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Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera Simuliidae)

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Abstract

A large material of larvae and nymphs of Ephemeroptera, Plecoptera, Trichoptera and Diptera Simuliidae from lotic biotopes in Lapland streams was used for an analysis of life cycle patterns. Flight-periods were determined from collection of winged insects. Although each species had its own distinctive life cycle, certain patterns prevailed and could be classified in several phenological types. The study area was situated on the border between the high boreal and subalpine zones and had an accordingly severe climate with a long period of ice-cover. However, life cycle patterns were not consistently different from those of the same or related species in regions with a milder climate.

The life cycles of some species varied from place to place. Some such differences are probably explicable in terms of local temperature differences.

The life cycles of some species varied from year to year.

Within the same species, some individuals took one year, others two years before reaching emergence.

No case of bi- or poly-voltinism was found.

Резюме

Обширный материал, состоящий из нимф и личинок видов Ephemeroptera, Plecoptera, Trichoptera и Diptera Simuliidae встречающихся в реках Лапландии, был использован для исследования жизненного цикла видов. Лётное время этих видов определялось наличием большого количества имаго. Даже если каждый вид имеет характерный для него жизненный цикл, то все же преобладают некоторые образцы, которые можно объединить в особые фенологические типы.

Исследуемая местность расположена в центральной части Лапландии, на границе между зоной тайги и зоной субальпийского березняка и отличается суровым климатом с долголежащим ледяным покровом. Однако жизненный цикл видов живущих в таких условиях не особенно отличался от жизненного цикла видов в областях с более мягким климатом.

У *Heptagenia dalecarlica* (Eph.) жизненный цикл изменялся в зависимости от местности и в некоторой степени это относится к *Baetis rhodani* (Eph.). Эти различия, по-видимому, можно объяснить разницей в температуре воды местных рек.

У *Diura nanseni* (Plec.) жизненный цикл был разным в разных годах. У *Heptagenia* spp. (Eph.) встречались индивиды так и с одногодичным, как и с двухлетним жизненным циклом. Никакой вид не имел больше 1 поколения в год.

У одних видов зимовка происходила в фазе яйца или нимфы – личинки в стадии покоя; другие виды скоро росли после вылупления и зимовали как крупные нимфы-личинки. Эта принципиальная разница встречалась так и у одногодичных, как и у двухлетних видов.

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1. Introduction

In the course of an ecological investigation of the benthic animals in the upper parts of the Vindelälven river system in central Swedish Lapland, the life cycles of the most important insect species were examined. This was considered to be of special interest in view of the unusual environmental conditions prevailing in the study area which is situated in the transition between the high boreal and subalpine zones.

Little information is available on the life cycles of stream-living invertebrates from northern Scandinavia. The most important studies devoted to taxa of interest in the present connection are those by Brinck (1949) and Svensson (1966) on Plecoptera and by Carlsson (1962) on Simuliidae; in addition data on flight-periods of Trichoptera have been published by Forsslund (1954) and Forsslund and Müller (1962).

2. Study area

The study area and its physiography are described elsewhere (Ulfstrand 1968). Only a few essential points need be repeated here. The area is centred upon the small village of Ammarnäs at approx. 66° N. lat. and 16° 15′ E. long. on the river Vindelälven in Lycksele lappmark, Swedish Lapland. The water courses investigated are of widely different sizes but are generally characterized by strong erosive forces producing for the most part naked stone bottoms, further by low conductivity values, high oxygen content and very little macroscopic vegetation. Temperatures will be discussed below (p. 186). Coniferous or mixed forests cover most of this sparsely-inhabited region, but the upper parts are within the subalpine birch zone. All the waters are practically unaffected by human activities.

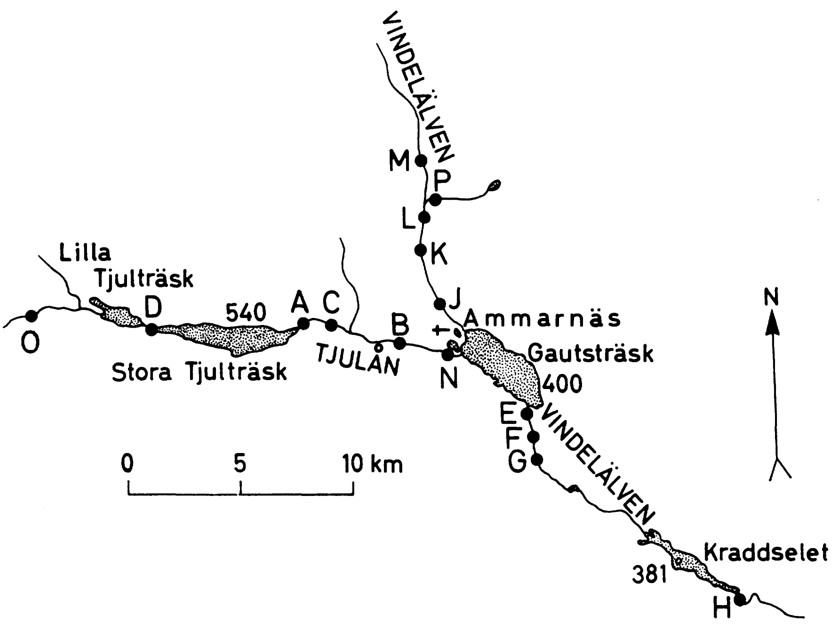

Fig. 1. Map of the investigation area around the village of Ammarnäs in central Swedish Lapland. Letters indicate main sampling localities. Figures show altitude in m above sea level.

3. Material and methods

I. The benthic stages

The material was collected at or near 15 sites located in strongly lotic parts of the streams around the village of Ammarnäs in the years of 1962 to 1964, with particularly extensive work in 1964. The sampling localities are described in detail in Ulfstrand (1968) and are shown in Fig. 1. Collections from several localities have sometimes been pooled for the present purpose. Thus all data from Vindelälven downstream of Lake Gautsträsk are combined under the designation GH. Similarly data from Vindelälven upstream of the same lake are pooled under KL and those from Tjulån under BN. Exceptions are the lake outlets, locs. A in Tjulån and E in Vindelälven which are kept separately. Data from locs. D, O and P have also been kept separately.

Sometimes, two collections were made with such short time between them at the same locality or within the same group of localities that it seemed justified to pool the data. In these cases the collections were never separated by more than seven days. For practical purposes, pooled data are ascribed to the middle date within the period concerned. This slight inaccuracy had to be introduced on four occasions only, and these four data are shown together with the rest in Tab. 1.

Life cycles were studied in terms of average total body length of the members of populations, changes in which were taken to indicate changes in the life cycles. This method is generally used in life cycle studies (e.g. Brinck 1949, Macan 1965/66). Although it is not quite without disadvantages (see Levanidova and Rubanenkova 1965, Svensson 1966), it is adequate for the purpose and suitable for handling extensive materials because of its simplicity.

Body length was measured from the front of the head to the rear of the last abdominal segment, excluding all appendages. The animals were measured under a binocular microscope fitted with a micrometer (specimens < 5 mm) or by placing them directly on graph paper (≥ 5 mm). Frequency distributions based on these measurements had a class interval of 1 mm. Often not all the material available could be measured, but representative subsamples were drawn from which only defective specimens were removed.

The sampling technique has certain drawbacks which must be kept constantly in mind. Many or all nymphs/larvae below a certain size are missed, either because they manage to pass through the nets employed or because they dwell in other microbiotopes than those from which the samples were drawn. Only after a certain growth will they appear in numbers in the samples. The growth processes during their earliest life are, thus, unavailable for analysis, and it is usually not possible to decide after how long time the eggs hatch. Their more or less sudden appearance in the catching net may depend on their having attained catchable size, but also on the fact

Tab. 1. Sampling dates.

Month	Year	A	BN	D	E	GH	KL	O	P
May	1964.....	13/5	14/5	–	9/5	19/5	18/5	–	23/5
June	1963.....	18/6	12/6	17/6	11/6	12/6	14/6	–	–
June	1964.....	5/6	3/6	11/6	8/6	12/6	7/6	2/6	7/6
July	1962.....	15/7	20/7	17/7	18/7	19/7	22/7	–	–
July	1963.....	18/7	21/7	12/7	11/7	17/7	12/7	16/7	–
July	1964.....	16/7	12/7	24/7	21/7	22/7	19/7	23/7	10/7
Aug.	1962.....	2/8	8/8	3/8	4/8	6/8	6/8	–	–
Aug.	1963.....	8/8	8/8	6/8	2/8	3/8	4/8	1/8	–
Aug.	1964.....	13/8	10/8	24/8	17/8	14/8	19/8	–	12/8
Sep.	1964.....	11/9	9/9	16/9	13/9	15/9	14/9	6/9	7/9
Oct.	1962.....	5/10	5/10	–	4/10	4/10	6/10	–	–
Nov.	1963.....	–	14/11	–	14/11	–	15/11	–	–

Tab. 2. Periods of light-trap operation. For position of localities, see Fig. 1.

