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Life cycles of four species of *Baëtis* (Ephemeroptera) in three Danish streams

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With 6 figures and 1 table in the text

Abstract

The study of life cycles of *Baëtis rhodani, B. niger, B. vernus* and *B. fuscatus* revealed two different patterns of life cycles. *B. rhodani* and *B. niger* had a life cycle with one or two winter and summer cohorts, whereas *B. vernus* and *B. fuscatus* had up to three summer cohorts and no winter cohort. The life cycle patterns reflected different strategies adapted to streams of different environmental stability and secured large egg or larval populations to be built up before the winter. Number of cohorts varied within years and localities and probably reflected variations in environmental conditions during egglaying or egghatching.

Introduction

A number of studies concerning the life cycles of running water invertebrates have been carried out at the Freshwater-Biological Laboratory, University of Copenhagen during the last several decades. Much of the research was accomplished as parts of MS-theses and is unpublished. The purpose of the present paper is to summarize the work done on four species of *Baëtis: B. rhodani* (Pictet), *B. vernus* Curtis, *B. niger* (L.) and *B. fuscatus* (L.).

Information comes from four localities, all different as regards flow, thermal regime, substrate and vegetation. Two of the species, *B. rhodani* and *B. vernus* occurred in three and two localities, respectively, and hence permit comparative considerations as to the influence of environmental factors on life cycle patterns.

A profound knowledge of the life cycles of a species is necessary in order to understand the mechanisms regulating population development, periodicity, size and productivity and to realize the relationships between species and environment.

Localities

The localities sampled were Rold Kilde I and VI in Northern Jutland (9°53′E, 56°46′N), Fønstrup Bæk in Northern Zealand (12°20′E, 55°58′N) and the Suså at Vetterslev in Southern Zealand (11°48′E, 55°23′N).

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Rold Kilde, being a spring, is primarily characterized by constant waterflow and has previously been described by NIELSEN (1942) and THORUP (1966). The two sections sampled, Rold Kilde I and VI, differ mainly in rate of flow.

Rold I is situated immediately downstream from a small sunexposed helokrene, yielding about 1 l sec^{-1}. The depth of the springbrook itself is only a few centimeters and the width is about 0.5 m. The current velocity is less than 30 cm sec^{-1} in spite of a slope of 16%. Water trickles among stones, most of which rise above the water surface. The springbrook is completely overgrown with herbs, mainly *Urtica dioica* (L.) during summer. The stream-bed itself is free of vegetation. The immediate surroundings are open land without trees or shrubs. Due to exposure of the helokrene and small flow, temperature fluctuated about 9 °C during the year (Fig. 1) and 0.3—3.7 °C during the day at the sampling site.

Rold Kilde VI is situated about 150 m downstream from Rold Kilde I. Brook width and depth have increased to 1.0—1.5 m and about 10 cm, respectively. The flow is close to 30 l sec^{-1}, and maximum current velocity is about 70 cm sec^{-1}. Substrates consist of sand, gravel, and stones which along the banks are densely overgrown with the submerged herbs (*Veronica beccabunga* L. and *Cardamine amara* L.). The sampling station was established in open land in order to eliminate shading by trees or bushes. Temperature fluctuations were about 6 °C during the year; daily amplitudes were 0.0—1.3 °C (Fig. 2).

Fønstrup Bæk is a forest brook, previously described by IVERSEN (1980). Its width varies between 1.2 and 2.3 m along the section studied, and depth varies between 5 and 16 cm, depending on variation in waterflow. Flows between 0.4 l sec^{-1} and 155 l sec^{-1} were measured during the investigation. Being strongly dependent on precipitation, they showed great variation from day to day. The study site is located in old beech forest which shades the brook during summer. Substrates consist of gravel and stones with intervening areas of sand and silt. Aquatic vegetation was extremely sparse, only a few tufts of *Berula erecta* (HUDS.) were present. Temperatures between 0.5 and 20.5 °C were recorded during the investigation (Fig. 3).

The Suså, described extensively by BERG (1943, 1948), was sampled near Vetterslev in the middle reach of the stream. Width of the studied section varied between 5 m and 9 m, and the depth ranged from 0.5 m to more than 2 m, depending on waterflow and macrophyte biomass. Waterflow varied between 175 l sec^{-1} and 10,900 l sec^{-1} in 1979—1980 (Det danske Hedeselskab, 1980, 1981). Since there was no shading from trees or shrubs, submerged macrophytes developed a rich community with a maximum biomass of 90 g dry weight m^{-2} in both years. The dominating species were *Potamogeton pectinatus* L., *P. crispus* L. and *Sparganium simplex* HUDS. *Cladophora* sp. was a conspicuous element in the flora from July to November 1979 and again in June—July 1980. On 1 August 1980 the stream vegetation was cut to prevent flooding of surrounding arable land. During summer fine particulate organic material and sand were deposited in the plant covered areas. Therefore, substrates were unstable sand and silt with areas of gravel and small stones in between. Daily mean temperatures, estimated from a water temperature model (JEPPESEN & IVERSEN, in press), varied from 2° to 20 °C during the sampling periods between May and November, and were close to zero in the winter when the stream was periodically covered with ice.

Methods

In Rold Kilde the winter population was sampled from September 1972 to May 1973 at about monthly intervals, whereas the summer population was sampled every three weeks from May to October 1978. In Fønstrup Bæk monthly sampling occurred from November 1974 until November 1975. Suså sampling periods were June to November 1979 and May to September 1980 at intervals varying from one week to one month.

