8.4.'94 With best wishes from the authors!

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Life cycle strategies of coexisting Ephemeroptera in an oligotrophic Norwegian lake

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With 3 figures and 3 tables in the text

Abstract

Life cycle, emergence, adult body size, fecundity and mortality were compared for three coexisting ephemeropteran species, *Leptophlebia vespertina*, *Siphlonurus aestivalis* and *S. lacustris*, in Myrkdalsvatn, an oligotrophic lake in western Norway. All species were univoltine, but have adopted different life cycle strategies. *L. vespertina* had small body size, high density, its main nymphal growth period during late summer and autumn, a short emergence period during mid-summer, low fecundity and low mortality. In contrast *S. aestivalis* had large body size, very low density, its main nymphal growth period during winter and spring, a very short emergence period during mid-summer and high fecundity, *S. lacustris* displayed large size, low density (compared to *L. vespertina*), its main nymphal growth period between ice break and emergence, a long emergence period during summer and autumn, high fecundity and high mortality. The life cycle strategies of *L. vespertina*, *S. aestivalis* and *S. lacustris* in Myrkdalsvatn appear to be influenced by interspecific competition and their coexistence is maintained by ecological segregation.

Introduction

Four species of Ephemeroptera *Leptophlebia vespertina* (L.), *Siphlonurus aestivalis* EATON, *S. lacustris* EATON and *Baetis rhodani* (PICTET) were recorded from the oligotrophic lake, Myrkdalsvatn, in western Norway. *L. vespertina* was the major species in the lake and constituted 72 % and 95 %, respectively, of total Ephemeroptera numbers in the benthic samples and emergence traps. *S. lacustris* was also common, but *S. aestivalis* only occurred in low numbers. Only a few spent female adults of *B. rhodani* were recorded in the emergence traps. However, it was abundant in the tributary streams and its presence in the emergence traps was probably an artifact and thus this species will not be considered further.

Data on nymphal growth and emergence in the Ephemeroptera from Myrkdalsvatn, has been published earlier by SÆTTEM & BRITTAIN (1985) and in

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the present paper only the major features will be reported. More details of the habitat, methods and the location of the sampling stations are also given in SÆTTEM & BRITTAIN (1985).

The aim of the present paper is to compare several ecologically important parameters such as nymphal growth, emergence, adult body size, fecundity and mortality for the sympatric ephemeropteran species in Myrkdalsvatn.

Habitat description

The oligotrophic, dimictic lake Myrkdalsvatn (60° 49′ N, 6° 28′ E) is part of the Voss river system in western Norway. The lake has a surface area of 1.66 km^2, a maximum depth of 107 m. It is ice-covered from late November until mid-May, although surface water temperatures reach a maximum of 23 °C during July. Further details are given in SÆTTEM (1981) and SÆTTEM & BRITTAIN (1985).

Material and methods

Nymphal growth of Ephemeroptera in Myrkdalsvatn was determined from material sampled by monthly kick samples (SÆTTEM, 1981) at 15 stations in the upper littoral during the ice free period in 1977 and 1978. Adult emergence was recorded daily in four box type emergence traps, with sides 1 m (DAVIES, 1950, BRITTAIN & LILLEHAMMER, 1978) located at different littoral sites around the lake. At the onset, peak and termination of emergence the body lengths of 50 male and female subimagos were measured.

Fecundity, defined as the total number of eggs produced by an individual female, was estimated by examining subimagos. The eggs were dissected from the abdominal and thoracic body cavity at peak emergence for the species in question and counted in a Sedgwick-Rafter cell (CLIFFORD & BOERGER, 1974; BRITTAIN, 1980).

Results and discussion

Leptophlebia vespertina, *Siphlonurus aestivalis* and *S. lacustris* were all univoltine in Myrkdalsvatn (Fig. 1). Nymphs of *L. vespertina* grew throughout the year with the highest growth rate during late summer and autumn. At this time nymphs of *Siphlonurus* were small and impossible to identify to species. However, during the winter *S. aestivalis* and *S. lacustris* became clearly separated in size due to winter growth in *S. aestivalis* (Fig. 1). Alternatively eggs of *S. aestivalis* may hatch earlier than those of *S. lacustris.*

The differences in timing of nymphal growth resulted in a succession in emergence. *L. vespertina* began its emergence period in late June, reaching a peak at the beginning of July and continuing sporadically from the end of July to late August. This emergence pattern in which 80 % of *L. vespertina* nymphs emerged within a period of only 10 days was in contrast to that of *S. lacustris* (Fig. 2). The latter species emerged over a long period from early July to the middle of October, with most specimens emerging from late July to the end of August. *S. aestivalis* was recorded for only a few days during the first half of