Light-trap at loc.: Year	H	B	N
1962....................	13/7 – 4/19	16/7 – 7/10	14/7–30/9
1963....................	10/6 –15/11	–	12/6–11/9, 4/10–16/11
1964....................	2/5 –15/9	–	20/4–15/9
1965....................	1/7 – 1/10	–	1/7–1/10

that they have moved from one microbiotope to another. It is well known that many species spend their earliest stages in the hyporheal biotope (Schwoerbel 1964). This environment is available for these species, which are not burrowing, only during their very first stages.

In the following, certain species are dealt with only briefly, as their life cycles were found to be uncomplicated. In such cases detailed measurements are not given in the descriptions. When the cycles were found to be more complicated, a full presentation is given.

II. The winged insects

During a preliminary survey in 1961 and, more consistently, from 1962 to 1965 when quantitative benthic sampling was carried out, winged insects were routinely collected with nets. From 1962 to 1965, light-traps were also operated and produced very large catches, particularly of Trichoptera. Adult blackflies (Simuliidae) were not collected.

The periods of light-trapping are shown in Tab. 2. Light-traps were placed at locs. H and N; in 1962 a third trap was operated at loc. B (see Fig. 1). The traps were fitted with UV lamps (with maximum emission at 3,655 Å, Philips HPW 125 W).

Although the light-trapping periods were not exactly the same every year and some irregularities in the netting efforts may have occurred, the temporal distribution of the catches is usually very regular, indicating that the material adequately reflects the true conditions. Netting was usually less intense in the last half of June which may account for some rather low figures of Plecoptera in that period.

4. Flight-periods

The material of winged insects belonging to lotic species of Ephemeroptera, Plecoptera and Trichoptera is shown in Tab. 3. Many more species were obtained, but these did not belong to lotic biotopes and are of no interest in this context. The combined net and light-trap material amounts to 101,387 specimens of the species referred to in the table.

Significantly, the temporal distribution in no case points to the occurrence of double flight-periods.

5. Quiescence and dormancy

At this point some clarification of the terms used herein is called for. The phenomenon of an organism's growth being temporarily arrested or slowed down is often loosely referred to as diapause. Andrewartha (1952) advocated restriction of the use of this term to endogeneous arrestment of the growth and adoption of the term quiescence for exogeneous arrestment. It is often difficult to decide whether a delay in the growth is caused by external or internal factors which of course frequently interact. Yet since most authors regard the periods of suspended growth in benthic insects as governed by, or at least strongly influenced by, environmental stimuli, it is more appropriate to use the term quiescence for the delay in the growth process found in many benthic nymphs/larvae.

The word dormancy will be applied to cases where no development of the eggs seems to take place for an appreciable period after deposition. As pointed out by Hynes (1962), a certain development may take place in eggs which superficially seem to be dormant. There is, then, no sharp demarcation line. Moreover, as pointed out above, the sampling technique is not suitable for obtaining the earliest nymphal/larval stages which may dwell in other biotopes than the larger animals. Therefore, true egg dormancy will rarely be detectable in field investigations of this type. When discussing life cycle patterns, however, this difficulty is often not very important.

6. Life cycles in Ephemeroptera

I. Ameletus inopinatus Etn.

This species may be briefly dealt with. It was only taken in a dozen individuals in late summer and autumn; these few nymphs were of very variable sizes and probably belonged to the preceeding generation. On the other hand, the species was often dominant in May and June, sometimes also in the beginning of July. The flight-period culminated in July.

Thus, *A. inopinatus* undergoes most of its growth after the streams freeze. When the ice breaks up, the nymphs are approaching maturity. It is not known when growth starts. As late as in November, the species was practically absent from the samples, indicating that the eggs were still dormant or that the nymphs were very small. In late winter and spring, most of the growth took place.

Gledhill (1959) reported that *A. inopinatus* has a very long flight-period in the English lake district. Some eggs hatched shortly after being laid, the remainder not hatching until the following spring. Landa (1962) characterizes the species by its rapid summer development.

II. Baetis rhodani Pict.

Six species of the genus *Baetis* occur in the Ammarnäs area. Whilst they were usually readily distinguishable in all life stages taken, young nymphs of *B. rhodani* and *B. subalpinus* Bgtn. were not. Judging from the flight-period and the occurrence in time of determinable nymphs of the latter species, such small nymphs probably belong to *B. rhodani* at any time except in July and August, when equally large nymphs of both species may occur together.

Young and older nymphs of *B. rhodani* were found to have different habitat pre-

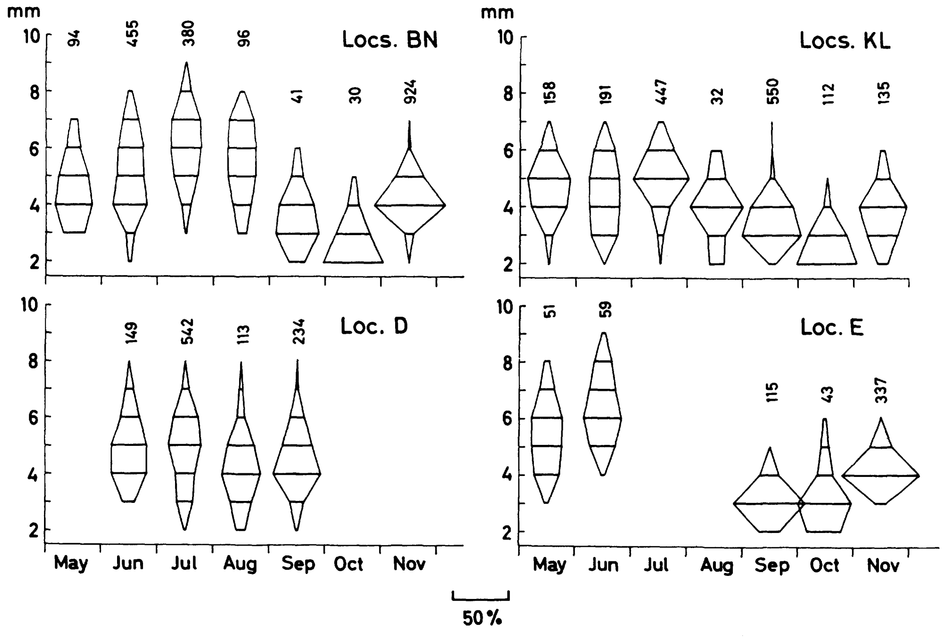

Fig. 2. *Baetis rhodani* Pict. Frequency distribution of nymphal size classes. Numbers of individuals shown above each polygon.

Tab. 3. Combined net and light-trap catches from 1962 to 1965 distributed on ten- or eleven-day periods. Only species of importance in the benthic community were included.

	May	Jun. I	Jun. II	Jun. III	Jul. I	Jul. II	Jul. III	Aug. I	Aug. II	Aug. III	Sep. I	Sep. II	Sep. III	Oct.	Nov.	Total
Ephemeroptera																
Siphlonurus lacustris Etn.[1] [2]	–	–	–	–	–	105	408	49	51	–	1	–	–	–	–	614
Ameletus inopinatus Etn....	–	–	–	15	80	114	11	3	1	–	–	–	–	–	–	224
Baetis fuscatus L..........	–	–	–	–	–	–	–	1	19	137	5	2	–	–	–	164
B. lapponicus Bgtn.........	–	–	–	–	–	–	40	42	17	6	–	–	–	–	–	105
B. macani Kimm.[1].........	–	–	–	–	1	15	28	84	74	6	–	–	–	–	–	208
B. pumilus Burm...........	–	–	–	–	–	15	69	30	–	1	–	–	–	–	–	115
B. rhodani Pict............	–	–	–	8	41	59	65	40	28	10	7	–	–	–	–	258
B. subalpinus Bgtn.........	–	–	–	–	–	–	–	1	85	43	48	20	–	–	–	197
Ecdyonurus joernensis Bgtn.[1] [2]................	–	–	–	–	–	–	–	–	1	24	27	17	–	–	–	69
Heptagenia sulphurea Müll./ *dalecarlica* Bgtn.........	–	–	–	–	–	161	182	55	5	1	–	–	–	–	–	404
Ephemerella aurivillii Bgtn...	–	–	–	9	44	134	37	3	–	–	–	–	–	–	–	227
E. mucronata Bgtn.........	–	–	–	–	–	22	175	7	–	–	–	–	–	–	–	204
																2789
Plecoptera																
Brachyptera risi Mort.[2]....	–	–	1	7	15	5	–	–	–	–	–	–	–	–	–	28
Taeniopteryx nebulosa L....	108	5	2	–	–	–	–	–	–	–	–	–	–	–	–	115
Amphinemura borealis Mort.	–	–	–	–	9	116	55	51	24	14	3	–	–	–	–	272
A. standfussi Ris...........	–	–	–	–	–	–	29	101	67	83	95	53	2	–	–	430
A. sulcicollis Steph.........	–	–	–	–	81	15	20	12	–	–	2	–	–	–	–	130
Nemoura cinerea Retz.[1] [2] ..	–	1	–	1	6	33	33	20	2	1	–	–	–	–	–	97
Protonemura meyeri Pict.[2]..	–	1	5	8	16	4	1	–	–	–	–	–	–	–	–	35
Leuctra digitata Kemp.[2]....	–	–	–	–	–	–	54	31	36	15	9	5	–	–	–	150
L. fusca L................	–	–	–	–	–	2	2	27	215	301	337	347	342	328	20	1921
L. hippopus Kemp.........	21	51	205	76	98	67	5	31	6	–	–	–	–	–	–	560
Capnia atra Mort..........	192	25	15	15	19	11	4	3	–	–	–	–	–	–	–	284
C. pygmaea Zett.[2].........	71	–	–	1	9	8	8	–	–	1	1	–	–	–	–	99
Capnopsis schilleri Rost.[2] ..	–	8	6	1	4	–	–	–	–	–	–	–	–	–	–	19

