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Life cycle strategies and seasonal distribution of mayflies (Ephemeroptera) in a small stream in Central Norway

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Mayfly nymphs were sampled from a stream in Trøndelag, Central Norway, about twice monthly throughout a single year. Seasonal distribution of nymphs of 16 species are documented and nymphal growth patterns of 7 species described. Retardation in growth during winter was seen in most species except *Ameletus inopinatus* Eaton in which 51 % of growth occurred during ice cover. A univoltine life cycle dominated, 5 species belonging to the category "winter species" and 2 species to "summer species". In *Heptagenia dalecarlica* Bengtsson some individuals took one year, others two years before reaching emergence. The coexistence of closely related species in terms of temporal separation in growth and life cycles is discussed.

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INTRODUCTION

Ephemeroptera are important components of the macroinvertebrate fauna of most northern rivers and streams. Marked seasonal variations in water flow and temperature characterize these habitats. Water temperature are considered to be a main factor affecting growth rates in mayfly and stonefly nymphs (Baekken 1981, Brittain 1976, 1982, 1983, Hynes 1961, Svennsson 1977). Reduced growth during winter has been described for several species among the two groups. However, the low temperature and the extensive ice periods in northern rivers severely limit the possibility to collect material for field studies on aquatic organisms in winter. Nevertheless, studies on overwintering strategies are of vital importance for the understanding of the ecology of boreal running waters.

Previous reports on life histories of mayflies from Norway do not include the coniferous areas of Central Norway. From other parts of Scandinavia life cycle information is available for many species, cfr. Larsen (1968), Ulfstrand (1968), Bengtsson (1973), Brittain (1974, 1978, 1980), Andersen et al. (1978), Lillehammer & Brittain (1978), Bengtsson (1981), Baekken (1981), Sættem & Brittain (1985, 1993), Söderström (1988). Life cycles appear to differ markedly in various localities and with altitude (Ulfstrand 1968, Brittain 1974, 1978, Wise 1980, Clifford 1982).

The purpose of the present investigation was to examine seasonal abundance and growth patterns of mayfly nymphs in a central Norwegian stream, as part of a study of seasonal variation in benthic invertebrate communities.

STUDY AREA

The study was carried out in the stream Sagelva which drains about 82 km^2 of a coniferous forest area in Trøndelag, Central Norway (63°21'N, 10°38'E). The stream is ice-covered from late November until early May. The water temperature ranged from 18.1 °C (4 July 1978) to 0.1 °C (winter) (**Figure 1**). During the period of sampling (April 1978-May 1979) the discharge varied from 5 to 3330 l sec^{-1}.

The area investigated was a moderate flowing part of the stream in a mixed forest zone, about 250 m a.s.l. At the sampling site the stream is 6-8 m wide and 5-30 cm deep at mean discharge. Water velocity varied from 5 to 40 cm s^{-1}. The bottom substrate was relatively homogenous and consisted of stones, 2-10 cm diameter.

METHODS

Sampling was carried out at one locality approximately twice monthly throughout a single year. Twenty bottom samples were taken each time, using a Surber sampler covering 1500 cm^2 and with a mesh size of 500 µ, or 0.5 mm. The substrate was disturbed to a depth of 10 cm and specimens sorted in the field. Additional sampling for growth studies was performed using a kicking technique (Frost et al. 1971). The material was preserved in 70 % ethanol.

The analyses of growth patterns were based on total length measurements. Each nymph was measured to the nearest 0.5 mm from the anterior margin of the labrum to the posterior margin of the last abdominal segment.

The method used by Macan (1970) and Elliot (1967) was used for illustrating the life cycles.

