Benthic Insect Communities of Streams in Stora Sjöfallet National Park, Swedish Lapland

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Abstract
Benthic animal communities in streams with varying environmental conditions in a national park in northern Swedish Lapland were analysed. Dominant taxa were Ephemeroptera, Plecoptera, Trichoptera and Diptera Simuliidae. Northeasterly or very widely spread species make up the fauna. Intrariverine distribution patterns were found to differ between taxa, and great variations of standing crop values between adjacent sampling sites were the rule. Day-to-day fluctuations of drift rate were unsynchronized between taxa. Some ecological properties of *Brachyptera risi* (Plec.) are discussed. Some lake shores and streams affected by hydroelectric exploitation appeared virtually devoid of macroscopic animals.

Introduction

Stora Sjöfallet National Park (henceforth abbreviated SSNP) in Swedish Lapland was established in 1909. It covers an area of ca 1500 km² and is part of a large block of national parks and forest and bird reserves, in all comprising over 8000 km² and said to constitute the biggest wilderness area in Europe west of the USSR (Curry-Lindahl, 1968). All the streams and lakes in SSNP belong to the River Lule älv draining system (Fig. 1).

In spite of its status as a national park, SSNP has been very heavily exploited for hydroelectric production. As early as ten years after its proclamation as a national park, its central valley was removed from its "protected" status in order to make the transformation of its lakes into water reservoirs legally possible. Some of these lakes were subsequently regulated in three steps, viz. in 1927, 1939 and 1963, and at present their fourth regulation is being carried out in order to increase manifold their water storage capacity.

For a long time the exploitation of SSNP was restricted to its central valley, the lakes of which were used as dams to ensure adequate flow volumes in a series of power plants further downstream. In the 1950's, the hydroelectric exploitation of north Swedish river systems culminated, and a much more extensive system of impoundments and power plants in the central parts of SSNP was planned. Today many of these plans have been implemented, others are still being contemplated, and still others have been cancelled. The steps already taken have resulted in a large-scale destruction of natural conditions in the rivers and lakes and their surroundings. The damage is so serious that many conservationists are presently urging that a large portion of SSNP be relegated from its status of a national park, since the objectives for which the park was established are no longer fulfilled.

Towards the end of the 1950's, the authorities decided that surveys of the flora and fauna should be carried out in areas about to be damaged by hydroelectric exploitation and allocated means for such purposes. The ensuing activities yielded a large body of floristic and faunistic information from many parts of north Sweden, although only exceptionally, viz. for River Vindelälven (Ulfstrand, 1968) the resources were adequate for long-term quantitative work. In the area with which we are presently concerned surveys of the invertebrate fauna were performed chiefly in 1961 and 1963. In addition, a special study has been undertaken to examine, over a sequence of years, the effects of a deluge caused by a dam catastrophe on certain terrestrial animal communities. Work has also been devoted to the

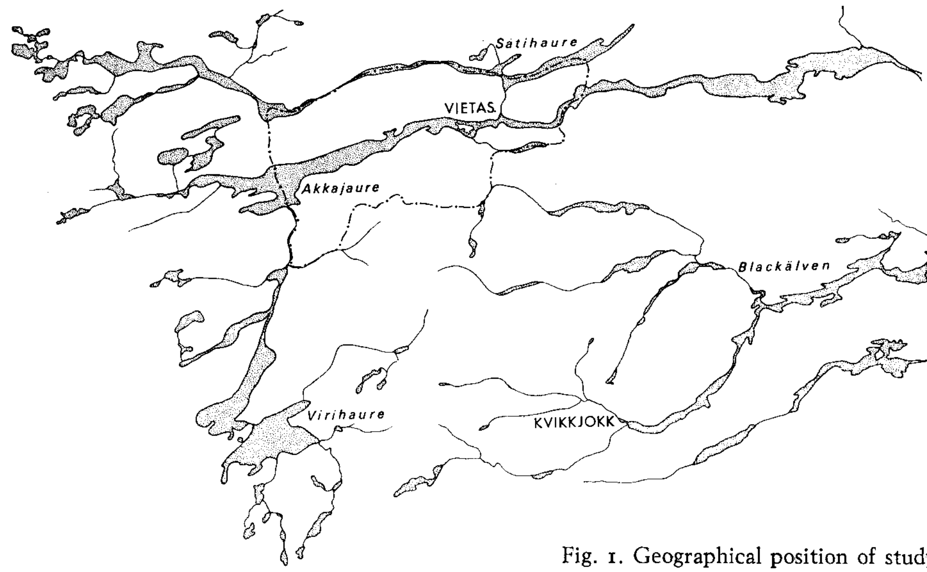


Fig. 1. Geographical position of study

small rodents of the area and to the forest bird communities; reports of the ornithological studies have been published by Andersson et al. (1967) and Eriksson et al. (1971).

This communication primarily reports on a quantitative survey of the benthic animal communities in several streams, which had not yet been seriously affected by the exploitation of the area. In particular, attention was devoted to the following aspects:

A) The qualitative composition of the regional fauna.
B) The quantitative composition of stream animal communities.
C) Intrariverine distribution patterns.
D) The quantitative relationship between drift and the benthic populations.