	May	Jun. I	Jun. II	Jun. III	Jul. I	Jul. II	Jul. III	Aug. I	Aug. II	Aug. III	Sep. I	Sep. II	Sep. III	Oct.	Nov.	Total
Arcynopteryx compacta McL.[2]	–	12	12	–	1	–	–	–	–	–	–	–	–	–	–	25
Diura bicaudata L.[1] [2]	–	26	21	31	78	77	–	10	1	–	–	–	–	–	–	244
D. nanseni Kemp	1	15	206	77	66	47	9	12	1	–	–	–	–	–	–	434
Dinocras cephalotes Curt.	–	–	–	–	–	16	169	6	–	–	–	–	–	–	–	191
Isoperla grammatica Poda	–	–	2	–	92	241	24	116	4	2	–	1	–	–	–	482
I. obscura Zett.	–	–	–	–	5	6	43	33	9	18	1	1	–	–	–	116
Chloroperla burmeisteri Pict.[2]	–	–	1	–	93	94	58	38	7	2	–	–	–	–	–	293
																5925
Trichoptera																
Rhyacophila nubila Zett.	–	–	–	–	–	5	1360	2231	8014	22956	24154	3197	1262	222	–	63401
Glossosoma intermedium Klap.	–	–	15	61	208	368	29	4	1	–	–	–	–	–	–	686
Philopotamus montanus Don.[2]	–	–	23	–	19	16	36	–	–	–	–	–	–	–	–	94
Arctopsyche ladogensis Kol.	–	–	–	–	17	71	41	–	1	–	–	–	–	–	–	130
Plectrocnemia conspersa Curt.[2]	–	–	–	–	–	4	2	4	–	–	–	–	–	–	–	10
Polycentropus flavomaculatus Pict.	–	–	–	–	–	59	169	89	9	–	–	–	–	–	–	326
Apatania stigmatella Zett.[3]	–	–	–	–	1	39	248	962	3065	17699	2616	1324	16	3	–	25973
A. wallengreni McL.[3]	–	62	352	144	130	57	1	–	–	–	–	–	–	–	–	746
Potamophylax stellatus Curt.[3]	–	–	–	–	38	290	573	266	76	36	23	2	2	1	–	1307
																92673

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[1] Not a truly regular inhabitant of the lotic biotopes.

[2] Not discussed in the text because of inadequate material of nymphs/larvae.

[3] Not discussed in the text because larvae inseparable from those of related species.

ferences (Ulfstrand 1967) illustrating that changes in the distribution on the river floor may occur in the course of a species' life cycle.

Four localities produced the most extensive material of *B. rhodani*, viz. BN, D, E and KL (Fig. 2). The samples from 1964 are basically used, but the data from October 1962 and November 1963 are entered in the graphs to complete the picture. The last-mentioned samples may be inserted in the time sequence only with reservation, since, deriving from other years, the populations may be out of phase phenologically.

Locs. BN and KL showed good agreement. During most of the year a wide variety of nymphal sizes were present. Small newly hatched nymphs were found at most seasons except in autumn. They were notably absent in the very rich November samples. There was a large increase of small nymphs in September and October, and in August the quantities of unidentifiable small nymphs were often extremely large; these were probably mainly *B. rhodani*. At these localities, then, the eggs hatched in two waves, one beginning in late summer and apparently ceasing about September, and another beginning sometime in winter and continuing until the following summer. Although the two hatching waves may have overlapped in July, the eggs were evidently divided into two well-defined categories. It remains an open question whether some of the last nymphs to hatch reached emergence in the same year.

Loc. D was inhabited by a relatively large proportion of medium-sized nymphs as late as September, i.e. after the flight-period even taking into account that this was distinctly later in this part of the study area (Tab. 4). The chance that some late-hatching nymphs do not reach emergence in the same year seems to be great at this site. Since no samples were taken at loc. D in October and November, it is not known when the accession of newly hatched individuals to the nymphal population stopped in autumn. As far as can be seen the somewhat aberrant picture of the nymphal populations at loc. D is mainly due to the hatching of nymphs from last year's eggs going on longer in summer.

At loc. E another local difference was observed. This locality became devoid of *B. rhodani* in July and August. This was found to be the rule in all years at locs. A and E (with some unimportant exceptions). It is probable that the hatching of new nymphs ceased relatively early in summer, so that a gap between the two cohorts arose.

B. rhodani has been found to have at least two generations in other areas of Europe (Harker 1952, Macan 1957 b, 1961 b, Pleskot 1958, Hynes 1961, Thorup 1963, Elliott 1967). In some areas, *B. rhodani* was found to be univoltine, viz. in the Central German Uplands (Illies 1952) and in a mountain stream in Poland (Sowa 1965). In a spring-fed trickle with almost constant temperature in Austria, Bretschko (1965) found that emergence took place almost round the year. In the maritime climate of Madeira, Brinck and Scherer (1961) found nymphs of varying sizes as well as winged insects at the same time.

Macan (1961 b) in England found that hatching ceased for a period about midwinter and that the animals emerging in spring were composed of two different groups, one ap-

Tab. 4. Differences in temporal distribution of catches of *Baetis rhodani* from the upper (D, O, P, KL) and lower (A, B, N, E, GH) localities.

Locs.	Jun./III	Jul./I	Jul./II	Jul./III	Aug./I	Aug./II	Aug./III	Total
KL, D, O, P	–	–	14	16	23	20	7	80
A, BN, E, GH	8	41	45	49	17	8	10	178
	8	41	59	65	40	28	17	258
		108				45		

$\chi^2 = 48.48$ df $= 3$ $P < 0.001$

parently deriving from eggs hatched in autumn, the other from those hatched in spring. This pattern is similar to that found in Lapland, except that the autumn-hatching and spring-hatching eggs yielded morphologically indistinguishable individuals.

Pleskot (1958) found in her Austrian study that *B. rhodani* did not winter in the nymphal stage, and Hynes (1961) suggested that this was due to the severe winter conditions. But ice-cover is still more persistent in Lapland where *B. rhodani* successfully hibernates as a nymph. The reason that nymphal hibernation does not occur in Austria may be that the nymphs hatching in autumn have time to emerge before winter, so that none remain in the benthos at the time of freezing. Conversely, it may be suggested that the individuals wintering as nymphs in Lapland might constitute the fraction of the population that emerges in late summer or autumn farther south. This explanation is in line with Pleskot's contention that the many differences found between the life cycles of different populations and species of *Baetis* are in fact modifications of one or a few basic patterns.

The flight-period of *B. rhodani* was longer than that of any other member of the genus represented in the material.

III. Other Baetis spp.

The following members of the genus, apart from *B. rhodani*, occur in the Ammarnäs area: *B. fuscatus* L., *B. lapponicus* Bgtn., *B. macani* Kimm., *B. pumilus* Burm., and *B. subalpinus* Bgtn. Of these, *B. macani* is a mainly lenitic species although invading the lotic areas from time to time. It will not be considered further here. For the taxonomy of *B. fuscatus*, see Ulfstrand (1968).

B. lapponicus, *B. fuscatus* and *B. subalpinus* were absent from the samples for the whole year except the four to eight weeks before their respective flight-periods (Ulfstrand 1968), when they suddenly occurred in large numbers. Evidently they spend most of the year either as dormant eggs or as quiescent, or very slow-growing small nymphs, perhaps in a different microbiotope. The final stages are undergone very rapidly in a period of intense growth.

B. pumilus possibly had a similar life cycle, but a number of medium-sized or small nymphs found in September and May to June indicate that part of the population overwintered as relatively large nymphs. This proportion was almost certainly small.

A very long period of dormancy and/or quiescence followed by a short period of explosive growth is a rather unusual pattern in the genus *Baetis*, although Pleskot (1958) recorded it in a less extreme form in *B. vernus* Etn. and *B. "bioculatus"* L. in Austria. According to Macan (1961 b) it does not occur in any species in Britain. Illies (1959) found a very long dormancy in *Baetis* eggs (average about 200 days) and also great variability within the same egg clutch. There were also differences between clutches, but it is difficult to evaluate the significance of this finding since it does not seem clear that all clutches belonged to the same species.

The pattern found in *B. lapponicus*, *B. fuscatus* and *B. subalpinus* resembles that found in the fraction of *B. rhodani* that was produced from eggs hatching in spring, although the cycle was more synchronized and the nymphal growth probably faster.

IV. Heptagenia sulphurea Müll. and H. dalecarlica Bgtn.

These two closely related species were found to have partly different local distribution ranges within the Ammarnäs area (Ulfstrand 1968). Unfortunately they could not be separated in the winged stages, so that in Tab. 3 they had to be combined. Evidently their flight-periods were coincident.