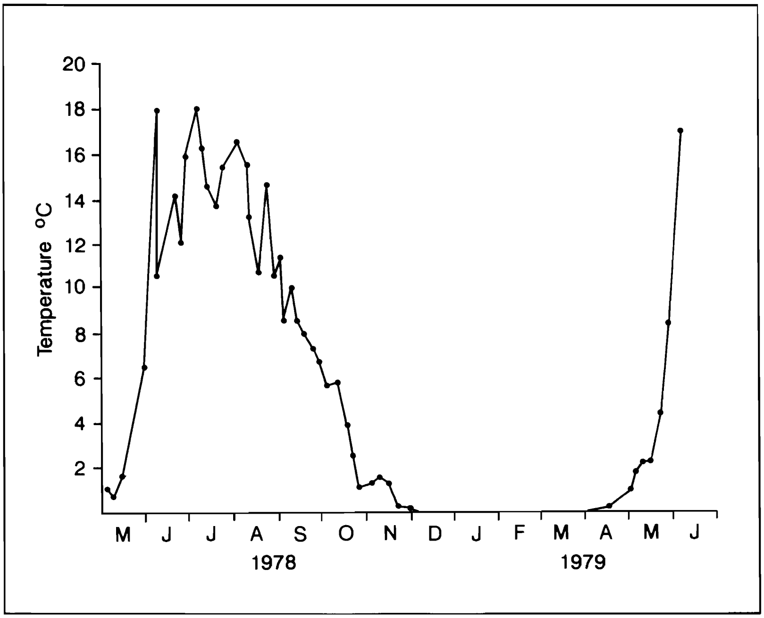

Figure 1
Water temperature in Sagelva, based on measurements between kl. 11 00 and 1500.

For species with large variations in body length, the growth was illustrated by size groups. Hatching periods were determined by the presence of small-sized nymphs (2-3 mm). Emergence periods were recognized by the presence of mature nymphs and from observations of imagines in the field.

RESULTS AND DISCUSSION

I Seasonal distribution

Mayflies were present throughout the year and constituted higher numbers than any other macroinvertebrate group. On average for the whole sampling period they constituted 44 % of the macroinvertebrate fauna. Within this single locality a total of 11 800 mayfly nymphs were collected and 16 species recorded. Their maximum abundance was in June-July and December-January (**Figure 2**). High numbers of nymphs in late June - early July was due to recruitment of small nymphs of *Baetis scambus* Eaton and *Heptagenia joernensis* (Bengtsson). The increase in number of nymphs from September to January was not caused solely by recruitment, but probably also resulted from a movement to the deeper part of the stream as water flow decreased and shallow areas became frozen. Such lateral movements and concentration of nymphs has been demonstrated by Olsson (1983).

