samples of nymphs of *L. vespertina* from the *Littorella* (L) and *Hydrocotyle* (H) zones at station 1 in Oak Mere. A standard sample covered 0.05 m^2.

tribution of nymphs was contagious and density-dependent. The mean density ($\bar{x}$) at which dispersion approaches randomness ($s^2/\bar{x}=1$) and below which it approaches regularity ($s^2/\bar{x}<1$) is given by the expression:

$$\bar{x}=^{b-1}\sqrt{1}/a \qquad (10)$$

or logarithmically:

$$\text{Log}_e\bar{x}=\frac{[\text{Log}_e(1/a)]}{b-1} \qquad (11)$$

The estimate of $\text{Log}_e\bar{x}$ is 0.1768, equivalent to a mean density of $1.193^{-0.05m^2}$ i.e. 23.86^{-m^2}. Population densities below this value were recorded only in late June and July at the extreme ends of the emergence periods. Thus spatial distribution was contagious and density-dependent for virtually the whole nymphal life cycle.

Production of L. vespertina

The field data collected during an annual cycle comprise three components. 1. Population densities m^{-2}, mean lengths and mean dry weights of nymphs in the *Littorella* zone (L), 2. similar data for the *Hydrocotyle* zone (H) and 3. population densities m^{-1} shore for emerging subimagines together with dry weights of fully mature nymphs (Figs 5, 6 & 8; Table 3). It was clear that nymphs increased in length rapidly during the emergence period but equally clear that data based on nymphs only did not fully reflect this change. Thus, emergence data were used in estimates of production by substituting the dry weights of fully mature nymphs for those of subimagines. Migration has been demonstrated between zones and hence it is not possible to be sure whether recorded changes occurred in a particular zone. Thus total production estimates are in terms of dry weight m^{-1} shore (m^{-1} shore is equivalent to 15 m^2 *Littorella* (L) and 4 m^2 *Hydrocotyle* (H) zones: total 19 m^2).

Two methods were applied for the assessment of production.

a) An Allen curve (Allen, 1951) was constructed by plotting population density m^{-1} shore against mean individual dry weight (mg) on each sampling date (Fig. 10). The data from the life cycle prior to emergence were converted from m^{-2} to m^{-1} shore by simple proportion (Fig. 6). The estimates were 23.81 g dry weight m^{-1} shore for 1978–79 and 15.31 for 1979–80.

b) A computational method (Chapman, 1978) derived from the equation:

$$P=G\bar{B} \qquad (4)$$

Table 3. Mean weights (mg±95% confidence limits) of some stages in the life cycle of L. vespertina.

Stage	Dry weight	n	Live weight	n
Mature nymphs	1.97*	12	–	–
Subimagines	1.86±0.21	61	6.72±0.34	14
Imagines	1.62±0.18	55	5.28±0.26	22

* Mean dry weight from 12 specimens of mean length 8.09±0.29 mm weighed together.

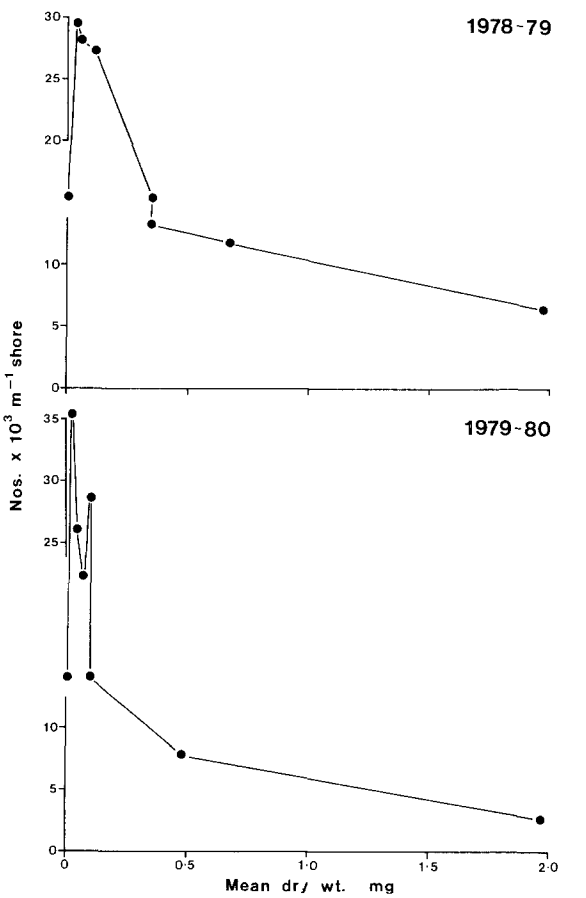


Fig. 10. Allen graphs showing population density (Nos. m^{-1} shore) in relation to mean individual dry weight (mg) of *L. vespertina* in the two generations of 1978–79 and 1979–80.

