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# Microdistribution of benthic species (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae) in Lapland streams

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## Abstract

At three localities in central Swedish Lapland (approx. 66°N, 16°E), areas of stream bottom were mapped with regard to depth, current and substrate conditions, and the benthic fauna of Ephemeroptera, Plecoptera, Trichoptera and Diptera Simuliidae was sampled in spring and autumn. The three environmental factors were found to be variously associated with each other, three combinations being dominant. The distribution of the benthic species was compared with these combinations, and it was found that most species showed a significant over-representation at sites characterized by one of these complexes. An attempt was made to establish which of the three factors was the most important for the different species. This analysis was complicated by the association between the environmental factors, but certain conclusions could be drawn from interspecific comparisons. Substrate is an especially important determinant of the life conditions of the fauna; besides other functions it usually has to provide food for the animals. Benthic species select their habitats on the basis of factor combinations, rather than isolated factors; in this interplay of environmental factors food was found to have a dominant influence in the biotope investigated.

## Резюме

В трех местообитаниях центральной Шведской Лапландии (примерно 66° с.ш. и 16° в.д.) участки с придонным течением картированы; указаны глубина, течения и характер субстрата. Весной и осенью исследовалась бентосная фауна *Ephemeroptera, Plecoptera, Trichoptera* и *Diptera-Simuliidae.* Три изученные фактора среды тесно связаны между собой. В исследованных точках выделено три типа местообитаний, различающихся комплексом условий существования. Изучение распределения бентосной фауны показало, что большинство видов приурочено к участкам с одним определенным комплексом условий. Исследовалось значение отдельных факторов среды для разных видов. Эти исследования осложняются тем, что все факторы среды тесно связаны между собой. Однако при сравнении распределения отдельных видов можно сделать определенные заключения о значении тех или иных условий. Субстрат – особенно важный детерминат жизненных условий беспозвоночных. Наряду с другими функциями, он обычно является источником жизни для животных. Местообитания бентосных видов определяются комбинацией факторов среды в большей степени, чем влиянием каждого фактора в отдельности. В этих комбинациях пищевые ресурсы играют особенно важную роль в исследованных местообитаниях.

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## 1. Introduction

Most students of the benthic fauna of running waters comment on the uneven distribution of the animals over the stream floor. Some general implications of this feature were discussed by Allen (1959). Needham and Usinger (1956) examined the variation between different sites within a small part of a riffle but did not analyse the possible causes of the differences. Percival and Whitehead (1929) made an early study in this general direction but were seriously hindered by taxonomic difficulties. Thorup (1966) published a valuable study on the detailed distribution of benthic animals in springs and spring trickles. Within a narrower taxonomic frame, microdistribution in lotic biotopes has been studied by e.g. Scott (1958), paying special attention to the significance of current and food on caddisfly distribution, and by Cummins (1964) who attempted to correlate the distribution of two American lotic limnephilid caddisflies with substrate, current and food conditions. Most authors have, however, restricted their attention to one factor only or have compared relatively large river sections with one another; reviews have been published by e.g. Macan (1961, 1962, 1963) and Cummins (1966).

The patchy distribution of the animals on the stream bottom may depend on either or both of two independent sets of factors. First, the distribution of the animals may reflect the heterogeneous distribution of some environmental factor. Second, the animals may have an uneven dispersion pattern of their own. For example, young larvae and nymphs are often found in aggregations as a consequence of the eggs having been deposited in clumps.

In this paper an attempt will be made to find out if and to what extent the microdistribution of the more numerous inhabitants of certain lotic biotopes conforms to that of certain environmental factors.

In this paper the terms "biotope" and "habitat" are used in the meanings given them by Macan (1963).

Several of the factors known to have or suspected of having an influence on the life conditions and distribution of the benthic species may be disregarded when microdistribution is being studied. Thus, within an area of a few square metres, temperature and chemical composition of the water may be considered uniform. Further, in a stream with fast current, strong turbulence, low temperature and practically no oxygen-consuming vegetation nor bottom deposits, it may be regarded as extremely improbable that oxygen is ever seriously deficient (cf. Eriksen 1966). Oxygen content in the free water layers of the streams investigated was found by Ulfstrand (in ms.) to be constantly around saturation; frequently slight supersaturation was recorded. This refers to summer conditions. The water of the boundary layer with strongly reduced current speed as well as the so-called dead-waters undoubtedly are in exchange with water masses holding fresh supplies of oxygen (cf. Ambühl 1959, 1962, Jaag and Ambühl 1964). It is, therefore, concluded that local differences in oxygen content of the water cannot be regarded as a factor of significance for the microdistribution of benthic animals in lotic biotopes of the kind discussed here (cf. Philipson 1954). Neither could differences in light conditions be of any importance, since the bottom areas investigated were not shaded by land vegetation (cf. Scherer 1962, Thorup 1966, Hughes 1966).

On the other hand, certain factors vary widely within very small distances, particularly water depth, current and substrate. It is therefore these factors with which we are at present concerned.

## 2. Study area, methods, material and taxonomy

The study area, situated at approx. 66° N. lat. and 16° 15′ E. long., is centred upon the small village of Ammarnäs in central Swedish Lapland; its environmental conditions have been described by Ulfstrand (in ms.) The area is situated on the border between the high-boreal and subarctic zones at altitudes ranging from 380 to 600 m above sea level on the eastern slope of the Caledonian mountain chain.

The present investigations were carried out in Vindelälven and its tributary Tjulån. These are rivers characterized by fast current, low temperatures, high oxygen contents and mainly stony bottoms.

The localities at which this work was carried out were called locs. B (Tjulån), D (a small stream between two lakes in the Tjulån system) and K (Vindelälven). The position

Figs. 1 to 6. Maps of sampling localities. Figures in circles show sampling sites. Figures without circles show water depth between depth contours. The current pattern is indicated by the orientation of the flow symbols.

o = negligible current speed
⚲ = current < 25 cm/s
⚲ = current 25 – 50 cm/s
⚲ = current 50 – 75 cm/s
⚲ = current > 75 cm/s

⁘ = substrate made up of naked stones
░ = substrate made up of silt
■ = substrate made up of detritus