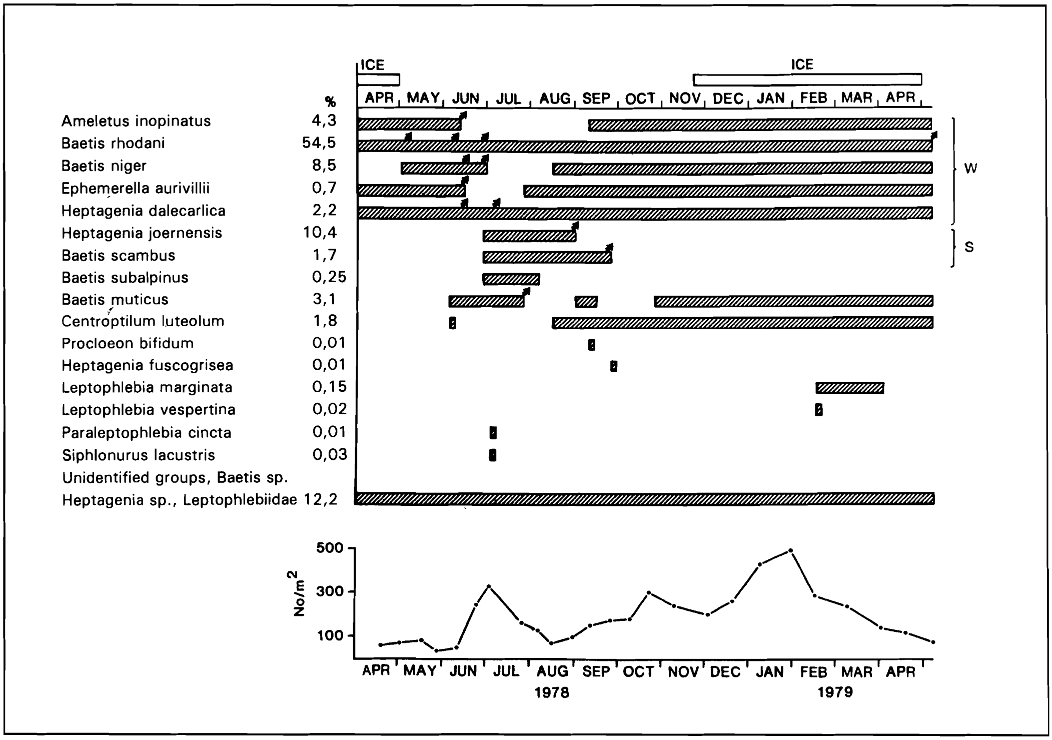

Figure 2

Seasonal distribution of mayfly nymphs in Sagelva, Central Norway, 1978-79. W shows winter species and S summer species. ↗ indicates time of emergence. Mean number of nymphs per m^2 is given in the lower figure.

Nymphs of *Baetis rhodani* (Pictet) and *Heptagenia dalecarlica* Bengtsson were present in benthic samples throughout the year. *Ameletus inopinatus* Eaton, *Baetis niger* (L.) and *Ephmerella aurivillii* (Bengtsson) emerged before July and nymphs of the new generation were present in the samples from August onwards. *Baetis scambus* and *Heptagenia joernensis* only occurred in the samples for a few months.

Baetis rhodani and *Heptagenia joernensis* were the dominant species, followed by *Baetis niger* and *Ameletus inopinatus*.

II Nymphal growth and life cycles

Growth patterns of the most abundant mayfly species are shown in **Figures 3-5**.

***Ameletus inopinatus* Eaton**

A. inopinatus was univoltine with growth period from August to May (**Figure 3**). There was no decline in growth during the winter, and 51 % of growth took place under the ice. Nymphs emerged in June after a fast growing period after ice-break in May.

Although temperature are considered as the main factor affecting growth rates (Brittain 1976, 1983, Humpesch 1979) the results from Sagelva show that growth in winter is not solely temperature related but depends also on other factors, at least in some species.

Other studies (Gledhill 1959, Larssen 1968, Ulfstrand 1968 and Brittain 1974, 1978) concluded that *A. inopinatus* was univoltine, growth taking place during the winter season and the species having a long flight period (May-August).

***Baetis niger* (Linnaeus)**

B. niger was univoltine in Sagelva (**Figure 3**). Nymphs were present throughout the whole year except in July. There were two periods of rapid growth; one from August to November and one from late April to June. At the end of the latter period the imagines emerged. The stagnation in growth occurred when temperatures were below 2 °C. Emergence and oviposition took place in June and July, and it seems reasonable to assume a short egg incubation period since small nymphs appeared in August and the length of the nymphs were rather uniform during autumn.

Andersen et al. (1978) describes an emergence period from June to late July in the river Ekso, Western Norway. This is in agreement with the present findings from Sagelva. Elliott (1967) found an univoltine life cycle with a winter and a summer generation in England.

***Baetis scambus* Eaton**

B. scambus (**Figure 4**) appeared as small nymphs and a few mature nymphs in July. The small nymphs grew rapidly, and emerged during September. The few mature nymphs in July may belong to a first summer generation, but lack of smaller nymphs in June makes this uncertain. It is therefore not possible to deduce whether *B. scambus* is univoltine or bivoltine in Sagelva.

Mayflies with two generations per year in Norway seem to have one winter generation and one summer generation (Brittain 1973, Larsson et al. 1978). In England, on the other hand, both *B. scambus* and *B. fuscatus* may have two fast-growing summer-generations (Elliot 1967, Wise 1980). The rapid development of the nymphs in summer makes it obvious that the timing of sampling is critical when interpreting growth patterns of this species.