where P is production, G is instantaneous rate of increase in dry weight and $\bar{B}$ is mean biomass between successive samples. In this method data for the life cycle prior to emergence were initially computed m^{-2} (Tables 4 & 5). The production estimates were 22.59 g dry weight m^{-1} shore for 1978–79 and 13.57 for 1979–80.

The production values derived from the two methods show close agreement. It is not possible to estimate total production m^{-2} accurately but an approximate value may be gained from computation. Furthermore, production may be expressed in terms of energy by using the conversion factor; 1 mg dry weight ≙ 21.6 J (Kjellberg, 1972; Lien, 1978; Zelinka, 1984). Thus, the mean values are 23.20 g dry weight m^{-1} shore (501.1 kJ m^{-1} shore; 1.22 g dry weight m^{-2}) for 1978–79 and 14.44 (311.9; 0.76) for 1979–80.

It should be noted that there was a period of negative production when biomass declined in spring in both generations (Fig. 8; Table 4).

The survival of L. vespertina *when maintained with other macroinvertebrates*

Field observations in 1978 revealed predation of nymphs of *L. vespertina* by Odonata and Coleoptera larvae. In April 1979 laboratory experiments confirmed the field observations (Fig. 11). Nymphs of *L. vespertina* showed particularly low survival

Table 4. The production (dry weight) of nymphs of *L. vespertina* prior to first emergence of subimagines in the two seasons 1978–79 and 1979–80.

Sampling date	Population density (Nos.m^{-2})		Mean dry weight, W (mg)		Population biomass (mg m^{-2})		Growth ($Log_eW_2 - Log_eW_1$)		Mean biomass between sampling dates (mg m^{-2})		Production (mg m^{-2})		Production (Litt.×15 + Hydro ×4) (mg m^{-1} shore)
	Litt.	*Hydro.*	*Litt.*	*Hydro.*	*Litt.*	*Hydro.*	*Litt.*	*Hydro.*	*Litt.*	*Hydro.*	*Litt.*	*Hydro.*	
19 Jul 78	103	0	0.0025	0	0.26	0	1.386	0	44.52	0	128.66	0	
29 Aug 78	-	0	0.010	0	-	0	1.504	0	-	0	-	0	
28 Sep 78	1973	0	0.045	0	88.78	0	0.299	0	101.61	0	30.38	0	
26 Oct 78	1876	0	0.061	0	114.44	0	0.648	0	163.01	0	105.63	0	
9 Dec 78	1824	0	0.116	0	211.58	0	1.127	0	290.52	0	327.42	0	
12 Mar 79	1032	0	0.358	0	369.46	0	-0.025	0	338.99	0	-8.47	0	
9 Apr 79	884	0	0.349	0	308.52	0	-0.306	0.732	167.36	1100.96	-51.21	805.90	
14 May 79	102	2608	0.257	0.726	26.21	1893.41				Totals	532.41	805.90	11209.75
15 Aug 79	820	480	0.006	0.006	4.92	2.88	1.299	1.299	26.18	10.02	34.01	13.02	
19 Sep 79	2156	780	0.022	0.022	47.43	17.16	0.801	0.801	61.40	37.44	49.18	45.42	
22 Oct 79	1538	-	0.049	0.049	75.36	-	0.412	0.412	84.82		34.95		
19 Nov 79	1274	780	0.074	0.074	94.27	57.72	0.229	1.201	130.65	77.57	29.92	93.16	
4 Feb 80	1796	396	0.093	0.246	167.03	97.42	-0.126	-0.237	120.25	70.05	-15.15	-16.60	
3 Mar 80	896	220	0.082	0.194	73.47	42.68		0.887	-	124.96	-	110.84	
1 Apr 80	-	440	-	0.471	-	207.24	1.539	0.917	123.83	256.76	190.57	235.45	
1 May 80	456	260	0.382	1.178	174.19	306.28							
										Totals	323.48	481.29	6777.36

Table 5. The production (dry weight) of nymphs during the emergence period (nymphal population immediately prior to emergence and fully grown nymphs estimated from trapped subimagines) in the two seasons 1978–79 and 1979–80.