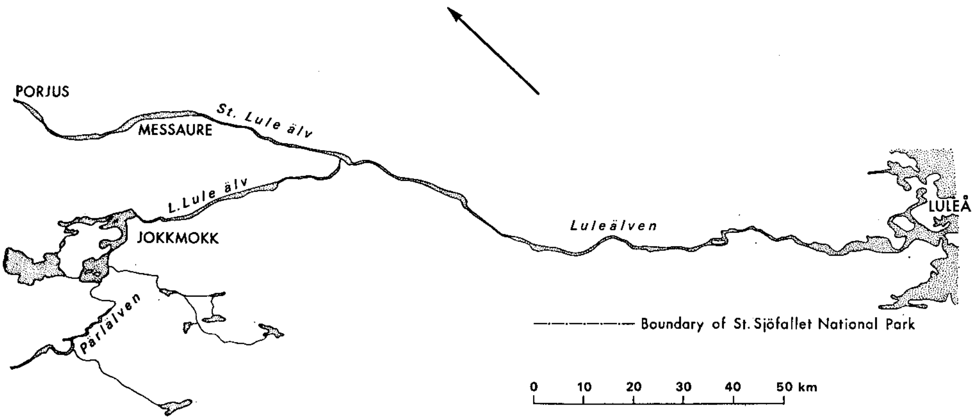
Mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) were identified to species level, the two former groups by S. Ulfstrand, the Trichoptera by B. Svensson. In the quantitative studies, all taxa were comprised. Blackflies (Diptera Simuliidae) were the only group of quantitative importance apart from the three taxa just mentioned. Two methods of benthic sampling were used, and the results obtained were compared.

A few lake and stream localities that have already become strongly affected by the exploitation of the area were also examined.

The field work covered the periods 11 July to 17 August and 11 to 16 October 1969.

Published information[1] about the invertebrates of the upper parts of River Stora Lule älv is limited to Brinck and Wingstrand (1949, 1951) who worked at Lake Virihaure 75 km SW of Stora Sjöfallet; their study area is well above the tree limit and characterized by much harder climatical conditions than the area in which the present study was performed. The stoneflies of River Lilla Lule älv have been dealt with by Brinck and Froehlich (1960). Around Messaure 120 km E of Stora Sjöfallet ecological research concerning stream insects has been intense over the past years (Müller, 1970). Some faunistic results concerning the caddisflies have been published by Tobias (1969). This area is in the midst of the taiga forest zone and thus differs markedly from our study area which is situated in the transition between the high boreal coniferous and subarctic birch forest zones.

[1] When this paper was in proof, an important contribution dealing with the chironomids of the same area, in part the streams, appeared by A. W. Steffan (Can. Ent. 103 (1971), pp. 477–486).



area and survey of River Lule älv.

Environmental conditions

Physiographical survey

The work was carried out in the central valley of SSNP and part of its northern branch draining Satihaure[1] and other lakes. The base was the village of Vietas, a temporary settlement erected for the staff of employees of the construction works. The approximate coordinates are 67° 30′ N, 18° 25′ E. Thus, the area is situated about 100 km north of the Arctic circle. For details, see Figs. 1 and 2. Many of the following data are taken from Curry-Lindahl's (1968) description of Stora Sjöfallet National Park.

River Lule älv originates in two main branches; the northern one, known as Stora Lule älv, derives from the block of national parks mentioned. Within SSNP, Stora Lule älv is made up of a series of long, narrow and deep lakes of which the uppermost one, known as Suorvajaure or Akkajaure, is presently subjected to its fourth regulation (alt. 420–440 m above sea level). Below its dam, the sequence of lakes bear the names Kårtjejaure (415 m), Paijeb Lulejujaure (375 m), Langas (374 m) and Stora Lulevatten (370 m). At Vietas, a still more northerly branch of the water system merges with Stora Lule älv through River Vietasätno. This stream derives from Lake Satihaure (440 m), which has been transformed into a large impoundment.

The upper reaches of Stora Lule älv flow through mountainous country with several peaks at 1600 m altitude and higher. Close to Vietas, some mountains reach 1200 to 1600 m. Further eastwards, the mountains give place to a country with lesser altitudinal amplitudes. Large areas are flat and covered with immense mires, but hills of modest heights are freely scattered over the region.

The total drainage area of Stora Lule älv at the point where it merges with Lilla Lule älv is approx. 9900 km^2. At Vietas the annual average flow volume is approx. 230 m^3/sec.

Much of the drainage area lies on archaic or cambrosilurian sedimentary rocks, but the latter are frequently covered with granites and syenites. Some big mountains, however, consist of amphibolites (Sundius, 1963). With nutritionally poor rocks prevailing, it is not surprising that, broadly speaking, the edaphic conditions are unfavourable to plant species with exacting demands (Björkman, 1965). Also the water in the lakes and streams is very poor in terms of ionic contents, and macrovegetation

[1] The spelling of Lappish place names varies a great deal. We follow the recent topographical map (Fältkarta 28 I Stora Sjöfallet, Stockholm 1965).