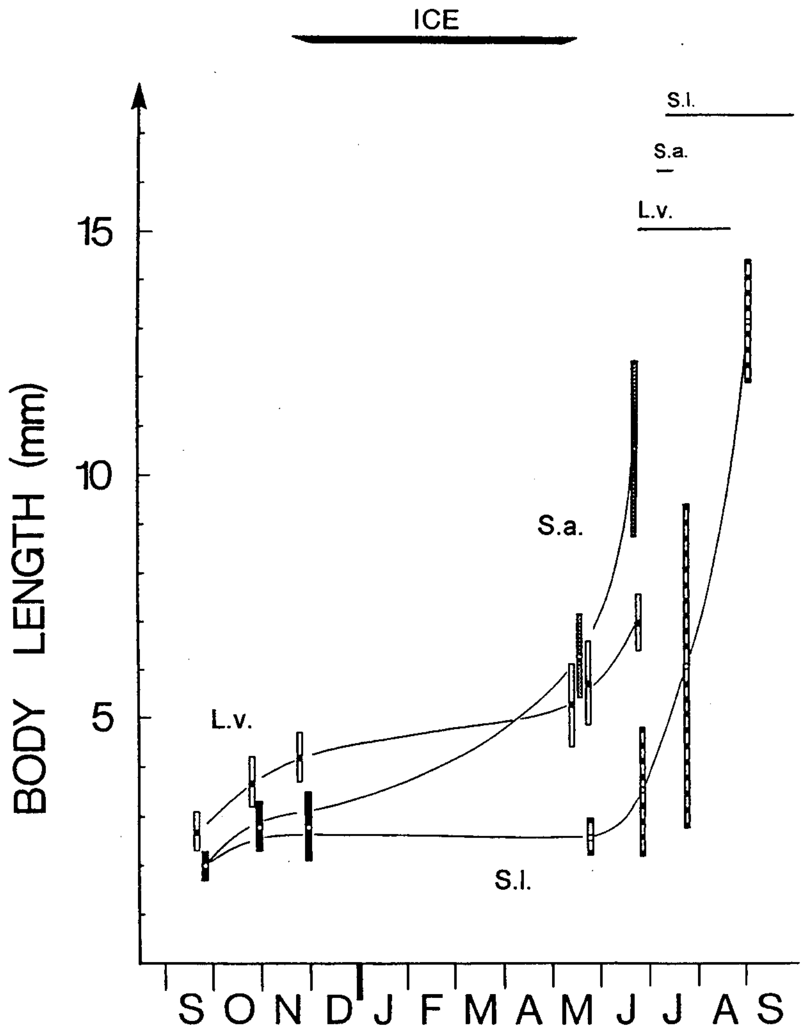

Fig. 1. Nymphal growth of *L. vespertina* (L.v.), *S. lacustris* (S.l.) and *S. aestivalis* (S.a.) in Myrkdalsvatn. Mean and standard deviation for 50 nymphs are given at each data point. The mayfly emergence periods and period of ice-cover are indicated.

July between the peak emergence of *L. vespertina* and *S. lacustris.* This serial emergence occurred in both 1977 and 1978.

During the emergence period there was a change in adult body size in both *L. vespertina* and *S. lacustris.* Late emerging *L. vespertina* of both sexes were significantly smaller than those emerging early in the summer ($p < 0.05$, t-test) (Table 1). In contrast, females and males of *S. lacustris* became significantly larger as emergence progressed ($p < 0.001$). The degree of size increase for *S. la-*