Loc. B 31/5 1964

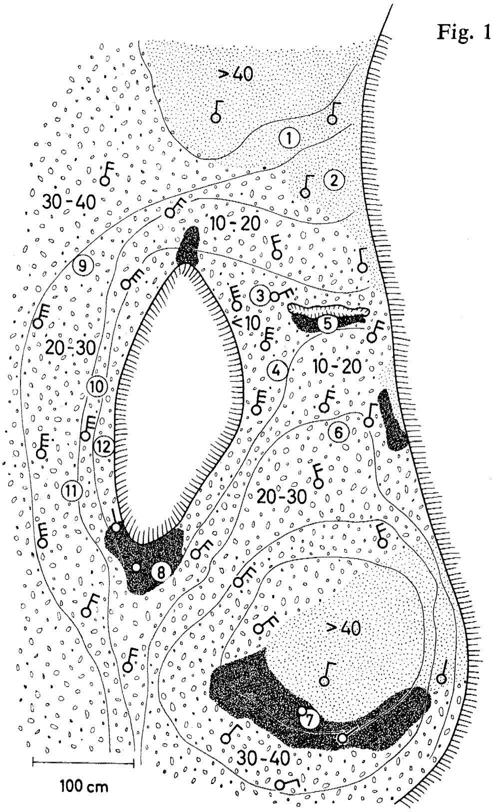


Fig. 1

Loc. B 16/8 1964

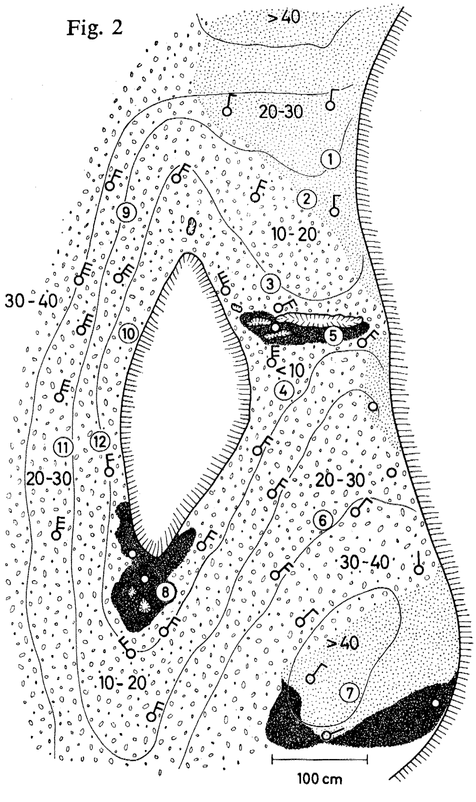
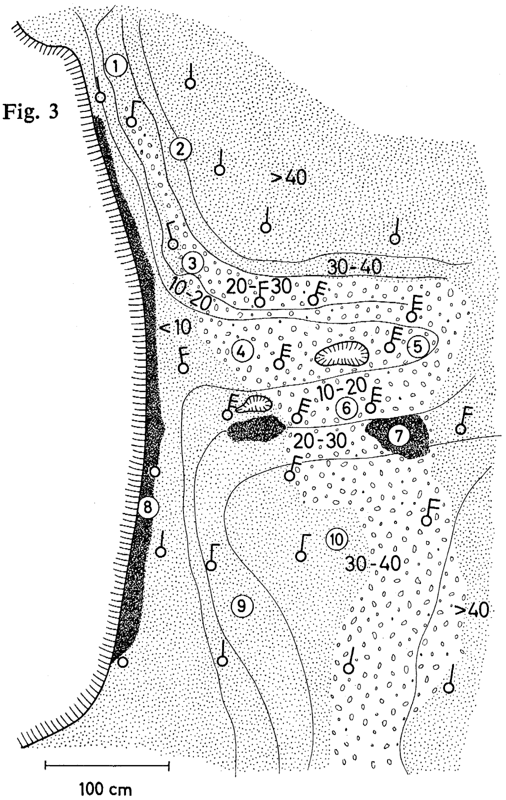


Fig. 2

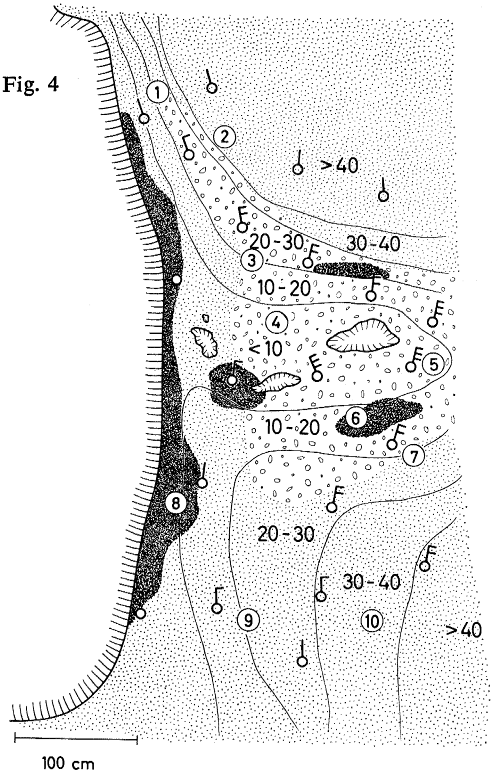
Loc. D 4/6 1964

Fig. 3



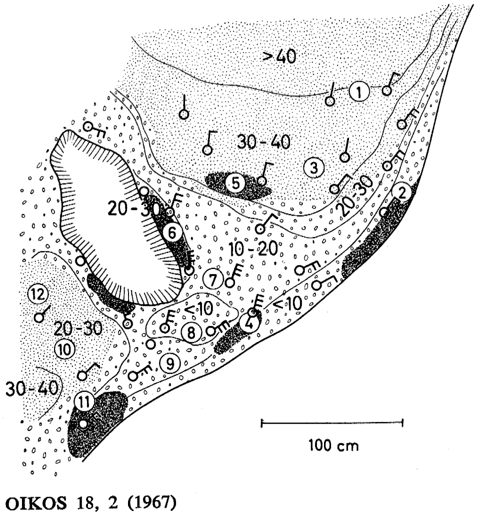
Loc. D 10/9 1964

Fig. 4



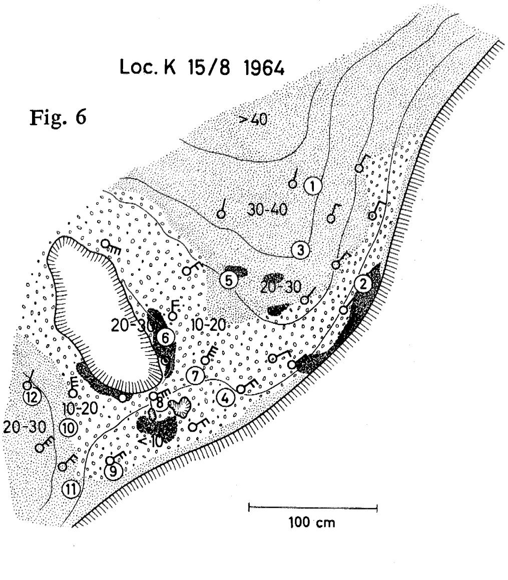
Loc. K 24/5 1964

Fig. 5



Loc. K 15/8 1964

Fig. 6



of the localities is shown on a map in Ulfstrand (in ms.) where they are also described in further detail.

For the present purpose a small area of the stream bottom was selected and mapped as accurately as possible with regard to water depth, current and substrate (Figs. 1 to 6). The current speed was measured by means of an Ott propeller held at 5 cm above the bottom. The substrate was classified into three categories, viz. 1) naked stones, 2) stones covered by a thin layer of silt and sometimes partly imbedded in sand or gravel, and 3) stones partly or wholly covered by detritus deposits mainly consisting of rotting litter from the terrestrial vegetation. Small tufts of the colonial diatom *Didymosphenia geminata* and aquatic moss were present.

The localities were sampled in late May to early June (spring samples) and again in August to September (autumn samples). The samples were taken on days with comparable water levels, but certain differences between the two sampling occasions were unavoidable. Therefore, the maps had to be re-made on the second occasion.

On each sampling locality ten or twelve samples were taken. Each sample consisted of one to three stones of a total surface area of $200 \pm 20$ cm$^2$. A net of the dimensions 85 × 65 cm and 18 meshes/cm was pressed against the bottom downstream of the stones to be removed. Those animals releasing their hold on the stones, as well as variable amounts of detritus, silt and sand, were caught in the net. The stones were placed in a bucket and were examined together with the contents of the net on the shore. The animals were preserved in 70% ethanol. The total macroscopic fauna was collected, but in this study only the mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera) and blackflies (Diptera: Simuliidae) are taken into account. The entire material of these groups amounts to 5173 specimens.

Taxonomically, Limnofauna Europaea (Illies 1967) is followed in all cases with the exception that *Ameletus alpinus* Bgtn. is merged with *A. inopinatus* Etn. Moreover, the generic name *Synafophora* is not accepted for what is here called *Glossosoma intermedium* Klap. (= *Mystrophora intermedia*).

The larvae belonging to the genus *Apatania* could not be identified specifically. In view of the flight-periods of these species and of the exclusive findings of *A. wallengreni* pupae before midsummer and of *A. stigmatella* pupae after midsummer, it seems safe to regard all *Apatania* larvae from the spring samples as belonging to the former species and those from the autumn samples to the latter.