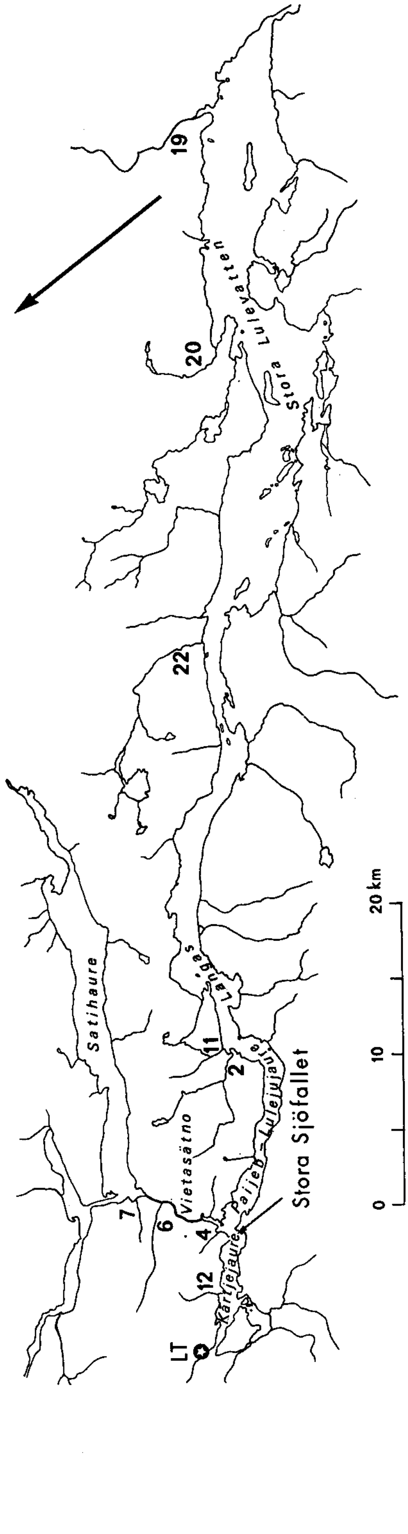


Fig. 2. Study area. Figures indicate sampling localities. The asterisk denotes position of light-trap.

at the bottom is sparse or entirely wanting.

The high latitude, of course, brings about violent seasonal fluctuations in most environmental features. Eradiation is markedly greater than irradiation on an annual basis, but the deficit is partly compensated for through convective heat transport from the south and west (Wallén, 1963). At Kvikkjokk, 50 km S of Vietas, the average number of sun hours during the whole of January amounts to 20, compared with nearly 300 in June. Monthly mean air temperatures rise above the freezing point for barely six months, and snow covers the ground for approx. 230 days/year (Sundius, 1963). Annual precipitation is as low as 400 mm at Saltoluokta, 20 km SE of Vietas, but exhibits extremely great local variations being much more abundant further west in the mountains than at the meteorological station at Saltoluokta.

The much reduced energy income in winter in combination with the thick cover of ice and snow brings about a nearly complete black-out of lake and stream benthos for many months (Rodhe, Hobbie & Wright, 1966). Another characteristic feature of these high latitudes is the virtual thermoconstancy of the water for upwards of five months (e.g. Müller 1970).

Björkman (1963, 1965) states that conifers in this area do not ascend above approx. 500 m altitude. Pine Pinus silvestris L. penetrates farther westwards than does spruce Picea abies (L.) H. Kerst. Considerable local variations are plainly visible, due, among other things, to differences in exposure. Most of our localities were in the coniferous forest, which usually includes a proportion of deciduous trees, but a few were surrounded mainly by birch Betula tortuosa Ledeb. or by open ground, such as Empetrum heath.

Description of main sampling localities

The quantitative community analysis was restricted to six localities. At another three localities, only qualitative collections were made. The localities will be described and discussed in order from west to east, i.e., at the same time, from higher to lower altitudes. Their positions are shown in Fig. 2 and are in the following descriptions geographically related to Stora Sjöfallet, the big water-fall that is now destroyed but is still to be found on the maps.

Loc. 7.

A small stream running down the eastern slope of Nieras into Lake Satihaure near the tiny islet of Kiettsavuolsuoloi (now submerged as a consequence of the impoundment), 6.5 km NE of Stora Sjöfallet. Gravel, pebble and cobble[1] at the bottom. Width approx. 1 m. Surroundings Empetrum—Betula nana L. heath with Rubus chamaemorus L. bogs, and a narrow fringe of small Salix and Betula bushes along the stream bed.

15 July: pH = 8.1 $\varkappa_{20} = 13$ mmho
7 August: pH = 7.8 $\varkappa_{20} = 16$ mmho

Loc. 6.

Parnejåkkå, a stream running down the eastern slope of Nieras into Vietasätno, 5 km NE of Stora Sjöfallet. Width 5 to 12 m, very shallow, steep fall gradient. Boulder and cobble at the bottom, with finer fractions in sheltered places, but virtually no organic litter. Surroundings Betula tortuosa forest with some Pinus silvestris, and tall Salix bushes along the bank. Exceptionally frequent and rapid flow fluctuations.

13 July: pH = 6.8 $\varkappa_{20} = 16$ mmho
7 August: pH = 6.8 $\varkappa_{20} = 17$ mmho

Loc. 12.

Stream from Juolme, southwestern slope of Nieras, falling into upper part of Kårtjejaure, 6 km NW of Stora Sjöfallet. Width 1–3 m with moderate fall gradient. Bottom substrate varying from cobble to sand. Surroundings Betula tortuosa forest.

26 July: pH = 5.8 $\varkappa_{20} = 12$ mmho
17 August: pH = 6.8 $\varkappa_{20} = 9$ mmho

Loc. 4.

Stream from Ippatjåkkå, southern slope of Nieras, falling into the northernmost part of Paijeb Lulejujaure, 1.5 km NE of Stora Sjöfallet. Width 1–2 m. Rather steep fall gradient. Boulder and cobble at the bottom with plant debris and finer minerogenic fractions in sheltered places. Surrounded by lush Betula tortuosa forest with some Pinus silvestris.

8 August: pH = 6.9 $\varkappa_{20} = 18$ mmho

Loc. 2.

Ripsojåkkå, stream from Juobmotjåkkå, falling into southern part of Paijeb Lulejujaure (near Kebnats), 11.5 km SE of Stora Sjöfallet. A true forest stream surrounded by dense Pinus and Picea forest with an admixture of Betula and Salix. Width 2–4 m. Gentle fall gradient. Shortly upstream of the sampling sites were several small deep pools interspersed in the stream course. The downstream part of the river stretch within which our samples were taken had recently been disturbed by the construction of a road and a bridge. Also the other parts had been modified in order to improve the spawning conditions for Thymallus thymallus L., but this had taken place so long ago that little could be seen of these measures. Boulder and cobble, and a dense cover of algae at many sites.

