Life cycle, energy fluctuations and sexual differentiation in Ephemera danica (Ephemeroptera), a stream-living mayfly

B. Svensson

Department of Animal Ecology, University of Lund

Svensson, B. 1977. Life cycle, energy fluctuations and sexual differentiation in *Ephemera danica* (Ephemeroptera), a stream-living mayfly. – Oikos 29: 78–86.

Larval growth of *Ephemera danica* Müller in a South Swedish stream was calculated from changes in the size distribution of the larvae between monthly samples. Part of the population completed a generation in two years, whereas the rest of the individuals spent three years as immatures. Adult and larval sex ratios equalled 3:2 with an excess of males. Stepwise development of external male characters accompanied by decreasing relative energy content of the nymphs took place in two periods (late spring and autumn). It is suggested that such a development of adult characters provides a mechanism allowing nymphs of different age to mature and emerge synchronously.

B. Svensson, Dept of Animal Ecology, Ecology Building, S-223 62 Lund, Sweden.

Рассчитывали рост личинок *Ephemera danica* Müller в реке южной Швеции на основе изменениий в размерного состава личинок в ежемесячных пробах. Часть популяции заканчивает развитие в два года, а остальные – в течение трех лет остаются неполовозрелыми. Соотношение полов у имаго и личинок составляет 3:2 с преобладанием самцов. Стадийное развитие внешних половых признаков у самцов сопровождающееся снижением относительного запаса энергии у нимф, наблюдалось в конце весны и осенью. Предполагаетсд, что характер развития половых признаков является механизмом, допускаюющим синхронное созревание и вылет насекомых разного возраста.

1. Introduction

During the last three decades the life histories of an increasing number of stream dwelling mayflies have been studied. Most investigations, however, have concerned uni- and polyvoltine species with rather straightforward life cycles. Few workers have dealt with the growth pattern of species spending two or more years as immatures and with the energetics and sexual differentiation in mayflies.

The present study comprises 3.5 years' observations of the life history of *Ephemera danica* Müller in a South Swedish stream. The nymphs of *E. danica* are common in slow-flowing waters all over Europe. They spend their lives burrowing in sandy substrate and feeding on fine particulate detritus. Several investigators have attempted to define the life span of *E. danica*. Thus, Macan (1970) in England, Pleskot (1958) in Austria and Jazdzewska (1971) in Poland suggest a one year life cycle, this opinion being contradicted by Landa's (1968) observations from Czechoslovakia where the species was found to complete a generation in two years. In addition to the dimensional growth and morphological differentiation I have used data on energy and fat contents in an attempt to identify periods of high energy expenditure.

2. Study area

This investigation was carried out in a small stream in southern Sweden, approx. 55° 37′ N, 13° 35′ E. The stream, herafter called Stampen, is about 10 km long with an average width of 1.7 m. For a general description see Hultin (1971) and Otto (1971). A 300 m stretch near its junction with a larger stream was chosen for this study. This part of the section is surrounded by cultivated fields and bordered with alder, *Alnus glutinosa* (L.). *Epilobium hirsutum* L. forms dense clumps in the lower part of the section, and some emergent *Sparganium* sp. occur in the upper part. The bottom consists of fine sand (average grain size 0.2 mm). The mean water depth amounts to 48 cm in the winter and 32 cm in the summer. Heavy rainfall or snow melting may occasionally cause the stream to flood, but generally only minor fluctuations in stream width occur within the section studied.

3. Terminology

All individuals deriving from eggs laid during one flight period and having the same emergence period are referred to as a cohort.

During a transitory period (Clifford 1970) larvae having reached a certain physiological stage suddenly accelerate and synchronize their development. Larvae not having reached this stage are left behind. Hence, transitory periods are periods of cohort differentiation or, with respect to the larger nymphs, cohort fusion leading to simultaneous emergence.

4. Material and methods

4.1. Field sampling

The field work was carried out from March 1972 until August 1975. About monthly samples were taken using a Neill cylinder (Macan 1958) which covered 0.05 m² and removed the bottom substrate to a depth of 5–7 cm. Each time, 6 to 50 such samples were taken, and, on average, 548 specimens were collected (max. 2063, min. 167). The larvae were generally sorted out in the field, using a sieve with 0.5 mm mesh size. This equipment collected all nymphs 4 mm or larger. The larvae were placed in glass jars filled with water and brought alive to the laboratory.

Occasionally during 1974, samples were also taken using a sheet-metal cylinder which covered an area of 113 cm² and removed the bottom substrate to a depth of about 10 cm. Three to five such samples were taken each time. The cylinder was emptied in a plastic pail, and the sample brought to the laboratory.

