Ephemeroptera and Plecoptera from River Vindelälven in Swedish Lapland

With a discussion of the significance of nutritional and competitive factors for the life cycles

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1. Introduction

One of the few major Swedish rivers that has not been regulated for hydroelectric purposes so far is River Vindelälven. Plans for its exploitation have, however, been published (Kungl. Vattenfallsstyrelsen 1962). In recent years the Swedish nature conservancy organisations have arranged for biological and other investigations to be carried out in such water systems that are threatened with destruction through technical exploitation. Within the compass of these activities the author had the opportunity of working in the upper part of River Vindelälven in 1961 to 1966, inclusively, for longer or shorter periods. The objective was both a qualitative survey of the aquatic fauna and a quantitative study of certain animal communities, viz. those of lotic biotopes; much of the latter work has been published (Ulfstrand 1967, 1968 a, b).

Using light-traps as well as manual collecting methods, a large material of certain insect groups (winged stages) was assembled from a variety of biotopes. In this paper the collections of mayflies (Ephemeroptera) and stoneflies (Plecoptera) will be described and discussed. The data yield a picture not only of the faunistical composition but also of various bionomical conditions. In addition, a more general discussion of the significance of certain nutritional and competitive factors for the life cycles of the species will be presented.

The Scandinavian stonefly fauna is well-known from Brinck's (1949) monograph. The mayflies, on the other hand, are extremely poorly known, nothing much having been published since Simon Bengtsson's days.

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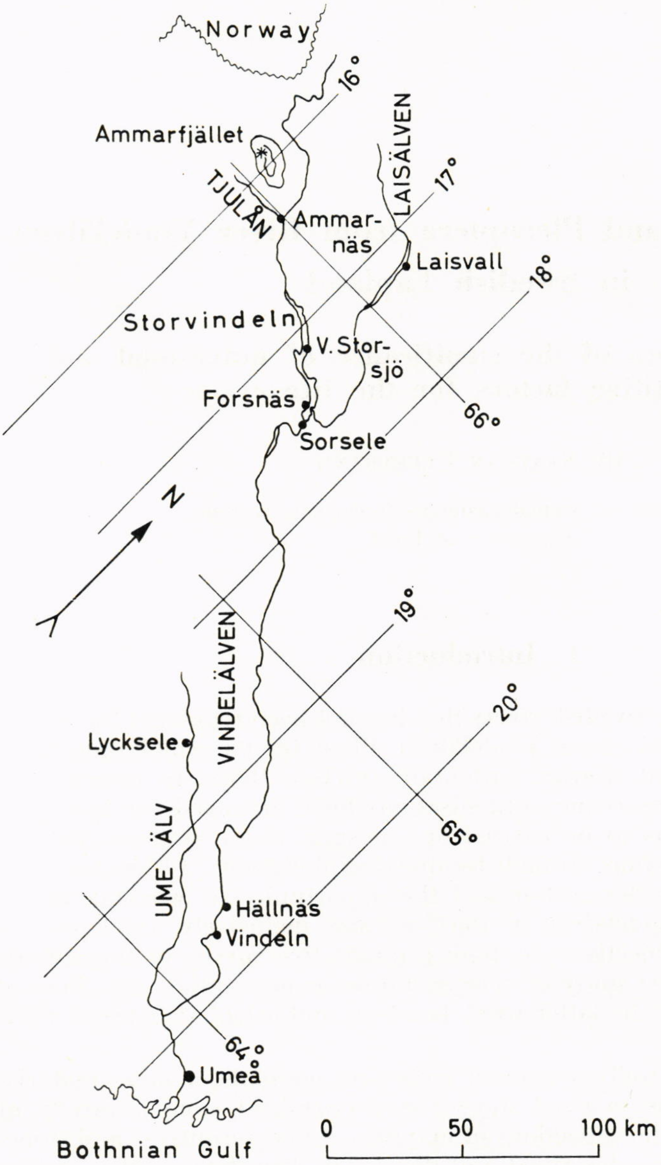


Fig. 1. Map of River Vindelälven showing the position of the study area and the village of Ammarnäs.

2. Study area and its physiographic features

A detailed description was given in Ulfstrand (1968 a) so that only some essential features need be repeated here.

River Vindelälven is the eighth largest river of Sweden. From its sources in the Scandian mountain chain to its mouth in River Ume älv near the coast of the Bothnian Gulf it traverses a distance of 444 km (Fig. 1). The present