## 3. Environmental conditions

*a) Classification.* – The environmental factors were codified as follows:

| | |
|---|---|
| depth < 20 cm (shallow water) .......... | *a* |
| " > 20 cm (deep water) ............ | *b* |
| current speed < 25 cm/s (weak current) .. | *c* |
| " " 25–75 cm/s (moderate current)................ | *d* |
| " " > 75 cm/s (fast current) ... | *e* |
| substrate made up of naked stones ........................ | *f* |
| substrate made up of stones covered by a thin layer of slit.... | *g* |
| substrate made up of stones covered by detrius ............. | *h* |

A sampling site can thus be short-hand described using a combination of these letters. Such combinations have been entered in Tabs. 2 to 4 and 6 to 8.

Silt is here used to indicate a fine fraction of mixed origin with no organic particles recognizable macroscopically. Two samples from June, 1967, contained 4 and 6% organic matter. The mineral particles were almost exclusively in the size ranges below 0.2 mm.

Detritus is used to denote very incompletely decomposed vegetable litter of allochthonous origin, with leaves and twigs still fully recognizable.

On the naked stones neither silt nor detritus were to be found, but they were partly covered by periphytic algae, especially diatoms.

*b) Association between depth, current and substrate conditions.* – As might be expected these environmental factors are partially

Tab. 1. Association between depth, current and substrate conditions according to the classification explained on p. 297.

Spring

| | c | d | e | f | g | h |
|---|---|---|---|---|---|---|
| a | 1 | 4 | 10 | 10 | 0 | 5 |
| b | 5 | 12 | 2 | 4 | 10 | 5 |

| | f | g | h |
|---|---|---|---|
| c | 0 | 4 | 2 |
| d | 2 | 6 | 8 |
| e | 12 | 0 | 0 |

Autumn

| | c | d | e | f | g | h |
|---|---|---|---|---|---|---|
| a | 1 | 9 | 7 | 10 | 2 | 5 |
| b | 4 | 10 | 3 | 5 | 10 | 2 |

| | f | g | h |
|---|---|---|---|
| c | 0 | 2 | 3 |
| d | 5 | 10 | 4 |
| e | 10 | 0 | 0 |

Total

| | c | d | e | f | g | h |
|---|---|---|---|---|---|---|
| a | 2 | 13 | 17 | 20 | 2 | 10 |
| b | 9 | 22 | 5 | 9 | 20 | 7 |

| | f | g | h |
|---|---|---|---|
| c | 0 | 6 | 5 |
| d | 7 | 16 | 12 |
| e | 22 | 0 | 0 |

associated with one another. This was examined by means of association grids where the degree of association between the three factors was quantified (Tab. 1).

From the grids it can be seen that certain combinations of factors are particularly frequent. Water depth is less strongly associated with the other two factors than these are between themselves. It was decided, therefore, to ignore depth conditions in the first analysis. Further, it seems ecologically legitimate, as well as being statistically very desirable, to unite the two lowest categories of current speed. Consequently the following factor combinations emerge:

I: *aef* + *bef*
II: *adg* + *bdg* + *bcg*
III: *adh* + *bdh* + *ach* + *bch*

These factor complexes differ with respect to current conditions (I vs. II + III) and in substrate conditions (I vs. II vs. III).

Among the spring samples 12 are of type I, 10 of type II and 10 of type III, whilst two fall outside all three types. In autumn the corresponding figures are 10, 12 and 7, respectively, which leaves five sites outside the categories.

The first task is to analyze the distribution of the species in relation to these three factor combinations, which prevail over most of the bottom and which obviously make up environmental complexes of ecological importance.

## 4. Distribution of species in relation to main combinations of environmental factors

*a*) *Statistical procedure.* – It was investigated whether the individuals of any given species were randomly distributed between the sampling sites, or whether significantly different numbers than expected on random basis were present on sites characterized by a certain factor combination. The probability of the distribution being random was estimated using $\chi^2$ analysis. When the probability was low, this was taken to indicate that the factor complex in question exerted a significant influence of the species. The factor combinations were thus examined in pairs. Spring and autumn samples were treated separately.

*b*) *Spring samples.* – The preferences of the species obtained in the spring samples (Tabs. 2 to 4) for the different factor combinations are summarized in Tab. 5. Nine species significantly preferred type I, three species type II and seven species type III. Two species showed no significant preference for type II compared with type III but avoided type I. One species showed no preference for type I compared with III but avoided type II.

Of the species making type I their first choice, all made type III their second choice or did not distinguish between types II and III.

Only three species exhibited a significant preference for type II, and in one of these, *Polycentropus flavomaculatus*, the significance was questionable. The other two species, viz. *Ephemerella mucronata* and *Chloroperla burmeisteri*, were only locally distributed in lotic biotopes within the study area (Ulfstrand in ms.). Specimens of these two species were often covered with inorganic particles when found in the net and obviously require at least a partially soft substrate. It is quite possible that their main distribution falls out-

Tab. 2. Samples from loc. B, 31 May 1964. Site description is explained in text (p. 297).

| Sample no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site description | bdg | bdg | aef | aef | adh | bdf | bch | adh | bef | aef | bef | aef | |
| *Ameletus inopinatus* Etn. | – | – | 16 | 12 | 1 | – | – | 1 | 20 | 37 | 44 | – | 131 |
| *Baetis rhodani* Pict. | – | – | 29 | 41 | 10 | 10 | 2 | 6 | 49 | 77 | 36 | 2 | 262 |
| *Baetis* sp. | 15 | 7 | 1 | – | – | 17 | 27 | 6 | 4 | 2 | – | – | 79 |
| *Ephemerella aurivillii* Bgtn. | 2 | 9 | 6 | – | 12 | 6 | 1 | 3 | 15 | 3 | – | – | 57 |
| *Heptagenia dalecarlica* Bgtn. | 6 | 3 | 1 | – | – | 1 | – | 4 | 5 | 6 | – | – | 26 |
| *Brachyptera risi* Mort. | 2 | 2 | – | – | 2 | 1 | – | 1 | – | – | – | 4 | 12 |
| *Amphinemura borealis* Mort. | – | 1 | – | – | 9 | – | 14 | 17 | – | – | – | – | 41 |
| *Nemoura cinerea* Retz. | 2 | – | – | – | – | – | 2 | – | – | – | – | – | 4 |
| *Leuctra hippopus* Kemp. | 9 | 5 | – | 13 | 16 | 2 | 17 | 9 | – | 2 | – | 19 | 92 |
| *Capnia atra* Mort. | – | 2 | 4 | 7 | – | 8 | – | 1 | – | – | 2 | 9 | 33 |
| *Diura nanseni* Kemp. | – | – | 9 | 19 | 3 | 1 | – | 1 | 16 | 14 | 10 | 14 | 87 |
| *Isoperla grammatica* Poda. | – | 2 | – | 1 | 8 | 12 | 9 | 16 | – | – | 2 | – | 50 |
| *Polycentropus flavomaculatus* Pict. | 4 | – | – | – | – | 11 | – | – | – | – | 1 | – | 16 |
| *Rhyacophila nubila* Zett. | – | – | 10 | 6 | 1 | 1 | – | 1 | 9 | 21 | 10 | 2 | 61 |
| *Glossosoma intermedium* Klap. | – | – | 14 | 14 | – | 5 | – | – | 28 | 9 | 1 | 1 | 72 |
| *Apatania wallengreni* McL. | – | 6 | 2 | – | 9 | 4 | 10 | 14 | 1 | 2 | – | 12 | 60 |
| *Potamophylax stellatus* Curt. | 9 | 1 | – | – | 6 | 2 | 16 | 2 | – | – | – | 12 | 48 |
| *Prosimulium hirtipes* Fries. | – | – | 27 | 40 | – | – | – | – | 55 | 70 | – | – | 192 |
| *Cnephia fuscipes* Fries. | – | – | 80 | 75 | 5 | – | – | – | – | 10 | – | – | 170 |
| *Odagmia monticola* Friedr. | – | – | – | – | 5 | – | – | 2 | – | – | – | – | 7 |
| | 49 | 38 | 199 | 228 | 87 | 81 | 98 | 84 | 202 | 253 | 106 | 75 | 1500 |