Emerging adults were trapped in net cages placed over the stream. During the flight periods of 1972 and 1973, three cages were used, each covering 0.8 m². These cages were emptied once a week, and both dead and alive specimens were collected. In 1974 and 1975, four traps were used, altogether covering 10.5 m². These cages were emptied each or every second day during the flight periods.

Stream water temperature was registered by means of a thermograph (Tab. 1).

4.2. Analytical procedures

Before being measured, the animals were anaesthetized using water saturated with carbon dioxide. This procedure evaded the distortive influence of preservatives on body parts. The nymphs were grouped into 1 mm size classes, based on total body length excluding the cerci. At the same time, the development of wing pads and external genitalia in the males were registered according to a standardized classification. Sex determinations and

Tab. 1. Monthly mean water temperature, °C, in Stampen during the study period.

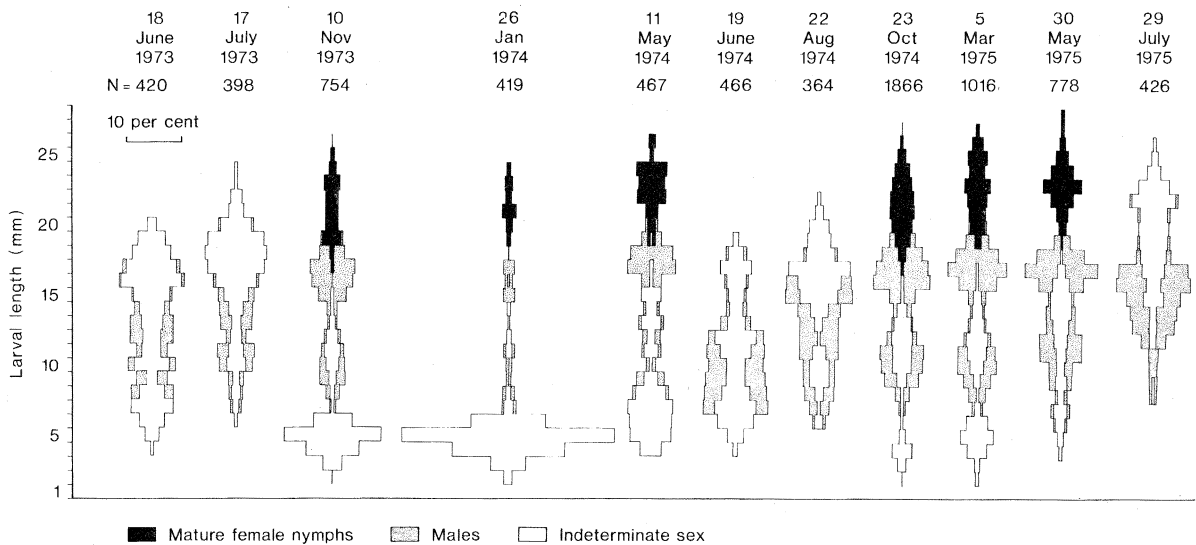|	J	F	M	A	M	J	J	A	S	O	N	D
1972			2.9	6.6	10.1	13.4	14.5	13.3	10.8	6.9	5.3	–
1973	3.2	2.6	3.6	5.7	10.8	13.1	14.6	13.1	10.9	6.2	3.3	0.8
1974	2.3	2.3	2.8	6.8	9.6	12.0	12.7	12.9	11.4	6.9	5.2	3.9
1975	3.8	2.4	3.1	5.7	10.1	12.1	14.3	14.9				

Fig. 1. Seasonal changes in the frequency of different size classes during part of the study period.

number of individuals in each size class were used for the construction of frequency histograms (see Fig. 1). Assuming a normal size distribution of individuals belonging to each sex and cohort, the different cohorts could then be separated according to the method described by Bhattacharya (1967). Having been measured and separated into sex and length classes, some animals were deep frozen for subsequent energy and fat analyses.

Growth was calculated from changes in body length between consecutive samples. When constructing the growth curves, body length was converted to dry weight using the formula

$$\log (\text{dry wt (mg)}) = -2.510 + 2.864 \times \log (\text{length (mm)})$$

No deviations from this relationship were observed during the study period. For the calculation of growth the total body length was used, because it agrees well with weight increase among larger nymphs. Among nymphs in the weight interval 1–12 mg head capsule width is directly related to body length.

Tab. 2. Comparison between wet oxidation and bomb calorimetry. Samples used in both methods are drawn from the same homogenized mixture of about 50 animals. Each value denotes the mean ± S.D. of six analyses. 1 cal. = 4.187 J.

		$\text{Cal} \times \text{g}^{-1}$ dry weight Wet oxidation	$\text{Cal} \times \text{g}^{-1}$ dry weight Bomb calorimetry
Nymphs	♂♂	4547 ± 183	5138 ± 166
	♀♀	4363 ± 67	4974 ± 179
Subadults	♂♂	4611 ± 188	5539 ± 83
	♀♀	4424 ± 162	5627 ± 190

The samples obtained by the sheet-metal cylinder were flotated using a 25% mangan sulphate solution. The first appearance of individuals <1 mm, signifying the beginning of the egg hatching period, was recorded.