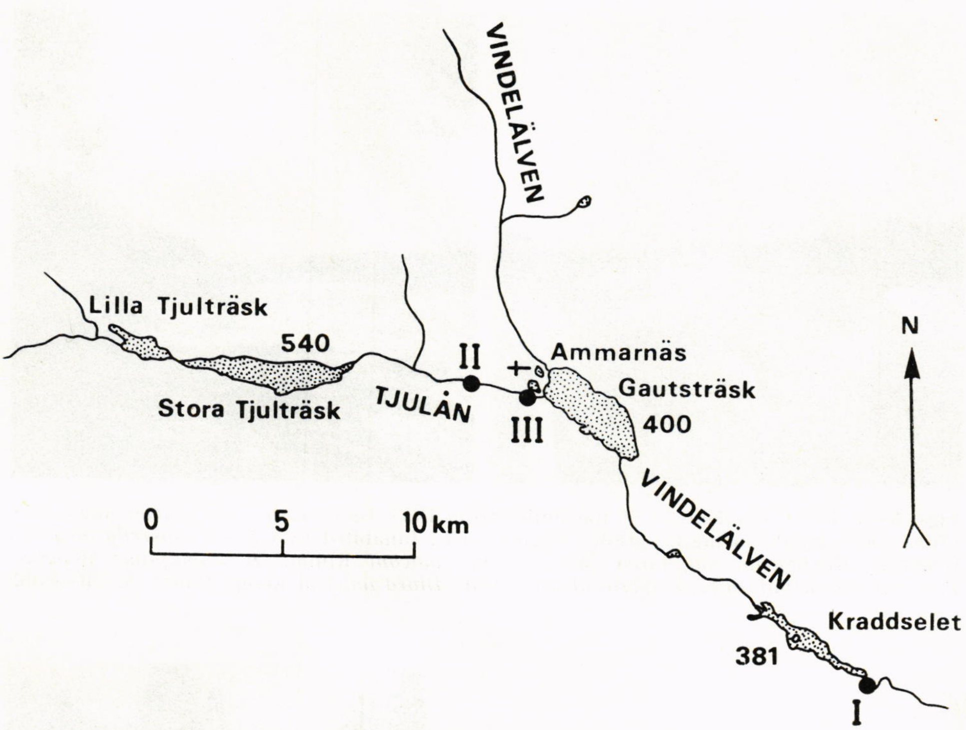
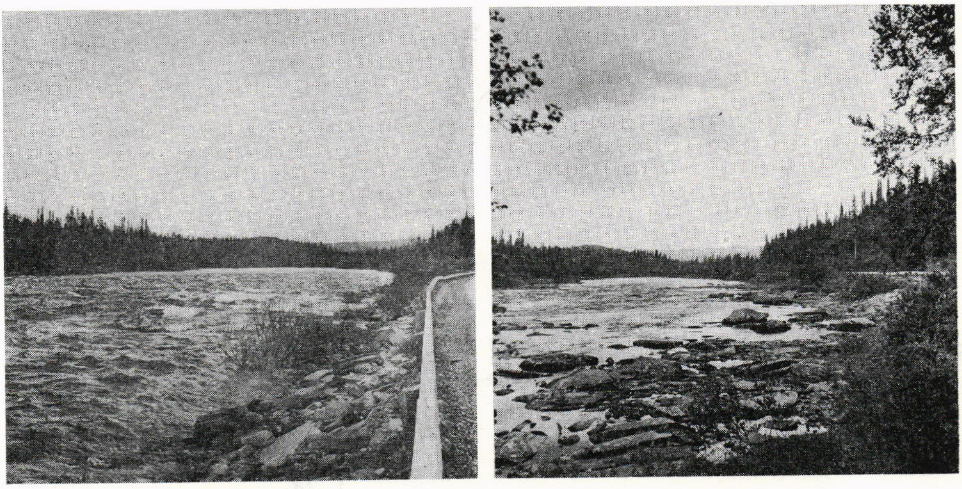


Fig. 2. Map of the Ammarnäs area. The altitude of the lakes is given in m above sea level. The position of the light-traps is indicated with Roman figures.

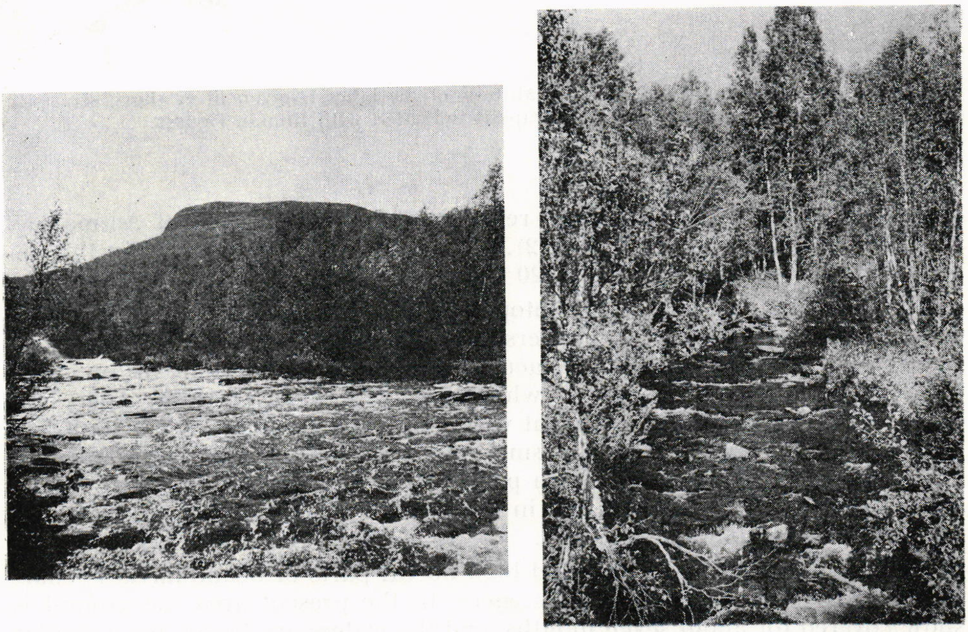
study was conducted in its upper reaches, around the village of Ammarnäs (lat. 65°58′N, long. 16°12′E; Fig. 2). The entire material included in this report derives from within approx. 20 km of Ammarnäs.

A great variety of freshwater biotopes occur within the study area. The running waters range from large rivers with rapid flow (Figs. 3 and 4) alternating with stretches of almost lacustrine character, to moderate or small streams (Figs. 5 and 6) some of which may dry up in summer. There are deep lakes with very little emergent vegetation, such as Lake Stora Tjulträsk (Fig. 7), but also various types of smaller and shallower lakes, tarns, springs, mires and marshes. In the western part of Lakes Lilla Tjulträsk and Gautsträsk (cf. map, Fig. 2) deltas are in the process of building up providing a mixture of many biotopes (Fig. 8).

The climate of the subarctic and high boreal parts of Scandinavia is characterized by violent seasonal differences. In the present area the ground is snow-covered for about seven months, and the waters are frozen for a similar length of time. The high latitude in combination with the cover of ice and snow blacks out the rivers and lakes for a long period, with obvious consequences for the photosynthetic productivity (cf. Rodhe, Hobbie and Wright 1966). The fast current in the streams in combination with low water temperatures guarantees a perpetually high oxygen content. This applies also to



Figs. 3—4. River Vindelälven at the outlet from Lake Gautsträsk. Left, during high flow (June 1964), right, during low flow (August 1963). Inhabited by e.g. *Ephemerella aurivillii* Bengtss., *Heptagenia sulphurea* Müll., *Baetis macani* Kimm., *B. subalpinus* Bengtss., *Taeniopteryx nebulosa* L., *Isoperla obscura* Zett., *Diura nanseni* Kemp. Photo: S. Ulfstrand.