Sampling date	Population density (Nos. m^{-1} shore)	Mean dry weight, W (mg)	Population biomass (mg m^{-1} shore)	Growth ($Log_eW_2 - Log_eW_1$)	Mean biomass (mg m^{-1} shore	Production (mg m^{-1} shore)
14 May 79	11962	0.666	7966.69	1.084	10500.11	11382.12
15 May–10 Jul 79	6616	1.970	13033.52			
1 May 80	7880	0.487	3837.56	1.397	4863.93	6794.91
9 May–7 Jul 80	2990	1.970	5890.30			

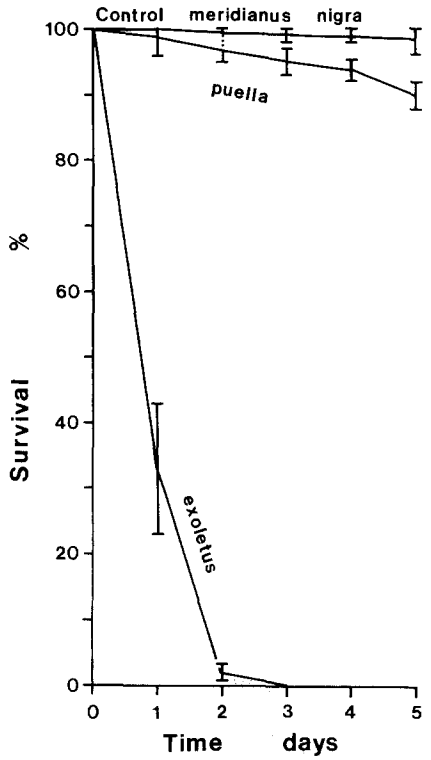


Fig. 11. The percentage survival (±95% confidence limits after Arcsin transformation) of nymphs of *L. vespertina* maintained in the laboratory alone (control) and with specimens of *P. nigra, A. meridianus, C. puella* and *R. exsoletus* respectively. Mortality (Z d^{-1}): control, *P. nigra* and *A. meridianus,* Z -0.003 ± 0.001; C. puella, Z -0.015 ± 0.004; R. exsoletus, Z -1.994.

when maintained with larvae of *R. exsoletus.* The beetles gripped the nymphs round the neck from below, holding them for 10–15 min., until struggling ceased. On many occasions the dead mayfly nymph was not eaten and the beetle immediately attacked another live nymph. Beetle larvae frequently killed mayfly nymphs larger than themselves. Predation by Odonata larvae was significant but much less marked. Survival in the remaining experiments did not differ significantly from the controls.

The behaviour of L. vespertina *in relation to environmental factors*

A series of null hypothesis choice experiments was used to investigate behavioural factors which might affect both the distribution and spatial distribution of nymphs (Fig. 12).

Background colour had no significant effect on behaviour (Fig. 12, A, B & C). It seems probable that the three components relating to the distribution of nymphs were texture, shade and shape. In the natural environment these components are provided by sand (texture) and *L. uniflora* (all three). There was a significant choice of shade at above 1000 lux when the substratum was glass which had an unnatural texture (Fig. 12, B & C); the nymphs were very active under these conditions. The nymphs were less active on the naturally textured sand substratum and significant numbers remained in shade at all light intensities (Fig. 12, D). When shape only was provided in the form of artificial *Littorella* (drawn from glass rod) on a glass substratum nymphs showed a significant preference for the appropriate shape at all light intensities (Fig. 12, E). When the same experiment was repeated with the substitution of a sand substratum shape was significantly preferred only between 1000–2000 lux. The nymphs showed high activity above 2000 lux and ceased resting on the artificial *Littorella* (Fig. 12, G). When all three components were provided in the form of real *L. uniflora* leaves nymphs showed a significant preference for the plant; it is noteworthy that choice was most marked when the natural substratum (sand) was absent (Fig. 12, F & H).

The foregoing observations suggest reasons why the distribution of nymphs in the lake was limited to zones where plants were present.

Discussion

The distribution of *L. vespertina* may be discussed from three distinct aspects; in relation to the biotopes within a given lake, in relation to different types of lakes, and the spatial distribution of individuals in relation to each other. The present paper is the only contribution to the latter aspect and it has been shown that spatial distribution is contagious and density-dependent.