Caloric contents were measured according to the wet oxidation method described by Winberg (1971). A comparison between this and the bomb-calorimetric method (Phillipson 1964) was made (Tab. 2). Although the latter method produced somewhat higher values, no correction was applied to the figures presented below.

Fat contents were determined using the method described by Södergren (1973).

Prior to these analyses the animals were dried at 60° for 24 h. As the guts of the nymphs often contained mineral particles which could greatly affect the weight measurements, the intestines were removed in all specimens $\geqq 14$ mm. In addition, non-combustible matter, appearing after the wet-oxidation of nymphs <14 mm, was filtered on a 0.45 μm Millipore filter. The weight increase of the filter was subtracted from the corresponding total dry weights. A comparison was made between intact animals and those from which the gut had been removed, and it was found that the gut-free animals achieved somewhat higher caloric values.

5. Results

5.1. Growth

The growth of an average individual in each cohort is illustrated in Fig. 2. The time of emergence is also indicated. Tab. 3 summarizes the life span of each cohort during the study period.

No attempt was made to follow the eggs from the time of laying until hatching occurred. However, as larvae
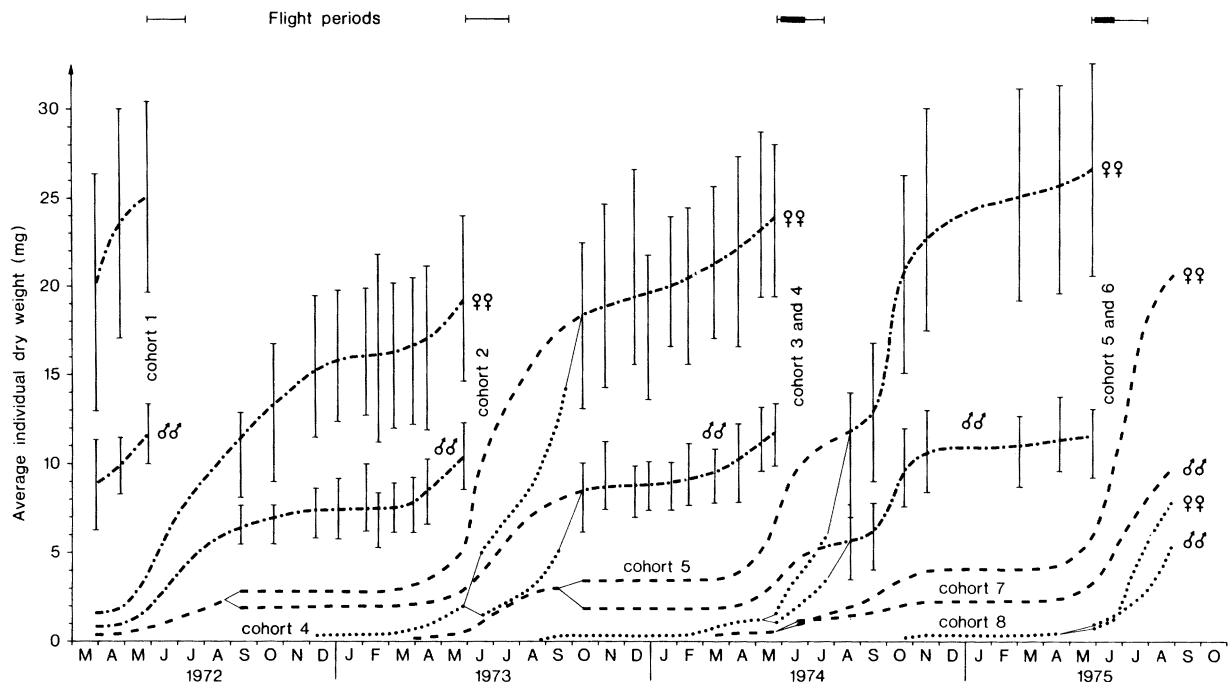
Fig. 2. Smoothed curves showing growth in terms of dry weight of average individuals during the study period. Dashed curves = three-year cohorts; dotted curves = two-year cohorts. Vertical lines denote S.D. Upper horisontal lines show time of emergence; thickened parts indicates the period during which 95% of the mayflies emerged.

<1 mm were obtained by the sheet-metal cylinder only from about one month after the main flight period until late winter, but not during spring and early summer, it is reasonable to assume that all eggs hatched between July and about March. Thus, eggs laid during one emergence season may give rise to either a two-year cohort or both a two-year and a three-year cohort.