The sampling method employed depended on the physical and biological conditions of the particular stream. In Rold Kilde 10 fist-sized stones were sampled. A handnet (frame size 16 × 16 cm, mesh size 0.44—0.48 mm) was pressed into the bottom immediately downstream from each stone. All loose material around and beneath a stone was washed into the net. The stone was then cleaned with a brush and replaced in the brook. Samples were preserved in 4 % formalin immediately. The unburied surface area of each stone was estimated, and the number of individuals m^{-2} was calculated (IVERSEN & JESSEN 1977).

In Fønstrup Bæk a kick-method was applied (IVERSEN 1980). A handnet (24 cm high and 30 cm wide, mesh size 0.1 mm) was pressed against the bottom, and the substrate upstream was disturbed intensively with the foot. 10 samples were taken each month throughout a year. These semi-quantitative samples were converted to quantitative values using a correction factor gained from simultaneous box samples (box size: 30 × 40 cm^2) taken on two occasions. Samples were preserved in 4 % formalin immediately.

All samples in the Suså were taken in the vegetation utilizing the method described by IVERSEN et al. (1985). All above ground plant parts were sampled with a 20 × 20 cm closing frame, on which a 1.2 m long net (mesh size: 0.045 mm) was mounted. Only samples from *Potamogeton pectinatus* are included in the present material. The samples were transferred to 1 l jars; sufficient formalin was added to give a 0.6 % concentration, which caused the invertebrates to relinquish their hold on the macrophytes. Samples were then preserved in 4 % formalin.

In the laboratory, Rold Kilde and Fønstrup Bæk samples were sorted by hand without magnification. Suså-samples were rinsed over a sieve (mesh size: 0.105 mm) and each plant then inspected for adhering animals. Nymphs were sorted manually under a dissecting microscope. In contrast to the methods applied to the Rold Kilde and Fønstrup Bæk samples, this procedure allowed for even the smallest instars of *Baëtis* spp. to be detected. Plants from the samples were dried and weighed. Plant biomass m^{-2} was derived from another part of the Suså project (IVERSEN et al. 1985), and from these data numbers of individuals m^{-2} were estimated.

Table 1. Total number of individuals of Baëtis species collected at each locality.

	Rold Kilde I	Rold Kilde VI	Fønstrup Bæk	Suså	Total
B. rhodani	2 862	8 777	6 394	0	18 033
B. niger	0	0	7 533	0	7 533
B. vernus	0	0	1 400	1 242	2 642
B. fuscatus	0	0	0	2 425	2 425
	2 862	8 777	15 327	3 667	30 633

When the total number of individuals exceeded 200—300 specimens per sample, a sub-sampling technique was applied. Even so, more than 30,000 specimens of *Baëtis* spp. were collected from the various localities in this study (Table 1).

After sorting, nymphs were measured, using an eyepiece micrometer. In the Rold Kilde and Fønstrup Bæk material, headcapsule width was determined at a magnification of 32 × to 1/10 of a micrometer unit (1 MU = 0.333 mm). In the Suså material, length of the second thoracic segment was measured at 40 × (1 MU = 0.025 mm).

In the following text the terms cohort and population are used according to the following definitions:

Cohort: A group of individuals of the same species which hatches within a limited time period and which can be followed as a detectable size group for some time, eventually until emergence.

Population: All the individuals of a species occurring in a particular locality at a given time.

The term generation will not be used due to confusion in the literature with definition and usage.

Results

Baëtis rhodani was sampled at both sections in Rold Kilde and in Fønstrup Bæk. The size distribution and estimated numbers m^{-2} at each sampling date are shown in Figs. 1, 2, and 3.

The size distribution in Rold Kilde I in September and October 1972 did not differ significantly from September and October 1978 (χ^2 test, $p > 0.05$). Neither did it differ in May 1972 and May 1978 (Fig. 1). Similar results were obtained in Rold Kilde VI (Fig. 2). Therefore, the life cycles could be generalized from the two studies.

In Rold Kilde I three cohorts can be identified during the year, one slow-growing winter cohort (September to June/July) with a maximum of 4,400 individuals m^{-2}, and two fast-growing, overlapping summer cohorts (June to September and July to October) with a maximum of 1,400 individuals m^{-2}. Winter cohort individuals were considerably larger than their summer counterparts.

In Rold Kilde VI, the life cycle showed the same main features, but numbers of individuals throughout the sampling periods were considerably higher