Figs. 5—6. Left, a moderately large stream in the *Betula* zone. Inhabited by e.g. *Baetis lapponicus* Bengtss., *Heptagenia dalecarlica* Bengtss., *Ephemerella mucronata* Bengtss., *Leuctra hippopus* Kemp., *Capnopsis schilleri* Rost., *Dinocras cephalotes* Curt. July 1963. Right, a small stream in mixed forest. Inhabited by e.g. *Amphinemura sulcicollis* Steph., *Protonemura meyeri* Pict., *Leuctra digitata* Kemp., *L. hippopus* Kemp., *Chloroperla burmeisteri* Pict., *Dinocras cephalotes* Curt. July 1965. Photo: S. Ulfstrand.

Fig. 7. Lake Stora Tjulträsk at break-up of ice (May 1964). Inhabited by e.g. *Siphlonurus lacustris* Etn., *Baetis macani* Kimm., *Centroptilum luteolum* Müll., *Metretopus* sp., *Leptophlebia marginata* L., *Nemoura avicularis* Mort., *Capnia atra* Mort., *Diura bicaudata* L. Photo: S. Ulfstrand.

most lenitic biotopes except small vegetation-rich pools. The water temperature at five lotic localities within the study area is shown in Fig. 9.

A prominent feature is the violent fluctuations of water flow in the streams, often differing by a factor of 100 between low and high flow.

The aquatic vegetation has not been studied in detail (cf. Wassén 1965). In the lotic biotopes the dominant macroscopically visible plant is the colonial diatom *Didymosphenia geminata* covering large areas of the river bottoms. Microscopical benthic algae, particularly diatoms, are also abundant. In shallow lakes and pools emergent macrophytes are usually present, sometimes covering vast areas.

Generally speaking, the running waters physiographically belong to the rhithron type, with the modifications induced by the geographical position of the area (Illies 1961, cf. Ulfstrand 1968 a, pp. 35—36).

In most of the study area the terrestrial vegetation is dominated by coniferous forests, with a variable admixture of deciduous trees. The western part, however, is within the subarctic *Betula* region which begins at about 475 m above sea level.

The human population is very sparse. Man has only to a negligible extent

Fig. 8. The delta in the western end of Lake Gautsträsk. In the foreground, part of the village of Ammarnäs. Inhabited by e.g. *Siphlonurus aestivalis* Etn., *Parameletus* sp., *Ecdyonurus joernensis* Bengtss., *Heptagenia fuscogrisea* Retz., *Arthroplea congener* Bengtss. August 1964. Photo: S. Ulfstrand.

interfered with the natural conditions of the waters of the area. The most important fish species are *Salmo trutta* L., *Salvelinus alpinus* L., *Thymallus thymallus* L. and *Coregonus* sp.

3. Methods

Adult insects were hand-collected and caught in light-traps.

Sweep-nets were used in vegetation along stream and lake shores, and likely hiding places such as stones and debris were searched and the animals collected. Since the quantitative work was directed at lotic biotopes, species from such biotopes became overrepresented in the catch, but efforts were made to secure adequate collections also from lenitic biotopes. It was attempted to spread the collecting activities as evenly as possible over the field work periods (Tab. 1).

In 1962 to 1965, inclusively, light-traps with UV-lamps (Philips HPW 125 W) emitting radiation with a maximum at 3655 Å were operated for long periods (Tab. 2). The traps were looked after by local people who were instructed to change the collecting jars when these were half-filled with insects

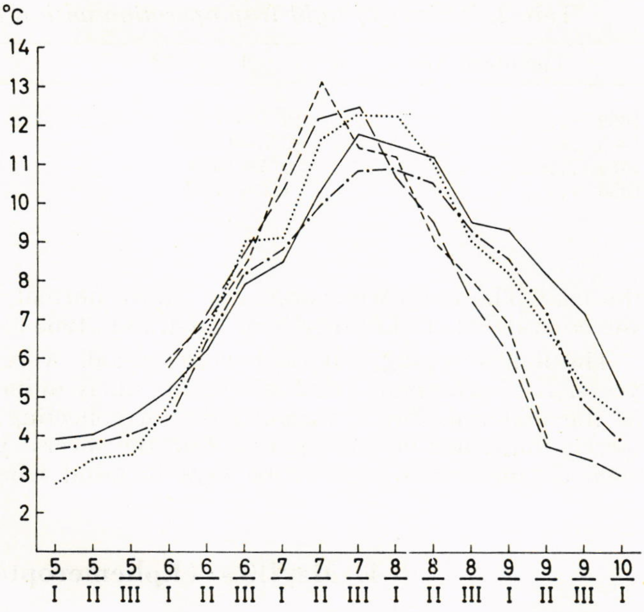


Fig. 9. Water temperature as recorded from thermographs at five lotic localities in 1964.

but at least every seventh day. For certain periods, the jars were shifted every day.

The location of the light-traps is indicated on Fig. 2. Light-trap I was situated at River Vindelälven about 18 km SSE of Ammarnäs. At this site a lake-like extension of the river ends (Kraddselet), and the river flowing out of it is broad, rapid and shallow. The trap was at the top of a river bank with the lamp about 5 m over normal summer water level. It was in view also from part of the lake-like extension. The site corresponds to Locality H in Ulfstrand (1968 a).

Light-trap II was at River Tjulån, a large tributary of River Vindelälven, and about 3 km W of Ammarnäs. There are practically no lenitic biotopes anywhere near the site, which corresponds to Locality B in Ulfstrand (1968 a). The lamp was about 2 m above normal summer water level.

Light-trap III was also at River Tjulån, within the village of Ammarnäs. About 200 m further downstream the river changes its character and runs slowly until discharging into Lake Gautsträsk. Its bottom is stony near the trap site but becomes more and more covered with finer fractions towards

Tab. 1. *Periods of field-work within the Ammarnäs area.*

1961	16—31/7
1962	14—28/7, 1—22/8, 3—8/10
1963	7/6—13/8, 12—17/11
1964	4/5—18/9
1965	13/7—23/8
1966	8—10/6, 29/9—2/10

Tab. 2. *Periods of light-trap operation within the Ammarnäs area.*

Light-trap No.	I	II	III
1962	13/7— 4/9	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

the lake. The lamp was about 2 m above normal summer water level. The site corresponds to Locality N in Ulfstrand (1968 a).

The light-trapping and field work periods were not the same in all the years. The earliest and latest species are likely to have been underrepresented in the material. Minor irregularities in collecting effort were presumably largely smoothed out through pooling the several years' material. However, such circumstances have to be kept in mind when discussing the results.