***Baetis rhodani* (Pictet)**

Nymphs of *B. rhodani* occurred throughout the year, and 3183 nymphs were measured for growth studies.

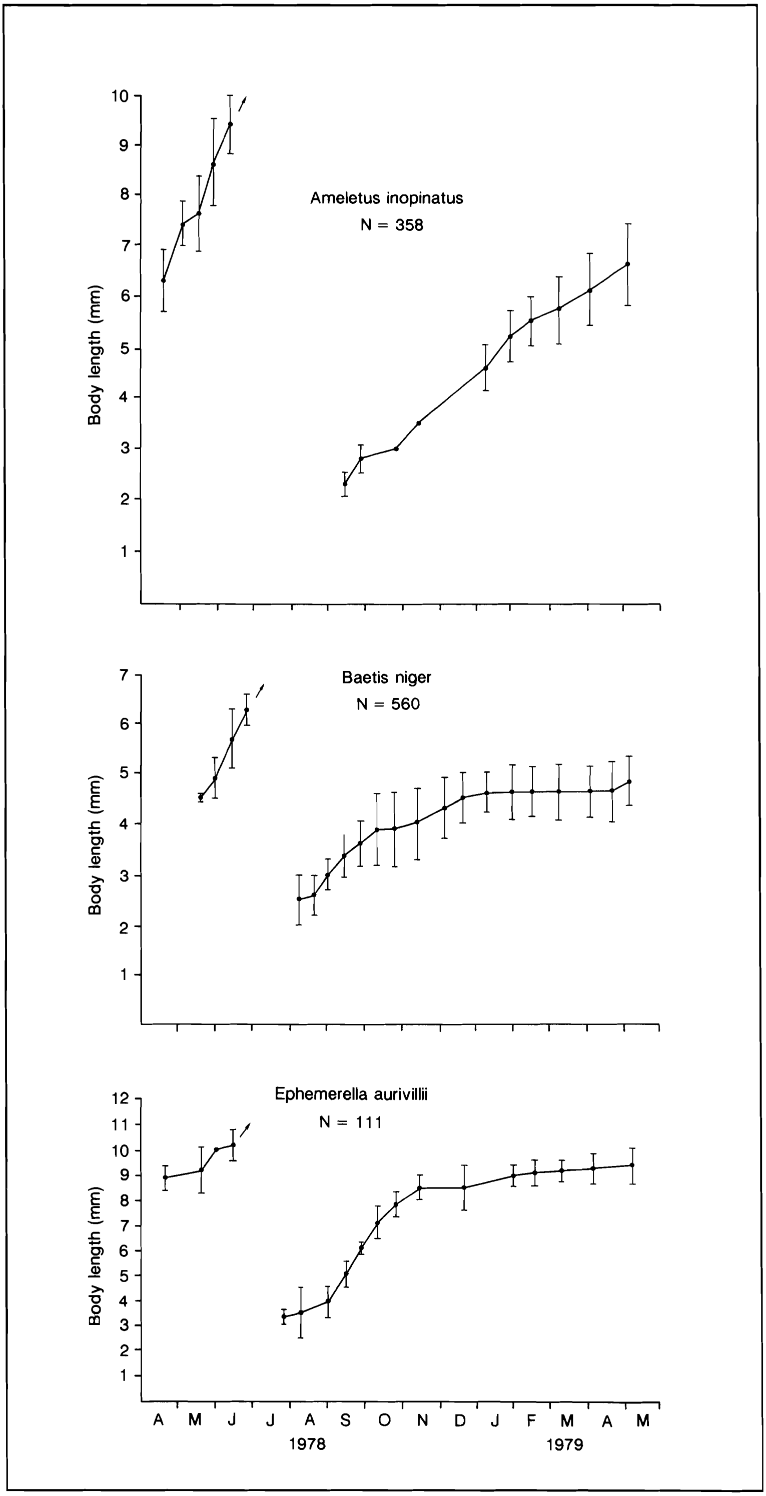

Figure 3
Growth pattern, as mean nymphal body length (± S.D.), for Ameletus inopinatus, Baetis niger *and* Ephemerella aurivillii *in Sagelva.*