21 July: pH = 7.2 $\varkappa_{20} = 30$ mmho
16 August: pH = 6.5 $\varkappa_{20} = 43$ mmho

Loc. 11.

Juobmojåkkå, stream from Juobmotjåkkå, falling into southern part of Paijeb Lulejujaure (near Kebnats), 12.5 km SE of Stora Sjöfallet. Closely resembling the previous locality, but the stream is somewhat smaller and had less abundant algal growth on the boulders and cobbles of the bottom.

18 July: pH = 6.8 $\varkappa_{20} = 28$ mmho
16 August: pH = 6.5 $\varkappa_{20} = 33$ mmho

Loc. 22 (only qualitatively sampled).

Stream at Ruokto, falling into Stora Lulevatten, 39 km SE of Stora Sjöfallet. Width 8 m. Boulder and cobble, very little epiphytic algae or moss. Surroundings mixed forest, but also some small hayfields.

9 August: pH = 7.8 $\varkappa_{20} = 17$ mmho

Loc. 20 (only qualitatively sampled).

Stream falling into Nabriluokto, a bay in Stora Lulevatten, 57 km SE of Stora Sjöfallet. Width 6–10 m, fairly deep with some deep pools interspersed in the course. Surrounded by mixed forests, partly swampy.

9 August: pH = 8.0 $\varkappa_{20} = 27$ mmho

Loc. 19 (only qualitatively sampled).

Sjaunjaätno, falling into Stora Lulevatten, 73 km SE of Stora Sjöfallet. A large, relatively slow-flowing river, width 10–20 m, deriving from an area of extensive coniferous forests and mires, and carrying heavily coloured water. The river is so

[1] The substrate classification of Cummins (1962) has been adopted in these descriptions.

deep that only the banks were accessible for manual sampling. The wide expanses of shallow and dark-coloured water further upstream probably absorb much heat, as illustrated by the fact that, at our visit on 9 August, the water temperature was as high as 20.8°.

9 August: pH = 8.7 $\varkappa_{20} = 38$ mmho

Water temperature

At locs. 7, 6, 4, 2 and 11, pairs of maximum-minimum thermometers were used to record the temperature during the field work periods. They were read and reset every day, usually late in the afternoon. Although the records cover only a brief period of the year, the results are interesting because they illustrate the very considerable local differences of temperature levels and fluctuations (Figs. 3 and 4). As apparent from the above descriptions and from Fig. 2, locs. 7, 6 and 4 all originate in the vast mountain block of Nieras, to the north of Stora Sjöfallet and of the village of Vietas. Locs. 7 and 6 run down the eastern slope and are partly screened by high mountains on the opposite side of the valley so they are not exposed to the sunshine apart from some hours before noon. Loc. 4 (as well as 12, from which we have no temperature records) runs down the southern slope of the same mountain and is fully exposed to the sunshine for many hours around noon. This explains the large temperature differences displayed in Figs. 3 and 4.

None of the three streams has any lakes worth mentioning in their courses. All of them derive from snow-fields on the high plateaux of Nieras. The summer of 1969 was characterized by exceptionally dry weather, practically no precipitation falling between 13 July and the end of our first field-work period. Thus, the rate of melting of the snow fields became the chief factor regulating the day-to-day and diel variations of run-off in the streams. The lack of precipitation obviously enhanced the temperature differences.

Figs. 3 and 4 demonstrate that loc. 4 had a very much higher water temperature than locs. 7 and 6 and in this respect resembled loc. 2, although the latter is a forest stream apparently much more sheltered from environmental vicissitudes. Loc. 4, however, exhibits larger diel fluctuations than loc. 2. This is readily explained not only by its more open exposure to the sun but also by its smaller water volume. The few data from loc. 11 suggest that this stream closely resembled loc. 2.

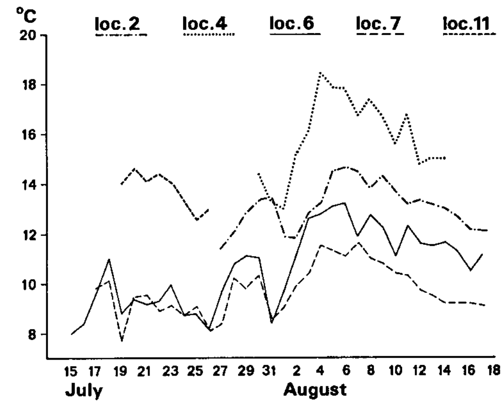


Fig. 3. Daily maximum water temperatures at five stream localities within study area.

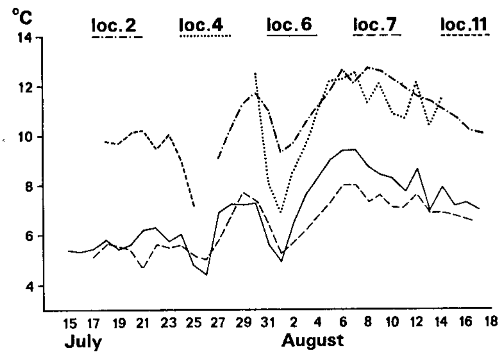


Fig. 4. Daily minimum water temperatures at five stream localities within study area.

Sampling methods

Benthic sampling methods

In north Scandinavian streams and rivers in which the bottom material frequently consists of boulders and generally coarse material, the more refined techniques of benthic sampling prove impracticable. Two methods are useful in streams characterized by this kind of substrate, viz. the Alm–Schräder and Surber sampling techniques, henceforth abbreviated

AST and ST, respectively. Methods of benthic sampling in lotic biotopes have been described and discussed by e.g. Macan (1958), Albrecht (1959), Cummins (1962), and Schwoerbel (1966).