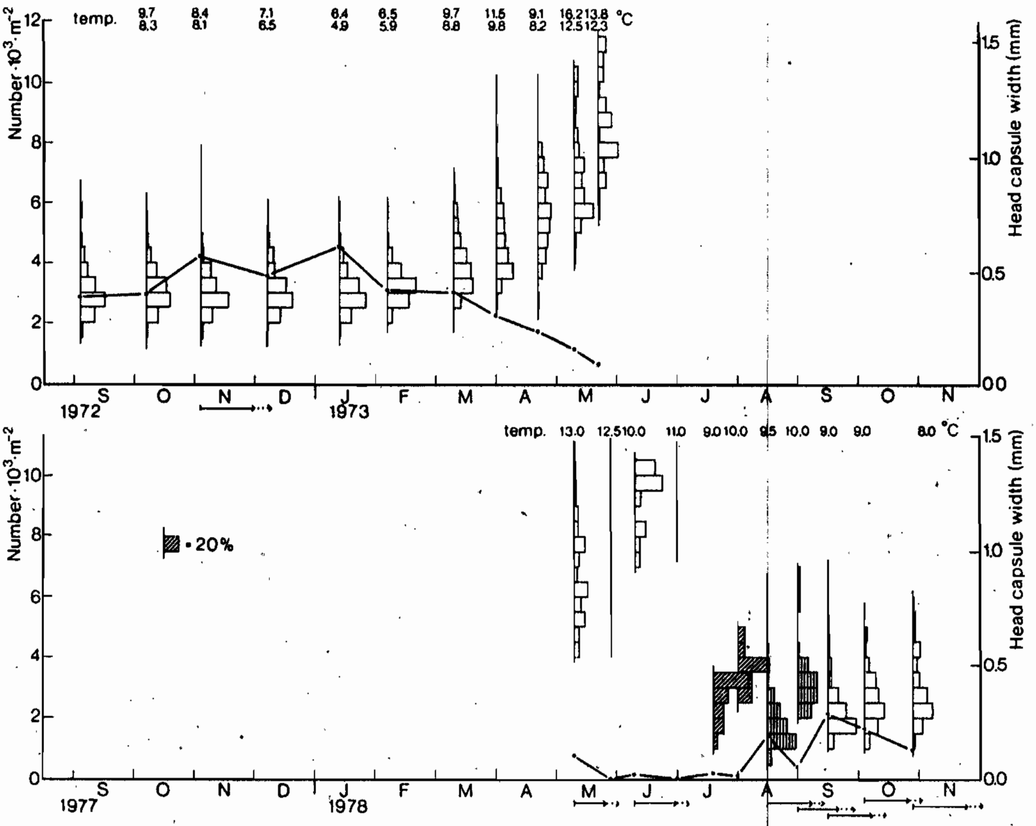

Fig. 1. Cohort size distribution by percent and estimated numbers m^{-2} (solid line) of *B. rhodani* in Rold Kilde I. Different cohorts are marked with different hatching. Actual temperatures on the sampling days are given above the histograms. Minimum and maximum hatching times estimated from ELLIOTT (1972) are marked with arrows below.

(12,000 individuals m^{-2} maximum). Winter cohort individuals were several size classes smaller in Rold Kilde VI than in Rold Kilde I.

The life cycle pattern was somewhat different in Fønstrup Bæk. Individual size during winter was larger than in Rold Kilde, and the winter cohort's emergence period ended in June, whereas it continued until the end of July in Rold Kilde VI. Two summer cohorts appeared, although they were difficult to separate, in July, August and September.

Baëtis niger was sampled in Fønstrup Bæk only. Size distribution and estimated numbers m^{-2} are shown in Fig. 4.

In May—June a small summer cohort hatched and grew up to emerge in August. The winter cohort became clearly distinguishable in July, and addition of young continued during the month. In the beginning of October an increase in the number of individuals occurred, and the histogram shows that it

