LIFE CYCLES AND NYMPHAL GROWTH OF TWELVE COEXISTING MAYFLY SPECIES IN A BOREAL RIVER.

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ABSTRACT

Bivoltine and univoltine life cycles were observed among twelve mayfly species in a boreal river. *Centroptilum luteolum* reached two generations per year. The winter generation hatched in mid-August but the nymphs did not grow during winter. Emergence took place in June. The summer generation hatched in mid-July and emerged in early August. The remaining species showed winter and summer univoltine life cycles.

Nymphs of the winter species were about half grown before winter, and all these species except *Baetis digitatus* grew markedly during winter.

The summer species, *Siphlonurus aestivalis* and *S. lacustris* hatched during late winter, while the remaining summer species accomplished their nymphal growth during a single summer.

INTRODUCTION

Life-history strategies of mayflies (Ephemeroptera) have been studied in a slow flowing part of a boreal river in northern Sweden since 1973. Some data have been published earlier (Olsson & Söderström 1978, Olsson 1983, Söderström and Nilsson 1987, Söderström 1988a, 1988b, 1988c, 1989, and Söderström and Johansson 1988). The aim of the present study is to give detailed information on life cycles and growth patterns of the dominant mayfly species.

STUDY AREA:

The investigation was carried out in a slow-flowing part of the river Vindelälven, near the village of Sirapsbacken (64°22'N, 19°28'E) in northern Sweden. The annual and seasonal fluctuations in discharge are very great, and as a consequence the width of the river varies between 160 and 230 m in the study section. The maximum flow (daily records) during 1971-1986 varied from 579 to 1484 m^3s-1, and the mean minimum and maximum flow (daily records) from 30 to 956 m^3s-1 (data from the Swedish Meteorological and Hydrological Institute). The river is normally ice-covered and the upper littoral zone frozen solid from the beginning of November to the beginning of May. In 1981 the river was completely ice-covered on 13 November, and the ice broke up on 11 May and 26 April in 1981 and 1982, respectively.

The marginal vegetation of the river in the study area was dominated by a dense belt of *Carex acuta* L.

MATERIALS AND METHODS

Mayfly nymphs were collected by a handnet. During winter, two types of handnet (mesh size 0.5 and 0.09 mm) were used, whilst only the 0.5 mm handnet was used during the spring, summer and autumn. Samples were taken at random at irregular intervals from December 1980 to July 1982.

The body length of mayfly nymphs was measured on preserved specimens (70% ethanol), the length from the front of the head capsule to the end of the abdomen being measured to the nearest 0.1 mm. As the body length did not differ between sexes in most occasions for all species studied (t-test, $P>0.05$), nymphs of both sexes were pooled for all species. The relationship between body length and time was best described by a linear regression when separate seasons (autumn, winter and summer), as well as the duration of the whole life cycle were examined. Because of this, growth rate (millimetres per day ± 95% C.L.) of nymphs of all species was estimated from the regression coefficient (b) in $L = a + bt$ where L (mm) denotes body length and t denotes time in days. For a few species, samples were obtained only twice during one season. In these cases, growth rate was estimated from the formula $(\bar{x}_2 - \bar{x}_1)/t$, where $\bar{x}_2$ and $\bar{x}_1$ represents mean body length at second and first sampling occasion, and t was number of days between the two sampling occasions. As a consequence no 95% C.L. could be calculated for these species during those seasons.

Comparisons of growth rates (regression coefficients) were performed by a sequential rejective multiple test according to Holm (1979). The seasons used in the growth rate (mm/day) calculations were defined as follows; autumn = mid August to 13 November (when ice was formed); winter = the period when the river was ice covered; summer= the period from ice break untill emergence started.

In the growth calculations (expressed as % of total nymphal growth) sizes of the first instar nymphs at hatching were estimated from Bengtsson (1913) and Clifford *et al.*(1979) and are given in Table 1. In these calculations first summer refers to the period from hatching of the first instar nymph untill mid August, while autumn, winter and second summer were defined as above.

RESULTS AND DISCUSSION

Of the twelve mayfly species studied, eleven had a one year life cycle and one species had a bivoltine life cycle. Of those species demonstrating a one year life cycle five could be classified as winter species (i.e. hatching and growing before winter) while six were summer species (i.e. hatching during late winter or later) (cf Figs. 1 and 2).