We used mainly the Surber sampling technique, but since the Alm–Schräder method has been used for many investigations of the benthic communities of north Scandinavian streams, we found it necessary to compare the results produced by the two different methods.

The frame of the Surber sampler used in the present study had the dimensions 60 × 34 cm, thus surrounding an area of approx. 2000 cm^2, and the net had 16 meshes/cm. When taking AST samples, the net held downstream of the stones which were removed was the same as that used for the ST samples.

Estimating the area sampled

Both the ST and the AST techniques have obvious disadvantages, as discussed by Albrecht (op. cit.). When comparing the results obtained, it is imperative to remember that different principles are involved in estimating the bottom area sampled. The Surber frame provides an absolute measure of the area from which the sample is drawn, but this area may include a variable portion of substrate unsuitable for the benthic community with which we are concerned (cf. Scott & Rushforth, 1959). AST samples, on the other hand, will include only substrate judged by the investigator to be suitable for this community. The area covered by AST samples is usually estimated by multiplying the length by the width of each stone in the sample and summing up the products. The measurement thus obtained is not immediately referable to the bottom as such but is an expression of a "standard area" useful for comparative objectives (cf. Ulfstrand, 1968). The question then is: how large a standard area corresponds to a Surber area ("correct" bottom area)?

This was examined through taking AST samples within the Surber frame, that is, removing all stones large enough to be regarded as suitable substrate for the benthic community. The stones removed were measured as described above.

Seventeen such comparisons were made. It was found that the 2000 cm^2 comprised within our Surber frame corresponded to a standard area of approx. 1400 cm^2. In average, then, 600 cm^2 of the area within the frame were largely unsuitable for the community. The variation was of course very great, the standard deviation being approx. 500. To compensate for the proportion of the area sampled being unsuitable, standing crop values obtained with the ST method have to be multiplied with a factor of approx. 1.4 to be comparable to those obtained with the AST method. Conversely, to refer AST samples to absolute bottom area a factor of approx. 0.7 has to be employed.

Comparison of AST and ST results

Apart from the difference between the two techniques in estimating the bottom area from which a given sample derives, one may also suspect the presence of differences in terms of sampling efficiency. In other words, it is far from clear that the same proportion of the animals present within the area sampled will be collected with the two methods. Furthermore, the efficiency may be different for different taxa. This question will be examined on the basis of samples taken at locs. 6 and 11.

Average *total standing crop* (TSC) at loc. 6 according to the results of 55 ST samples amounted to 55 mg/2000 cm^2, equal to, after correction for "unsuitable substrate", 79 mg/2000 cm^2. Average TSC according to the results of 6 AST samples, covering in all about 1 m^2, was found to be 248 mg/2000 cm^2. This figure is approximately three times higher than the corrected ST value. At loc. 6, the community consisted mainly of nymphs of the stonefly *Brachyptera risi* and of simuliid larvae. Closer inspection of the data shows that the average number of simuliids in the ST samples were 8 (after correction = 12)/2000 cm^2 but 57/2000 cm^2 in the AST samples. Corresponding values are for the stonefly nymphs 5 (after correction = 8)/2000 cm^2 in the ST samples and 16/2000 cm^2 in the AST samples.

Loc. 11 was found to yield a TSC of 331 mg (after correction = 473 mg)/2000 cm^2 on the basis of 21 ST samples. Six AST samples covering in all approx. 9000 cm^2 produced a TSC value of 664 mg/2000 cm^2. The AST samples yielded higher values per unit area for all taxa, but the difference was particularly great for simuliid pupae, which occurred in twenty times higher abundance in the AST samples.

With respect to the different handling of the

Table 1. List of species of Ephemeroptera, Plecoptera, and Trichoptera obtained at the different localities, which have been placed in sequence from west to east (approx. from higher to lower altitudes). N. B. Locs. 19, 20, and 22 were only briefly visited on a few occasions. Locs. 11, 19, and 20 were not visited during the field work period in October.
i = imago, j = juvenile stage.

	Localities:								
	7	6	12	4	2	11	22	20	19
Ephemeroptera									
Siphlonurus lacustris Etn.	—	—	—	—	j	—	—	—	—
Ameletus inopinatus Etn.	ij	—	ij	ij	j	i	—	—	—
Parameletus chelifer Bgtss.	—	—	j	j	—	—	—	—	—
Baetis fuscatus L.	—	—	—	—	j	j	j	j	—
B. lapponicus Bgtss.	j	—	ij	j	j	j	—	—	—
B. macani Kimm.	—	—	ij	—	j	j	—	—	—
B. muticus L.	—	—	—	—	j	j	—	j	—
B. rhodani Pict.	—	—	j	j	j	ij	j	j	j
B. subalpinus Bgtss.	—	—	—	—	j	—	—	j	—
Heptagenia dalecarlica Bgtss.	—	—	—	—	—	—	j	j	j
H. sulphurea Müll.	—	—	—	—	—	—	—	—	j
Arthroplea congener Bgtss.	—	—	—	—	—	—	—	i	—
Leptophlebia vespertina L.	—	—	—	—	—	—	—	i	—
Paraleptophebia strandi Etn.	—	—	—	—	—	—	—	—	i
Ephemerella aurivillii Bgtss.	—	—	—	—	j	—	j	—	—
E. mucronata Bgtss.	—	—	—	—	—	i	—	—	—
Plecoptera									
Brachyptera risi Mort.	j	j	j	—	j	—	—	—	—
Taeniopteryx nebulosa L.	—	—	—	—	j	—	j	—	—
Amphinemura standfussi Ris	j	—	ij	ij	j	j	j	—	—
A. sulcicollis Steph.	—	—	—	—	—	j	ij	i	j
Nemoura arctica Esb.-P.	j	j	ij	i	—	—	—	—	—
N. cinerea Retz.	ij	ij	j	ij	i	i	i	—	i
Nemurella picteti Klp.	j	—	—	ij	—	—	—	—	—
Protonemura meyeri Pict.	—	—	—	j	—	—	j	—	—
Leuctra digitata Kmp.	—	—	—	ij	ij	j	ij	i	—
L. fusca L.	—	—	—	j	j	j	j	j	j
L. hippopus Kmp.	j	—	—	—	—	—	—	—	—
L. nigra Ol.	—	i	—	—	—	—	—	—	—
Capnia atra Mort.	—	ij	—	j	—	—	—	—	—
Capnopsis schilleri Rost.	—	i	—	ij	—	—	—	—	—
Arcynopteryx compacta McL.	j	—	j	—	—	—	—	—	—
Diura nanseni Kmp.	j	—	j	ij	j	ij	j	j	j
Isoperla grammatica Pod.	ij	—	—	ij	j	—	—	i	—
I. obscura Zett.	i	i	i	ij	—	—	—	—	—
Chloroperla burmeisteri Pict.	j	—	—	—	i	—	—	i	—
Trichoptera									
Rhyacophila nubila Zett.	—	—	j	ij	ij	ij	ij	ij	j
Philopotamus montanus Don.	—	—	—	—	—	j	—	—	—
Arctopsyche ladogensis Kol.	—	—	—	—	—	—	—	—	j