Tab. 3. Samples from loc. D, 4 June 1964. Site description explained in text (p. 297).

| Sample no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Site description | bcg | bcg | bdf | aef | aef | aef | bdh | ach | bdg | bdg | |
| *Siphlonurus lacustris* Etn. | 5 | 5 | 2 | – | – | – | – | 4 | – | – | 16 |
| *Ameletus inopinatus* Etn. | – | – | 9 | 15 | 33 | 11 | 12 | – | 1 | 1 | 82 |
| *Baetis pumilus* Burm. | – | – | – | 2 | 2 | – | 13 | – | – | – | 17 |
| *Baetis rhodani* Pict. | – | – | 12 | 29 | 17 | 40 | 38 | – | 2 | 1 | 139 |
| *Baetis* sp. | 5 | 3 | 19 | 5 | – | 3 | 19 | 2 | 26 | 18 | 100 |
| *Ephemerella aurivillii* Bgtn. | – | – | 4 | 2 | – | 13 | 15 | – | – | – | 34 |
| *Ephemerella mucronata* Bgtn. | 3 | 11 | 3 | – | – | – | 1 | – | 9 | 6 | 33 |
| *Heptagenia dalecarlica* Bgtn. | – | 1 | 4 | 8 | 13 | 10 | 3 | – | 3 | – | 42 |
| *Brachyptera risi* Mort. | 3 | 1 | 6 | 1 | – | – | 1 | 4 | 3 | – | 19 |
| *Leuctra hippopus* Kemp. | 6 | – | 16 | 11 | 8 | – | 18 | 13 | – | – | 72 |
| *Capnia atra* Mort. | 1 | – | 18 | – | 1 | – | 2 | 3 | – | 4 | 29 |
| *Diura nanseni* Kemp. | – | – | – | 9 | 18 | 8 | 4 | 10 | – | – | 49 |
| *Isoperla grammatica* Poda. | – | – | 5 | 3 | 1 | 2 | – | – | – | – | 11 |
| *Polycentropus flavomaculatus* Pict. | – | 6 | 15 | 9 | 4 | 4 | – | – | – | 7 | 45 |
| *Apatania wallengreni* McL. | – | 5 | 13 | – | 4 | – | 17 | – | 2 | 4 | 45 |
| *Potamophylax stellatus* Curt. | 4 | – | 1 | – | – | – | – | 4 | – | – | 9 |
| *Prosimulium hirtipes* Fries. | – | – | – | 86 | 64 | 21 | – | – | – | – | 171 |
| *Cnephia fuscipes* Fries. | – | – | – | 31 | 47 | – | 5 | – | – | – | 83 |
| *Odagmia ornata* Meig. | – | – | 9 | 2 | – | – | 5 | – | 2 | – | 18 |
| | 27 | 32 | 136 | 213 | 212 | 112 | 153 | 40 | 48 | 41 | 1015 |

Tab. 4. Samples from loc. K, 24 May 1964. Site description explained in text (p. 297).

| Sample no.<br>Site description | 1<br>bcg | 2<br>adh | 3<br>bdg | 4<br>adh | 5<br>bdh | 6<br>bdh | 7<br>aef | 8<br>aef | 9<br>aef | 10<br>bdg | 11<br>bdh | 12<br>bcg | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ameletus inopinatus* Etn. | – | 6 | 1 | 15 | – | 29 | 36 | 35 | 20 | – | – | 4 | 146 |
| *Baetis rhodani* Pict. | – | 6 | – | 20 | 19 | 47 | 36 | 14 | 29 | 2 | 10 | – | 183 |
| *Ephemerella aurivillii* Bgtn. | – | 2 | 4 | 8 | 9 | 13 | 6 | – | 10 | – | 16 | – | 68 |
| *Ephemerella mucronata* Bgtn. | 8 | – | 14 | – | 4 | – | – | – | – | 8 | 6 | – | 40 |
| *Heptagenia dalecarlica* Bgtn. | 2 | – | 1 | 4 | – | – | 9 | 6 | 6 | 1 | – | – | 29 |
| *Brachyptera risi* Mort. | – | 2 | – | – | – | – | – | – | – | – | – | – | 2 |
| *Amphinemura borealis* Mort. | – | – | – | – | 6 | 4 | – | – | – | – | 5 | – | 15 |
| *Amphinemura sulcicollis* Steph. | – | 6 | – | – | 1 | – | – | – | – | – | – | – | 7 |
| *Nemoura avicularis* Mort. | 1 | – | – | 2 | 1 | – | – | – | – | – | 2 | – | 6 |
| *Nemoura cinerea* Retz. | 2 | 4 | – | – | – | – | – | – | – | – | 2 | – | 8 |
| *Protonemura meyeri* Pict. | 15 | 2 | 10 | – | – | – | – | – | – | 19 | 15 | 6 | 67 |
| *Leuctra hippopus* Kemp. | 1 | 10 | 5 | 13 | 16 | 2 | – | – | 17 | 1 | 9 | 1 | 75 |
| *Capnia atra* Mort. | 1 | – | – | – | – | – | – | – | 8 | – | – | – | 9 |
| *Capnopsis schilleri* Rost. | 1 | – | – | – | – | – | – | – | – | – | – | – | 1 |
| *Diura nanseni* Kemp. | – | 12 | – | 8 | – | 13 | 9 | 9 | 4 | – | – | 2 | 57 |
| *Isoperla grammatica* Poda. | 6 | 9 | 9 | 16 | – | – | – | – | 1 | 4 | 9 | 1 | 55 |
| *Chloroperla burmeisteri* Pict. | 16 | 4 | 15 | – | – | 5 | 1 | – | – | 8 | – | 1 | 50 |
| *Arctopsyche ladogensis* Kol. | – | – | – | – | – | – | – | – | – | 2 | – | 1 | 3 |
| *Polycentropus flavomaculatus* Pict. | 12 | – | – | – | – | – | – | – | 1 | 1 | – | – | 14 |
| *Rhyacophila nubila* Zett. | – | 3 | – | – | 2 | 6 | 6 | 1 | 3 | 1 | 5 | – | 27 |
| *Apatania wallengreni* McL. | – | 1 | 5 | – | 2 | – | 1 | – | 16 | 1 | 12 | 4 | 42 |
| *Potamophylax stellatus* Curt. | – | 7 | – | 2 | – | – | – | – | – | – | 10 | 4 | 23 |
| *Prosimulium hirtipes* Fries. | – | – | – | – | – | – | – | 80 | – | – | 10 | – | 90 |
| *Cnephia fuscipes* Fries. | – | – | – | – | – | – | 2 | 20 | – | – | 13 | – | 35 |
| *Odagmia ornata* Meig. | – | – | – | – | 4 | 2 | 20 | – | – | – | – | – | 26 |
| | 65 | 74 | 64 | 88 | 64 | 121 | 126 | 165 | 115 | 48 | 124 | 24 | 1078 |

Tab. 5. Distribution of species on the three site types, based on spring samples. Statistical significance of preference indicated by asterisks: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Bracketed figures show number of individuals.

| type I | type II | type III |
|---|---|---|
| *Ameletus inopinatus**** (350) | ←—— *Baetis* sp.*** (143) ——→ | |
| *Baetis rhodani**** (562) | *Ephemerella mucronata**** (70) | *Ephemerella aurivillii** (149) |
| *Heptagenia dalecarlica**** (92) | ←—— *Brachyptera risi** (26) ——→ | |
| *Capnia atra**** (45) | *Chloroperla burmeisteri**** (50) | *Amphinemura borealis**** (56) |
| *Diura nanseni**** (192) | *Polycentropus flavomaculatus** (49) | *Protonemura meyeri**** (67) |
| *Rhyacophila nubila**** (87) | | *Leuctra hippopus**** (221) |
| *Glossosoma intermedium**** (67) | | *Isoperla grammatica**** (97) |
| *Prosimulium hirtipes**** (453) | | *Apatania wallengreni**** (130) |
| *Cnephia fuscipes**** (288) | | *Potamophylax stellatus**** (77) |

| types I + III |
|---|
| *Odagmia monticola* + *O. ornata**** (42) |

scarce species:

*Siphlonurus lacustris, Baetis pumilus, Amphinemura sulcicollis, Nemoura avicularis, Nemoura cinerea, Capnopsis schilleri, Arctopsyche ladogensis* side the biotope range investigated. Both species were entirely absent from type I sites. *P. flavomaculatus* was entirely absent from type III bottoms.