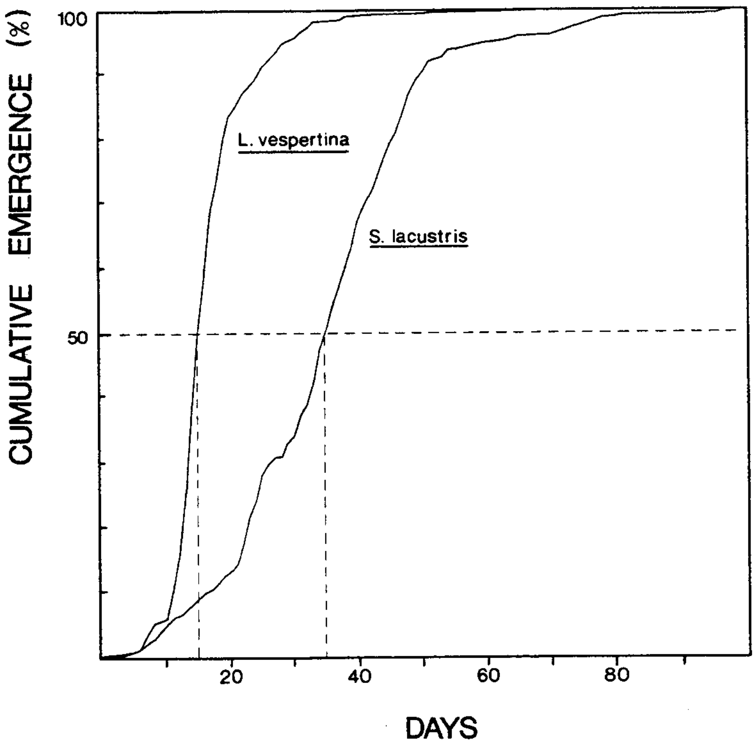

Fig. 2. Cumulative emergence of *L. vespertina* (n = 16521) and *S. lacustris* (n = 1029) in Myrkdalsvatn.

Table 1. Male and female body length of *L. vespertina*, *S. lacustris* and *S. aestivalis* during emergence in Myrkdalsvatn. Each mean, is based on 50 specimens.

		Onset			Peak			Termination		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
L. vespertina	male	7.9	0.2	7.3– 8.1	7.2	0.3	6.5– 7.9	6.4	0.3	6.0– 6.8
	female	7.7	0.6	6.3– 8.5	7.0	0.4	6.1– 7.6	6.2	0.5	5.5– 7.1
S. lacustris	male	11.2	0.8	10.0–12.4	11.2	0.8	10.2–12.4	11.5	1.0	9.9–12.6
	female	11.4	1.0	10.0–13.0	11.7	0.5	11.1–12.8	12.9	0.6	12.2–13.7
S. aestivalis	male				13.0	0.9	12.0–13.8			
	female				14.6	1.6	11.9–17.2			

custris was greater for females than males and late in the emergence period females were significantly larger than males ($p < 0.001$).

Size decrease during emergence is a general trend in many ephemeropteran species (e.g. Thibault, 1971; Benech, 1972; Sweeney, 1978; Brittain, 1980). However, an increase in body length during emergence is rare. This phenomenon has only previously been recorded in certain species of *Baetis* with long

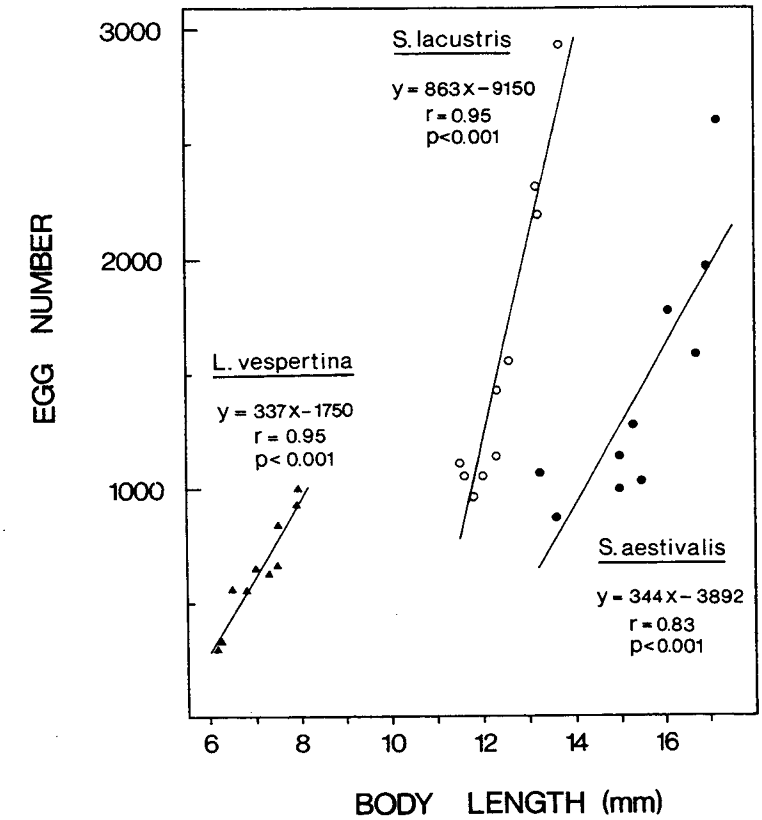

Fig. 3. Female body length and fecundity of *L. vespertina*, *S. lacustris* and *S. aestivalis* in Myrkdalsvatn. All values are for subimagos.

emergence periods (BENECH, 1972; ILLIES, 1979). Temperature and water level are key factors in the physical explanation of this emergence pattern (SÆTTEM & BRITTAIN, 1985; BRITTAIN, 1978). However, adult body length is important in view of the relationship between size and fecundity (THIBAULT, 1971; BENECH, 1972; CLIFFORD & BOERGER, 1974; SWEENEY, 1978; BRITTAIN, 1980) and an attempt to outline the success of particular life cycle strategies can be based on studies of fecundity and mortality of single populations.