As can be seen in Fig. 2, female nymphs (including non-differentiated males, see below) above 1.5 mg grew faster and became larger in comparison with males. In addition, different cohorts showed different growth rates. There were also marked between-year differences in the mean weight of full-grown nymphs. These differences were most pronounced in the females.

Tab. 3. Life span of the different cohorts during the study period. Cohort numbers refer to Fig. 2. Figures in brackets denote expected years of emergence. See text for definition of cohort.

Cohort	Yr of hatching	Yr of emergence	Life span, yr
1	?	1972	?
2	?	1973	?
3	(1971)	1974	(3)
4	1972	1974	2
5	1972	1975	3
6	1973	1975	2
7	1973	(1976)	(3)
8	1974	(1976)	(2)
9	1975	?	?

5.2. Energy storage

The seasonal changes in caloric content per weight unit of average individuals in two cohorts are illustrated in Fig. 3. In the same figure are shown the average relative growth rates, calculated from the growth curves. Fig. 4 demonstrates the changes in the proportion of fat of large nymphs from September until emergence at the end of May. Note that caloric and fat analyses were largely performed in different years. Thus, these values do not allow of direct comparisons. Obviously the caloric content fluctuated synchronously in males and females. For both cohorts, the highest caloric values were achieved in February/March with a second peak among the younger nymphs in the beginning of summer. The lowest values were found in April and early autumn.

5.3. Sexual differentiation and sex ratio

In E. danica differentiated male nymphs differ from female nymphs by the presence of claspers on the ninth abdominal segment, and by the relatively large size of the eyes. As these two characters develop at the same time in this species, only the former has been used in this study. Male characters first became visible in larvae belonging to the 8 mm size class. Occasionally, differentiated males were found already among the 5 mm larvae. Thus, animals without a forceps had to be classified as either females or non-differentiated males.

The proportion of males among the total number of individuals (Fig. 5) in each of the 8 cohorts included two conspicuous enlargements between egg hatching and
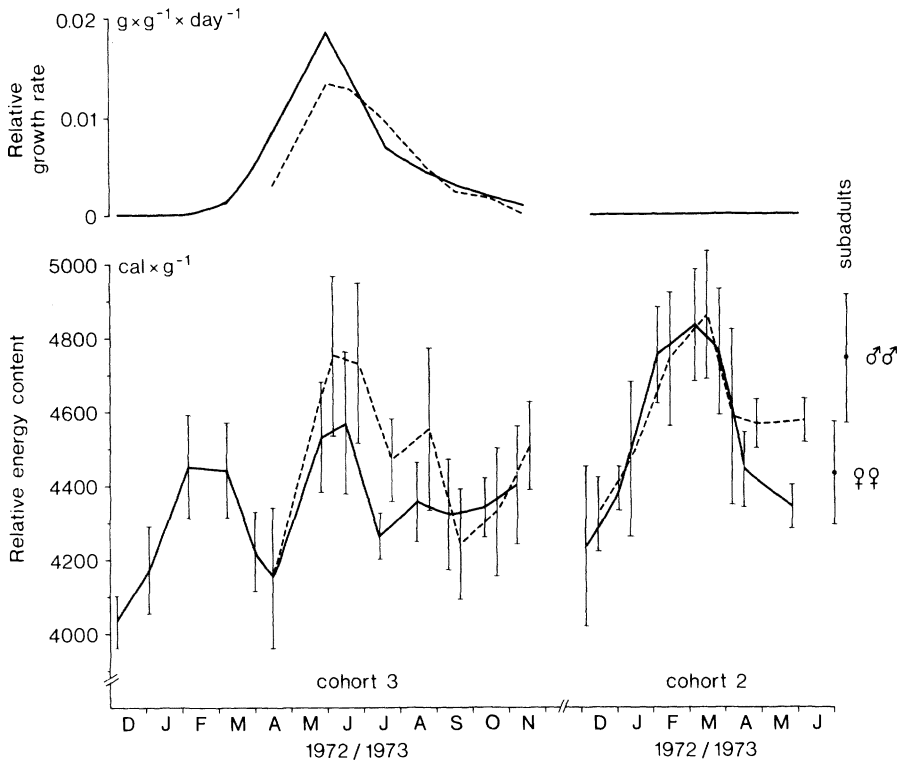
Fig. 3. Relative growth rates (upper graph), and seasonal changes in relative caloric content (lower graph) of average individuals of two different cohorts. Dashed lines = males; solid lines = females. Vertical lines denote S.D. Cohort numbers refer to Fig. 2. Values from Oct and Nov also include cohort 4. Each caloric value represents the average of 31–83 analyses.

emergence, each of which was followed by a period of relatively stable sex ratios. As already stated, the first rise was seen when the larvae approached a total body length of 8 mm, while the second change in sex ratio involved nymphs which had reached almost their final body size. A close examination of the development of the three-segmented claspers among the older male nymphs showed, however, that owing to a retarded development of their external sex characters, a certain proportion of males had been classified among the females in earlier periods.