The most extensive material of *H. sulphurea* was obtained at locs. A and E, and of *H. dalecarlica* at locs. BN and KL. These localities were selected for detailed presentation (Figs. 3 and 4). Although the two species usually did not dominate at the same localities, they frequently occurred together, and in September 1964 a relatively rich material of *H. dalecarlica* was obtained at locs. A, E and H, where *H. sulphurea* was usually the commonest species. This material is shown in Fig. 5.

The absence of *H. sulphurea* (Fig. 3) from the May samples is remarkable, since in June

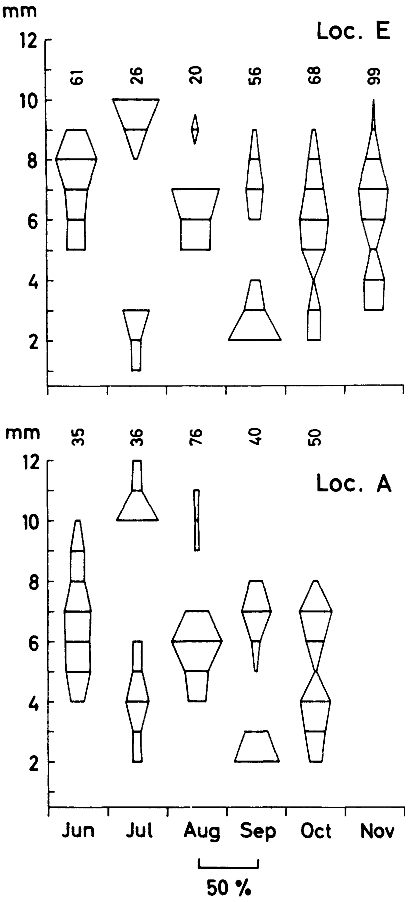

Fig. 3. *Heptagenia sulphurea* Müll. Frequency distribution of nymphal size classes. Numbers of individuals shown above each polygon.

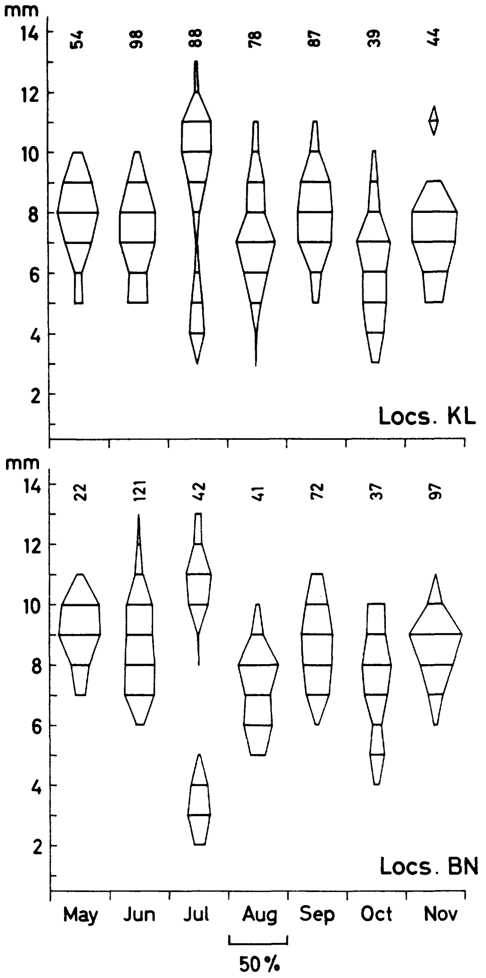

Fig. 4. *Heptagenia dalecarlica* Bgtn. Frequency distribution of nymphal size classes. Numbers of individuals shown above each polygon.

it was obtained in considerable numbers. The nymphs were by then very variable in size, but there was no sign of a bimodal size distribution. In July, however, the population was divided into two quite distinct groups, one consisting of nymphs larger, the other of nymphs much smaller on average than in June. The larger-sized fraction were certainly of the same origin as the individuals found in the preceeding month. These nymphs were approaching emergence. The smaller nymphs cannot derive from the same year's eggs, for the flight-period had only just begun. Hence it must be concluded that they derived from eggs laid in the previous year. In August, the larger-sized fraction had vanished almost completely, as was to be expected, while the smaller-sized nymphs had grown considerably. In September, when they were larger still, they were joined by a new cohort of small nymphs. These most probably derived from eggs laid during the preceeding flight-period. They grew so rapidly that in the following two months they caught up and merged with the preceeding cohort, and no trace of the dual origin of the overwintered population could be seen in spring.

Since all the nymphs taken in June were obviously destined to emerge in the same summer, *H. sulphurea* evidently has two very different life histories. Some individuals spend a year as eggs before hatching, or as very small quiescent nymphs, grow in the following summer and emerge at an age of approximately two years. Others start growing soon after oviposition and emerge at an age of approximately one year. In both cases, the period of most intense growth is in July to September/October.

H. dalecarlica (Fig. 4) was represented in May and June by a homogeneous nymph population. The nymphs seemed to grow slowly at first, then more rapidly to reach emergence in July. In this month a cohort of small nymphs appeared which could not possibly cone from eggs laid in the simultaneous flight-period. Evidently they derived from eggs laid in the previous year and had spent almost a whole year as dormant eggs and/or quiescent nymphs. They grew rapidly and by August to September had almost reached the size of mature nymphs. Like *H. sulphurea, H. dalecarlica* underwent greatest growth in late summer and early autumn. At locs. BN and KL (Fig. 4) there was no indication of an additional cohort appearing in September.

However, at locs. A, E and H in September 1964 there was in fact a cohort of small nymphs precisely as in *H. sulphurea* (Fig. 5), and it seems highly probable that these derived from the same year's eggs.

In *H. dalecarlica*, then, the interesting situation is found that not only do some individuals take one year, others two years, to complete their development, but these two patterns occur with unequal frequency at different localities. At localities which were not lake outlets (BN, KL), *H. dalecarlica* spent one year as an egg and another as a nymph before emerging. At lake outlets (A, E, partly H; cf. Ulfstrand 1968), some individuals compressed their development to one year, reducing the period of egg dormancy and/or early nymphal quiescence.

The scanty material from October 1962 and November 1963 indicates that the presence of two nymphal cohorts in autumn is a regular feature in *H. dalecarlica* at the lake outlets.

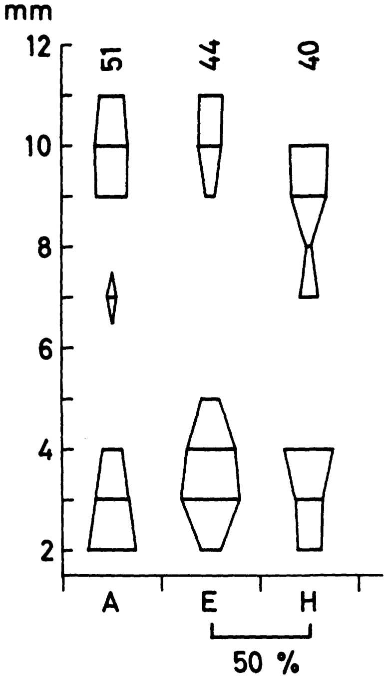

Fig. 5. *Heptagenia dalecarlica* Bgtn. Frequency distribution of nymphal size classes in September 1964. Numbers of individuals shown above each polygon.

It is comparatively rare for Ephemeroptera to have life cycles covering more than one year. *Ephemera* spp. are often cited as having two- or even three-year cycles (cf. Illies 1952), and Landa (1962) states that he has evidence that two *Ephemera* spp. have two-year cycles. But Pleskot (1958) and Macan (1961 b) refused to accept the evidence presented.

It is common among Ephemeroptera that the eggs are divided in two or more groups with respect to dormant period, as shown by Pleskot (1958), Illies (1959), Gledhill (1959), Macan (1961 b) and others. A remarkable feature in the Ammarnäs area is the extremely rapid growth of the nymphs coming from overwintered eggs and/or quiescent small nymphs during late summer and autumn.

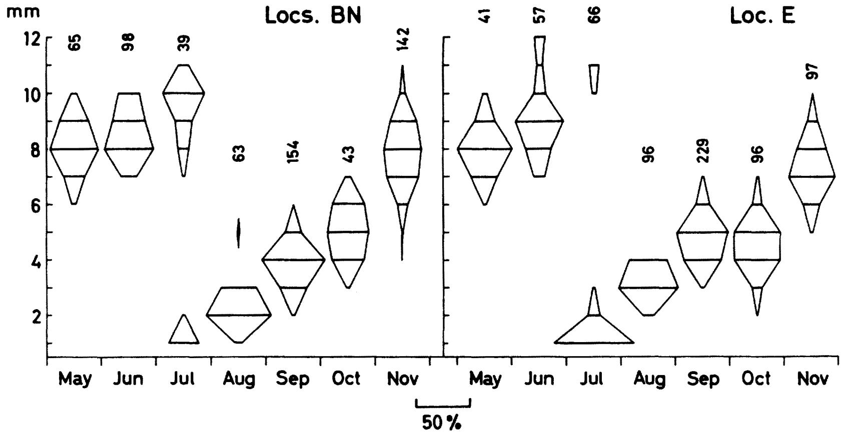

Fig. 6. *Ephemerella aurivillii* Bgtn. Frequency distribution of nymphal size classes. Numbers of individuals shown above each polygon.