	Localities:								
	7	6	12	4	2	11	22	20	19
Hydropsyche sp.	—	—	—	—	—	—	j	—	j
Plectrocnemia conspersa Curt.	—	—	—	—	j	ij	—	—	—
Polycentropus flavomaculatus Pict.	—	—	—	—	—	—	i	ij	i
Micrasema sp.	—	j	j	j	—	—	—	—	—
Apatania stigmatella Zett.	ij	ij	ij	j	ij	ij	—	—	—
A. zonella Zett.	ij	i	—	—	—	—	—	—	—
Limnephilus borealis Zett.	—	—	—	—	—	—	i	—	—
L. femoratus Zett.	—	—	—	—	—	i	—	—	—
L. rhombicus L.	—	—	—	—	i	—	—	—	—
Phacopteryx brevipennis Curt.	—	—	—	—	—	i	—	—	—
Rhadicoleptus alpestris Kol.	—	—	—	—	—	—	—	—	i
Potamophylax cingulatus Steph.	ij	j	j	ij	—	i	i	j	i
Halesus radiatus Curt.	—	—	—	—	—	i	—	—	—
Lepidostoma hirtum Fbr.	—	—	—	—	—	—	—	—	j
Athripsodes nigronervosus Retz.	—	—	—	—	i	—	i	—	—
Molannodes tincta Zett.	—	—	—	—	i	—	—	—	—

Unidentified nymphs of Siphlonurus sp. were found at locs. 7, 4, 2, and 11; imagines of Heptagenia sulphurea/dalecarlica at loc. 19; limnephiline larvae at locs. 7, 6, 4, and 2.

substrate it is scarcely surprising that animals that cling to the stones become strongly underrepresented in the ST samples. Clearly AST sampling will produce results that approach correctness much better than ST sampling. On the other hand, AST work is extraordinarily time-consuming. Therefore, when the purpose is a survey covering a considerable number of localities or when seasonal or other comparisons are the main objective, ST sampling may yield adequate information to a much lower cost.

Both AST and ST samples cover only that part of the benthic community that exists on the bottom surface or immediately below the larger stones. Certain species or stages dwell in deeper layers and require special sampling techniques.

Drift sampling

The drift of macroscopic animals was sampled using an acryl tube with an inner diameter of 7 cm and a length of 200 cm. The tube was placed in the stream where a small waterfall made it possible to mount it in such a position that its downstream end protruded above the water surface. From the tube the water passed through a net with 25 meshes/cm. This was arranged in such a way that clogging did not occur. The quantity of water passing through the tube was estimated by clocking the time it took to fill a 15 litre bucket. The net was emptied and reset every day, and at the same time the flow through the tube was measured.

Composition of the fauna

Tab. 1 lists all species of Ephemeroptera, Plecoptera and Trichoptera collected at the nine sampling localities during the present investigation. Some additional species were taken in a light trap, as discussed below. The nomenclature follows Limnofauna Europaea (Illies, 1967) with certain exceptions for which reasons have been given elsewhere (Ulfstrand, 1968, 1970). The list includes no faunistically unexpected species. Sixteen species of mayflies, nineteen of stoneflies and the same number of caddisflies were identified in this collection.

Certain species were found only as adults, not as juveniles. This applies to the mayflies *Arthroplea congener, Leptophlebia vespertina,* *Paraleptophlebia strandi* and *Ephemerella mucronata*, the stonefly *Leuctra nigra* and the caddisflies *Limnephilus borealis, L. femoratus, L. rhombicus, Phacopteryx brevipennis, Rhadicoleptus alpestris, Halesus radiatus, Athripsodes nigronervosus* and *Molannodes tincta*. Limnephiline caddis larvae are often impossible to identify to species, and our material includes a limited number of such larvae, usually of small size. Although certain aquatic insects have excellent powers of dispersal, there is nothing speaking against the acceptance of all species included in Tab. 1 as members of the local fauna. Many of them, however, do not belong to communities inhabiting lotic biotopes.

As our field work only covered two restricted periods, the list must be regarded as far from complete. In particular, the caddisflies are poorly represented. As a matter of fact caddisflies were unexpectedly scarce during our field work periods. Whether this was caused by some temporary condition or reflected a true poverty in terms of species and individuals is of course impossible to decide.