Of the species preferring type III some were equally sparse in II and I. *Ephemerella aurivillii*, however, only slightly preferred type III to I but was almost entirely absent from II. *Protonemura meyeri*, on the other hand, avoided type I. *Leuctra fusca* showed a very distinct preference for type III over I and equally clearly for type I over II. *Isoperla grammatica* made type II its second choice and was strongly under-represented in type I. Neither *Apatania wallengreni* nor *Potamophylax stellatus* made any differentiation between types I and II but significantly preferred type III.

Tab. 6. Samples from loc. B, 16 August 1964. Site description explained in text (p. 297).

| Sample no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site description | bdg | adg | aef | aef | adh | bdf | bch | adh | bef | aef | bef | adf | |
| *Baetis lapponicus* Bgtn. | – | – | 10 | 12 | – | – | – | – | 8 | 2 | 5 | – | 37 |
| *Baetis pumilus* Burm. | – | 2 | 2 | 5 | 2 | – | 2 | – | – | 6 | 1 | – | 20 |
| *Baetis fuscatus* L. | – | – | 9 | 26 | – | 17 | – | – | 35 | 9 | 21 | 6 | 123 |
| *Baetis rhodani* Pict. | – | – | 2 | 6 | – | – | – | – | – | 3 | – | – | 11 |
| *Baetis subalpinus* Bgtn. | – | – | – | – | 13 | 20 | 7 | 5 | 1 | – | 10 | 16 | 72 |
| *Baetis* sp. | 16 | 30 | 2 | – | 10 | 6 | 17 | 15 | – | – | – | 1 | 97 |
| *Ephemerella aurivillii* Bgtn. | 14 | – | – | – | 1 | – | 18 | – | – | – | – | – | 33 |
| *Heptagenia dalecarlica* Bgtn. | – | – | 7 | 2 | – | 1 | 7 | 2 | 5 | 10 | 3 | 1 | 38 |
| *Amphinemura standfussi* Ris | 1 | – | – | – | 12 | 1 | 16 | 10 | – | 1 | – | 2 | 43 |
| *Leuctra fusca* L. | – | 8 | 13 | 2 | 19 | 6 | 12 | 15 | 4 | 8 | 2 | 21 | 110 |
| *Diura nanseni* Kemp. | – | – | 2 | 4 | – | – | – | – | 4 | 1 | – | – | 11 |
| *Polycentropus flavomaculatus* Pict. | – | – | 1 | – | – | 3 | – | – | 2 | – | – | – | 6 |
| *Rhyacophila nubila* Zett. | – | – | 1 | 3 | – | – | – | 1 | – | – | – | – | 5 |
| *Apatania stigmatella* Zett. | 6 | 6 | 1 | 3 | – | 11 | – | 1 | 4 | 14 | 17 | 12 | 75 |
| *Odagmia monticola* Friedr. | – | – | – | 1 | 1 | – | – | 3 | 2 | – | 1 | – | 8 |
| *Simulium truncatum* Lundstr. | – | – | 4 | – | – | 5 | – | – | 2 | – | – | – | 11 |
| | 37 | 46 | 54 | 64 | 58 | 70 | 79 | 52 | 67 | 54 | 60 | 59 | 700 |

Tab. 7. Samples from loc. D, 10 September 1964. Site description explained in text (p. 297).

| Sample no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Site description | bcg | bdg | bdf | aef | aef | adh | bdg | ach | bdg | bdg | |
| *Baetis pumilus* Burm. | – | – | 2 | 3 | – | 4 | 1 | – | – | – | 10 |
| *Baetis rhodani* Pict. | – | – | 5 | 11 | 23 | 6 | 17 | – | – | 5 | 67 |
| *Baetis subalpinus* Bgtn. | – | 12 | 3 | – | – | 2 | – | – | 10 | 12 | 39 |
| *Baetis* sp. | 7 | 9 | 5 | – | – | 9 | – | – | 13 | 17 | 60 |
| *Ephemerella aurivillii* Bgtn. | – | – | 26 | – | – | – | 19 | – | – | 1 | 46 |
| *Heptagenia dalecarlica* Bgtn. | 1 | – | 2 | – | 6 | – | – | – | – | 3 | 12 |
| *Taeniopteryx nebulosa* L. | 2 | 4 | – | 1 | – | 4 | – | – | 1 | 3 | 15 |
| *Leuctra fusca* L. | – | – | – | 2 | – | 4 | – | 9 | – | – | 15 |
| *Capnia atra* Mort. | 2 | 6 | – | – | – | 14 | – | – | 7 | 10 | 39 |
| *Diura bicaudata* L. | – | – | – | – | – | – | – | – | 2 | – | 2 |
| *Diura nanseni* Kemp. | – | – | 1 | 3 | 3 | – | – | – | – | – | 7 |
| *Polycentropus flavomaculatus* Pict. | – | – | 2 | 4 | – | 1 | 4 | – | 1 | 6 | 18 |
| *Rhyacophila nubila* Zett. | – | – | – | – | 1 | 2 | 1 | – | – | – | 4 |
| *Apatania stigmatella* Zett. | – | – | 2 | – | – | – | – | 4 | 1 | – | 7 |
| Limnephilinae sp. | – | – | – | – | – | – | – | 4 | – | – | 4 |
| *Odagmia monticola* Friedr. | – | – | – | – | 3 | 1 | – | – | – | 4 | 8 |
| | 12 | 31 | 48 | 24 | 36 | 47 | 42 | 17 | 35 | 61 | 353 |

Tab. 8. Samples from loc. K, 15 August 1964. Site description explained in text (p. 297).

| Sample no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site description | bcg | adh | bdg | adf | bdg | bch | aef | aef | adf | bef | adg | bdg | |
| *Baetis pumilus* Burm. | – | – | – | – | – | – | 3 | 9 | 3 | – | – | – | 15 |
| *Baetis fuscatus* L. | – | – | – | – | – | – | 10 | 6 | 20 | – | – | 1 | 37 |
| *Baetis rhodani* Pict. | – | – | – | – | 1 | 12 | 5 | 11 | 13 | 5 | – | – | 47 |
| *Baetis subalpinus* Bgtn. | – | 7 | 2 | 29 | – | 17 | 5 | 3 | – | 15 | 10 | 8 | 96 |
| *Ephemerella aurivillii* Bgtn. | – | – | 2 | – | – | – | – | – | – | 35 | 2 | – | 39 |
| *Heptagenia dalecarlica* Bgtn. | 5 | 2 | 9 | – | 5 | 1 | 6 | 6 | – | – | 3 | – | 37 |
| *Taeniopteryx nebulosa* L. | 2 | – | – | – | 1 | – | – | – | – | – | – | – | 3 |
| *Amphinemura standfussi* Ris | – | 3 | 1 | 9 | – | 17 | – | – | – | 1 | 7 | – | 38 |
| *Protonemura meyeri* Pict. | 5 | 3 | 16 | 4 | 4 | – | – | – | – | – | 3 | 5 | 40 |
| *Leuctra fusca* L. | 2 | 5 | – | 14 | – | 1 | 2 | 1 | 5 | – | – | – | 30 |
| *Diura nanseni* Kemp. | – | – | – | 2 | – | – | 1 | 4 | – | – | – | – | 7 |
| *Arctopsyche ladogensis* Kol. | – | – | 1 | – | 1 | – | – | – | – | 2 | – | 4 | 8 |
| *Polycentropus flavomaculatus* Pict. | 10 | – | – | – | 1 | – | 3 | – | – | – | – | 5 | 19 |
| *Rhyacophila nubila* Zett. | – | 2 | – | – | – | 1 | 3 | 6 | 2 | – | – | 1 | 15 |
| *Apatania stigmatella* Zett. | – | 4 | – | 8 | 1 | 1 | – | – | 7 | 6 | 2 | – | 29 |
| *Eusimulium* sp. | – | – | – | – | – | – | 1 | 1 | – | – | – | – | 2 |
| *Odagmia monticola* Friedr. | – | – | – | – | – | – | 3 | 15 | 47 | – | – | – | 65 |
| | 24 | 26 | 31 | 66 | 14 | 50 | 42 | 62 | 97 | 64 | 27 | 24 | 527 |