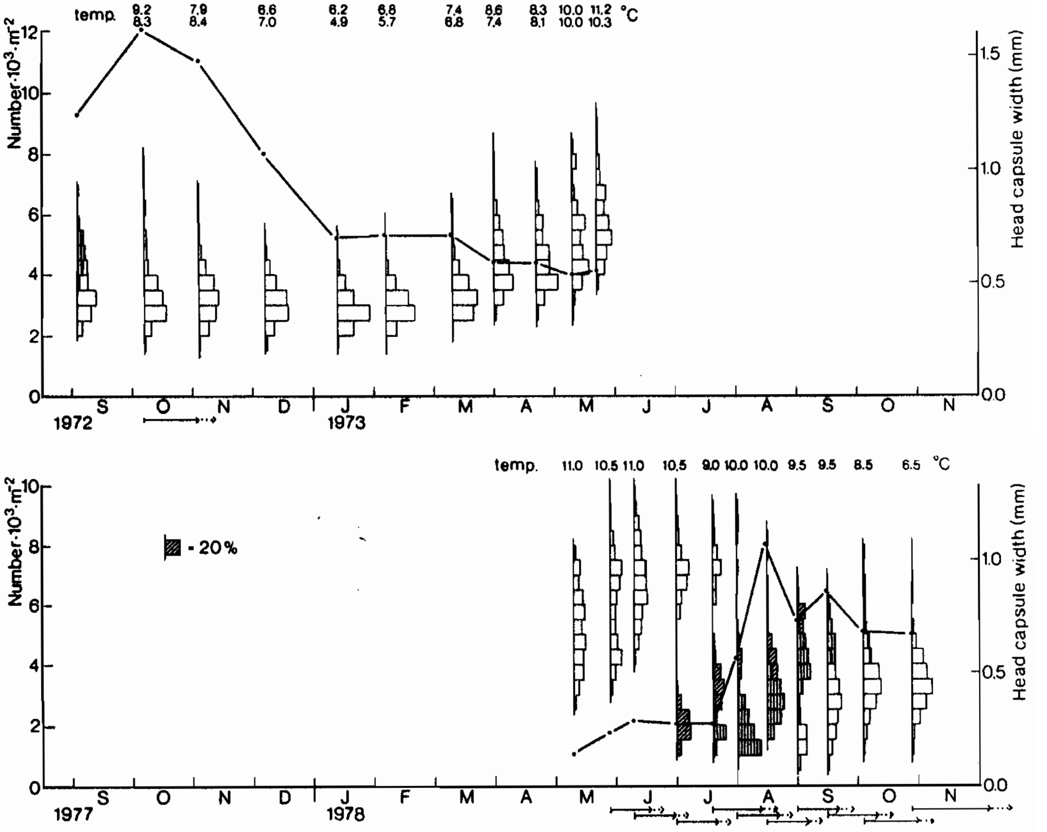

Fig. 2. Cohort size distribution by percent and estimated numbers m^{-2} (solid line) of *B. rhodani* in Rold Kilde VI. Different cohorts are marked with different hatching. Actual temperatures on the sampling days are given above histograms. Minimum and maximum hatching times estimated from Elliott (1972) are marked with arrows below.

was primarily due to increase in the number of small individuals. There are indications in the histograms for November 1974 and 1975 that the winter population might be composed of two cohorts, although size distribution in the previous and following months do not support this. The shape of the March histogram indicates a new supply of young specimens in the preceding period.

Baëtis vernus occurred in the material from Fønstrup Bæk and from the Suså. Size distribution and estimated numbers m^{-2} are shown in Figs. 4 and 5.

Fønstrup Bæk populations were very small except during June. In the Suså, *Baëtis* spp. mainly occurred from May to November. (Four series of 48 winter bottom samples, each with an area of 21 cm^2, contained only five specimens of *Baëtis*).

In Fønstrup Bæk summer and fall cohorts could be identified. The abundant summer cohort grew up and emerged in June/July. The fall cohort

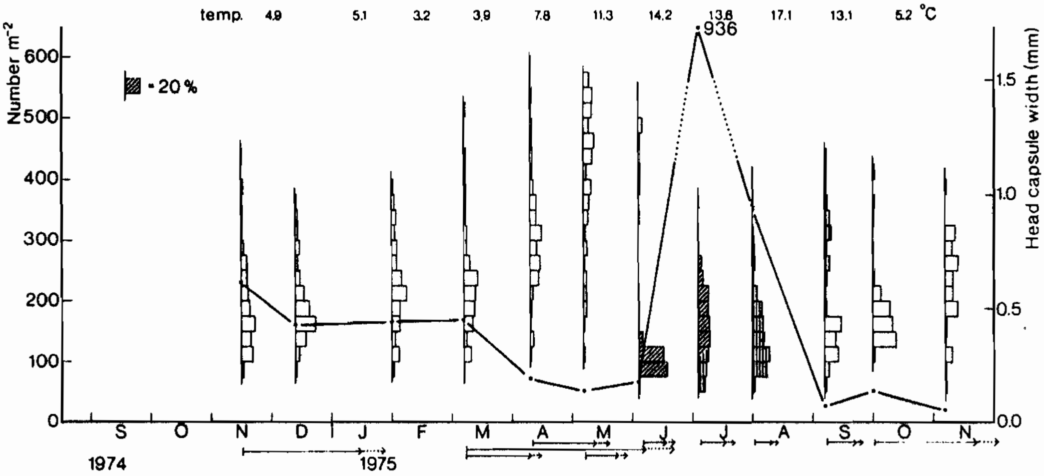

Fig. 3. Cohort size distribution by percent and estimated numbers m $^{-2}$ (solid line) of *B. rhodani* in Fønstrup Bæk. Different cohorts are marked with different hatching. Mean temperatures between sampling dates are given above histograms. Minimum and maximum hatching times estimated from ELLIOTT (1972) are marked with arrows below.

started in August grew faster and ended emergence in November. The start of an unsuccessful winter cohort was seen in November/December 1974.

In the Suså samples, three short summer cohorts could be distinguished. The first began in May and emerged in June (1980), the second began in June/July and emerged in July/August, and the third began in August and emerged in September/October. In 1979 the start of a winter cohort was indicated in October/November, and the few large specimens in May and June samples (1980) can be regarded as the remnants of this cohort.

Baëtis fuscatus was only found in the Suså. Size distribution and number of individuals m $^{-2}$ is seen in Fig. 5.

In May 1980 the beginning of an early summer cohort was found. It attained emergence size a mongh later. In June/July/August the next cohort started, and emerged in August/September. The last summer cohort began in September and in October/November, but seemed to be without success in 1980, as no fullgrown specimens were found.

In November 1979 indications of a beginning winter cohort was found, but this also seems to have been unsuccessful, although a few large specimens in May 1980 could represent its last remnant.

Discussion

A complete understanding of the life cycle of *Baëtis* species is not possible without knowledge of the duration of egg development. Unfortunately, such