Neither species of *Heptagenia* has been subjected to detailed analysis elsewhere.

V. Ephemerella aurivillii Bgtn. and E. mucronata Bgtn.

A large material of *E. aurivillii* exists from several localities. For a detailed presentation one outlet and one non-outlet locality were selected (Fig. 6).

The life cycle of *E. aurivillii* is uncomplicated. Small nymphs appeared shortly after the flight-period and began to grow rapidly. Egg hatching was completed within a brief span, as was seen from the absence of small nymphs only one or two months later. The nymphal material remained homogeneous with regard to size throughout the cycle. Most of the growth took place in late summer and autumn, so that the nymphs were in November only slightly smaller than those in May.

E. mucronata had an entirely different cycle. Nymphs were obtained in the samples only for a short period before the flight-period (Ulfstrand 1968). The species was completely absent in the samples from September and November, whilst two specimens were found in October. In May only half a dozen nymphs were obtained. Thus, *E. mucronata* spends a very long time as a dormant egg and/or a quiescent nymph, and this long period is followed by a short period of intense growth (in June and July). The pattern closely resembles that described for *Baetis lapponicus*, *B. fuscatus* and *B. subalpinus*.

Both *Ephemerella* spp. are northeasterly (Illies 1967) and have been little studied, except that *E. mucronata* was found in Siberia to have a life cycle resembling that of *E. aurivillii* in the present study area (Levanidova and Rubanenkova 1965). *E. ignita* Poda – a very wide-spread species – has been studied in many areas (Illies 1952, Dittmar 1955, Jensen 1956, Macan 1957 a, Pleskot 1958, Hynes 1961, Petr 1961, Maitland 1965, Elliott 1967). All these authors are agreed that the egg dormancy of *E. ignita* is exceptionally long and that nymphs are present in the benthos for only a short time before emergence – the same pattern as in *E. mucronata* in Lapland. Levanidova and Rubanenkova (op. cit.) studied a closely related species – perhaps, in fact, the same species – in Siberia and found the same thing.

In the Canadian Rocky Mountains, Hartland-Rowe (1964) found both types of cycle within the genus *Ephemerella*. In Central Europe, *E.* (*Torleya*) *belgica* Lest. and *E.* (*T.*) *major* Klap. were reported by Petr (1961) to spend long periods as large nymphs, resembling *E. aurivillii* in Lapland. The same author stated that *E.* (*Chitonophora*) *krieghoffi* Ulm. had a long egg dormancy, like *E. mucronata* in Lapland and *E. ignata* in central and western Europe. Landa (1962), on the other hand, placed *E. krieghoffi* among the species having a long period of nymphal life. In this species there may be regional differences. *E. notata* has been found to have a long nymphal period (Frost, quoted from Hynes 1961).

Within the genus *Ephemerella* (s.l.) there are, thus, no consistent differences in life cycle pattern between geographical regions with widely different climates.

7. Life cycles in Plecoptera

I. Taeniopteryx nebulosa L.

This species was often abundant in late autumn samples. Small numbers of nymphs were found as early as August, but at that time most of them were too small to be catchable. In November the nymphs were about half-grown. Since emergence took place as soon as the first holes appeared in the ice-cover in spring (cf. Brinck 1949), much growth evidently took place under the ice.

T. nebulosa is wellknown to have a very early flight-period and is a good example of the hiemal growth type (Brinck op. cit.). However its growth is not restricted to the period of very cold water, since the nymphs were about half-grown at the time of the ice-cover.

II. Nemouridae

In the lotic biotopes, four species were regularly present, viz. *Amphinemura borealis* Mort., *A. standfussi* Ris, *A. sulcicollis* Steph. and *Protonemura meyeri* Pict. Too few specimens were obtained of the last-mentioned species to permit analysis.

All the three *Amphinemura* spp. were present in catchable sizes for only a short period before emergence. Thus, they obviously spent most of the year as dormant eggs or – in the case of Plecoptera – more probably as small, more or less quiescent nymphs. Their main growth periods were, for *A. borealis* and *A. sulcicollis*, June and July, and for *A. standfussi*, July and August.

Data on these species supplied by Brinck (1949), Lillehammer (1965) and Svensson (1966) generally agree with the present findings.

III. Leuctra fusca L. and L. hippopus Kemp.

These two species had partially different habitat preferences, the former being absent from the smallest streams in which the latter reached its maximal abundance. However in many places they occurred together.

Their life cycles are basically similar, although differently timed. Only a very small number of *L. fusca* nymphs were found before July, when rapid growth started, and emergence of the first imagines occurred within weeks. No nymphs were found after September.

Only eight specimens of *L. hippopus* were found in the material from September to November, whereas they occurred in abundance in May and early June. In July and August a few large nymphs were obtained.

Both species spend most of the year as dormant eggs or more or less quiescent nymphs. With respect to Brinck's (1949) demonstration of the short egg dormancy periods of most Plecoptera, the latter alternative is the more likely. These small nymphs may dwell in the hyporheal biotope.

L. fusca is the most characteristic example of the estival growth type (Brinck op. cit.), whilst *L. hippopus*, undergoing almost its entire growth under the ice, is an equally good example of the hiemal growth type.

IV. Capnia atra Mort.

The relative scarcity of this species in benthic samples from all seasons suggests that it dwelt in other biotopes than those represented at the sampling localities. However from the number of nymphs found in August to November, it is evident at least that many eggs hatched and the nymphs started growing in late summer. Therefore, the cycle of *C. atra* seems to resemble that of *Taeniopteryx nebulosa.*

V. Diura nanseni Kemp.

A preliminary survey of the data revealed that there were considerable differences between the summers of 1963 and of 1964. A very extensive material had therefore to be considered in order to analyze this com-

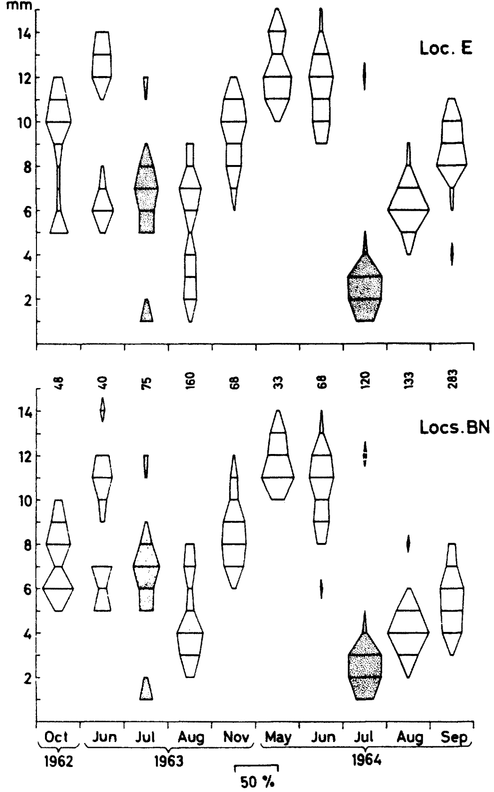

Fig. 7. *Diura nanseni* Kemp. Frequency distribution of nymphal size classes. In July, samples from all localities were combined; these graphs are dotted. Numbers of individuals shown above each polygon.

plexity (Fig. 7). Locs. BN and E were selected since they yielded the most extensive material.

As is seen from the data from July and later, eggs started hatching shortly after the flight-period. The hatching period was limited, as may be seen from the absence of small nymphs in autumn. Growth was intense until November, but relatively little additional length increase took place during the winter. The final stages were rapidly passed through in May and June. This pattern is quite unambiguous, if the period from November 1963 to September 1964 is considered by itself.

In July 1963, however, the situation was complicated by the presence of an intermediate cohort, whose members were obviously too small to reach emergence in the same year but much too large to derive from newly laid eggs. These nymphs grew very slowly in the summer, and the nymphs hatched from the eggs of the year caught up with them in early autumn. In November, the two cohorts had merged completely. This intermediate population was present at both localities represented in the graphs, and a survey showed that it was present at all localities samples in the relevant period except locs. D and O.

Two explanations are forthcoming; either, that in the winter of 1962 to 1963, delayed egg-hatching occurred, or, that some of the nymphs which hatched normally in the late summer of 1962, lagged behind in their development. The incipient division of the population in October 1962 supports the latter alternative.

The flight-period of *D. nanseni* culminated about one month after the break-up of the ice. The species does not belong to the very early ones, such as *Taeniopteryx nebulosa* and *Capnia* spp. Since its most intense growth took place in late summer and autumn and the rest in spring, it is difficult to place it with either the estival or hiemal growth types. In view of its early flight-period, it may be best grouped with the latter category.

Interestingly, Svensson (1966) also reported annual variations in the life cycle of *D. nanseni.* Much more growth took place in the autumn of 1964 than in 1963, and accordingly more remained to be completed in the spring of 1964 than in 1965. His finding that this deviation was due to a disturbance in autumn supports the above conclusion concerning the similar circumstance in the Ammarnäs area.