Tab. 9. Distribution of species on the three site types, based on autumn samples. Statistical significance of preference indicated by asterisks (see Tab. 5). Bracketed figures show number of individuals in the study.

| type I | type II | type III |
|---|---|---|
| *Baetis lapponicus**** (37) | ←—— *Baetis* sp.*** (145) ——→ | |
| *Baetis pumilus**** (40) | *Protonemura meyeri**** (36) | *Baetis subalpinus*** (139) |
| *Baetis fuscatus**** (116) | ←—— *Capnia atra**** (39) ——→ | |
| *Baetis rhodani**** (107) | *Polycentropus flavomaculatus** (38) | *Amphinemura standfussi**** (69) |
| *Heptagenia dalecarlica*** (77) | | *Leuctra fusca**** (109) |
| *Diura nanseni**** (22) | | |
| *Apatania stigmatella**** (71) | | |
| *Odagmia monticola**** (31) | | |
| types I + II + III | | |
| *Ephemerella aurivillii* (92) | | |

scarce species:

*Taeniopteryx nebulosa*, *Diura bicaudata*, *Arctopsyche ladogensis*, *Rhyacophila nubila*, Limnephilinae sp., *Eusimulium* sp., *Simulium truncatum*.

Unidentifiable small *Baetis* nymphs were found distinctly to prefer types II and III to I. It is probable that they chiefly belonged to the species *B. rhodani.*

Blackfly larvae of the species *Odagmia monticola* and *O. ornata* occurred in comparatively low numbers and were found to avoid type II as against both I and III between which they did not discriminate.

*c) Autumn samples.* – The material obtained in autumn (Tabs. 6 to 8) was less extensive than that in spring. The results are summarized in Tab. 9. Eight species significantly preferred type I, two type II and three type III. In addition, two species were equally frequent in types II and III but avoided type I, whilst one species was found equally frequently in all three types.

The list of species preferring type I includes four species of the genus *Baetis*. Of these, *B. pumilus* showed the least strong preference for this site type, whilst *B. lapponicus* and *B. fuscatus* were entirely absent from both II and III. *B. pumilus* and *B. rhodani* showed no significant differentiation between II and III.

*Heptagenia dalecarlica* showed a clear if not absolute preference for type I and did not differentiate between II and III.

*Diura nanseni* was taken in small numbers only. Every specimen was taken in type I. Because of this clear demonstration of preference the species was not included in the list of scarce species to which it belongs on numerical grounds.

*Apatania stigmatella* clearly preferred type I but did not distinguish between types II and III. The same applied to *Odagmia monticola*, although its numbers were small.

Young *Baetis* nymphs showed the same preference as in spring, i.e. were more frequent in types II and III than in type I; they did not differ between the two former types. It is possible to state confidently that the large majority of these small nymphs were *B. rhodani*, for no other species occurs in this stage in autumn. All other species spend the winter almost invariably as eggs. Thus, *B. rhodani* must have a different habitat as a tiny nymph in autumn than as a more or less full-grown nymph in spring.

*Ephemerella aurivillii* did not show any clear preference for any of the three site types. This may indicate that its microdistribution was governed by some factor not included in the present analysis.

*Protonemura meyeri*, although obtained in relatively small numbers, showed a distinct preference for type II. Like *Ephemerella mucronata* and *Chloroperla burmeisteri*, its habitat seems only just to reach within the range of biotopes sampled. *Amphinemura standfussi* was almost exclusively confined to type III bottom.

*Polycentropus flavomaculatus* showed a weak preference for type II. As in spring, it avoided type III.

Blackfly larvae were present in small numbers only. It was found that *Odagmia monticola* was almost entirely restricted to type I.

*d*) *The agreement between the distribution of species and that of environmental factor complexes.* – In spring, 19 species showed a significant over-representation in one of the three bottom types. In all cases except two, the probability of the distribution being random was $< 0.001$. Only three species did not show any over-representation in one site type. One of these three species was very scarce. The other two species demonstrated a very clear preference for two of the types as against the third; thus, they too showed a clear dependence on the factors under study. Both of these last-mentioned "species" are in fact aggregates known or suspected to consist of more than one species.

In autumn, 13 species showed a significant over-representation in one of the three site types. In ten of them the probability of random distribution was $< 0.001$. Three species had a less restricted preference. Two of them, viz. *Baetis* sp. and *Capnia atra*, preferred two of the types when compared with the third, whilst one species, viz. *Ephemerella aurivillii*, was equally distributed over all three types. The unidentified *Baetis* nymphs with almost absolute certainty can be referred to one species only, viz. *B. rhodani*.

Thus, a large majority of the species exhibited patterns of microdistribution indicating that they are under strong influence of environmental factor complexes as defined in this study.

## 5. Distribution of species in relation to separate factors

*a*) *Procedure of analysis.* – The next task is to break down the factor complexes and analyze which of the separate factors are the most important for habitat selection. Because of the close association of the factors this is difficult and sometimes impossible. However, a partial analysis along the following lines was carried out. Water depth, current and substrate were treated separately. It was calculated how many individuals of a given species were to be excepted on the total number of sites characterized by a given environmental condition, if the distribution were random with regard to the alternatives examined. For example, of the 359 individuals of *Ameletus inopinatus* included in the 34 spring samples, 158 were to be expected on the 15 shallow water sites and 201 on the 19 deep water sites, if water depth was of no consequence for the habitat selection of the species. Exactly the numbers expected were very rarely found. Tabs. 10 and 11 show the numbers found in percent of the numbers expected. A figure above 100% indicates that the sites in question were selected more often than would be expected on random basis; that is, the factor characterizing these sites positively influenced the habitat selection of the species. The opposite is of course true for sites showing a figure below 100%.

Only species represented by at least 100 individuals were analysed, an exception being made in the case of *Heptagenia dalecarlica.*

The association between different factors was of course not affected by this procedure. However, interspecific differences in the percentage figures can only be interpreted as indicating differences in the relative importance of the separate factors for the different species.

*b*) *Spring samples.* – The data are assembled in Tab. 10. Certain species showed a very clear preference for shallow as opposed to deep water, particularly *Diura nanseni* and the two blackfly species. The only species showing a high percentage in the deep water is *Baetis* sp. Several species were rather evenly distributed over the two depth classes, viz. *Ephemerella aurivillii*, *Isoperla grammatica* and *Apatania wallengreni.*

With respect to current velocities, only *Baetis* sp. showed a figure over 100% in the lowest category. *Leuctra hippopus*, *Isoperla grammatica* and *Apatania wallengreni* also showed a certain tolerance, if not preference for slow current. In the fastest current class, *Ameletus inopinatus*, *Baetis rhodani*, *Heptagenia dalecarlica*, *Diura nanseni* and both blackfly species were all very clear over-represented, indicating strong preference. Among the species having their highest figure in the medium current class, interesting differences appeared. Thus, *Baetis* sp. and *Isoperla grammatica* had their second highest value in the slow current, whilst the opposite was true for *Ephemerella aurivillii.* Finally *Leuctra hippopus* and *Apatania wallengreni* were about equally distributed over strong and weak current categories.