Tab. 4 summarizes the sex ratios of the fullgrown nymphs and of the adults during the study period. Immediately after the second differentiation of male characters, the ratio approached 2:3 with an excess of males. Such a proportion between the sexes at this stage is considered a normal feature in Stampen, since hardly any aberrations occurred between years. However, among the emerging adults, sex ratio variations did oc-

cur. The most obvious departure from the normal ratio was found during the flight period of 1974, when males constituted only 45% of the total. This ratio could be traced back to the end of November 1973, when cold weather caused the bottom substrate to freeze. Many dead nymphs, mostly males, were found during that period (Svensson 1976).

Tab. 4. Sex ratios in six cohorts during the study period. All values differ significantly from a 1:1 sex ratio. Sex ratios among the fullgrown nymphs refer to samples taken in October the year before emergence.

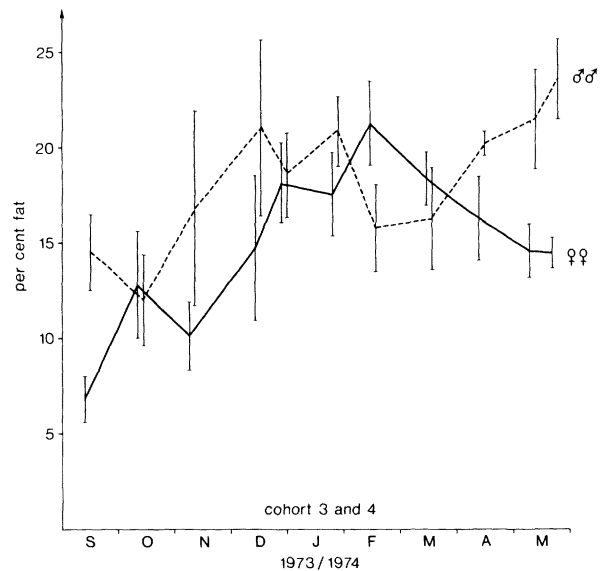| Cohort	Fullgrown Nymphs		Subadults	
	% ♂♂	N	% ♂♂	N
1	–	–	60	206
2	65	184	64	375
3 and 4	61	286	45	3119
5 and 6	60	1102	56	1096

Fig. 4. Seasonal changes in relative fat content of average individuals during one year. Each value is the mean of 5 analyses. 5–7 nymphs were used in each analysis. Vertical lines denote S.D. Cohort numbers refer to Fig. 2.
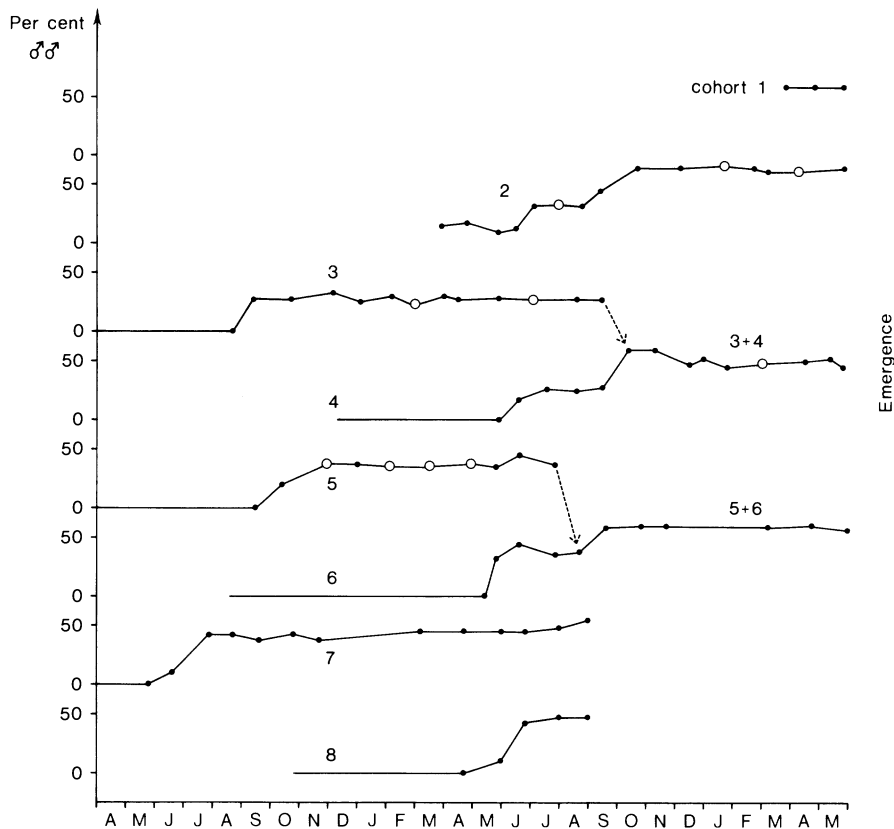
Fig. 5. Relative proportion of discernible males among the total number of individuals in each cohort during the study period. Cohort numbers refer to Fig. 2. When the number of individuals were less than 100, combined values of two consecutive samples have been used (open circles).