Univoltine winter species:

Heptagenia fuscogrisea Retz., *Leptophlebia marginata* L., *L. vespertina* L., *Ephemerella mucronata* Bgtss., and *Baetis digitatus* Bgtss. all belong to this life cycle type. Small nymphs first appeared in the samples from August to October (Figs. 1, 2a). At the onset of winter nymphs of these species were about half grown. In spring and early summer they grew rapidly. Emergence took place from the beginning to the end of June. *L. marginata* emerged first (early June) followed by *H. fuscogrisea* and *L. vespertina* (mid June). *E. mucronata* and *B. digitatus* emerged from the middle to the end of June. The two *Leptophlebia* species did not temporarily overlap in size, and their emergence periods were well separated. This observation is in agreement with data from Norway (Brittain 1978, 1980). The timing and life cycle type of *H. fuscogrisea*, *L. marginata* and *E. mucronata* agree well with those described by Bengtsson (1981) from northern Sweden. Data for *L. vespertina* from central Sweden obtained by Kjellberg (1973) were similar to mine. In contrast to my results, Ulfstrand (1968) found *E. mucronata* to be a summer species in the mountain area of northern Sweden. In Fig. 1c an indication of the life cycle of *Ephemerella aurivilli* Bgtss. is given. Although the samples were extremely small (the species is rare at this locality), they indicate that *E. aurivilli* has this type of life cycle. A few adults of this species were captured at the end of June. Ulfstrand (1968) also classified *E. aurivilli* as a typical winter species. For *B. digitatus* (Fig. 2a) this is probably the first full description of the life cycle, although Olsson (1983) indicated that this is a winter species.

L. vespertina showed a significantly lower growth rate during the autumn compared with the other species in this category (Fig. 3). During winter, all winter species except *B. digitatus* showed a small but significant length increase (F-test, $P<0.001$). Compared with the other seasons all winter species but one (*L. marginata*) showed their highest growth rate during summer. In *L. marginata*, growth rate during autumn and summer could not be significantly separated ($P>0.05$).

Table 2 shows seasonal growth expressed as percentage of total nymphal growth. Compared with the other winter species, nymphs of *L. marginata* had their highest growth during autumn, while a very slow growth took place during the first summer. In a Norwegian subalpine lake *L. marginata* accomplished nearly 60% and *L. vespertina* 30% of their total nymphal growth during the period of ice cover (Brittain 1980). This is not in accordance with my results and may be explained by both a much longer period of ice cover in the subalpine lake and that the water of a frozen lake probably is warmer than a frozen stream.

Univoltine summer species:

Siphlonurus aestivalis Etn., *S. lacustris* Etn., *S. alternatus* Say., *Arthroplea congener* Bgtss., *Metretopus borealis* Etn. and *Procloeon bifidium* Bgtss. all belong to this life cycle type. *S. aestivalis* and *S. lacustris* hatched from eggs when the river was still ice-covered, while the remaining four species probably hatched during summer (Figs. 1a-b, 2a, 2c). All six species showed a rapid length increase, and emergence took place from late June to early August. Subimagoes of *S. aestivalis* first appeared in late June/beginning of July, followed by *S. lacustris* in early July, while *S. alternatus* first appeared as subimago from late July/beginning of August. Subimagoes of the remaining three species first appeared from the beginning of August. There was no contemporary overlap in size distribution of nymphs of the three *Siphlonurus* species. However, their emergence periods were not completely separated in time. The size distributions of *S. alternatus*, *A. congener*, and *M. borealis* were completely mixed, while that of *P. bifidium* was separated from the other five summer species. The timing and life cycle type of *S. aestivalis* and *S. lacustris* agreed well with those described for these species by Otto & Svensson (1981) and Brittain (1980), respectively. Contrary to these findings, *S. aestivalis* seems to be a typical winter species in central Europe (Bretschko 1985). The timing and life cycle type of *S. alternatus* agreed well with that described for this species by Clifford (1969, 1982). For *P. bifidium* almost nothing is known. In England adults have been recorded from April to October (Elliott and Humpesch 1983), and in central Europe it is thought to be a summer species with more than one generation per year (Landa 1968, Sowa 1975). In my study area *P. bifidium* was a summer species with only one generation per year. For *M. borealis* and *A. congener* these are probably the first full descriptions of their life cycles, although some details are given by Jensen (1956), Hirvenoja (1964), Landa (1968), and Olsson (1983). Contrary to my findings, there is an indication that *M. borealis* is an univoltine winter species in Canada (unpublished data of Daniel Soluk, cited in Clifford 1982). In Figure 1c an indication of the life cycle of *Ephemerella ignita* Poda is given. Although the samples were extremely small it is probable that *E. ignita* has a one year life cycle and belongs to the summer species at my study area. Although extensive sampling was performed during winter no nymphs could be found. A few *E. ignita* adults were captured at the end of July. It seems that *E. ignita* belongs to this type of life cycle in upland streams of Europe while it shows an univoltine winter life cycle in lowland European streams (Elliott 1978).