Only *Baetis* sp. had its highest substrate over-representation in the silt bottom. *Ameletus inopinatus*, *Baetis rhodani*, *Diura nanseni*

Tab. 10. Differences between actually found distribution and that expected on the basis of random dispersion within factor groups, expressed as specimens found in percent of number expected. Spring samples.

| | Factors | a | b | c | d | e | f | g | h |
|---|---|---|---|---|---|---|---|---|---|
| | Number of samples | 15 | 19 | 6 | 16 | 12 | 14 | 10 | 10 |
| | no. of inds. | | | | | | | | |
| *Ameletus inopinatus* | 359 | 150.3 | 60.3 | 6.3 | 44.7 | 219.7 | 194.6 | 6.6 | 60.4 |
| *Baetis rhodani* | 584 | 138.0 | 69.7 | 1.9 | 66.5 | 193.7 | 174.7 | 2.9 | 91.9 |
| *Baetis* sp. | 179 | 23.9 | 158.9 | 115.6 | 149.4 | 23.4 | 68.9 | 139.6 | 101.9 |
| *Ephemerella aurivillii* | 159 | 92.2 | 105.3 | 3.6 | 137.3 | 98.2 | 98.5 | 31.9 | 168.1 |
| *Heptagenia dalecarlica* | 97 | 154.0 | 54.4 | 17.6 | 65.2 | 182.9 | 168.3 | 58.6 | 37.9 |
| *Leuctra hippopus* | 239 | 124.8 | 81.2 | 90.5 | 117.0 | 83.3 | 89.8 | 40.0 | 175.7 |
| *Diura nanseni* | 193 | 170.9 | 42.6 | 35.3 | 46.2 | 204.4 | 175.0 | 3.5 | 89.5 |
| *Isoperla grammatica* | 116 | 111.8 | 90.8 | 80.0 | 166.7 | 24.4 | 56.3 | 64.7 | 197.1 |
| *Apatania wallengreni* | 147 | 94.6 | 105.3 | 73.1 | 130.4 | 73.1 | 91.7 | 62.8 | 151.1 |
| *Prosimulium hirtipes* | 453 | 194.0 | 25.7 | [1] | 4.7 | 276.9 | 238.2 | [1] | 7.5 |
| *Cnephia fuscipes* | 288 | 210.9 | 11.1 | [1] | 16.9 | 259.8 | 222.7 | [1] | 27.1 |

[1] No specimens in this class.

and both blackflies were over-represented on the naked stones. Several species covered a fairly wide range of types.

Comparing Tab. 5 with Tab. 10 it is found that all type I species had as expected high percentages in columns *a*, *e* and *f* separately. In the two blackfly species this was so pronounced that it seems probable that each separate factor has a positive value for these animals. *Ameletus inopinatus* also showed a very pronounced preference for each of the factors but also occurred with some frequency in moderate current and on detritus bottom. *Baetis rhodani* was still more spread over two current and substrate classes, although retaining its clear preference for *aef* conditions. *Heptagenia dalecarlica* carried this tendency still further, particularly by its tolerance of silt bottom. *Diura nanseni* very clearly avoided silt but showed some tolerance for varying current conditions.

Of the type III species of Tab. 5, *Ephemerella aurivillii* showed a clear over-representation in detritus compared with naked stones and was only infrequently found on silt, whilst it showed only a weak preference for fast as compared with moderate current. *Leuctra hippopus* demonstrated a clear preference for detritus but was rather indifferent for current conditions. *Isoperla grammatica* did not seem to have very sharply defined requirements, except for its intolerance of fast current. *Apatania wallengreni* covered a wide spectrum of types but exhibited a clear preference for detritus substrate.

*Baetis* sp. clearly avoided the fastest currents but showed only a weak preference for silt bottom as against other substrates.

*c*) *Autumn samples.* – The data are assembled in Tab. 11. Only two species showed marked discrimination between the depth classes, viz. *Ephemerella aurivillii* prefering deep and *Leuctra fusca* shallow water.

*Baetis fuscatus* showed a very strict preference for the fastest current conditions, and was completely absent from the slowest class. *B. rhodani* likewise preferred strong current but did not distinguish between moderate and weak current. *Heptagenia dalecarlica* demonstrated an unusual pattern in having its lowest figure in the medium class; it cannot be excluded that this depends on the relatively small material of this species. *Baetis subalpinus* and *Baetis* sp. (= young *B. rhodani*) were over-represented in the moderate current; the latter was almost absent from the fast current sites.

*Baetis fuscatus* had a very clear preference for naked stones, being virtually absent from other substrates. *Baetis rhodani* and *Apatania stigmatella* also preferred naked stones but much less strictly. Still less pronounced was the over-representation on this substrate by *Heptagenia dalecarlica*. *Baetis subalpinus* exhibited a wide distribution, and *Baetis* sp.

Tab. 11. Same as Tab. 10 for autumn samples.

| Factors | | a | b | c | d | e | f | g | h |
|---|---|---|---|---|---|---|---|---|---|
| Number of samples | | 17 | 17 | 5 | 19 | 10 | 15 | 12 | 7 |
| | no. of inds. | | | | | | | | |
| *Baetis fuscatus* | 160 | 107.5 | 92.5 | [1] | 49.4 | 246.8 | 223.9 | 1.8 | [1] |
| *Baetis rhodani* | 125 | 126.9 | 71.4 | 63.1 | 67.1 | 178.4 | 150.0 | 52.3 | 69.2 |
| *Baetis subalpinus* | 207 | 86.5 | 112.5 | 77.4 | 128.5 | 55.7 | 110.9 | 74.0 | 118.6 |
| *Baetis* sp. | 157 | 84.8 | 113.9 | 104.3 | 150.6 | 4.3 | 20.3 | 167.3 | 159.4 |
| *Ephemerella aurivillii* | 118 | 5.1 | 194.9 | 100.0 | 97.0 | 100.0 | 115.1 | 90.5 | 76.0 |
| *Heptagenia dalecarlica* | 87 | 102.3 | 95.4 | 107.7 | 57.1 | 173.1 | 125.6 | 83.9 | 66.7 |
| *Leuctra fusca* | 155 | 164.1 | 34.6 | 104.3 | 111.5 | 73.9 | 115.9 | 18.2 | 203.1 |
| *Apatania stigmatella* | 111 | 110.7 | 87.5 | 29.4 | 96.8 | 136.4 | 170.0 | 40.0 | 43.5 |

[1] No specimens in this class.

did not discriminate between naked stones and detritus. *Ephemerella aurivillii* was probably indifferent to substrate, whilst *Leuctra fusca* clearly preferred detritus and avoided silt.

Comparing Tabs. 9 and 11 it is seen that, as in the spring samples, the type I species usually preferred each of the factors involved, although in varying degrees. In *Baetis fuscatus* preference for fast current and naked stones was very distinct, but less for shallow water. In *B. rhodani* the selection with regard to substrate and current was somewhat less marked than in *B. fuscatus*, whilst the preference for shallow water was more distinct than in the latter species. The selection was generally still less distinct in *Heptagenia dalecarlica*. *Apatania stigmatella* seemed to be more dependent on naked stones than on fast current, although it did not occur in the weakest current. *Baetis subalpinus* in general showed fairly weak preference for the slower current.

## 6. Discussion

*a) Water depth.* – The flow of the north Scandinavian rivers and streams exhibits violent seasonal and sometimes daily fluctuations. It might be pointed out that all sampling sites were below normal low water level and were at no time observed to dry up between 1962 and 1965, inclusively.

The static pressure experienced by a benthic organism increases with approx. 5% from 0 to 40 cm water depth. Differences in static pressure within the depth range occurring in this study cannot have an influence on distribution.