Brinck (1949) and Hynes (1961) found a similar life cycle in *Diura bicaudata* L.

VI. Isoperla grammatica Poda and I. obscura Zett.

The pattern in these two species was uncomplicated. The eggs hatched shortly after being deposited, and the nymphs started growing, but comparatively slowly, having

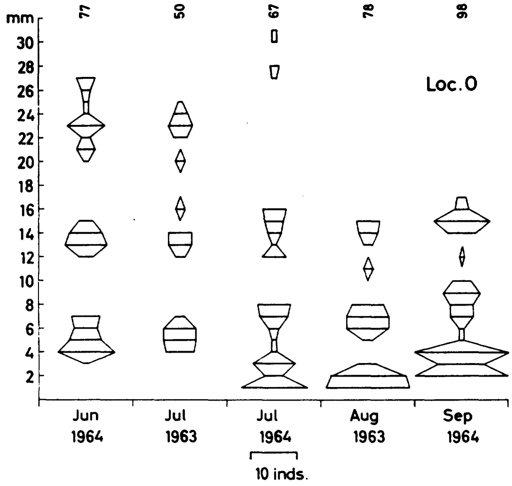

Fig. 8. *Dinocras cephalotes* Curt. Frequency distribution of nymphal size classes. Numbers of individuals shown above each polygon.

reached a length of 2–3 mm in November. By May, their mean length had more than doubled, but still much growth remained to be performed before emergence, which took place in late July and August.

These species, thus, seemed to have a very long growth period, covering part of two summers and the intervening winter. It is difficult to place them with either the estival or the hiemal growth types. Svensson (1966) established a long period of winter quiescence in his study area in northeastern Sweden, and this was also found in southern Sweden by Brinck (1949).

VII. Dinocras cephalotes Curt.

This species is known to have a three-year cycle in Europe including southern Sweden (Schoenemund 1912, Brinck 1949, Dittmar 1955, Hynes 1958, Aubert 1959).

In the Ammarnäs area, *D. cephalotes* occurred almost only at loc. O (Fig. 8). In July and August very small nymphs were numerous. They may derive from newly laid eggs having hatched immediately (cf. Tab. 3). But in the light of Brinck's (op. cit.) finding of a relatively long period of egg dormancy in this species it seems probable that the eggs had been deposited the preceeding year. This would harmonize with the presence of young nymphs almost at the beginning of the flight-period. Thus, the species presumably has a four-year cycle in Lapland.

8. Life cycles in Trichoptera

I. Rhyacophila nubila Zett.

This too was a species with a complex composition of the larval populations. The data from locs. BN and E are shown in Fig. 9. It

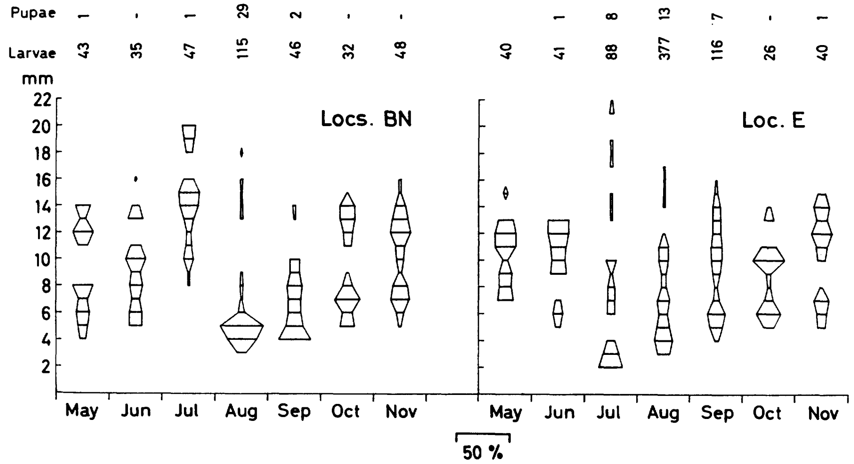

Fig. 9. *Rhyacophila nubila* Zett. Frequency distribution of larval size classes. Numbers of larvae and pupae shown above each polygon; pupae are not included in the polygons.

was considered sufficient to use the material from 1964 (with the usual inclusion of October 1962 and November 1963) as there were no traces of annual differences of pattern as in *Diura nanseni*.

At both localities rather heterogeneous populations divided into two, more or less clearly demarcated cohorts occurred in spring. All these larvae grew rapidly and emerged in the following summer. In July to August a new cohort appeared consisting of small but by no means newly hatched larvae. Since they had evidently been growing for some time and the flight-period had only barely begun at the time for the first appearance, they obviously derived from the preceeding year's crop. It is difficult on the basis of the present material to prove that none of these larvae reached emergence in the same year, towards the close of the long flight-period, but there is no evidence for this. Probably they all spent the following winter as larvae of the third, fourth and fifth instars. Addition to the population of young larvae seemed to cease in autumn, as witnessed by the absence of small larvae after September.

Evidently, *Rh. nubila* normally had a two-year cycle in the study area.

At loc. E a complication was found in the form of a cohort of intermediate-sized larvae in June and July. It is difficult to interpret their significance. The most probable explanation seems to be that they were larvae that had lagged behind in the development and that they were bound to emerge towards the end of the year's flight-period. They would then be comparable with the intermediate-sized nymphs of *D. nanseni* discussed above except they were able to catch up with the normal larvae and emerge in the "right" year. However, it cannot be excluded that they derived from eggs hatching earlier than most and thus constituted individuals able to dispense with the second year in the normal two-year cycle.

This intermediate cohort was not discernible in July and August 1962 and 1963. But the extraordinarily large variation of larval sizes at most times may easily conceal divergent fractions.

Pupae were found in numbers for only a very short period, mainly in August. Their scarcity in September is surprising considering that the flight-period continues until the beginning of October.

By far the majority of all larvae in the samples belonged to the third, fourth and fifth instars. In July and August a number of second instar larvae were also obtained, whilst first instar larvae were only occasionally obtained. Either they dwelt in other microbiotopes, or they were able to pass through the catching net and were thus missed.

The evidence thus, indicates that *Rh. nubila* had a two-year cycle. The eggs had a long period of dormancy or the first and second larval instars long periods of relative quiescence. A cohort of aberrant larvae raised the suspicion that the life cycle may under special circumstances be abbreviated, but this could not be conclusively shown.

Rh. nubila has not been studied in detail elsewhere. The flight-period seems generally to be very long in northern Sweden (Forsslund 1954, Forsslund and Müller 1962). In Central Europe, Dittmar (1955) and Petr (1961) found that larvae of widely different sizes occurred throughout the year.

More extensive work has in the past been devoted to *Rh. septentrionalis* McL., especially Nielsen's (1942) careful investigations. This species wintered exclusively in the fifth larval instar which was of very long duration. Many of the larvae spent a long time as "Ruhelarvae" – a condition rare in *Rh. nubila* as noted also by Nielsen. It should be remembered that the populations studied by Nielsen inhabited a very special biotope, viz. springs with reduced annual temperature fluctuations.

Many data on *Rhyacophila* in the literature are of limited value, since it is often open to doubt whether one or more species were involved. Hynes (1961) was reasonably sure that two *Rhyacophila* spp. in his study area had widely different cycles. In *Rh. obliterata* McL. the eggs had a very long dormant period followed by rapid growth of the larvae, a pattern appearing similar to that of *Rh. nubila* in Lapland, in which, however, the cycle took longer time. In *Rh. dorsalis* Curt. the flight-period covered most of the year, and since the eggs hatched almost immediately, larvae of all sizes were present throughout the year. Hynes thought that *Rh. dorsalis* had a one-year cycle, as did Scott (1958), whereas Mackereth (1960) suspected, for good reasons, that at least part of the population had a two-year cycle. Décamps (1967) established the occurrence of a large variety of life cycle in different *Rhyacophila* spp. in southern France. Even within one species an extraordinary variability was found. For example, *Rh. evoluta* McL. had one-, two- or three-year cycles at different sites within Décamps' restricted study area. He also found that small and large larvae sometimes occurred in different biotopes within the streams.

II. Glossosoma intermedium Klap.

This species had a very early flight-period for a caddisfly (Tab. 3). Larvae were found from August onwards. In November practically all had pupated, and in May only pupae were found. Thus this species had a relatively short larval period of intense growth followed by a long pupal period.

III. Arctopsyche ladogensis Kol.

Since this species was obtained in relatively small numbers, the data from all localities and all years had to be pooled (Fig. 10). The majority of the larvae derived from locs. E, GH and KL. Remarkably, no pupa was ever found.

As is shown by the graphs, the species had an uncomplicated two-year cycle. In contrast to *Rh. nubila* the eggs hatched shortly after being deposited and larval growth commenced. These small larvae apparently continued growing under the ice, for they increased in body length from November to June. Growth continued in the following summer and was completed in their second year after a second hibernation. Generations were quite distinct, and larvae of the same year class well concentrated.