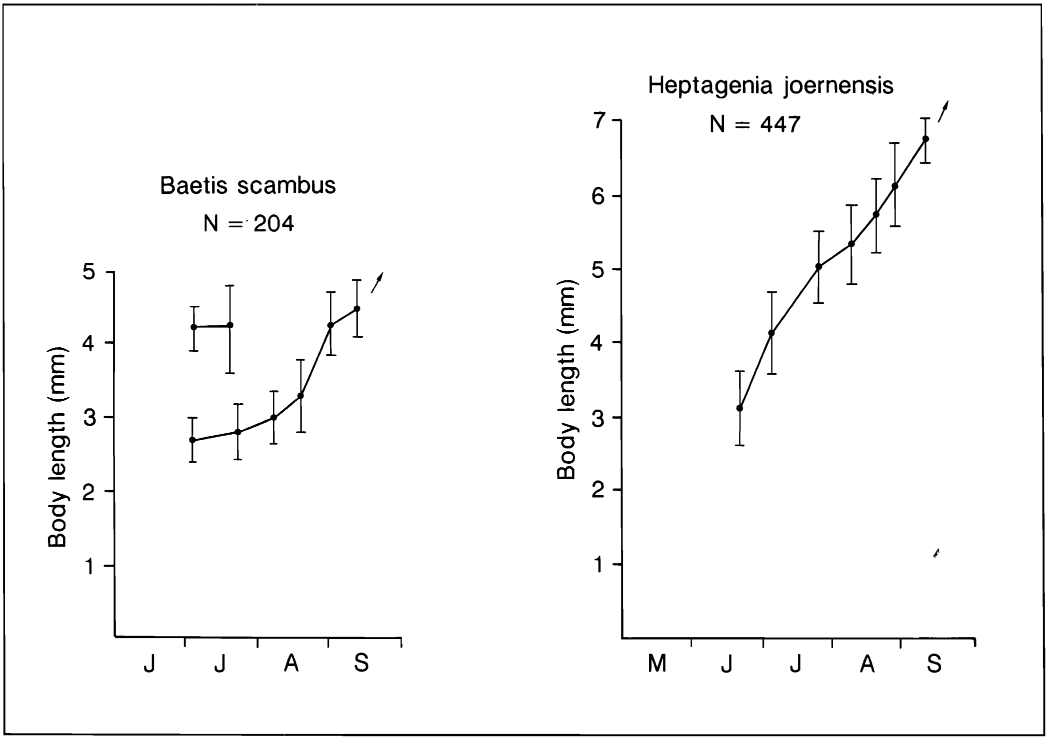

Figure 4
Growth pattern, as mean nymphal body length (± S.D.), for Baetis scambus *and* Heptagenia joernensis *in Sagelva.*