6. Discussion

Despite the fact that emergence in *E. danica* was restricted to a rather short period, small larvae occurred during most of the year (see Fig. 1), indicating an extended period of egg hatching. The same phenomenon has been recorded in several other mayfly species (Hynes 1970). Bohle (1969), Benech (1972b) and Elliott (1972) examined the relationship between temperature and the time of hatching of the eggs of *Baetis rhodani* Pictet. They found an inverse exponential relationship between temperature and the duration of embryogenesis in this species. In Stampen, however, the temperature was rather uniform during the comparatively short *Ephemera* oviposition period, hence giving all the eggs an equal start. Therefore, the protracted period of egg hatching in *E. danica* in accordance with observations made by Hunt (1951) in *Hexagenia limbata* (Serville), may be caused by quiescence of egg masses that were clumped together or buried in mud.

The protracted period of egg hatching contrasts with the synchronous emergence of two cohorts with unequal life span that has been established in this study. Clearly this adjustment must involve differential growth rates between cohorts. In May 1974 five cohorts were present (Fig. 2). However, only three of them were size-different at this time (Fig. 1). One month later, the fullgrown nymphs had transformed and emerged, but still there were three cohorts. The reason for this appa-

rent paradox was that larvae, forming cohort 6, hatched earlier and grew faster than larvae belonging to cohort 7. In May these two cohorts could be partly separated due to the more developed wing pads in the cohort 6 larvae. In August only two cohorts could be distinguished. At this time the cohort 6 nymphs overlapped the cohort 5 with respect to size, despite the fact that the latter were nearly one year older.

Similar growth patterns have been observed among zygopteran dragonflies, e.g. *Ischnura elegans* (van der Linden) and *Coenagrion puella* (L.) (Parr 1970, Lawton 1972). In these two species the pattern has been explained in terms of presence of facultative diapauses in the slow-growing cohorts.

What then determines the rate of growth in different cohorts? Clifford (1970) working with *Leptophlebia cupida* Say suggested that its nymphs, at a certain time, pass a threshold or switch-point, and that individuals having passed this threshold are able to develop and continue to grow. Before this critical point, in contrast, growth and development are inhibited. Prior to this transition, therefore, nymphs in the mature stage accumulate, leading to synchronous emergence.

For *E. danica* the development of the forceps in the males coincides with the growth of other adult structures, e.g. the wing pads. However, these characters are not simply related to body size. They display a rather stepwise development, which, as indicated above, may
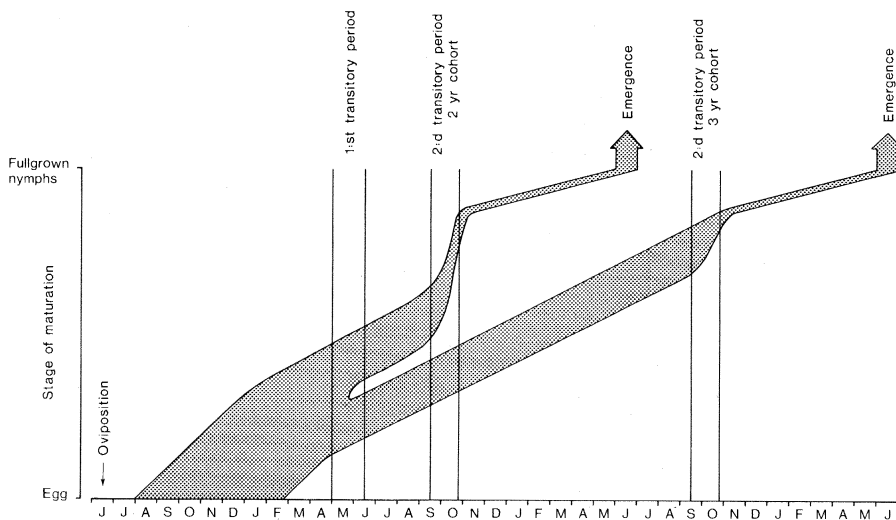
Fig. 6. Generalized life cycles of two cohorts deriving from eggs laid during one emergence season. Consult text for definition of transitory period.

lead to sudden changes in the sex ratio as judged from inspection of external characters. As each increase of the proportion of recognizable males reflects a sudden development of male characters, and probably also a shift in the physiological state of the nymphs concerned, possible transitory periods have been looked for in connection with these increases. As mentioned above, the outcome of the second differentiation of male characters was an equalized maturation of males from two previously unequally developed cohorts. This observation suggests the presence of a transitory period at this time. Another critical event in the life cycle of *E. danica* is the time when the larvae of one generation separate into two cohorts with unequal life span. The sharp limit between these two cohorts indicates the occurrence of another transitory period at the time of this division. As the different growth rates of the two cohorts became apparent at about the same time as male characters among the two-year cohort nymphs first became visible (see Figs 2, 5), this transitory period was also accompanied by a spurious change of the observed sex ratio. As indicated in Fig. 5 the second period is restricted to September/October, while the first period is confined to May/June.