Present evidence suggests that distribution within a lake is related to the distribution of detritus and macrophytes together with seasonal patterns of migration (Brittain, 1978; Brittain & Lillehammer, 1978; Kjellberg, 1972, 1973; Macan, 1965, 1975,

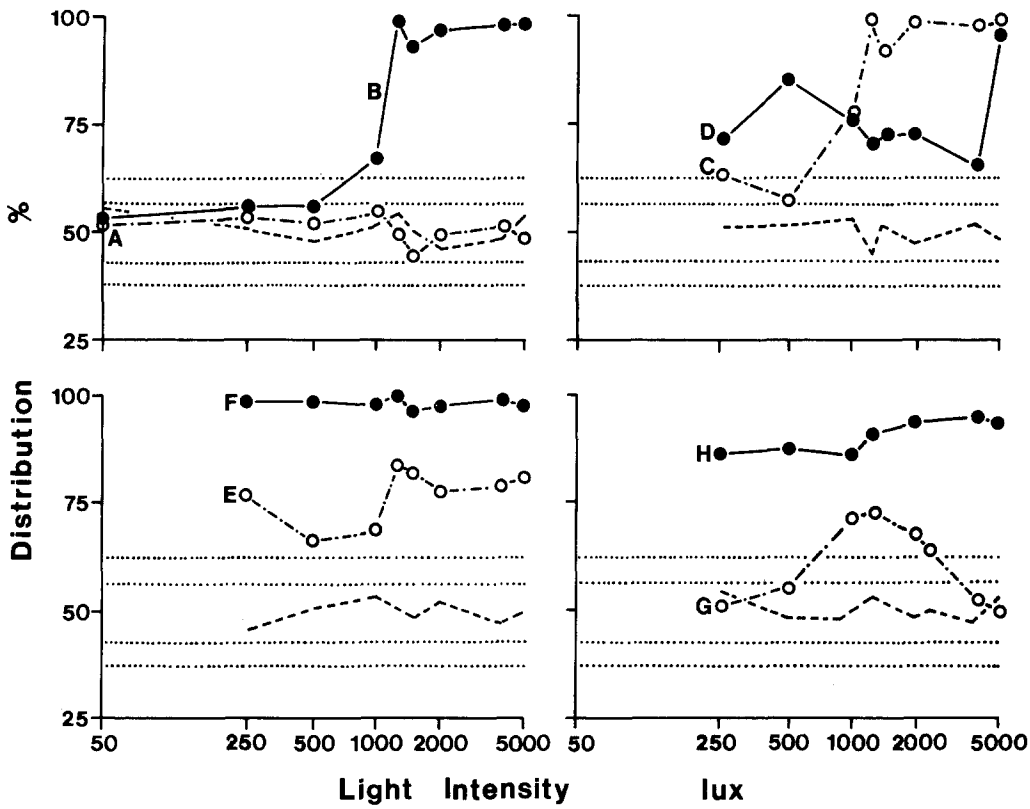


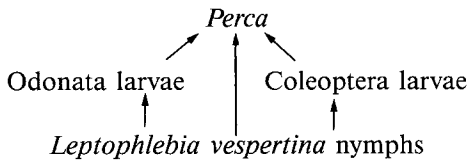
Fig. 12. The percentage of nymphs of *L. vespertina* present in one half of a chamber when provided with a choice between two environmental factors at a series of different light intensities (lux). The sets of factors, with % indicated on graphs named first in each pair, were: A, Black/White backgrounds on glass substratum; B, Shade/Light on black glass substratum; C, Shade/Light on white glass substratum; D, Shade/Light on sand substratum; E, Simulated Glass *Littorella*/Nil on glass substratum; F, *Littorella*/Nil on glass substratum; G, simulated Glass *Littorella*/Nil on sand substratum; H, *Littorella*/Nil on sand substratum. Controls are indicated by broken lines. $p = 0.05$ and $p = 0.001$ significance levels from Chi-squared are indicated by dotted lines.