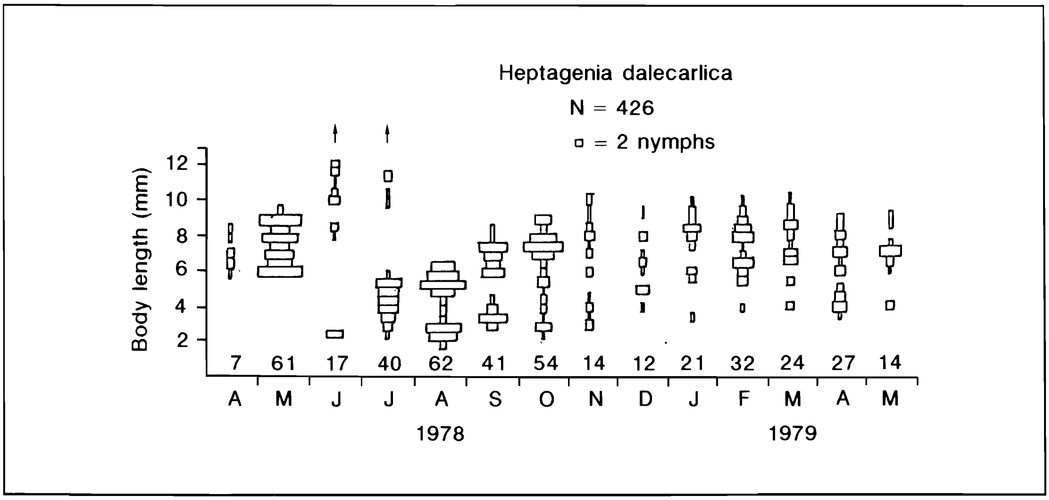

Figure 5
Frequency distribution of nymphal size classes of Heptagenia dalecarlica *in Sagelva. Sample size is given.*

B. rhodani is univoltine in Sagelva (**Table 1**). The life cycle is complex and there is a continuous overlap between developmental stages during the year. Obviously, one winter generation can be distinguished. Mature nymphs emerged from May to July. No fully grown nymphs were captured in August and September. In these months and in October small nymphs (group I) dominated. These must belong to a first cohort of the new winter generation. They grew into group II and III in late autumn, but there was soon considerable variation in nymphal size from November. Nymphs appeared in group IV from October, but they were not fully grown before April.

Small nymphs (group I) were present in all months. Presumably nymphs hatched from eggs over a long period as the emergence period for *B. rhodani* is reported to be long (Ulfstrand 1968, Andersen et al. 1978). Diapausing eggs may give rise to several cohorts (Humpesch 1979), which were not detected because of too large mesh size in the Surber net. The results therefore do not permit any interpretation of several cohorts of nymphs in the winter generation as shown in the river Ekso, Western Norway (Baekken 1981).

B. rhodani has been found to have two generations per year in several localities in Scandinavia (Larsen 1968, Ulfstrand 1968, Baekken 1981) but also one generation has been recorded in mountain areas (Brittain 1978). In Sagelva, no rapid growing summer generation was detected.

Continuous overlap between developmental stages has also previously been recorded for this species (Elliot 1967, Larsen 1968, Ulfstrand 1968, Humpesh 1979, Baekken 1981). Baekken (1981) found two cohorts in the winter generation in Ekso, and the growth pattern described for the first cohort is in agreement with that found in Sagelva.

Humpesch (1979) showed a more complicated situation with ten cohorts over a period of 30 months for *B. rhodani* in Austria. This shows the flexibility of life cycle strategies in *B. rhodani* and explains its wide distribution (Illies 1978).

Heptagenia dalecarlica Bengtsson

H. dalecarlica has a complicated life cycle in Sagelva. Nymphs were present throughout the year and with a wide size distribution during most of the year (**Figure 5**).

Table 1. Percentage composition of size groups, based on body length measurements of Baetis rhodani. n is the sample size.

Month	A	M	J	J	A	S	O	N	D	J	F	M	A	M
Gr. IV (6.0-8.5 mm)	6	15	9	2	1		1	9	9	8	14	8	11	12
Gr. III (5.0-6.0 mm)	18	29	15	15		3	13	25	25	26	43	39	34	21
Gr. II (4.0-5.0 mm)	41	27	27	27		22	35	29	35	34	31	34	36	34
Gr. I (2.0-4.0 mm)	34	29	48	57	99	75	50	37	31	33	13	19	19	34
n	70	238	277	122	63	176	531	226	386	341	239	158	243	119

Nymphs belonging to the winter generation were fully grown in late June and July, and emerged in this period. In June and July a cohort of small nymphs appeared and grew rapidly until October. These nymphs most probably derived from eggs laid the previous year since the flight period had only just began when they appeared. In August and September another cohort of small nymphs appeared. Evidently they derived from eggs laid during the preceding flight period. In October and November they mixed with the preceding cohort, and for the whole winter the population consisted of variable sized nymphs with no indication of a bimodal size distribution.