S. lacustris and *S. alternatus* showed significantly higher growth rates ($P<0.05$) during both summer and the whole life cycles compared with the other four summer species (Fig. 3). It is also evident that growth rate during the summer period is significantly higher in the summer species compared with the winter species ($P<0.05$) (Fig. 3).

S. aestivalis achieved between 16 and 38 per cent of its total growth during the period of ice cover (Table 2). In *S. lacustris* the corresponding figures are 16 and 21 per cent, and this finding is in good agreement with the data on this species given by Brittain (1980). As can be seen from Table 2 all the remaining four summer species performed all their growth during the ice free season.

Bivoltine life cycle:
Centroptilum luteolum Müll. was the only species that had more than one generation per year (Fig. 2b). Generation one showed a small but significant length increase during the 1981 winter (F-test, $P<0.001$). In spring and early summer 1981 the nymphs grew rapidly and emergence took place in late June/beginning of July. The second generation appeared in mid-July, grew rapidly and emerged in mid-August. The third generation appeared from the middle of August and showed no significant length increase during autumn and winter 1981/1982 (F-test, $P>0.05$). The third generation emerged in late June 1982. *C. luteolum* also showed two generations per year in a river in nothern England (Wise 1980).

The winter generation showed a low growth rate during autumn and winter (Fig. 3). During early summer the growth rate of the winter generation of *C. luteolum* was equal to that of the winter species during the same period. The growth rate of the summer generation of *C. luteolum* could not be distinguished from that of the summer species during the same period.

In addition to the twelve mayfly species described in this study, another ten species are found in the same study area (Olsson 1983, Söderström and Nilsson 1987, Söderström and Johansson 1988, Söderström unpubl.). The co-occurrence of so many closely related species is probably possible partly due to differences in habitat utilization (Olsson 1983, Söderström and Johansson 1988, Söderström 1989), and partly to temporal segregation (Olsson 1983, Söderström 1989). The most closely related species seem to be the ones demonstrating clear temporal segregation (Figs. 1b, 2c). These patterns may result from intense competition in congeneric species (cf Grant and Mackay 1969, Brittain 1974, Bengtsson 1981).

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Table 1. Estimated size of first instar mayfly nymphs (mm) and number of specimens measured of each species in each generation from December 1980 to July 1982.

Species	Estimated size of 1 st instar nymphs (mm)	Generation 1	Generation 2	Generation 3
Heptagenia fuscogrisea	0.5	853	1 076	
Leptophlebia marginata	0.5	108	146	
L. vespertina	0.4	405	588	
Ephemerella mucronata	0.4	422	195	
Baetis digitatus	0.4	298	144	
Siphlonurus aestivalis	0.5	167	74	
S. lacustris	0.5	244	219	
S. alternatus	0.5	389	145	
Arthroplea congener	0.5	75		
Metretopus borealis	0.5	289		
Procloeon bifidium	0.4	318		
Centroptilum luteolum	0.4	447	44	286

Table 2. Per cent of total nymphal growth accoplished during separate seasons of the different mayfly species.