Notes on the benthic community of a disturbed stream

Vietasätno (see Fig. 2) is a big river with a strong fall gradient. Shortly upstream of the village of Vietas, however, the slope becomes less steep and the stream widens, covering extensive areas with only shallow water. Speaking from considerable experience, such a locality can be expected to harbour a benthic community rich in both species and individuals.

Since River Vietasätno has been very drastically affected by the impoundment of Lake Satihaure—in fact, this river has been almost dry for certain periods but on the other hand has transported abnormally large water volumes on other occasions—we regarded it as important to examine its benthic animal communities.

On 12 July nine AST samples were taken at the site described above, covering a total surface area of approx. 1.3 m^2. The total content was two simuliid larvae and a few chironomid larvae.

On 22 July fifteen ST samples were taken at the same site, covering 3 m^2 (4.2 m^2, after correction for "unsuitable area"). The total result consisted of five blackfly larvae and one pupa, twenty chironomid larvae and one mayfly nymph (*Siphlonurus sp.*—a genus of largely lenitic species).

On this evidence, it seems justified to classify Vietasätno as something of a biological desert. The few animals we obtained had probably drifted in from some undisturbed or at least less damaged tributary. With respect to the violent interference with natural conditions that has affected Vietasätno, the absence of a benthic animal community on its bottom is hardly astonishing (cf., e.g. Chutter, 1969).

Notes on the insects of disturbed lake shores

As mentioned previously the lakes in the central valley of SSNP have been subjected to repeated regulations.

At Lake Kårtjejaure, attempts were made to investigate whether any number of amphibiotic insects emerged from the litoral zone. Therefore, a great number of stones along the shore were examined. At undisturbed lake shores this work usually yields a rich harvest of Ephemeroptera, Plecoptera and Trichoptera. We were, however, able to obtain only an extremely small number of specimens, belonging to *Diura bicaudata* L. and *Potamophylax latipennis* Curt.

From 23 July to 30 September, 1969, a light trap fitted with a UV lamp (Philips HPW 125 W) with maximal emission at 3655 Å was operated at the eastern part of Lake Suorvajaure. The total catch during this period of more than two months amounted to 791 individuals of 19 species of Trichoptera (Tab. 2); no mayflies and only a very few stoneflies (*Isoperla obscura, Diura bicaudata, Leuctra fusca*) were obtained. Moreover, since a small stream fell into the lake only some 50 m from the trap site, a certain proportion of the caddisflies trapped probably derived from that stream. This is, for example, almost certain for *Rhyacophila nubila* and quite likely for *Apatania stigmatella*. An excess of males over females in most limnephilids has been found elsewhere and has been tentatively interpreted as indicating that males tend to travel over larger distances than females; in the present collection, *Potamophylax latipennis* is the only exception which would fit in with the fact

Table 2. Trichoptera obtained in a light-trap at the eastern end of Lake Suorvajaure from 23 July to 30 September, 1969.

	Males	Females	Total
Rhyacophila nubila Zett.	37	19	56
Polycentropus flavomaculatus Pict.	—	1	1
Limnephilus rhombicus L.	1	—	1
L. borealis Zett.	25	—	25
L. externus Hag.	1	—	1
L. stigma Curt.	1	—	1
L. coenosus Curt.	26	—	26
L. algosus McL.	1	—	1
Asynarchus lapponicus Zett.	5	—	5
Rhadicoleptus alpestris Kol.	1	—	1
Potamophylax nigricornis Pict.	9	—	9
P. cingulatus Steph.	7	—	7
P. latipennis Curt.	5	13	18
Halesus radiatus Curt.	1	—	1
H. tesselatus Ramb.	1	—	1
H. digitatus Schrk.	24	—	24
Chaetopteryx villosa F.	2	1	3
Apatania stigmatella Zett.	235	367	602
A. zonella Zett.	—	8	8
			791

that this species seems to reproduce in big lakes and therefore the individuals trapped might have hatched closer to the trap site then those of most other species (Ulfstrand, 1970).

It is difficult to compare the trapping result with those achieved elsewhere in northern Sweden, but it is legitimate to state that both qualitatively and quantitatively the catch was very poor indeed (cf. Ulfstrand, op. cit.; Tobias, 1968).

The depauperization of the littoral benthic community accompanying lake impoundments has been studied in detail by Grimås (1962, 1965). The present findings confirm the general validity of his results.

Benthic communities of the six main study localities

Standing crop values in summer and autumn

Relevant data concerning the standing crop values in summer and autumn are presented in Tab. 3. ST samples yielded total standing crop[1] values below 1 g/m^2 in summer except at loc. 11 with a value twice that of any other locality. After correction of "unsuitable substrate" (p. 315) the values reached or passed 1 g/m^2. As expected, AST samples produced much higher values. Comparing the localities at which AST samples were taken, loc. 6 stands out having a remarkably low TSC. The general distinctiveness of loc. 11 was largely due to the abundance of blackfly larvae.

Autumn TSC values were invariably much lower than summer values. Locs. 6 and 12 were almost devoid of animal life in autumn. The relatively high value at loc. 7 is largely accounted for by the presence of a small number of very heavy tipulid larvae. An important reason for the low autumn values is the virtual absence of blackfly larvae; the species inhabiting the small streams examined apparently spend the winter in the egg stage.

[1] The total standing crop of all taxa sampled is abbreviated as TSC and the standing crop of any particular taxon as SC.

Table 3. Total standing crop values in summer and autumn assessed using Surber (ST) and Alm-Schräder (AST) sampling techniques. For the relationship between bottom area and standard area, see p. 315.