4. Mayflies (Ephemeroptera)

4.1. *Taxonomical and nomenclatorial remarks*

The list in Limnofauna Europaea (Illies 1967) seems to be the best available and will be followed with the same exceptions as in my previous papers (Ulfstrand 1968 a, p. 8).

The winged stages of *Heptagenia sulphurea* Müll. and *H. dalecarlica* Bengtss. were impossible to separate, while the nymphs were readily distinguishable using the reverse asymmetry of the mouth-parts (Bengtsson 1917). This, of course, may appear a character of very low taxonomical value, but since it has been demonstrated that the two forms have different local distribution patterns and life cycles (Ulfstrand 1968 a, p. 31, 1968 b, pp. 175 et seq.) it would seem rash to merge them into one species. The relationship between them should be examined more closely before such a step is justified.

4.2. *Survey of the mayfly collection*

The total mayfly collection is presented in Tab. 3 from which may be seen that a total of 3447 specimens were obtained, of which 532 came on the light-traps and the rest were hand-collected. If *Parameletus* sp. and *Metretopus* sp. are provisionally taken to represent one species each and *Heptagenia sulphurea/dalecarlica* on nymphal evidence are counted as two species, the total list from the study area includes 24 mayfly species.

Illies (1967) considered that the presence in Europe of some 200 mayfly species was established and that another 55 were likely to occur. Our knowledge about the distribution of most of these species is imperfect or nonexistent. If one compares the list from Ammarnäs with that for the British Isles (Macan 1961) it is striking how few species are common to both areas. The following species do not occur in the British Isles: both *Ephemerella*

Tab. 3. *The collection of mayflies* (*Ephemeroptera*). Italicized figures indicate the ten-day period during which the median specimen was obtained. In *Centroptilum luteolum,* this happened exactly on the border between two periods.

	Light-trap collection				Manual collection				6 III	7 I	7 II	7 III	8 I	8 II	8 III	9 I—III	Total light-trap	Total manual collection	Grand total
	Im ♂♂	Subim ♂♂	Im ♀♀	Subim ♀♀	Im ♂♂	Subim ♂♂	Im ♀♀	Subim ♀♀											
Siphlonurus aestivalis Etn.	1	—	—	—	27	32	52	36	—	2	*112*	33	—	—	—	1	1	147	148
S. lacustris Etn.	331	1	5	—	74	63	71	69	—	—	105	*408*	49	51	—	1	337	277	614
S. linnaeana Etn.	1	—	—	1	—	—	—	—	—	—	1	—	—	—	1	—	2	—	2
Ameletus inopinatus Etn.	4	5	—	14	21	62	15	103	15	80	*114*	11	3	1	—	—	23	201	224
Parameletus sp	—	—	—	—	—	—	2	—	—	—	2	—	—	—	—	—	—	2	2
Baetis fuscatus L.	16	1	—	—	8	50	23	66	—	—	—	—	1	19	*137*	7	17	147	164
B. lapponicus Bengtss.	2	—	7	1	45	12	25	13	—	—	—	40	*42*	17	6	—	10	95	105
B. macani Kimm.	—	—	3	—	28	62	30	85	—	1	15	28	*84*	74	6	—	3	205	208
B. pumilus Burm.	1	—	2	—	13	20	40	39	—	—	15	*69*	30	—	1	—	3	112	115
B. rhodani Pict.	3	2	13	—	6	76	48	110	8	41	59	*65*	40	28	10	7	18	240	258
B. subalpinus Bengtss.	19	—	34	—	35	25	60	24	—	—	—	—	1	85	*43*	68	53	144	197
Cloeon simile Etn.	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	1	1
Centroptilum luteolum Müll.	—	—	4	—	21	38	38	34	—	—	*67*	*44*	17	5	2	—	4	131	135
Metretopus sp.	3	—	11	1	7	24	9	31	—	—	—	—	11	*40*	21	14	15	71	86
Ecdyonurus joernensis Bengtss. ..	6	—	9	—	—	28	—	26	—	—	—	—	—	1	24	*44*	15	54	69
Heptagenia sulphurea Müll./ *dalecarlica* Bengtss.	4	—	1	1	71	94	65	168	—	—	161	*182*	55	5	1	—	6	398	404
H. fuscogrisea Retz.	3	—	5	—	70	—	29	1	—	2	21	*84*	1	—	—	—	8	100	108
Arthroplea congener Bengtss.	7	1	5	—	—	11	4	8	—	—	—	7	*9*	13	7	—	13	23	36
Leptophlebia marginata L.	—	—	—	—	17	22	16	49	—	1	33	*43*	27	—	—	—	—	104	104
L. vespertina L.	—	—	—	—	—	2	5	2	—	—	1	7	1	—	—	—	—	9	9
Paraleptophlebia strandi Etn.	—	—	—	—	1	9	1	16	—	—	—	—	—	4	8	*15*	—	27	27
Ephemerella aurivillii Bengtss. ..	1	—	2	1	12	59	32	120	9	44	*134*	37	3	—	—	—	4	223	227
E. mucronata Bengtss.	—	—	—	—	8	18	151	27	—	—	22	*175*	7	—	—	—	—	204	204
																	532	2915	3447

spp., *Heptagenia dalecarlica, Ecdyonurus joernensis, Arthroplea congener,*[1] *Paraleptophlebia strandi, Siphlonurus aestivalis, Parameletus* sp., *Metretopus* sp., *Baetis subalpinus, B. macani* and *B. lapponicus.* On the other hand, taking into account recent nomenclatorial and taxonomical changes, the Ammarnäs species are almost without exception included in the lists from Finland (Tiensuu 1939) and the European part of the U.S.S.R. (Tchernova 1964). This points to the strong northeasterly affinity of the north Scandinavian mayfly fauna.

Fourteen of the 23(24) species on the list were obtained in 100 to 300 specimens; two were taken in more than 300 specimens, viz. *Siphlonurus lacustris* (cf. below) and *Heptagenia sulphurea/dalecarlica.* Only four species were obtained in very low numbers (less than 25 specimens). These four species are all distinctly lenitic which at least partly explains their scarcity in the material.