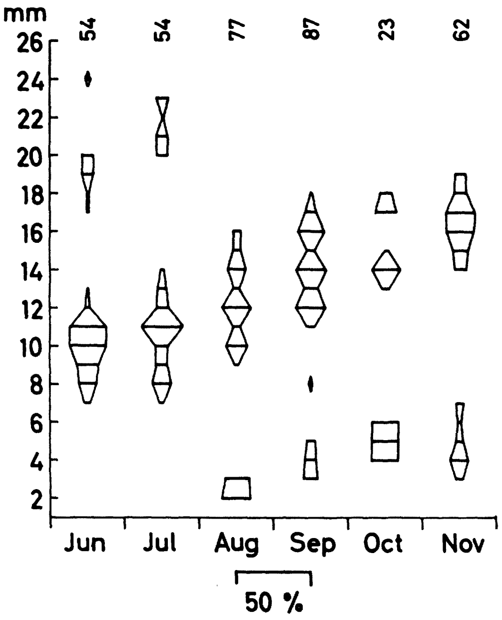

Fig. 10. *Arctopsyche ladogensis* Kol. Frequency distribution of larval size classes. Numbers of larvae shown above each polygon.

Whilst there are no studies of *A. ladogensis* from elsewhere, species of *Hydropsyche* have been extensively studied. Hynes (1961) found that *H. instabilis* Curt. had larval populations composed of very different sizes in spite of a strictly univoltine cycle, and assumed that individual growth rates varied strongly. Illies (1952) found two distinct size-classes present at the same time and was of the opinion that at least some individuals took one-and-a-half years to complete their cycle.

A. ladogensis has its two-year cycle in common with *Rh. nubila*. In contrast to the latter species, larvae reach a considerable body-length shortly after hatching.

IV. Polycentropus flavomaculatus Pict.

All catchable sizes of larvae were present at all seasons, although proportions varied (Fig. 11). Most of the larvae belonged to the fourth and fifth instars; the earlier instars were possibly of relatively short duration, as found by Nielsen (1942) for *Plectrocnemia conspersa* Curt.

P. flavomaculatus provides an extreme example of composite larval populations. Very little can be stated with confidence concerning

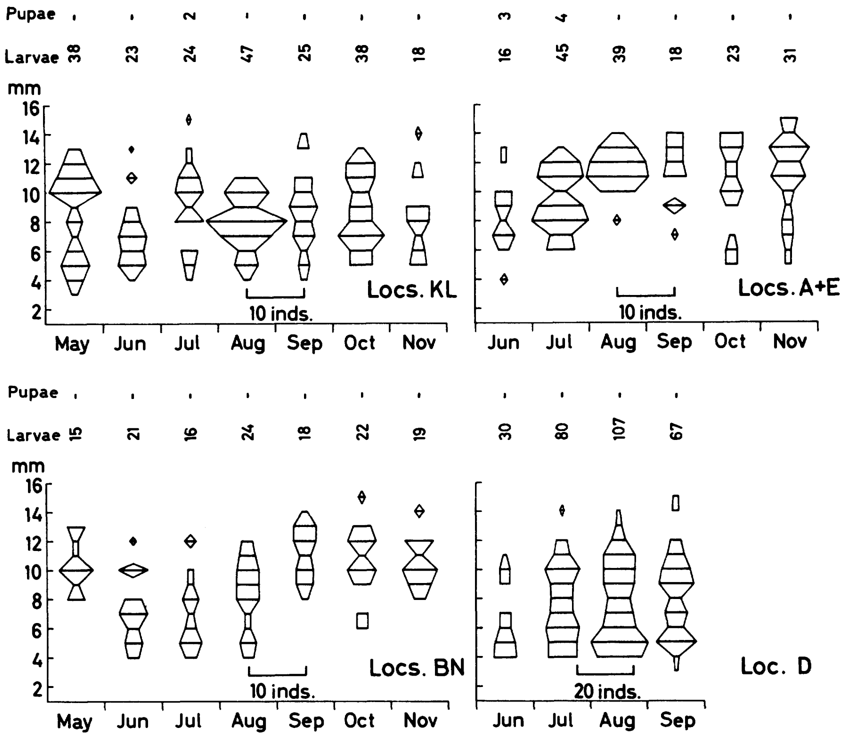

Fig. 11. *Polycentropus flavomaculatus* Pict. Frequency distribution of larval size classes. Numbers of larvae and pupae shown above each polygon; pupae are not included in the polygons.

its life cycle because of this. Relatively large larvae occurred during and after the flight-period, indicating that many individuals have a two-year cycle.

9. Life cycles in Simuliidae

Most of the blackflies had simple life cycles. Practically no blackflies were on the wing outside the period late June to middle August. A very long period of egg dormancy (usually about 10 months) was followed by a short period of explosive growth, leading through pupation to emergence within weeks (cf. Ulfstrand 1968). In this family the occurrence of small larvae dwelling in a different microbiotope seems to be out of the question. This applies to the following species listed in approximate chronological order of emergence: *Prosimulium hirtipes* Fries, *Cnephia fuscipes* Fries, *C. tredecimata* Edw., *C. trigonia* Lundstr., *C. lapponica* End., *Helodon ferrugineus* Wahlb. (having a locally variable emergence time), *Gnus forsi* Carlss. (same remark), *Schönbaueria* Zett., *Simulium truncatum* Lundstr. and *S. argyreatum* Meig.

A few species were present also in autumn and early spring as larvae and in contrast to all the species listed above, obviously wintered as larvae (never as pupae). This applies to *Odagmia monticola* Friedr., *O. ornata* Meig. and *Eusimulium latipes* Meig., perhaps also to some scarcer species. The wintering larval populations were usually very thin and more or less restricted to the smaller water courses. Wintering larval populations were notably absent from lake outlets. It is not known whether these species always wintered as larvae, or whether this was true only for part of the population. In these species two annual generations might occur, a possibility that can be excluded for all the other species listed above. *O. monticola* and *E. latipes* were mentioned by Zahar (1950) as hibernating in the larval stage in Britain.

Most of these results agree with those published by Carlsson (1962). Many of the species present in the Ammarnäs area are known to have two or three generations annually in central Europe; many records in the literature are, however, unreliable because of uncertain identification. In Saskatchewan, Fredeen et al. (1951) found a *Simulium* species having a life cycle conforming with the commonest pattern in the Ammarnäs area. The records by Doby et al. (1959) of rapid development of blackflies under laboratory conditions support the field data.

10. Phenological types

The benthic insect species of the Lapland streams may be classified in several phenological categories. Such classifications which may offer a means of ecological analysis have been repeatedly suggested. Brinck (1949) distinguished estival and hiemal growth types in Plecoptera, and Hynes (1961) and Landa (1962) described slow and fast growth types among Ephemeroptera and Plecoptera. Landa also pointed to the occurrence of intermediate types, with certain stages growing very fast and others much more slowly. Strongly retarded growth may, under field conditions, be indistinguishable from no growth at all (cf. Hynes 1962). Hartland-Rowe (1964) whose study area was more like the present area than any other, concluded that the life cycles in the north were easily identifiable with those described from more southerly areas with shorter winters. Pleskot (1951 a, 1958, 1961) has presented detailed descriptions and analyses concerning life cycle patterns in Ephemeroptera, whilst Hynes (1961) and Macan (1957 a, b, 1958, 1961 b) have contributed further important information.

Among species discussed in this paper the following phenological types (life cycle patterns) may be discerned:

A) One-year cycles:

- I) Considerable growth commencing shortly after oviposition leading to the presence of more or less large-sized nymphs/larvae during a long period: *Baetis rhodani* (partim), *Heptagenia sulphurea* (partim), *H. dalecarlica* (partim), *Ephemerella aurivillii*, *Taeniopteryx nebulosa*, *Capnia atra*, *Diura nanseni* (mostly), *Isoperla grammatica*, *I. obscura*; possibly *Odagmia* spp. and *Eusimulium latipes* (?partim).
- II) Intense growth concentrated to a period preceeding emergence: *Ameletus inopinatus*, *Baetis rhodani* (partim), *B. fuscatus*, *B. lapponicus*, *B. pumilus* (mostly), *B. subalpinus*, *Ephemerella mucronata*, *Amphinemura borealis*, *A. standfussi*, *A. sulcicollis*, *Leuctra fusca*, *L. hippopus*, all Simuliidae except those listed under A I.
- III) Egg and larval stages short, pupal stage long: *Glossosoma intermedium*.

B) Two-year cycles:

- I) Considerable growth before and during (part of) the first winter: *Diura nanseni* (at times), *Arctopsyche ladogensis*.
- II) First winter spent as egg or as more or less quiescent early nymph/larva: *Heptagenia sulphurea* (partim), *H. dalecarlica* (partim), *Rhyacophila nubila* (chiefly).

C) Three- or four-year cycle: *Dinocras cephalotes*.

D) Doubtful cases: *Rhyacophila nubila* (the intermediate cohort at loc. E, as described on p. 182), *Polycentropus flavomaculatus* (probably mainly a two-year cycle).