1977a, 1977b). Brittain (1978) showed that there was a significant positive correlation between the population density of *L. vespertina* and detritus (organic matter) in Øvre Heimdalsvatn. In Oak Mere *L. vespertina* was absent from the sand zone and at low population densities at all zones on peat; it reached highest density at intermediate levels of organic matter. Descriptions of Øvre Heimdalsvatn suggest that this sub-alpine lake, dependent on allochthonous material, may lack areas containing high levels of organic matter comparable to those found in Oak Mere (Brittain, 1978; Vik, 1978). Thus Brittain's relationship is modified by the concept of an optimum in relation to percentage organic matter in the substratum. The optimum range in Oak Mere was 1.2–7.0%.

L. vespertina is invariably found among aquatic macrophytes; in particular *L. uniflora* (Brittain, 1972, 1976a; Kjellberg, 1972; Macan, 1965, 1975, 1977a, 1977b; Moon, 1939). The field observations in Oak Mere support this conclusion and the behavioural responses described suggest a causal explanation. Two patterns of migration have been described within the littoral zones; into deeper water during winter and a shorewards movement prior to emergence (Brittain, 1976a, 1978; Macan, 1965; Macan & Maudsley, 1968). The latter pattern of migration was confirmed in Oak Mere in 1979 and 1980. In addition, it was shown to be differential in relation to larger nymphs. There was a suggestion of migration towards deeper water in February 1980 but it did not extend beyond a depth of 0.4 m where macrophytes ceased. Furthermore, the shorewards migration did not occur in 1978 when there was

bare sand only between the *Littorella* zone and the shore. *L. vespertina* is an algal-detrital feeder (Brittain, 1978; Kjellberg, 1972) and hence macrophyte zones provide a source of food which may not be available elsewhere in Oak Mere. It seems probable that the trophic and behavioural responses ensure that *L. vespertina* stays among plants and detritus while migration is a more secondary phenomenon which occurs only once primary needs have been satisfied.

Lack of food may explain the absence of *L. vespertina* from zones of low organic matter but this factor is not applicable at high concentrations. It has been shown that Coleoptera larvae are common at high levels of organic matter in Oak Mere and are rapacious predators. Thus predation is almost certainly responsible for the low population densities. Odonata larvae are less rapacious predators throughout the range of *L. vespertina* in Oak Mere. This interpretation is in accord with present evidence (Brittain, 1978; Kjellberg, 1972; Lien, 1978; Macan, 1977b). A probable food-chain for Oak Mere is:



This is virtually identical with a food-chain described in a small woodland lake in Sweden (Kjellberg, 1972).

Brittain (1974) has described the distribution of *L. vespertina* in a series of Norwegian lakes. It was absent from alpine lakes where he suggested that low temperature was a limiting factor. It was found in waters with a conductivity range 7.4–74.4 μS cm^{-1} (18 °C). In the British Isles it has been found in a conductivity range 38–110 μS cm^{-1} (25 °C) (Brittain, 1972; Carrick & Sutcliffe, 1982; Macan, 1965; Moon, 1939) until the present study where the upward range is extended to 185 μS cm^{-1} (Table 1). Only a single specimen of *L. vespertina* was recorded in 25 north-west midland meres in England with a conductivity range 130–870 (mean 447) μS cm^{-1} (25 °C) (Savage & Pratt, 1976) and it was not recorded from Borrevan, near Oslo (134 μS cm^{-1} (18 °C)), in Brittain's (1974) survey. Clearly, it is associated with unproductive or oligotrophic waters. However, the author has maintained nymphs of *L. vespertina* in Hatch Mere water in the laboratory (Table 1) and it has been reported from saline water (9800 μS cm^{-1}) by Lingdell & Müller (1979). Thus the absence of *L. vespertina* from productive or eutrophic lakes cannot be explained directly in terms of water chemistry.

The majority of north-west midland meres are characterised by abundant emergent vegetation, highly organic substrata and high population densities of Corixidae, Coleoptera, Odonata, Mollusca and Gammaridae (Reynolds, 1979; Savage, 1982, 1985; Savage & Pratt, 1976). Thus conditions in eutrophic lakes are an extension of conditions in the more organic zones of Oak Mere. Hence, increased predation is a probable explanation for the absence of *L. vespertina* from such waters. There is already evidence that eutrophication leads to the disappearance of Ephemeroptera (Morgan, 1970).