Hence, the results indicates that *H. dalecarlica* has two life cycle strategies. Part of the population spend a year as eggs or small quiescent nymphs, grow in summer and autumn and emerge the second summer. Another part of the population start growing soon after oviposition and complete their development in one year. These findings agrees with the results presented by Ulfstrand (1968) from Swedish Lappland.

Heptagenia joernensis (Bengtsson)

H. joernensis belongs to the category of summer species (**Figure 4**). No published information on the nymphal growth of this species is available from Scandinavia. In Sagelva *H. joernensis* was univoltine with a very rapid growth in summer. The first small nymphs appeared in late June and mature nymphs in mid-August. The emergence of imagines terminated in early September. The species probably overwinter in the egg stage or as small nymphs. However, interpreting the length of egg development from field data are uncertain, as pointed out by Brittain (1982). Small nymphs may be deep down in the substratum or too small to be detected by normal sampling methods. The status of *H. joernensis* in winter therefore remains unknown.

Ephemerella aurivillii (Bengtsson)

This species had an univoltine life cycle in Sagelva (**Figure 3**). Mature nymphs were caught from late May to 12 June, and small nymphs appeared for the first time on 25 July. Nymphs grew considerably in the period September-November, followed by a reduced growth during the whole winter period. Nymphal material showed little variation in size distribution at any time, indicating a homogenous population. The results agrees with finding from Western Norway (Larsen 1968) and Swedish Lapland (Ulfstrand 1968).

Notes on uncommon species

Some species were too rare or occurred too sporadically to allow any interpretation of life cycle.

A few large nymphs of *Baetis subalpinus* Bengtsson occurred in June and July, but were absent from samples in other months. In total 355 nymphs of *Baetis muticus* (Linnaeus) were caught during the period. Nymphs were absent in the spring of 1978, but median-sized nymphs occurred in June and mature nymphs in July. Small nymphs appeared again from late October and seemed to grow little until May.

Small nymphs of *Centroptilum luteolum* (Müller) were present in the benthos from late September and now and then through the winter. Presence of a few large nymphs with dark wing pads in late July and August 1978 suggested that emergence was imminent.

Six other mayfly species occurred only occasionally in the benthic samples (**Figure 2**).

III Coexistence and growth strategies

In Sagelva, six major species were univoltine and occured together in the same habitat, but their strategies differed markedly. There was considerable difference in growth strategy from *A. inopinatus* in which nymphs were present for about 10 months of the year and much of the growth occurs during the period of ice cover, to *H. joernensis* in which nymphal growth and occurrence are restricted to about 2 months during the summer.

The competitive exclusion principle, discussed by Illies (1952) states that no two species which occupy the same ecological niche can occur together indefinitely in the same habitat. This situation is avoided of species in the same genus by different distribution in space or in time. Occurrence of closely related mayflies in Sagelva seems mainly in agreement with this principle. Related species are separated in time both in nymphal growth and emergence periods (**Figure 2**).

Five species of the genera *Baetis* coexist in the same locality in the stream. These can be grouped in two categories according to morphology and habitat utilization. One category consists of *B. rhodani*, *B. scambus* and *B. subalpinus*. These are closely related species which are good swimmers (Müller-Liebenau 1969, Ulfstrand 1968b). In *B. scambus*, growth takes place after the emergence of *B. rhodani*, and large nymphs of *B. scambus* coexist with small nymphs of *B. rhodani* in August and September. The two species are clearly separated in the time of emergence. There is, however, a certain degree of overlap of nymphal size of the two species in September, due to the wide size distribution of *B. rhodani*. Nymphs of 4-5 mm size of both species occurs simultaneously, but they are in a different level of development. While fully grown nymphs of *B. scambus* had a body length of about 4.5-5 mm, those of *B. rhodani* reached about 7.5-8 mm. Change in diet and microdistribution with stage of development have been found in several mayfly species, among them in *B. rhodani* (Moore 1977, Baekken 1981). Even-sized nymphs of the two species *B. rhodani* and *B. scambus* may therefore have different demands for food and shelter. It seems likely that such differences in habitat utilization enable them to coexist.