Species	Year	Per cent of growth during First summer	autumn	winter	Second summer
Heptagenia fuscogrisea	81/82	32.5	24.7	9.1	33.7
Leptophlebia marginata	81/82	19.9	33.3	12.8	34.0
L. vespertina	81/82	23.9	21.2	13.8	41.1
Ephemerella mucronata	81/82	26.5	17.1	13.0	43.4
Baetis digitatus	81/82	38.0	17.5	0.0	44.5
Siphlonurus aestivalis	80/81			38.5	61.5
	81/82			16.0	74.0
S. lacustris	80/81			16.4	83.6
	81/82			21.6	78.4
S. alternatus	80/81				100.0
Arthroplea congener	80/81				100.0
Metretopus borealis	80/81				100.0
Procloeon bifidium	80/81				100.0
Centroptilum luteolum	81				100.0
	81/82	44.2	6.7	3.1	46.0

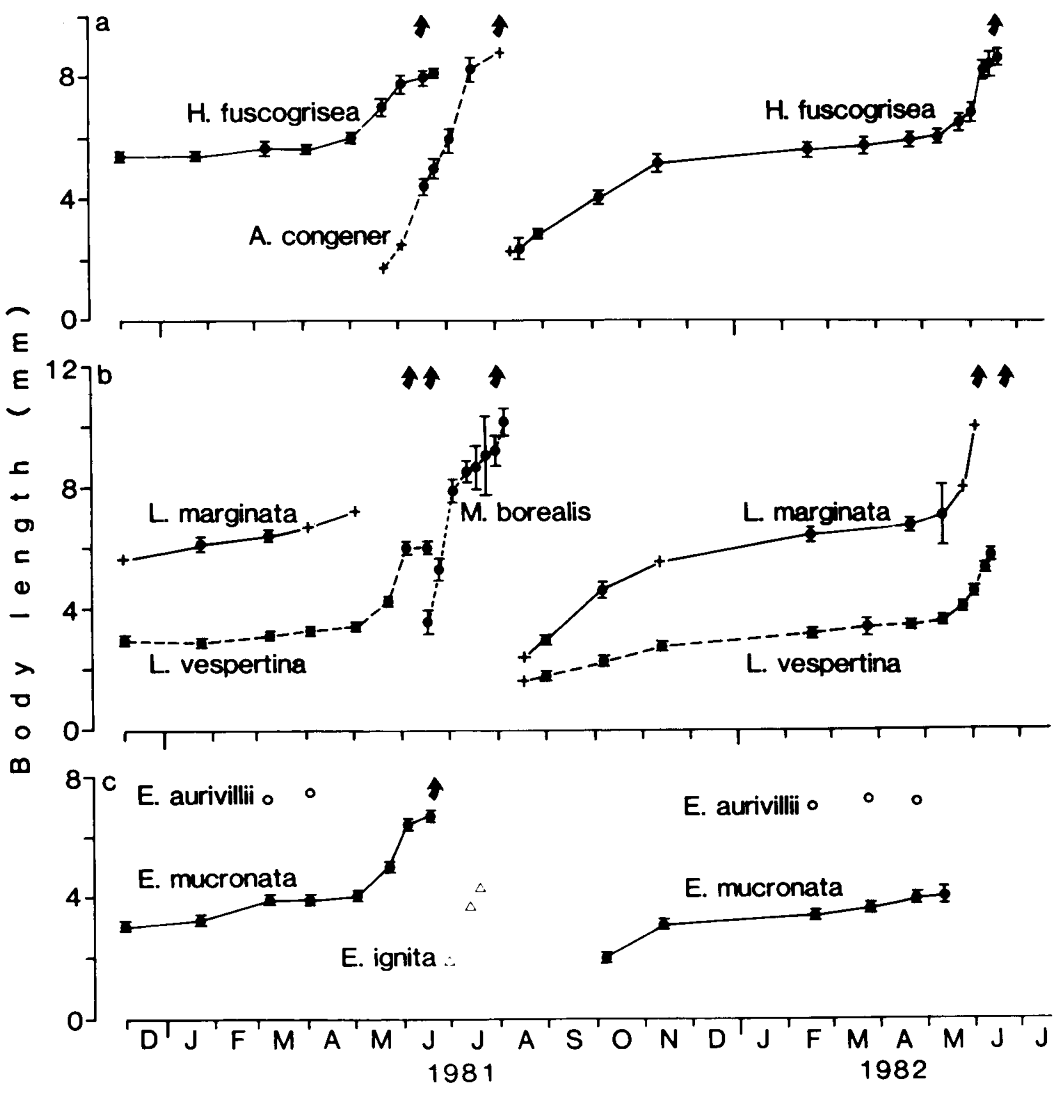

Fig. 1. Size (body length ± 95 % C.L.) of nymphs of different mayfly species during 2 years. Number of nymphs measured per species on each occasion ranged from 10 to 96 when denoted by a solid circle and less than 10 when denoted by a + sign or an open symbol. Emergence time of each species is denoted by an arrow. (a) *Heptagenia fuscogrisea* and *Arthroplea congener*. (b) *Leptophlebia marginata*, *Leptophlebia vespetina*, and *Metretopus borealis*. (c) *Ephemerella mucronata* and notes of the size of *Ephemerella aurivilli* (open circles) and *Ephemerella ignita* (open triangles).