L. vespertina maintains a consistent univoltine life cycle strategy throughout its range (Clifford, 1982) with the possible exception of the Swedish mountains where it may be semivoltine (Kjellberg, 1973). Growth is rapid in autumn and spring while continuing slowly in winter, even under ice (Brittain, 1972, 1978; Kjellberg, 1972, 1973; Macan, 1965). A similar cycle occurred in Oak Mere but, in addition, there was an indication of negative growth in early spring. Existing evidence shows that the major factor affecting growth is temperature (Brittain, 1976b; Macan & Maudsley, 1966). However, only one of the two annual cycles described in Oak Mere fully supported this conclusion. The period of negative growth, accompanied by a fall in biomass, occurred at higher temperatures than in winter when positive growth took place. Thus a factor other than temperature was responsible for the control of growth for at least a part of the life cycle. Negative growth may be interpreted as differential survival in favour of small nymphs. It was noted also in a population of *Caenis robusta* Eaton from a eutrophic lake (Bradbeer & Savage, 1980). It was most marked in Oak Mere in the season when production was higher and it seems that shortage of food might produce the effects described.

Data on population density and production of *L. vespertina* are available for a number of habitats. However, it is difficult to be certain of making valid

comparisons. An attempt has been made in relation to the littoral margin of lakes where plants are usually present. Following Brittain & Lillehammer (1978) it is termed the exposed zone.

The maximum population density in the exposed zone of Oak Mere was 2600 nymphs m^{-2}. This is similar to Hodgsons Tarn (Macan, 1965), marginally higher than in Llyn Dinas (Brittain, 1972) and considerably higher than in Scandinavia (Brittain, 1978; Eriksson *et al.*, 1974; Kjellberg, 1972, 1973). Similarly, production was higher in Oak Mere; 0.76–1.22 g dry weight m^{-2} exposed zone compared with Lake Vitalampa, 0.043 g dry weight m^{-2} (Eriksson *et al.*, 1974); a Swedish forest lake, 0.38–0.58 g dry wt. m^{-2} (Kjellberg, 1972, 1973) and Øvre Heimsdalvatn, 0.6 g dry wt. m^{-2} (Brittain, 1978).

The relatively high production of *L. vespertina* in Oak Mere may be associated with the atypical relationship between temperature and growth. There was a significant correlation between temperature and growth in 1979–80 when biomass and production were relatively low but not in 1978–79 when they were high (Fig. 7). It has been shown that the relationship between temperature and growth in laboratory and field populations of Ephemeroptera was closer in a species from a cold upland stream than in species from a warm lowland stream (Humpesch, 1979, 1983). It may be inferred that production would be higher in the warm lowland stream where, like Oak Mere in 1978–79, there was disparity between temperature and growth. Thus it appears probable that factors other than temperature affect growth, and hence production, in eutrophic waters. For *L. vespertina*, these factors are probably food and predation.

Summary

L. vespertina was confined to zones of littoral macrophytes. There was a significant ($p<0.01$) difference in population density on peat (organic matter c. 40%) and sand (1.2–7.0%) substrata; 112 m^{-2} and 1600 m^{-2} respectively. There were significant ($p<0.05$) differences in other taxa: Coleoptera larvae, 10 m^{-2} and 0 m^{-2}; Trichoptera larvae, 20 and 1; *P. nigra,* 56 and 1, *A. meridianus,* 39 and 2. Odonata larvae were not significantly different, 26 and 19. Laboratory experiments demonstrated a significant positive choice by nymphs of features associated with macrophytes. There was significant ($p=0.05$) predation by Coleoptera and Odonata larvae (Coefficients of Mortality (Z) were −1.997 and −0.015 respectively). Evidence is discussed which suggests that the occurrence of *L. vespertina* in lakes of the oligotrophic-eutrophic series is limited by temperature in the former, predation in the latter and detritus in both. The spatial distribution of nymphs showed a significant ($p<0.001$) agreement with a power law and hence was contagious and density-dependent. *L. vespertina* had a univoltine winter life cycle with marked shorewards migration of larger nymphs immediately prior to emergence. The maximum population density was 2600 m^{-2}. Growth rates varied from −0.09 – 5.01% increase dry weight d^{-1}. In 1979–80 there was a highly significant ($p<0.001$) correlation between growth and water temperature but not in 1978–79 when biomass and production were higher ($p<0.1$). Production estimates were 23.2 g dry weight m^{-1} shore (1.22–1.40 m^{-2}) in 1978–79 and 14.4 (0.76) in 1979–80. There was a period of negative production during early spring in both generations; it is suggested that food may have been a limiting factor during this period.

Acknowledgements

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