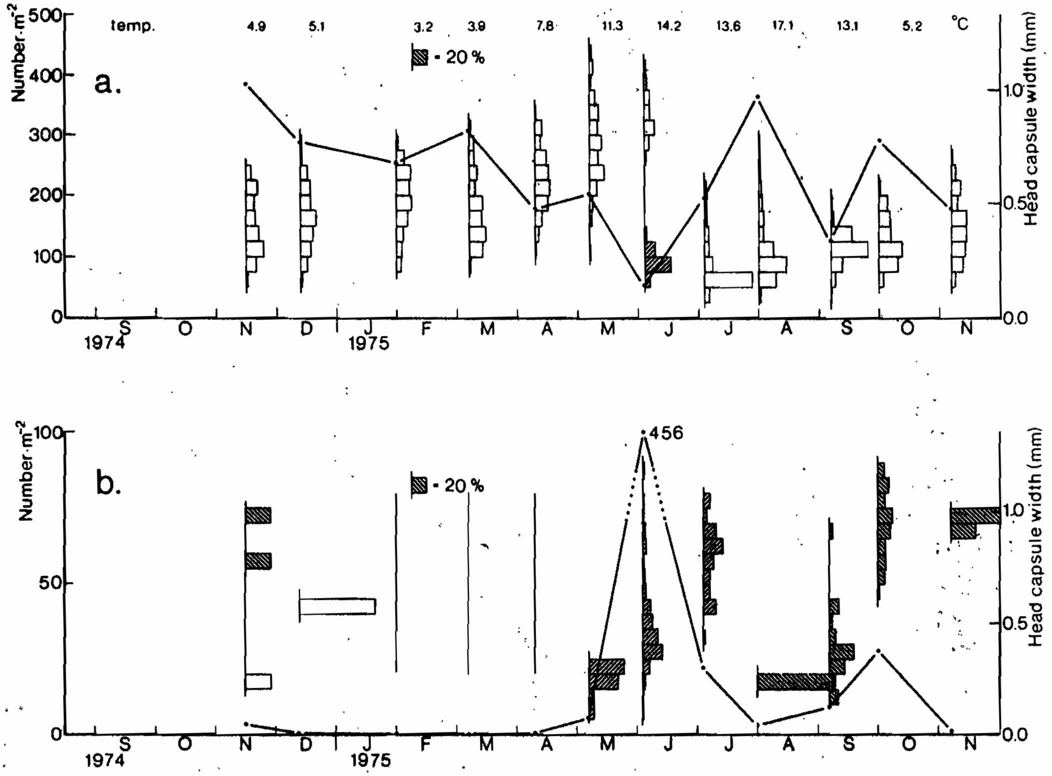

Fig. 4. Cohort size distribution by percent and estimated numbers m^{-2} (solid line) of *B. niger* (a) and *B. vernus* (b) in Fønstrup Bæk. Different cohorts are marked with different hatching. Mean temperatures between sampling dates are given above histograms.

information is scarce. To the authors' knowledge, the hatching period is known only for *B. rhodani* and *B. vernus* (Benech & Vignes 1972 a, Bohle 1969, Elliott 1972, Illies 1959).

The hatching period for eggs of *B. rhodani* given by Benech & Vignes (1972 a), Elliott (1972) and Bohle (1969) are in close agreement. Such hatching times, for eggs deposited at any field temperature, can be found from an established relationship between temperature and time required for hatching (Elliott 1972). By applying these hatching periods to the data from Rold Kilde I and Fønstrup Bæk (Figs. 1 and 3) the winter cohort is shown to probably be the parental cohort for the first and second summer cohorts (Fig. 6 A). Progeny from the first summer cohort comprised the beginning of the winter cohort, whereas progeny from the second summer cohort were probably recruited to the winter cohort from October throughout the winter. However, the expected distinct bimodal size distribution in the winter population was