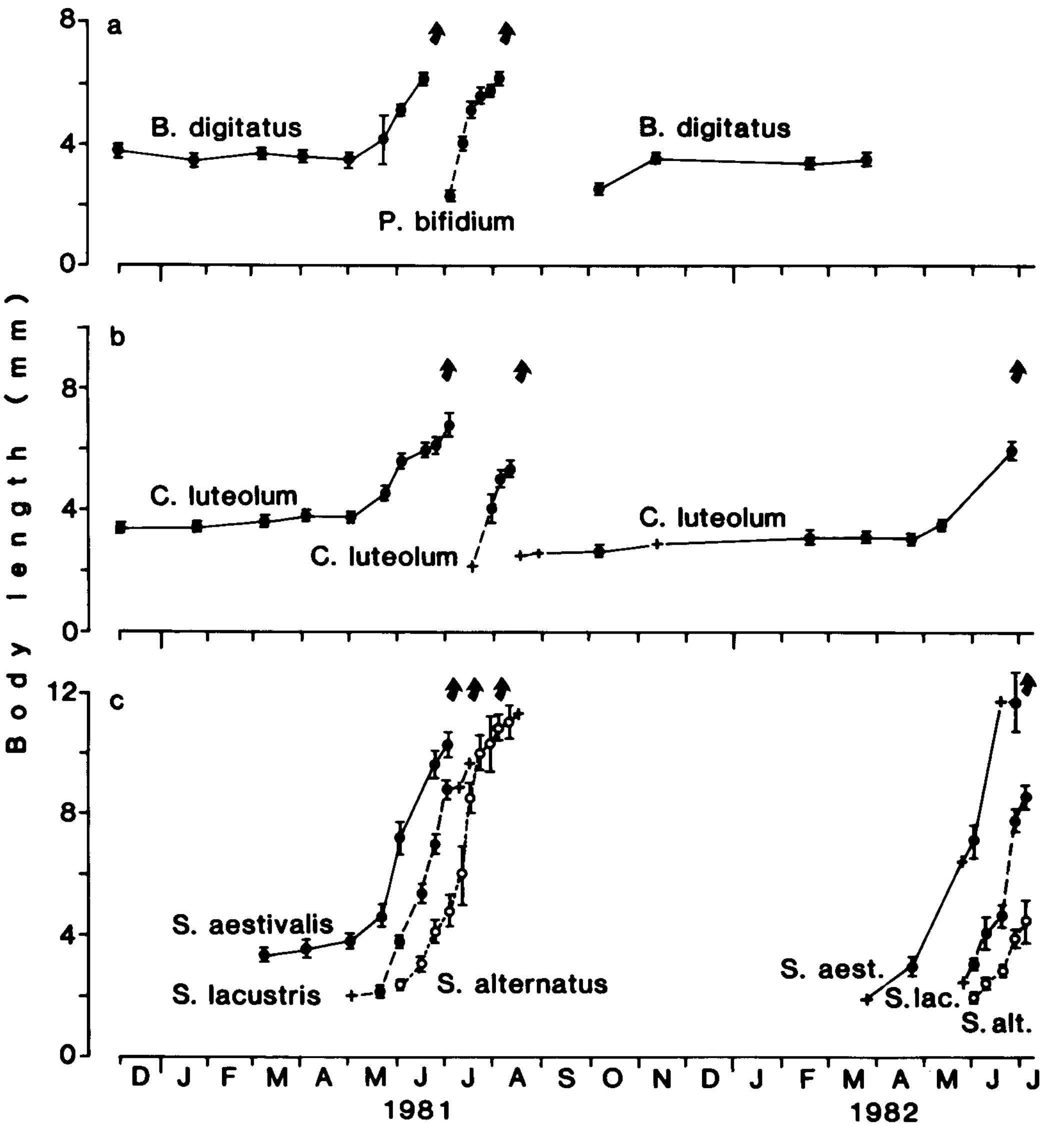

Fig. 2. Size (body length ± 95 % C.L.) of nymphs of different mayfly species during 2 years. Number of nymphs measured per species on each occasion ranged from 10 to 96 when denoted by a solid circle and less than 10 when denoted by a + sign. Emergence time of each species is denoted by an arrow. (a) *Baetis digitatus* and *Procloeon bifidium*. (b) *Centroptilum luteolum*. (c) *Siphlonurus aestivalis*; *Siphlonurus lacustris* and *Siphlonurus alternatus*.