Nymphs of *B. subalpinus* were also found together with nymphs of *B. scambus* and *B. rhodani*. These nymphs occurred in low numbers and were at that time larger than nymphs of both other species.

Another category of *Baetis* spp. consists of *B. muticus* and *B. niger*. Nymphs of these species have a more cylindrical body shape and may occupy other parts of the substratum than nymphs of the first category (Müller-Liebenau 1969, Hynes 1970, Ulfstrand 1967, 1968). Mature nymphs of *B. muticus* were present in July, while *B. niger* had fully grown nymphs in late May and June. This indicates a separation in the time of emergence. In autumn and especially winter both species occurred together, but *B. niger* dominated and was present with larger nymphs than *B. muticus* at the same time.

Other investigations have also demonstrated the importance of size as a factor in ecological segregation in mayflies (Brittain 1980, 1982). Smaller specimens can inhabit smaller crevices and so do not compete with larger ones for shelter and food (Hynes 1970, Söderström 1989). Life cycle separation also was demonstrated for *B. rhodani*, *B. fuscatus* and *B. subalpinus* in Swedish Lappland (Ulfstrand 1968), but here there also was a separation in habitat.

Differences in nymphal growth periods have also demonstrated for the species *Heptagenia dalecarlica* and *Heptagenia joernensis*. Both species occurred together from June to September, with *H. joernensis* dominating. The two species have adopted different life cycle strategies, whereby *H. joernensis* is present in the nymphal stage for just 2-3 months and has a rapid growth after the emergence period of *H. dalecarlica*. During the whole growing period (June-September) *H. joernensis* had larger nymphs than *H. dalecarlica*. The two species also differ in their size at maturity, average length of the fully grown nymph being 6.7 mm in *H. joernensis* and 10.7 mm in *H. dalecarlica*.

Although temporal separation in growth and life cycles is one of the most common mechanisms permitting coexistence among closely related mayflies (Brittain 1982), other differences also may be important in permiting a variety of species to coexist in the same locality. In a Norwegian mountain lake differences in nutrition, fecundity, predation pressure and size at maturity were found among the four mayfly species *Baetis macani*, *Siphlonurus lacustris*, *Leptophlebia marginata* and *Leptophlebia vespertina* (Brittain 1980). Baekken (1981) found that relatively small changes in food composition could result in considerable shifts of microhabits, enabling a different habitat choice among the different size groups of *B. rhodani*. This was considered to reduce the interaction between nymphal stages both within *B. rhodani* and between two coexisting detrivorous species. Such consideration may also be done to explain the great numbers of nymphs with a wide size distribution and the flexibility of *B. rhodani* and *H. dalecarlica* in Sagelva.

Based on the field data, the growth strategies and life cycles of lotic Ephemeroptera in Sagelva can be grouped into three categories. The first, represented by *B. scambus* and *H. joernensis*, spend the period of ice cover either as eggs or small quiescent nymphs and have a rapid growth before emergence and oviposition in late summer (summer species). The second type of strategy is also a univoltine life cycle. Nymphs hatch from eggs in the summer or in several cohorts during the autumn. Nymphal growth then continues throughout the period of ice cover. Growth is often reduced in winter, but may be considerable as in the case of *Ameletus inopinatus*. There may be another short burst of growth after ice break before emergence occurs, as shown for *Baetis niger*. This strategy with a nymphal winter generation is the most common in Sagelva, and species belonging to this group are *Ameletus inopinatus*, *Baetis rhodani*, *Baetis niger*, *Ephemerella auriviillii* and *Heptagenia dalecarlica* (partly). The latter species also represents the third group of strategy in which part of the population seems to have a two-year life cycle with the first year spending as egg or quiescent nymphs in the hyphoreal zone. The nymphs grow in the following year and emerge at an age of about two years. Multivoltine life cycle are scarce among mayflies and besides *H. dalecarlica* are described within the genus *Ephemera* (Svensson 1977), *Hexagenia* and some other species - see Clifford 1982.

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