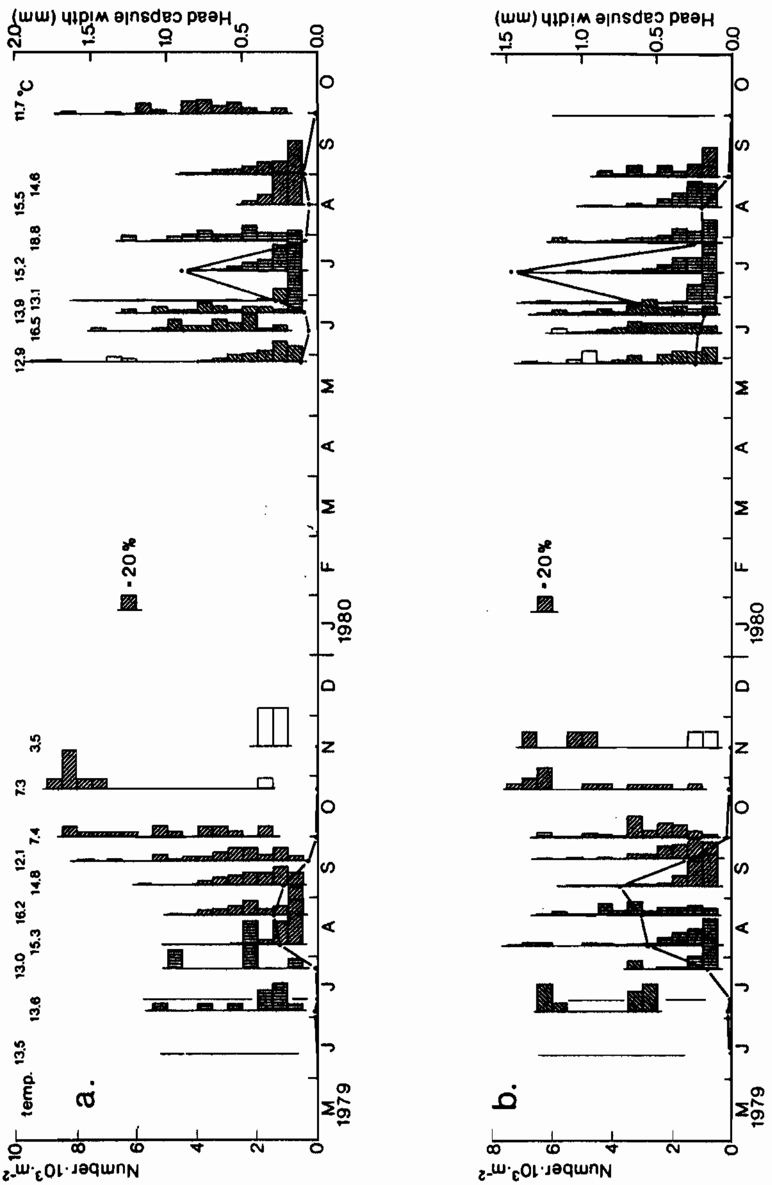

Fig. 5. Cohort size distribution by percent and estimated numbers m^{-2} (solid line) of *B. vernus* (a) and *B. fuscatus* (b) in the Suså. Different cohorts are marked with different hatching. Weekly mean temperatures around sampling date are given above histograms.

not found, probably due to interference of the temperature dependent hatching period and growth rate, and overlapping flight periods of the two summer

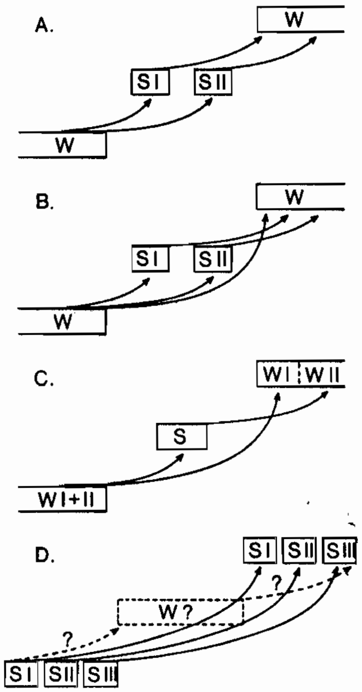

Fig. 6. Simplified outline of the studied *Baëtis* life cycles. W: winter cohort, S: summer cohort. First, second and third cohorts are marked with roman numerals I, II and III. A: *B. rhodani* from Rold Kilde I and Fønstrup Bæk, B: *B. rhodani* from Rold Kilde VI, C: *B. niger* from Fønstrup Bæk, D: *B. vernus* from Fønstrup Bæk, and *B. vernus* and *B. fuscatus* from the Suså.

cohorts. Fønstrup Bæk did suggest a weak bimodality, perhaps due to minor recruitment in winter and early spring.

In Rold Kilde VI (Fig. 2) the lower summer temperatures resulted in another linking of the various cohorts (Fig. 6 B). The first summer cohort's progeny could not develop fast enough to initiate the winter cohort, the beginning of which came only from offspring of the preceding winter cohort. The two summer cohorts were important, however, in prolonging recruitment to the winter cohort throughout the entire winter.

From midsummer until autumn the temperature in Fønstrup Bæk was several degrees centigrades higher than in the Rold Kilde localities. The result was faster growth of *B. rhodani* in Fønstrup Bæk, giving higher modal and maximum sizes of the winter cohort throughout the winter. Therefore, full-grown nymphs occurred in March in Fønstrup Bæk, whereas they did not reach maturity until April in Rold Kilde. Emergence of the winter cohort was finished in Fønstrup Bæk in June, but not until July/August in Rold Kilde.

B. rhodani is one of the most common and widespread mayflies in European watercourses, and many authors have dealt with its life cycle (Benech & Vignes 1972 b, Bretschko 1965, Elliott 1967, Fahy 1973, Harker 1952, 1953, Humpesch 1979, Langford 1971, Larsen 1968, Macan 1957, Pleskot 1958, Thibault 1971, Thorup 1963, 1973, Ulfstrand 1968, Welton, Ladle & Bass 1982, Wise 1980). Most authors agree that there is only one winter cohort. Important exceptions are MACAN's (1957) suggestion of two overlapping winter cohorts, and the absence of wintering nymphs in the study of PLESKOT (1958). MACAN (1957) also proposed that the summer cohort may be divided into two. Most researchers have found several summer cohorts, but the exact number is difficult to specify due to methodological difficulties. Because nymphs grow rapidly during summer, the sampling interval must be shorter than usual in order to determine the number of cohorts with certainty. However, the number of cohorts and their temporal occurrence undoubtedly varies between and perhaps within localities.

The emergence period was found in most studies to last from early spring to late autumn, with variation in length due to the thermal regime of the water course. Variation in emergence intensity often gives peaks in spring, early summer and autumn. In a few cases no emergence took place in July or August, resulting in distinct flight periods for the winter and summer cohorts (PLESKOT 1958, WISE 1980). The more usual situation is for the summer population to be composed of several cohorts, resulting in more uniform emergence throughout the summer.

Hatching period information is lacking for *B. niger*, but it seems realistic to assume that the summer cohort is based on progeny from the winter cohort. This implies a hatching period for *B. niger* of equal or shorter length than for *B. rhodani*. That the beginning of the winter cohort is based on progeny from the summer cohort seems unlikely. It must be based on progeny from the latest emergence of the preceding winter cohort (Fig. 6 C). Here, too, the importance of the *B. niger* summer cohort lies in extending recruitment of the winter population. In turn, extended recruitment may be the cause of the large number of nymphs in October—November and possibly the bimodal size distribution in November.