In Myrkdalsvatn the fecundity of *L. vespertina* was less than the two *Siphlonurus* species. The number of eggs produced per female was correlated positively with adult body length for all three species (Fig. 3).

By knowing the number of eggs produced from a given area and the number of males and females emerging from the same area in the following emergence period, an estimate of life cycle mortality from the unfertilized egg to the subimago stage can be made (CLIFFORD & BOERGER, 1974). The two emergence periods of *L. vespertina* in 1977 and 1978 gave very similar numbers: 10.959 adults (5775 ♀♀, 5184 ♂♂) and 10.199 adults (4540 ♀♀, 5659 ♂♂), respectively. *L. vespertina* was univoltine in Myrkdalsvatn (Sættem & Brittain, 1985) and the number of adults in 1978 was the result of the egg numbers produced in 1977. This egg number can be estimated by multiplying the average fecundity by the number of females (Table 2). The number of eggs necessary to produce one adult is then found by dividing the total emergence catch in 1978 by the number of egg laid in 1977 (Table 2). This gives an estimated total mortality of 99.7 %.

In the case of *S. lacustris* fecundity and emergence data are only available for 1977. We therefore made the same assumption as Clifford & Boerger (1974), that the number of adult *S. lacustris* in Myrkdalsvatn in 1977 (1029 adults) approximated the number that emerged the following year. Based on this assumption on a similar mortality calculation for *S. lacustris* gives a total mortality of 99.9 %. Thus, *S. lacustris* in Myrkdalsvatn needs about twice as many eggs to produce one adult as in *L. vespertina*, although of course fecundity is twice as high in *S. lacustris* (Table 2). A similar interspecific difference in mortality was found for the same species in the mountains of central southern Norway (Brittain, 1980).

Average fecundity and total life cycle mortality both give a measure of success and provide an indication as to whether the species inhabits a favourable environment (Clifford & Boerger, 1974; Sweeney & Vannote, 1978). Body length, fecundity and total life cycle mortality were greater in Norwegian mountain populations of *L. vespertina* and *S. lacustris* (Table 3, Brittain, 1980). This seems to reflect the less favourable environment for these species at higher altitudes, probably due to the short, capricious summer disturbing swarming and oviposition as well as a longer nymphal period at lower water temperatures increasing predation pressure (Sweeney & Vannote, 1978). The late emerging females of *S. lacustris* became significantly larger than the males indicating an ecological adaptation in the form of increased fecundity to compensate for higher mortality due to increased predation and/or to decreased probability of finding a mate (Sweeney, 1981, 1982).

Table 2. Egg and adult cumulative frequencies of *L. vespertina* and *S. lacustris* in Myrkdalsvatn.

	Average fecundity pr. female	Females emerging /m²/year	Number of eggs /m²/year	Males and females emerging /m²/year	Number of eggs required to produce one subimago	Total life cycle mortality
L. vespertina	645	5775	3722565	10199	365	99.7 %
S. lacustris	1575	470	740250	1029	720	99.9 %

Table 3. Comparison of size and fecundity data from Myrkdalsvatn and the Norwegian subalpine lake, Øvre Heimdalsvatn (BRITTAIN, 1978).

	Average body length at peak emergence	Average fecundity pr. female	Number of eggs required to produce one subimago
L. vespertina			
Myrkdalsvatn	7.1 mm	645	365
Ø. Heimdalsvatn	8.7 mm	1079	461
S. lacustris			
Myrkdalsvatn	11.5 mm	1575	720
Ø. Heimdalsvatn	13.2 mm	1740	931

Based on this study the sympatric ephemeropteran species in Myrkdalsvatn appeare to have adopted three quite different life cycle strategies. In summary, *L. vespertina* had opted for small size, very high density, a main nymphal growth period during late summer and autumn, a short emergence period during midsummer and low fecundity and mortality. *S. aestivalis* has been selected for large size, very low density, a main nymphal growth period during winter and spring, very short emergence period and high fecundity. The third species *S. lacustris,* has large size, low density (compared with *L. vespertina*), a main nymphal growth period between ice break and emergence, a long emergence period during summer and autumn, high fecundity and high mortality. These strategies seem to be influenced by interspecific competition and the coexistence of *L. vespertina, S. aestivalis* and *S. lacustris* in Myrkdalsvatn appears to have been established by ecological segregation through natural selection (ULFSTRAND, 1968).

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