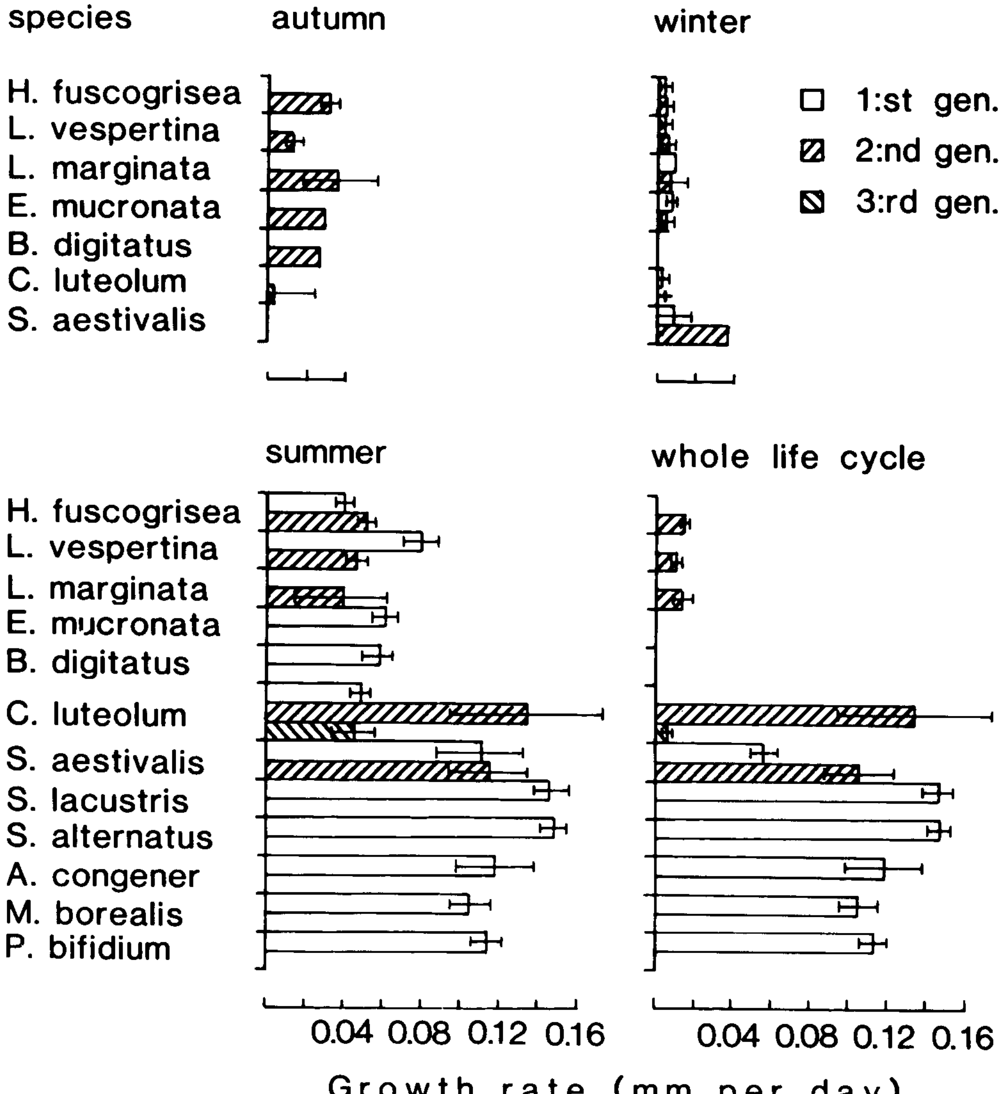

Fig. 3. Growth rates (when possible with 95% C.L.) for different generations (1-3) of mayfly nymphs during separate seasons and for the whole life cycle.