In the benthic samples, two species were outstandingly dominant, being present everywhere in lotic biotopes, viz. *Baetis rhodani* and *Ephemerella aurivillii,* followed by *Ameletus inopinatus, Baetis subalpinus* and *Heptagenia dalecarlica* (Ulfstrand 1968 a, p. 29). The relative dominance of the species in the benthic communities is not reflected in the material of the winged stages, although this was collected to a large extent along the same rivers from which the benthic material derives.

4.3. *Comparison between the light-trap and manual collections*

All species were taken in so low numbers in the light-traps that their presence in them seems almost accidental.

The only exception is *Siphlonurus lacustris* of which a considerable number was taken in light-trap III, viz. 89 inds. in the period of 15—22/7 1964 (probably all or most of them on a single night) and 244 on the night of 24—25/7 1964. On the latter occasion the events could be directly watched. In the afternoon of 24/7 the sun was coming out after a series of heavy showers, the air temperature rose and air humidity was very high. Suddenly large quantities of mayflies appeared over River Tjulån near the site of light-trap III, forming a longish swarm over the stream and heading upstream. All specimens netted were *S. lacustris* males. Specimens (females) taking off from the shore and moving up towards the swarm were instantly seized in the air (cf. Brinck 1957, p. 24), and mating couples fell out of the swarm and descended on the shore vegetation, where copulation was completed. This intense activity continued for hours and still went on when the moderate darkness of the subarctic summer night fell; it could not be ascertained when it ceased. In the morning the trap contained many *S. lacustris* males.

A tentative explanation of the unusual number of mayflies trapped on this occasion is that, because of particularly favourable meteorological conditions at a moment when many mayflies physiologically were ready to swarm, swarming activity became extraordinarily intense and therefore was prolonged to later hours than usually, and that the lamp became more attractive

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[1] There is a single record of this species from the British Isles. My doubts about the authenticity of this record are shared by Mr. D. E. Kimmins who agrees (in litt.) that the species had better be deleted from the British list.

under the different conditions. Yet its power was only moderate also on this occasion, to judge from the small proportion of the animals present that were eventually trapped.

It is notable that the fundamentally lenitic *S. lacustris* whose nymphs were obtained only irregularly and in small numbers in the benthic samples from lotic biotopes, was swarming over the lotic biotope. I have seen the same thing in *S. aestivalis,* another lenitic mayfly.

According to the field observations, mayflies are in Lapland diurnal animals, with maximal swarming activity in the afternoon or early evening (cf. Brinck 1957), when the air temperature is falling and the relative humidity rising. On the European continent certain species are crepuscular or even nocturnal (Brehm quoted from Brinck 1961, Verrier 1956). Tjönneland (1960) found that tropical mayflies are nocturnal and suggested that this would be favourable under the tropical climatical conditions. The heat, drought and high winds of the tropical day would be dangerous for the fragile mayfly imagines. The prevalence of diurnalism in northern latitudes fits in with this explanation. In the north mayflies often avoid the warmest hours of the day, even though swarming may be seen in strong sunlight; probably the air humidity is more important than the temperature itself. On the other hand, the very low temperatures frequently occurring in the night may operate against displacement of the activity into the dark hours. Moreover, the extraordinary development of the eyes of mayfly males suggests that these animals are basically adapted to visual orientation in space, in other words, that diurnalism probably is the original feature and nocturnalism a later adaptation.

4.4. *Sex and imago/subimago ratios*

With the exception of *Ameletus inopinatus,* subimagines were virtually absent from the light-traps. In the manual collection most species were represented by many more subimagines than imagines, although there are several exceptions. Also the sex ratio is extremely variable.

No consistent pattern is discernible. The differences observed may be explained by many factors. A longer life-span in the subimago than in the imago stage probably explains, at least partly, the dominance of subimagines in the manual collection. Shortly after emergence, mayflies are very easy to catch in numbers, but later they spread over larger areas, gathering again for swarming and egg-laying. In so short-lived animals, chance will play a large role for the composition of the catch. Thus, the extraordinary figures for *Ecdyonurus joernensis* (all 54 hand-collected specimens being subimagines) and *Heptagenia fuscogrisea* (99 out of 100 being imagines) have to be viewed in this light.

4.5. *Flight periods*

The ten-day period during which the median specimen was obtained is regarded as the peak of the flight period and has been marked out in Tab. 3. Three species have their peak in 7/II, seven in 7/III, one exactly between 7/II and 7/III, three in 8/I, one in 8/II, two in 8/III, and two in 9/I—III. The remaining species were too scarce to be so classified.

The flight periods of mayflies in Lapland, thus, generally fall in the middle of the summer. Not even the earliest ones, such as *Ameletus inopinatus* and *Ephemerella aurivillii,* can properly be called vernal. *Ecdyonurus joernensis* and *Paraleptophlebia strandi* are so late that they may be called autumnal; probably they are underrepresented in the material because of their late flight periods.

Baetis rhodani is known to have a very long flight period in various parts of its vast range, often because of its polyvoltine annual cycle (e.g. Pleskot 1961, Brinck and Scherer 1961). In the present study area its very long flight period was found to depend on different local populations having differently timed flight periods (Ulfstrand 1968 b, pp. 174, 188). There is no clear distinction between early and late species in terms of length of flight periods. All species have clearly univoltine annual cycles.

5. Stoneflies (Plecoptera)

5.1. *Taxonomical and nomenclatorial remarks*

A comparison between the taxonomy and nomenclature used by Brinck (1949) and Illies (1967) reveals the high degree of stability in these respects achieved in this group. I have followed the last-mentioned reference.

5.2. *Survey of the stonefly collection*

In Tab. 4 the stonefly collection is presented. It is made up of 6064 specimens and 25 species. The light-traps yielded 1641 stoneflies, while 4423 specimens were manually collected.

The Swedish list includes 35 species (Brinck 1949, Illies 1953 a), while the European list features 340 species, of which, however, no less than $^2/_3$ have much restricted ranges in central and south European mountain areas (Illies 1967, p. 220).