Fig. 6 generalizes the life cycle patterns of two cohorts deriving from one set of eggs. By the time of the first transitory period, nymphs having reached a certain stage will increase their growth to attain maturity later that year, whereas the smaller, or less developed nymphs, have to await the corresponding transitory period the following year. Consequently, the second transitory period will tend to equalize the maturation of nymphs belonging to two different cohorts, and thus to synchronize emergence, whereas the first period will split up each generation into two different cohorts.

The above conditions are further illustrated by the pattern of energy fluctuations (Figs 3, 4). Low caloric and fat values, indicating the occurrence of energy consuming processes, were established during September/October the year before emergence. Decreasing values in the younger nymphs in the beginning of summer were probably related to accelerated growth and/or food shortage. The spring energy decrease in the fullgrown nymphs was probably coupled with an increased metabolic activity due to the formation of gonads and other adult structures at that time (see Eriksen 1964). On the other hand, values indicating increasing relative energy contents, probably reflecting low metabolic activity, were obtained during periods when no apparent development of adult structures occurred. Thus, simultaneous energy changes in both sexes probably reflect the periods of synchronous maturation within each cohort.

Slowed down growth and development of insects are often related to dormancy periods. Several investigators have dealt with diapause and related phenomena in the immature stages of aquatic insects. Thus, Khoo (1964, 1968) found that increased day length or rising temperatures induced nymphal diapause in *Capnia bifrons* (Newman). On the other hand, exposure to long photoperiod in the post-diapause instars accelerated the differentiation of adult structures (Khoo 1968). In contrast, Corbet (1956) showed that decreasing photoperiod induced diapause in the dragonfly *Anax imperator* Leach. There is no trace of the presence of a true diapause in the larval life of *E. danica*. This obviously does not mean that its growth and development proceed at the same rate. As shown above, the rate of increase of the body length may sink at the same time as development of adult structures accelerates. These shifts exemplify the transitory periods mentioned above. However, the factors inducing these periods probably are the same as those releasing the diapause in the above cases. For example, Maxwell and Benson (1963) measuring the wing pads of mayfly nymphs of the genus *Epeorus* found that these characters grew faster than the tergites in the winter.

Even though the presence of transitory periods de-

termines the formation of cohorts and the nymphal growth rates, still a considerable capability of modifying its development must persist in each nymph.

In mayflies emerging synchronously, small nymphs must mature as quickly as the larger nymphs. As the latter usually have passed a larger number of moults, the smaller nymphs must be able to reduce the number of instars they would otherwise go through. This capability has been confirmed in studies of the univoltine *Hexagenia bilineata* Say (Fremling 1973). Both body size and number of moults probably are related to the duration of the immature life. Thus, in the polyvoltine *B. rhodani* the nymphs of the spring generation grow faster, run through fewer moults and turn out smaller than the summer and winter generations (Benech 1972a). In mayflies, the fecundity of the adult females usually is directly related to their size (Clifford and Boerger 1974). Consequently, in populations with two cohorts in each generation, there must be a balance between the duration of the life span and the production of offsprings, among other things because an extended developmental cycle is likely to involve a larger natural mortality among the larvae, at the same time as the survivors become larger and are able to lay more eggs. There also exists a possibility that the size of the adults will affect their power of dispersal; thus, in a lotic caddisfly (Trichoptera) in Stampen a higher proportion of large than of small individuals probably left the hatching area (Svensson 1975).

With respect to *E. danica* the average weight of the fullgrown female nymphs was rather variable between years during the study period. These variations may partly be due to different proportions of three-year and two-year nymphs hatching in different years.

In the above discussion environmental factors are supposed to account for the cohort differentiation within each generation. Such differences may also emanate from polymorphism. However, environmental factors probably account for the entrainment of periodicity of emergence and transitory periods, since these events, regardless of the age of the nymphs, are confined to certain times of the year.

References

Benech, V. 1972a. Le polyvoltinisme chez *Baetis rhodani* Pictet (Insecta Ephemeroptera) dans un ruisseau à truites Pyrénées-Atlantiques, Le Lissuraga. – Ann. Hydrobiol. 3: 141–171.
– 1972b. Etude experimentale de l'incubation des oeufs de *Baetis rhodani* Pictet. – Freshwat. Biol. 2: 243–252.