Classifications of this kind, although useful for several purposes, may conceal important specific differences. Naturally, every species has its particular features and, accordingly, there are variations within each of the phenological types as defined above. For example, in type A I, the period between oviposition and the appearance of catchable nymphs is a matter of weeks in *Ephemerella aurivillii* but of months in *Capnia atra*. Yet both differ from the species in group A II, which spend the winter as eggs or as more or less quiescent small nymphs and larvae. Most of the growth is in the latter group of species postponed to the following year.

Winter quiescence is a common feature in Plecoptera (Brinck 1949, Svensson 1966). It may comprise only part of the period of ice-cover, as demonstrated by several species in the Ammarnäs area, which showed a length increase between November and May.

The species possessing both one- and two-year cycles are of special interest. *Diura nanseni* usually, but not invariably, completed its life cycle in one year. The two *Heptagenia* spp. were able to do so only at certain localities, and even there only in part of the population. In *Rhyacophila nubila*, the two-year cycle dominated, and it was not possible to obtain evidence for a one-year cycle.

It is interesting to relate these findings to those by Jónasson (1965) concerning *Chironomus anthracinus* Zett. in a Danish lake. This species was found to have a one-year cycle in shallow water and a two-year cycle in deep water, with a transitional zone in between. The length of the cycle was strongly influenced by conditions prevailing during a short period immediately preceeding summer stagnation. This indicates that the different cycles in e.g. *Heptagenia* spp. at different places in the Ammarnäs area may be determined by special conditions prevailing for only a brief time.

Mackereth (1960) demonstrated the occurrence in the caddisfly *Agapetus fuscipes* Curt. of considerable annual differences in life cycle pattern. Such differences have not otherwise been convincingly shown in lotic insects. In the lenitic mayfly *Cloeon dipterum* L., Macan (1965/66) and Macan and Maudsley (1966) recently showed essentially similar annual differences.

Superficially the variable life cycles of *Diura nanseni*, *Heptagenia* spp. and *Rhyacophila nubila* appear hazardous. But in fact the flexibility which is a prominent feature in their life cycle patterns may be of great advantage and represent an important factor for the success of these species.

11. Life cycles and local temperature differences

Much of the work and speculation about the influence of temperature on the life conditions of aquatic insects has been summarized by Macan (1961 a, 1962 a, 1963). In this context no attempt will be made to discuss faunistic composition or life cycle differences between species in terms of temperature conditions, but only to demonstrate some local temperature differences and discuss their possible effect on local differences of life cycle patterns.

Local temperature differences within a river system and their ecological implications have been discussed by e.g. Pleskot (1951 b etc.), Macan (1957 b), Kamler (1965) and Edington (1966).

In 1964, temperature was continuously recorded by means of mercury-in-copper thermographs which incorporated compensation devices so as to eliminate the effect of air temperature. The thermographs were checked every week against a high precision mercury thermometer. Records were obtained from five localities, viz. E, K, N, O and P (cf. Fig. 1).

The stations were chosen so as to reflect a variety of conditions. Loc. E is at a lake outlet, whereas loc. K is in Vindelälven upstream of the same lake; at the latter place, the river upstream is not in connexion with any lake which can influence the temperature conditions. Loc. N is at the lower end of Tjulån which flows very rapidly for 10 km from the lake Stora Tjulträsk. Its partly torrential character causes the water mass to come into close contact with the air, so that air temperature has a relatively strong influence on the water temperature. Locs. O and P are situated in smaller water courses, and the differences between them are described in Ulfstrand (1968).

The temperature measurements are shown in Fig. 12. Low air temperatures in May caused loc. N to have a particularly low value in the first measurements. In June all differences were largely smoothed out which was largely due to the large quantities of melt water that filled all streams. The two smallest water courses reached their annual temperature peak earlier than the others, and the peaks

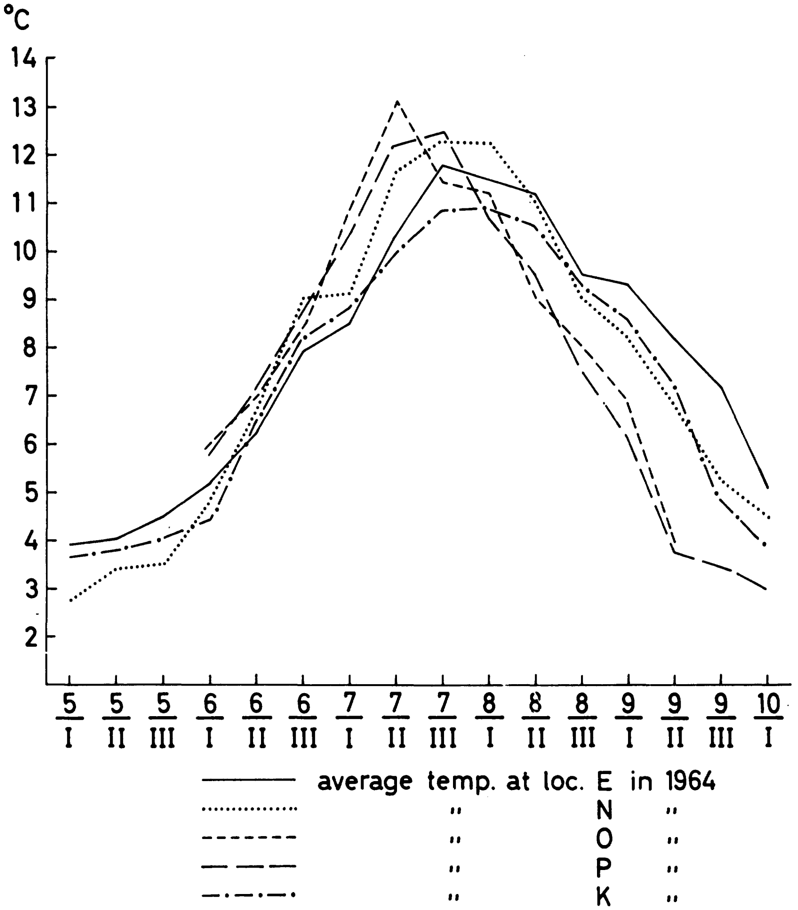

Fig. 12. Water temperature curves for five localities, May to October 1964. The values are averages of the temperatures recorded every three hours during the ten- or eleven-day periods.

were also comparatively high, particularly at loc. O. It is noteworthy that this locality, the one at the highest altitude, thus had a higher temperature peak than those situated at lower altitudes. The outlet locality lagged behind in early summer, and loc. K had a distinctly lower peak than any other. In autumn, differences were still more marked than in spring and summer. The outlet received relatively warm water from the lake and had a distinctly higher temperature than any other locality. The two small water courses cooled down much faster than the larger ones. The effect of the lake may give the downstream river stretch a slightly higher temperature also in winter, but the effect is likely to be very local (Melin 1947).

The marked difference in autumn between the temperature at the outlet and elsewhere seems to be an important causative factor for the local differences in the life cycles of *Heptagenia* spp. They were able to complete their life cycle in only one year at the outlets, but not elsewhere; *H. sulphurea* was almost restricted to these places. It seems very probable that the elevated temperatures at the outlets permit the rapid development of the eggs and maybe the first nymphal stages and thus the elimination of one whole year's life in the benthos.

Similarly, the elevated temperature at the outlet may cause in *Baetis rhodani* the eggs to hatch and the nymphs to grow more rapidly. This would explain why this species disappeared earlier from the outlets than from other localities in summer.

The early fall of temperature in autumn at loc. O probably also occurred at loc. D, because the small and very shallow lake upstream of this site could hardly act as a heat reservoir to any extent. If this was so, it would explain why the accrual of newly hatched nymphs to the population of *B. rhodani* at loc. D was more protracted in summer than elsewhere.

Several factors probably cooperate to raise the temperature at the uppermost localities, as exemplified by loc. O. Above the birch forest the streams are exposed to strong and almost continuous irradiation around the summer solstice. Most streams, lakes and tarns are shallow and this permits an efficient heat absorption. The high temperature reached in these streams may be of importance for certain species. Thus, for example, the large stonefly *Dinocras cephalotes* which is generally of a southerly distribution occurs in the Ammarnäs area mainly in streams in the upper birch zone or even above (Ulfstrand, unpublished records).

As reported in Ulfstrand (1968) the main peak of the blackfly zoome of small streams occurs about a month earlier than at the lake outlets. This may be explicable in terms of local temperature differences, this interpretation not being invalidated by the fact that different species were involved at the two biotopes. But the most important factor is probably the nutritional conditions.

Whilst it has been shown that local temperature differences probably have a considerable influence on the life cycle patterns of certain species, it has to be remembered that various other factors may vary concomitantly with temperature – in time and/or space (Knöpp 1952). Under the circumstances prevailing in the Ammarnäs area, oxygen is hardly ever likely to be a limiting factor, in contrast to many study areas where the reduced oxygen content at rising temperature makes the analysis of temperature effects very difficult. The nutritional conditons at outlets are different from those prevailing further downstream, there being more seston and periphyton at the outlets (more fully described in Ulfstrand 1968) and more in summer than at other seasons. Temperature has an important effect on the plankton production in a lake and its timing (Lindström 1958); and lacustrine plankton serves as food for the inhabitants of the outlet. It is therefore to be expected that it is the coaction of several factors operating in combinations which usually govern the life cycle patterns actually undergone by the different species.

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