Several records are of faunistical interest. *Nemoura arctica* had previously been found only much farther to the north (Brinck op. cit., Brinck and Froehlich 1960). *N. flexuosa,* on the other hand, has only once before been taken in Lapland (Tärna, approx. 40 km SSW of Ammarnäs; sub. nom. *N. erratica* Claass., Brinck op. cit.). *Capnopsis schilleri* is known from only a small number of localities widely scattered over the country. *Dinocras cephalotes* has a distinctly southerly distribution in Sweden, but evidence is accumulating that it is a good deal commoner, and extends to higher altitudes, than previously known; the two localities in the Ammarnäs area were in and just below the subarctic *Betula* region, respectively.

The zoogeography of stoneflies has been thoroughly discussed by Illies (e.g. 1953 b, 1966). Eight of the species on the Ammarnäs list are absent from the British Isles (Hynes 1967), but some have advanced outposts in north-central Europe. The stonefly fauna of north Scandinavia therefore is not so strongly divergent from the general "European" fauna as the mayfly fauna (cf. p. 154).

Almost one third of the total catch consists of one species, *Leuctra fusca,*

Tab. 4. *The collection of stoneflies* (*Plecoptera*). Italicized figures indicate the ten-day period during which the median specimen was obtained.

	Light-trap collection		Manual collection		5 I—III	6 I	6 II	6 III	7 I	7 II	7 III	8 I	8 II	8 III	9 I	9 II	9 III	10 I—III	Total light-trap	Total manual collection	Grand total
	♂♂	♀♀	♂♂	♀♀																	
Brachyptera risi Mort.	—	—	20	8	—	—	1	7	*15*	5	—	—	—	—	—	—	—	—	—	28	28
Taeniopteryx nebulosa L.	6	9	14	86	*108*	5	2	—	—	—	—	—	—	—	—	—	—	—	15	100	115
Amphinemura borealis Mort.	32	67	106	67	—	—	—	—	9	116	*55*	51	24	14	3	—	—	—	99	173	272
A. standfussi Ris.	13	13	191	213	—	—	—	—	—	—	29	101	67	*83*	95	53	2	—	26	404	430
A. sulcicollis Steph.	2	4	46	78	—	—	—	—	*81*	15	20	12	—	—	2	—	—	—	6	124	130
Nemoura arctica Esb.-P.	—	—	—	2	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	2	2
N. avicularis Mort.	2	9	18	21	—	9	7	*11*	10	6	5	2	—	—	—	—	—	—	11	39	50
N. cinerea Retz.	8	9	14	66	—	1	—	1	6	33	*33*	20	2	1	—	—	—	—	17	80	97
N. flexuosa Aub.	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—	1
Nemurella picteti Klap.	—	1	46	33	—	—	—	2	14	*33*	11	19	—	—	—	1	—	—	1	79	80
Protonemura meyeri Pict.	—	—	14	21	—	1	5	8	*16*	4	1	—	—	—	—	—	—	—	—	35	35
Leuctra digitata Kemp.	1	1	71	77	—	—	—	—	—	—	54	*31*	36	15	9	5	—	—	2	148	150
L. fusca L.	428	684	341	468	—	—	—	—	—	2	2	27	215	301	*337*	347	342	348*	1112	809	1921
L. hippopus Kemp.	48	42	172	298	21	51	205	*76*	98	67	5	31	6	—	—	—	—	—	90	470	560
L. nigra Ol.	—	—	4	2	—	—	—	—	—	2	4	—	—	—	—	—	—	—	—	6	6
Capnia atra Mort.	5	11	168	100	*192*	25	15	15	19	11	4	3	—	—	—	—	—	—	16	268	284
C. pygmaea Zett.	11	6	37	45	*71*	—	—	1	9	8	8	—	—	1	1	—	—	—	17	82	99
Capnopsis schilleri Rost.	—	—	14	5	—	8	*6*	1	4	—	—	—	—	—	—	—	—	—	—	19	19
Arcynopteryx compacta McL.	—	—	10	15	—	12	*12*	—	1	—	—	—	—	—	—	—	—	—	—	25	25
Diura bicaudata L.	—	—	96	148	—	26	21	31	*78*	77	—	10	1	—	—	—	—	—	—	244	244
D. nanseni Kemp.	61	55	181	137	1	15	*206*	77	66	47	9	12	1	—	—	—	—	—	116	318	434
Isoperla grammatica Pod.	17	19	194	252	—	—	2	—	92	*241*	24	116	4	2	—	1	—	—	36	446	482
I. obscura Zett.	20	10	43	43	—	—	—	—	5	6	43	*33*	9	18	1	1	—	—	30	86	116
Dinocras cephalotes Curt.	—	—	128	63	—	—	—	—	—	16	*169*	6	—	—	—	—	—	—	—	191	191
Chloroperla burmeisteri Pict.	15	31	120	127	—	—	1	—	93	*94*	58	38	7	2	—	—	—	—	46	247	293
																			1641	4423	6064

* Incl. 20 inds. from first week November.

which dominates the light-trap and, though to a lesser extent, the hand-collected material. Including *L. fusca,* fourteen species were taken in more than 100 specimens. *Brachyptera risi, Nemoura arctica, N. flexuosa, Leuctra nigra, Capnopsis schilleri* and *Arcynopteryx compacta* were taken in less than 30 specimens. Of these both *Nemoura* spp. and *C. schilleri* are locally rare, while *L. nigra* and *A. compacta* are known to have large populations not far from the study area. It is difficult to see why *B. risi* should be so scarce, since the nymphs of this species were frequent at some sampling sites.

Judging from the nymphal populations on the river bottom, *Leuctra fusca* and *Diura nanseni* are the dominant stonefly species of the Ammarnäs area (Ulfstrand 1968 a, p. 29). The abundance of the former is reflected even to a disproportionate degree in the imago collection, but not that of the latter. Other abundant species in the benthic samples were relatively poorly represented in the imago collection which thus gives only a very imperfect picture of the quantitative relationships between the nymphal populations in adjacent biotopes.

5.3. *Comparison between the light-trap and manual collections*

Every species except the rare *Nemoura flexuosa* was obtained in the manual collection, while the following are absent in the light-trapped catch: *Brachyptera risi, Nemoura arctica, Leuctra nigra, Capnopsis schilleri, Arcynopteryx compacta, Diura bicaudata* and *Dinocras cephalotes.* Apart from the first-mentioned of these species, their absence is readily explained by the fact that they are more or less scarce and not at home anywhere near the trap sites.