An increase in the number of small individuals occurred in March. These small nymphs may have hatched from eggs laid in late autumn, as temperatures in Fønstrup Bæk were very low (2.5—5.5 °C) during the winter. At such low temperatures we know that embryogenesis of *B. rhodani* lasts 4—5 months (ELLIOTT 1972), and embryogenesis of approximately the same length might be expected for *B. niger*. The 1975 autumn temperature of Fønstrup Bæk was much higher than the preceding year, so similar recruitment would not be likely during March 1976.

ELLIOTT (1967) described the life cycle of *B. niger* in Walla Brook as being bivoltine, with the same emergence period as we found.

In conclusion, the life cycle patterns of *B. rhodani* and *B. niger* in Fønstrup Bæk were very much alike, the main difference being that *B. rhodani* had two hardly distinguishable summer cohorts and *B. niger* possibly two winter cohorts. Further, maximum numbers due to hatching of the summer cohorts occurred a month later for *B. niger* than for *B. rhodani*. A small difference in species growth rate under the common existing ecological conditions could be responsible for the different life cycles observed.

The most characteristic feature of the life cycle of *B. vernus* in Fønstrup Bæk and the Suså is the near lack of specimens during winter. Since sampling was conducted throughout the winter, nymphal absence must be a function of the species biology.

According to Bohle (1969), an obligate diapause occurs in the egg development of *B. vernus*. Diapause lasts from one month at 0 °C to 12 months at 15.6 °C. Pre- and postdiapause development is also temperature dependent, and takes several months whatever the temperature conditions are. The information thus indicates that *B. vernus* overwinters as eggs. Because eggs must diapause, it is improbable that the successive cohorts during summer are parent and progeny. So, for each summer cohort the parental cohort must be found among the preceding years' cohorts (Fig. 6 D). However, as the duration of the diapause and other embryonic phases are temperature dependent in a rather complicated manner (Bohle 1969), it is not possible with any certainty to link the various cohorts. Pleskot (1958) suggested that diapause for all eggs is not obligatory, and a small percentage from the first summer cohort develops rapidly and gives rise to a second summer cohort. Published information on embryogenesis offers no explanation for the presence of two summer cohorts in Fønstrup Bæk.

Pleskot's (1958) data indicate two well-separated summer cohorts in the Schwechat, Austria. These appear to correspond to the first and second summer cohorts in the Suså population. She also found five nymphs in September which must represent our third cohort.

Illies & Masteller (1977) found that the number of summer cohorts varied between one and three in Breitenbach, Germany, depending on the temperature regime during the preceding winter. Low winter temperatures induced development of more summer cohorts than did high winter temperatures. This, however, is not consistent with the present results as, in spite of the fact that the winter 1978—79 was very severe with longlasting ice cover of the Suså, *B. vernus* apparently had only two cohorts during the summer of 1979. Low temperature is important in breaking egg-diapause (Bohle 1969) and, therefore, the times at which low temperatures occur are important as well. In the published literature only Langford (1971) noted the presence of *B. vernus* nymphs during winter. He found them in small numbers in River Severn, England. Our present studies revealed a few small individuals at the beginning of winter and a few large ones at the end of the winter, indicating the presence of a negligible winter cohort.

Compared to the other *Baëtis* species evaluated, the development of the *B. vernus* populations seems to differ greatly between years and localities. Perhaps this can be taken as an indication of the sensitivity of the diapausing egg to varying temperature conditions, especially during winter.

Although no embryogenesis information is available, Pleskot (1958) implies a winter egg-diapause in her interpretation of the life cycle of *B. fuscatus* (sub. nom. *B. bioculatus* L.). The life cycle of *B. fuscatus* in the Suså resembles that of *B. vernus* (Fig. 6 D) and might be explained in the same way, assuming the same type of embryogenesis but a differing temperature dependency.

In addition to Pleskot (1958, 1960, 1961), the life cycle of *B. fuscatus* has been studied by Langford (1971), Sowa (1975), Ulfstrand (1968), and Wise (1980). All conclude that the species hibernates in the egg stage, but Langford and Ulfstrand found one summer cohort, while Sowa and Wise desbribe two. While none of these authors found three cohorts, an overly long sampling interval or, as this study shows, variability between years due to environmental influence might be responsible. In Swedish Lapland *B. fuscatus* occurred only from the beginning of August to the middle of September (Ulfstrand 1968), just time enough for one cohort under the prevailing temperatures.

Although the patterns were the same for the two species each year, *B. vernus* and *B. fuscatus* demonstrated great difference in the development of population size in 1979 and 1980. In 1979 the number of individuals was very small until July—August, probably due to the severe and prolonged winter. Not until the beginning of the second cohort of *B. fuscatus* and the third of *B. vernus* was significant population increase seen. The number of *B. fuscatus* was further increased by the appearance of a third cohort. In 1980 the populations received a much better start because of a mild winter. The first cohort of both species contained significant numbers, and the population increased considerably with the hatching of the second cohort in July. However, a sudden decrease in numbers was noticed at the end of July shortly after a severely increased stream flow. Weed clearance on August 1st impeded the third cohort of both species from rebuilding their populations.