The fact that certain species, such as blackflies, exhibited a very strong overrepresentation in shallow water deserves comment. It cannot depend on static pressure. A likely explanation seems to be the change in flow conditions occurring with decreasing depth. As the water becomes shallower, a nozzle effect is produced with increasing velocity and dynamic stability; at increasing depth, the flow is separated from the substrate with dynamic instability and eddy formation. The latter conditions seem less favourable to filter feeders than the former.

Another factor which may explain overrepresentation in shallow water is the tendency of many species to approach the shore some time before their emergence (e.g. Wesenberg-Lund 1943, Lillehammer 1966 for stoneflies; Harker 1953 for mayflies). Distance from shore was analysed as a separate factor in some species, amongst other *Diura nanseni*, but no statistically significant differences between sites at different distances from the shore-line could be ascertained.

*b) Current.* – A bottom-living organism is exposed to a dynamic pressure which reaches its maximal value where the flow encounters some complete obstacle (see e.g. Kresser 1953). The dynamic pressure is mainly a function of the current velocity. This is very variable over the bottom. There are frequently pockets of still or almost still water and no or little dynamic pressure. It is an established fact that many species preferably or exclusively live in such pockets; it may be said that these animals, although inhabiting a stream, live in still water.

Moreover, even if a benthic animal occurs on the upper surface of a stone exposed to the current, the stratification of current is such that an animal of the order of size of insect larvae and nymphs is in fact surrounded by slowly flowing or even standing water. The significance of this boundary layer for the benthic animals has been elucidated particularly by Ambühl (1959, 1962). Although the extreme turbulence to be found in this type of stream characterized by "rushing" rather than "streaming" flow (Ruttner 1963) and very coarse bottom substrate must be expected to reduce the thickness of this layer to a very low value, it is still sufficient to protect the animals from being fully exposed to the full mechanical force of the current. It is also difficult to believe that the extremely streamlined body form of many benthic species has not evolved in part as a response to the difficulties presented by the fast current.

There exist several studies concerning the correlation between current and distribution of species in nature and still more laboratory investigations of the tolerance and preference of species for current velocities (see e.g. Dorier and Vaillant 1948, 1954, Philipson 1954, Scott 1958, Ambühl 1959, Edington 1965). Whilst it is of course interesting to acquire information on the reaction of animals to different current conditions, it should always be kept in mind that in nature current is an extremely heterogeneous factor. A full scale of variation usually exists within small bottom areas. The direct effect of current on the animals is regarded as relatively unimportant by many workers, as pointed out by Macan (1963) who summarized much of the discussion and pointed to the very great significance of the indirect effects of current (cf. Scott 1958, Eriksen 1966). Philipson (op. cit.) found that certain caddisflies were entirely dependent on current for their respiration but that they survived in a wide variety of current velocities, including very slow ones. This seems to confirm Ruttner's (1963) concept of the physiologically enrichening effect of current. As pointed out by e.g. Berg (1948), Nielsen (1950), Linduska (1942) and Maitland (1966) the current is unsuitable as a basis for biotope classification because its direct effect on the animals is so relatively small. The netspinning caddisflies constitute an exception to this in that they make use of the dynamic pressure of flow to hold their sieving devices open.

Oxygen transport, seston load, and influence on bottom substrate are some of the chief indirect effects by current. In addition many animals are transported with the current, but if these movements are a means of population redistribution or simply a result of accidental detachment from the substrate on the part of a fraction of the population is at present an unsolved question (cf. Müller 1954, Elliott 1967).

c) *Substrate and food.* – Substrate has a many-sided importance for the benthic fauna. Certain species require a hard bottom, for example blackfly larvae. For most species, substrate has a much more complicated significance than merely as a support. Apart from such secondary aspects as shelter from predatory animals, substrate has to provide food for a large number of benthic animals; the most notable exception from this being the seston feeders which will be disregarded in the present connection.

The food factor has been surprisingly neglected in most discussions of stream ecology – an important exception being the work of Scott (1958).

For the benthic fauna three groups of food are of evident importance: 1) autochthonous matter in the form of periphytic algae, particularly diatoms, 2) allochthonous matter (cf. Nelson and Scott 1962) in the form of vegetable detritus from land and from lakes and slow-flowing parts of the stream, including microorganisms living on the detritus and lacustrine plankton adhering to the bottom and the periphyton, 3) other animals – the food of predatory species.

The first kind of food is most plentiful on naked stones exposed to light. The growth of periphyton is usually adversely affected by sedimentation. The second kind is particularly in evidence as accumulations of detritus in dead-waters or other sheltered places. In the study area, most of this food came from the terrestrial vegetation surrounding the streams. The species exploiting the third kind of food are on a higher trophic level and are regulated in their distribution by that of the prey species.

The food choice of the species in question is relatively well known. If any species in the present study has not been studied, some near relative usually has, and it is probable that such species are closely similar in this respect.

For mayflies, information is provided notably by Bengtsson (1925), Wissmeyer (1926), Schoenemund (1930) and Brown (1961), for stoneflies by Grau (1926), Hynes (1941) and Brinck (1949) and for caddisflies by Siltala (1907), Slack (1936) and Scott (1958). Meierjürgen (1935), Jones (1950) and Chapman and Demory (1963) contain useful information on all three taxa.

Narrow food specialization seems to be absent from the benthic species of lotic biotopes within this general area. Mayflies are generally herbivore. Some of them are primarily algal grazers, others detritus consumers, but there are no sharp differences. Actively swimming species, such as *Baetis* spp., are known to graze periphyton as well as feed on detritus. Young stages living in the interstitial spaces under the river bottom proper may live on both detritus and the microorganism film adhering to the mineral particles, as was suggested by Brown (1961) and in analogy to what has been found for marine interstitial organisms (e.g. Gray 1966). *Ephemerella* spp. are omnivore scavengers, while heptageniids are predominantly algal grazers.

In the stoneflies, Brinck (op. cit.) found that filipalpians eat almost exclusively vegetable matter, whilst setipalpians are primarily predatory. Among the latter, however, some genera have a more mixed diet than others. In particular *Chloroperla*, but also *Isoperla*, ingest a considerable amount of vegetable matter as well, whilst *Diura* and *Dinocras* are strictly predatory.

Among the caddisflies, limnephilids are herbivorous or omnivorous, whilst the genus *Rhyacophila* includes exclusive predators. A species of *Glossosoma* has been found to be an exclusive algal grazer, and this is probably also the condition of the species in the present study. Polycentropids and hydropsychids catch most of their food in nets, but *Polycentropus flavomaculatus* is said sometimes to behave as a predator; the species is exclusively carnivorous.

When viewing the microdistribution of the species from the angle of food preferences, the evident conclusion is that their distribution is more closely related to this factor than with any other.

Algal grazers are found on naked stones – most *Baetis* spp., *Ameletus inopinatus*, *Glossosoma intermedium*, *Heptagenia dalecarlica*. Detritus consumers are not unexpectedly more or less restricted to this kind of substrate, the importance of which has been emphasized by e.g. Elton (1959), Egglishaw (1954), Nelson and Scott (1962) and Hynes (1963). It is interesting that the two *Apatania* species fall in different categories; this requires further study. Young *Baetis* nymphs are frequent in silt; they probably also occur in the hyporheal biotope (Schwoerbel 1964) which was not included in this study. Baetid nymphs are known to be a preferred food source for predatory stoneflies, and the density of the former may well influence that of the latter as well as of other predators, such as *Rhyacophila*. Chironomids also figure prominently on the diet lists of predatory stoneflies, but their distribution has not been examined.

*d) The interplay of environmental factors.* – The interplay of several environmental factors is evidently a most important aspect of the problem of the microdistribution of the benthic fauna, even though the food factor is of paramount significance. Animals in nature respond to combinations of factors; within certain limits, suboptimality in one respect may be compensated by optimality in another. However, each species of course has certain fundamental requirements that cannot remain unsatisfied. Food is one such basic requirement and has a very large influence on the microdistribution of animals in the comparatively nutrition-poor environments of north Scandinavian rivers.

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