Bhattacharya, C. G. 1967. A simple method of resolution of a distribution into Gaussian components. – Biometrics 23: 115–135.
Bohle, H. W. 1969. Untersuchungen über die Embryonalentwicklung und die embryonale Diapause bei *Baetis vernus* Curtis and *Baetis rhodani* (Pictet) (Baetidae, Ephemeroptera). – Zool. Jb. Anat. 86: 493–575.
Clifford, H. F. 1970. Analysis of a northern mayfly (Ephemeroptera) population, with special reference to allometry of size. – Can. J. Zool. 48: 305–316.
– and Boerger, H. 1974. Fecundity of mayflies (Ephemeroptera), with special reference to mayflies of a brown-water stream of Alberta, Canada. – Can. Ent. 106: 1111–1119.
Corbet, P. S. 1956. Environmental factors influencing the induction and termination of diapause in the emperor dragonfly, *Anax imperator* Leach (Odonata, Aeshnidae). – J. exp. Biol. 33: 1–14.
Elliot, J. M. 1972. Effect of temperature on the time of hatching in *Baetis rhodani* (Ephemeroptera: Baetidae). – Oecologia 9: 47–51.
Eriksen, C. H. 1964. Evidence of a spring rise in metabolic rate in the burrowing mayfly *Ephemera simulans* Walker. – Hydrobiologia 23: 506–510.
Fremling, C. R. 1973. Environmental synchronization of mass *Hexagenia bilineata* (Ephemeroptera) emergences from the Mississippi River. – Verh. Internat. Verein. Limnol. 18: 1521–1526.
Hultin, L. 1971. Upstream movements of *Gammarus pulex pulex* (Amphipoda) in a South Swedish stream. – Oikos 22: 329–347.
Hunt, B. P. 1951. Reproduction of the burrowing mayfly *Hexagenia limbata* (Serville), in Michigan. – The Florida Entomologist 34: 59–70.
Hynes, H. B. N. 1970. The ecology of running waters. – Liverpool Univ. Press, Liverpool.
Jazdzewska, T. 1971. Jetki (Ephemeroptera) rzeki Grabi. – Pol. Pismo ent. 41: 243–304.
Khoo, S. G. 1964. Studies on the biology of *Capnia bifrons* (Newman) and notes on the diapause in the nymphs of this species. – Gewässer Abwässer 34/35: 23–30.
– 1968. Experimental studies on diapause in stoneflies. I. Nymphs of *Capnia bifrons* (Newman). – Proc. R. ent. Soc. Lond. (A) 43: 40–48.
Landa, V. 1968. Developmental cycles of Central European Ephemeroptera and their interrelations. – Acta ent. bohemosl. 65: 276–284.
Lawton, J. H. 1972. Sex ratios in odonata larvae, with particular reference to the Zygoptera. – Odonatologica 1: 209–219.
Macan, T. T. 1958. Methods of sampling the bottom fauna in stony streams. – Mitt. Verein. Theor. angew. Limnol. 8: 1–21.
– 1970. A key to the nymphs of the British species of Ephemeroptera with notes on their ecology. – Freshw. Biol. Ass. Sci. Publ. No. 20.
Maxwell, G. R. and Benson, A. 1963. Wing pad and tergite growth of mayfly nymphs in winter. – Am. Midl. Nat. 69: 224–230.
Otto, C. 1971. Growth and population movements of *Potamophylax cingulatus* (Trichoptera) larvae in a South Swedish stream. – Oikos 22: 292–301.
Parr, M. J. 1970. The life histories of *Ischnura elegans* (van der Linden) and *Coenagrion puella* (L.) (Odonata) in south Lancashire. – Proc. R. ent. Soc. Lond. (A) 45: 172–181.
Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. – Oikos 15: 130–139.
Pleskot, G. 1958. Die Periodizität einiger Ephemeropteren der Schwechat. – Wass. u. Abwass. (1958): 188–219.
Södergren, A. 1973. A simplified cleanup technique for organochlorine residues at the microliter level. – Bull. Env. Cont. Tox. 10: 116–119.
Svensson, B. W. 1975. Morphometric variation of adult *Potamophylax cingulatus* (Trichoptera) reflecting environmen-

tal heterogeneity in a South Swedish stream. – Oikos 26: 251–263.

Svensson, B. 1976. The association between *Epoicocladius ephemerae* Kieffer (Diptera: Chironomidae) and *Ephemera danica* Müller (Ephemeroptera). – Arch. Hydrobiol. 77: 22–36.

Winberg, G. G. 1971. Methods for the estimation of production of aquatic animals. – Academic Press, London.