Fluctuations in population size in Fønstrup Bæk were conspicuous during summer. All three species had maxima occurring successively in June, July and August for *B. vernus*, *B. rhodani* and *B. niger*, respectively. In this way the three closely related species shared resources in spite of two of the species' life cycles being much alike. There was no biological indication of a second and smaller maximum coinciding for *B. niger* and *B. vernus* about the first of October.

The different nature of the three localities did not have any discernable influence on the life cycle pattern of *B. rhodani* other than the effect of the different temperature regimes on embryogenesis and maximum size already discussed. The main difference between the populations appeared in population size and dynamics. The population of *B. rhodani* in Rold Kilde was an order of magnitude larger than the total populations of *Baëtis* spp. in Fønstrup Bæk. Better food conditions in Rold Kilde, it being an exposed locality with higher periphyton production, might be responsible. However, the occurrence of two other species of *Baëtis* in Fønstrup Bæk might influence total population size there (Langford 1971). That the maximum population size in Fønstrup Bæk was attained by the summer cohorts rather than the winter cohorts as in Rold Kilde is remarkable. However, no explanation of this difference can be given with our present knowledge.

The population of *B. vernus* in Fønstrup Bæk was substantially smaller than in the Suså, because ecological conditions and carrying capacity differ considerably. The important differences were the dense vegetation and high water level which increase the area of surfaces with good food conditions in the Suså. The difference in timing of the population maxima at the different localities and years is accounted for by temporal and local variations in environmental factors such as stream flow and weed clearance as already described.

Most studies of Ephemeroptera life cycles reveal a characteristic difference between maximum size of nymphs belonging to different cohorts. The slow-growing winter cohorts always attain larger size than the fast-growing summer cohorts. Even differences between the various summer cohorts have been demonstrated (Benech & Vignes 1972 b, Fahy 1973, present study).

The life cycle patterns dealt with in the present study are clearly classified into two groups characterized by different wintering strategies. *B. rhodani* and *B. niger* exemplify one pattern. They hibernate as small and half-sized nymphs that grow rapidly in late winter and early spring and are followed by one or two fast-growing summer cohorts. The summer cohorts are apparently unnecessary for the continuity of the population, but provide a continuous input of newly hatched individuals, thus assuring a numerous and secure winter population. Such a life cycle is advantageous to species living on stable substrate which affords nymphs suitable winter habitats.

In temperate latitudes *B. vernus* and *B. fuscatus* hibernate as diapausing eggs. Such eggs hatch in spring or early summer, producing two or three cohorts during summer. This type of life cycle is well adapted to life in vegetation in larger streams. In such streams, such as the Suså, the vegetation withers in autumn and does not grow again until the following summer, thus eliminating winter nymphal habitats.

In order to evaluate the effect of environmental stress on *Baëtis* sp. populations, an intimate knowledge of the parent—progeny relationship is necessary. In three small Danish streams with high winter concentrations of Fe^{++} (0.9—1.3 mg $Fe^{++}\ l^{-1}$) and summer concentrations < 0.5 mg $Fe^{++}\ l^{-1}$ *B. rhodani* was found in August/September, but not in January nor May/June (Skriver 1984). As *B. rhodani* does not have overwintering eggs, this occurrence could only be explained as immigration from neighbouring streams, where *B. rhodani* occurred abundantly.

Although studies on Ephemeroptera life cycles show that each species has a fixed life cycle pattern, they also show that the number of cohorts varies within the same species, reflecting the environmental conditions. For example might an egg-hatching period with optimal conditions give rise to one cohort, whereas bad conditions in the middle of the egghatching period might give rise to two cohorts. In theory, numbers of cohorts are unlimited, but in practice numbers of cohorts are limited by the length of egghatching period, the nymphal growth rates, sampling interval and sample size.

In this study we have demonstrated that numbers and sizes of cohorts of a given *Baëtis* sp., do vary between localities and years due to variations in the abiotic or biotic environment. In studies of secondary production the use of production curves (ALLEN 1951) therefore makes it necessary each time to delimit discrete cohorts, which makes the method very tedious.

When estimating secondary production by the size frequency method (WATERS 1977, BENKE 1979) nymphal maximum size and the cohort production interval (CPI) must be known. We think that it is possible to establish a model which relates growth rates or the cohort production interval of various *Baëtis* species to easily measured abiotic parameters as for example temperature and light. It will probably still be necessary to separate the winter and summer cohorts, but no doubt estimation of secondary production will be greatly facilitated.

Summary

The life cycles of *Baëtis rhodani*, *B. niger*, *B. vernus* and *B. fuscatus* were studied on a quantitative or semiquantitative basis in three Danish streams, differing with regard to flow, thermal regime, substrate and vegetation. The association between *Baëtis* spp. varied among the studied streams as well. Two different life cycle patterns were revealed; one possessed one or two winter and summer cohorts (*B. rhodani*, *B. niger*), and one had three summer cohorts but no winter cohorts (*B. vernus*, *B. fuscatus*). The two types of life cycles represent different strategies for dealing with the different environments in which the species overwinter. Both strategies function to build up a large population of nymphs or eggs during summer and autumn. Species living on stable substrates such as stones and gravel establish a big population of nymphs during summer, autumn and the beginning of the winter, while species associated with vegetation build up a large population of winter-diapausing eggs. Number of cohorts merely reflects variations in environmental conditions and may differ within years and localities. Therefore, growth rate or cohort production interval under specified environmental conditions are much more important than number of cohorts.

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