Even if such species, which inhabit biotopes near a light-trap, usually will be trapped in a low number, it is quite clear that stoneflies are very weakly attracted by light of the quality used in these traps. This presumably depends on the fact that they are diurnal animals.

There is one notable exception, viz. *Leuctra fusca,* a large number of which was obtained in the light-traps. This species obviously is attracted by light. The most outstanding feature in its ecology is its very late flight-period. Possibly the natural light conditions in autumn, not only in terms of intensity but also of spectral composition, may render the UV lamps used in these traps more powerful in attracting the insects (cf. Verheijen 1958).

5.4. *Sex ratio*

Even closely related species show very different sex ratios. It seems impossible to analyse the reasons for this on the basis of the present material.

5.5. *Flight periods*

As seen in Tab. 4, three species had their peak in 5/I—III, three in 6/II, two in 6/III, three in each of 7/I, 7/II and 7/III, two in 8/I, one in 8/III and one in 9/I. Between themselves the species cover practically the whole ice-free period. In comparison with the mayflies (and the caddisflies, Trichoptera) the stoneflies are, as is well-known, very early: thus, eleven of the stoneflies had their peak (measured in terms of the median specimen collected) before the earliest mayfly. Only *Amphinemura standfussi* and, particularly, *Leuctra fusca* culminate in late summer and autumn. The earliest species, *Taeniopteryx nebulosa* and *Capnia* spp., emerge as soon as the first gaps in the ice appear. Not only these species, but also many others which are numerous in June, carry through their winged life including reproduction under a period of very difficult climatical conditions with frequent strong frosts.

The early species have conspicuously short flight periods. In many species there is a trail of scattered specimens, usually females, occurring long after the flight period proper of the species.

6. Discussion

6.1. *Light attraction*

Although both mayflies and stoneflies in Scandinavia are chiefly diurnal or at most crepuscular animals and basically unattracted to light, certain exceptions were found. In the mayfly *Siphlonurus lacustris,* large numbers were light-trapped on a couple of occasions only, and it seems likely that special meteorological conditions during a critical phase of the life of a large number of imagines caused a prolongation towards dusk of the swarming activity. The mayflies were consequently active in an exceptional light climate, and this, for a short period, made them "trappable".

In the stonefly *Leuctra fusca,* the attraction to light was a more consistent attribute. Possibly the late flight period caused the animals to live under light conditions which render the light sources effective and which other stoneflies only rarely experience.

The mechanism of the attraction to artificial light sources in animals is a most complex problem (Verheijen 1958). It seems worth noting that a species not usually attracted to light may become attracted on special occasions (the first-mentioned instance) and that one species may be attracted although all other species of its order within the same geographical area are unattracted (second above-mentioned instance).

6.2. *Dispersal in the winged stages*

Several species known to be absent from nearby biotopes were obtained in small or moderate numbers in the light-traps. This indicates that certain specimens had flown in to the traps from considerable distances. This would be the case in e.g. *Arthroplea congener, Metretopus* sp., *Nemoura avicularis,* and *Chloroperla burmeisteri.*

On the whole, the mobility of the winged stages of mayflies and stoneflies should not be underrated (Brinck 1949, pp. 175—179, Illies 1953 b). It is a common experience when working in Lapland to come across mayflies and stoneflies far from any suitable biotope of the species in question. They come flying with the wind over the heaths and may then easily be carried across water sheds from one drainage system to the next. Brinck and Froehlich

(1960) comment on the presence in "abnormal" biotopes of several stonefly species as a consequence of wind or water transport. Long-distance movements have been seen by myself most often in *Ameletus inopinatus, Baetis rhodani, Heptagenia sulphurea/dalecarlica, Isoperla grammatica, I. obscura* and *Capnia atra.* These species are partly or exclusively lotic, and it seems reasonable that lotic species should be particularly liable to air-borne cross-country transports in connection with their upstream movements (Roos 1957).

The very high frequency of endemic species among European stoneflies (Illies 1966) cannot be exhaustively explained with reference to their allegedly poor power of dispersal. Other circumstances have to be looked for as well.

A number of stoneflies have reduced wings, although always in one sex only, e.g. *Diura bicaudata* and *Arcynopteryx compacta.* The importance from the view-point of dispersal to retain the ability of flight in the females was pointed out by Brinck (1949). Similar views are held by Lindroth (1949, pp. 572 et seq.) for Coleoptera Carabidae. The general adaptive significance of aerial locomotion in insects was discussed in detail by Southwood (1962) and, in particular, Johnson (1966).

6.3. *Interspecific segregation mechanisms in the adult and juvenile stages*

The principally important problem of how mutual interference (competition) between species living together is prevented has been discussed for the lotic community by e.g. Illies (1952) and Macan (1958) who considered the possible role of differences in flight periods. It seems reasonable that the comparatively species-poor rhithron communities may provide a particularly suitable basis for such analysis, and the comparative approach, using unregulated as well as regulated stream sections, has much to recommend itself (cf. Grimås and Nilsson 1965, Grimås 1967).

A glance at Tab. 3 shows that the flight periods of a number of mayfly species deriving from similar biotopes and including congeneric species groups overlap widely. The most species-rich genus is *Baetis* of which six species were obtained in considerable numbers. Two of them, viz. *B. fuscatus* and *B. subalpinus,* have later flight periods than the rest. Still, however, they overlap partly with the other four, which have largely simultaneous flight periods. The interspecific differences in terms of microhabitat distribution of the nymphs were discussed elsewhere (Ulfstrand 1968 a, pp. 32—33). Siphlonurids, ephemerellids and heptageniids also overlap more or less broadly.

Tab. 4 shows that the position is similar in the stoneflies. It is true that *Leuctra fusca* is largely, if not wholly, isolated in time from other *Leuctra* spp., but the general pattern is one of wide temporal overlapping of the flight periods of the different species.

Thus, only traces of temporal interspecific segregation of the winged stages may be found in the Ammarnäs fauna of mayflies and stoneflies. On the other hand, Illies (1952) showed very clearly the existence of such segregation (temporal succession) in his central European study area. He is of the opinion that this feature has been evolved as a response to the need for interspecific sexual isolation.

Interference between species (competition), in amphibiotic insects, may occur during two very distinct life phases, viz. in the nymphal and winged stages. These insects are, during their lives, members of two completely separate communities. Interspecific segregation is imperative in both cases. It is conceivable that the selective pressures during the two phases might conflict.

Disregarding the cases of microptery and brachyptery among stoneflies, it is obvious that amphibiotic insects are much more mobile in their winged than in their juvenile aquatic stages. Therefore spatial isolation between the imagines of different species is difficult to achieve and uphold. Small-scale habitat differences are not sufficient to prevent imagines of different species to meet. Thus, it seems probable that interspecific isolation between the sexual stages would be much more easily achieved through differences in the timing of the flight period than in habitat distribution.

In nymphs, on the other hand, even small-scale interspecific differences in habitat might preclude interference with respect to e.g. food requirements, to mention a factor likely to play an important role in nymphal ecology. Because of the small range of routine movements of the nymphs (cf. Allen 1959), it is possible for two or more species to avoid competitive interference through evolving small-scale differences in biotope requirements, such as, for example, current, substrate, light or temperature (e.g. Scherer 1965, Thorup 1966, Oláh 1967, Ulfstrand 1967, Madsen 1968, Egglishaw 1969). This will lead to differentiation in their utilization of the food resources. If the nymphs are transported over a more or less considerable distance by organic drift (Müller 1954 and other works), the interspecific habitat segregation may be rapidly restored at the new site (Ulfstrand 1968 a, pp. 94—99).

While overlapping of the flight periods is seen to be frequent, an examination of the pattern in the benthic community in which the nymphs live suggests that the nymphs usually are segregated in terms of microhabitat differences, sometimes with temporal separation as an auxiliary mechanism (e.g. Svensson 1966). This was discussed in more detail elsewhere. It is reasonable that the nymphal populations require a clear interspecific separation. Nymphs are long-lived; in the Ammarnäs area, all species spend at least one year in the benthos before emerging, with quite a few having still longer life cycles (Ulfstrand 1968 b). During this time they have to feed actively and grow, obviously using up much energy. Prevention of interspecific interference in the exploitation of the food resources would therefore seem imperative (cf. Macan 1962).

Not at all so during the winged stages. These usually are short-lived, although some stoneflies have been found exceptionally to live for up to 84 days (Khoo 1964). They ingest little or no food; those that do feed seem to have small and unspecified nutritional requirements and make use of resources that are very unlikely to occur in short supply (Hynes 1942, Brinck 1949, pp. 165—167). In this stage, therefore, the selective pressure for segregation is based solely on the importance of avoiding interspecific matings (cf. Mayr 1963, pp. 89 et seq.).

Recently the significance of a behavioural mechanism for the prevention of hybridization in stoneflies has been elucidated by Rupprecht (1969). Several setipalpian species were found to possess highly species-specific precopulatory displays. This would seem to be a most effective means to this end and will no doubt be found in many other aquatic insects so far not examined in this respect. The existence of such a mechanism reduces the urgency for other kinds of interspecific barriers during the sexual stage.

Against this background, therefore, temporal segregation, when present, seems to have been evolved primarily to assist in reducing interspecific interference during the nymphal life stage with its manifold demands on various resources, rather than as a means of sexual isolation. In other words: it is a product of competitive factors in the benthic rather than in the terrestrial/aerial community.

Thus, the flight period of a given species may be determined by conditions in the benthic biotope rather than by factors operating during the adult life. In other words, interspecific differences in flight periods may be by-products from selective processes during the juvenile stages. This, of course, cannot be carried too far. It is, for instance, obvious that the flight periods of northern insects cannot fall at any time of the year. Because of the climate they will be restricted to a certain period. Not only is emergence impossible during the period of ice cover, but also the climatical conditions for some time after the break-up of ice are too adverse for many insect species.

6.4. *Nutritional factors, stenothermy and flight periods*

Still, some species carry through their aerial stage immediately after the break-up of ice, particularly a number of stoneflies. It is frequently held that stoneflies are strictly cold-stenothermous animals and that this is an exhaustive explanation for their main growth period being placed in winter. However, as discussed elsewhere, the nutritional conditions probably are also highly important (Ulfstrand 1968 a, pp. 104—107). As detritus consuments, filipalpian stonefly nymphs find food most abundant between the autumnal leaf-shed of the terrestrial vegetation (cf. Kaushik and Hynes 1968) and the vernal high flow which removes much of the detritus. That cold-stenothermy is only part of the truth is suggested by the fact that some northern stoneflies have a different annual cycle growing in summer and emerging towards autumn. In the present area this is seen most clearly in *Leuctra fusca* but also, although less extremely, in *Amphinemura standfussi*. Such cases prove that stoneflies, as a group, are not immutably cold-stenothermous; if other selective forces press for a displacement of the growth period to a warmer part of the year, there are no unchangeable physiological properties preventing such a change taking place (cf. Sheldon and Jewett 1967). This is not to say that early emergence per se cannot have a positive value. Possibly, for example, synchronization is more effectively accomplished when emergence follows directly upon ice break-up (cf. Corbet 1964). Temperature levels may be utilized as proximate time cues for the timing of the annual cycle (cf. Minshall and Minshall 1966), even though the ultimate factor determining its pattern may be related to competitive and/or nutritional conditions.

Again, the much later flight periods of mayflies in comparison with stoneflies may be at least partially explicable in terms of nutritional rather than thermal conditions. A great many mayfly nymphs graze periphytic algae which are, because of the light conditions, most productive in the ice-free part of the year (cf. Kownacka and Kownacki 1968). Consequently, it would seem advantageous for these animals to have their main growth period in summer, and incidentally the flight period will be later than the stoneflies.

6.5. *Conclusion*

Although stoneflies, as a group, are earlier than mayflies, the flight periods of each of the two groups in fact cover a very large part of the ice-free period. Generalizations about the significance of reaction to abiotic factors, food habits and other ecological properties of whole groups of animals composed of, as in the present cases, twenty or more species, are legitimate only under full appreciation of all the interspecific differences which are a prerequisite for the co-existence of the several species in the community. The above discussion tries to emphasize that competitive and nutritional factors are among the important elements in the rhithron community ecology, a fact the significance of which is frequently underestimated in comparison with the importance attached to thermal and other abiotic factors.

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