Loc.	Date	Method	Area (m^2)	Total standing crop (g/m^2 bottom area)	Total standing crop (g/m^2 standard area)
7	15/7	ST	1.2	0.83	1.16
	12/10	ST	1.8	0.33	0.46
6	13/7	ST	1.2	0.32	0.45
	12/10	ST	1.2	0.01	0.01
12	27/7	ST	2.4	0.74	1.04
	13/10	ST	1.2	0.06	0.08
4	1/8	ST	1.2	0.43	0.60
	11/10	ST	1.2	0.18	0.25
2	25/7	ST	2.4	0.77	1.08
	11/10	ST	1.2	0.11	0.15
11	18/7	ST	1.0	1.64	2.30
7	16/7	AST	1.0	3.55	5.06
6	14/7	AST	0.9	0.89	1.27
11	19/7	AST	0.9	2.24	3.20

The AST samples produced TSC estimates which agree well with those obtained by Ulfstrand (1968) in the upper parts of River Vindelälven and its tributaries, if lake outlet localities are excluded. Apart from such places, north Scandinavian streams are usually characterized by low TSC values compared with, for example, streams in central and western Europe (cf. Albrecht, 1959). One of the reasons is that some taxa that are of great quantitative significance in more southerly regions, such as amphipods, isopods, gastropods and bivalves, are practically lacking in north Scandinavian running waters.

Small-scale intrariverine differences

Method

At the six main localities the "microdistribution" of standing crop values of the different taxa was studied. At a number of sites one Surber sample was taken, and at the same time certain environmental features were recorded, viz. current velocity (measured with an Ott propeller at 5 cm above the bottom), depth and substrate, including presence of accumulated litter and macrovegetation. The distance between sampling sites varied between approx. 25 and 100 cm. Sites were selected to represent a full variety of environmental conditions at the locality studied.

The results are presented for each locality in Figs. 5 to 10. It should be kept in mind that the standing crop weights are based on ST samples the results of which have not been corrected for the proportion of "unsuitable substrate" (cf. p. 315) but are expressed in relation to absolute bottom area.

It is clear that the present procedure hardly allows a refined analysis of the relationships between various environmental features and the microdistribution of the different species. Still, however, with regard to the very scanty information available about the benthic communities of north Scandinavian streams, we believe that the survey achieved is of considerable interest.

Results

Loc. 7. 15 July. 27 samples. Fig. 5.

The stream bottom was covered by naked stones, in places with relatively coarse detritus and moss tufts. The average TSC of the 27 samples amounted to 249 mg/200 cm^2 = approx. 1.2 g/m^2. Of the TSC, 42 per cent consisted of blackfly larvae and pupae. Stoneflies and caddisflies each made up approximately one quarter of the TSC, while mayflies were scarce. Dipteran larvae other than simuliids were relatively important; chironomids were numerous but weighed so little that they were insignificant in terms of standing crop, while tipulids were few but very heavy.

By far the dominant stonefly was *Brachyptera risi*, but several other species were present in so many samples that they no doubt belonged to the local community rather than being stragglers from neighbouring ones. Among the caddisflies, *Apatania stigmatella* dominated in terms of numbers, but *Potamophylax cingulatus*, though not numerous, was also important because of the heaviness of its larvae and pupae.

As apparent from Fig. 5, high blackfly SC values were usually found at sites with naked stones, sometimes also at those with some detritus, while mossy sites were avoided. Blackflies also seemed to be favoured by high current velocity (but see site 20). Sites 22 to 24 were characterized by particularly abundant moss, and showed very low SC values for all the three dominant taxa. High SC values of caddisflies were rarely found at sites with high current velocity.

High SC values for all three taxa coincided at no site. Two of the taxa showed high values at sites 10, 21, 25, and 26; at three of these, high values of stoneflies and blackflies coincided and at the fourth, caddisflies and stoneflies.

Loc. 6. 13–14 July. 55 samples. Fig. 6.

This locality was characterized by particularly uniform substrate conditions, there being only negligible amounts of debris and of moss. The average TSC was extraordinarily low, 55 mg/2000 cm^2 = approx. 0.28 g/m^2. Blackflies made up 51 per cent, and stoneflies, almost exclusively *Brachyptera risi*, 45 per cent of the TSC. The remainder consisted of chironomid larvae, a few small oligochaets and a few larvae and pupae of *Apatania stigmatella*. Obviously, the number of species was low.

The microdistribution pattern as reflected in our samples is rather difficult to interpret. Sites 1 to 13, for no apparent reason, exhibited very low SC values for both blackflies and stoneflies. It is true that the current was relatively weak in the area of the stream within which these sites were located, but comparison with other sites outside this limited area having weak current reveals that this cannot be the whole explanation.

There was a high degree of correlation between the microdistribution of the blackfly larvae and the *B. risi* nymphs ($r = +0.48$, $t = 3.97$, $P < 0.001$). However, *B. risi* seemed slightly more dependent on high current speed, for all six sites without any stoneflies were among those with lowest speed.

Loc. 12. 26 July. 17 samples. Fig. 7.

This locality and the next one were characterized by a much more variable substrate than the preceding ones. Stones were of more varying size, and at some sites there were a great deal of coarse litter. Also the current and depth conditions fluctuated within wide limits. The average TSC was 431 mg/2000 cm^2 = approx. 2.2 g/m^2. More than three quarters of the TSC consisted of blackfly larvae and pupae, the remainder being mainly mayflies, among which *Baetis lapponicus* prevailed, with *B. rhodani* constituting only a small minority. Nymphs of the stonefly *Amphinemura standfussi* were frequent but were so small that they did not influence weight measurements appreciably.

As a general rule mayfly nymphs are abundant at places with much detritus. However, at this locality, two of the highest values were obtained at sites having no or very little detritus. This depends on the fact that, according to extensive field experience, *B. lapponicus* differs from most mayfly species in frequently being abundant on substrate consisting of almost purely naked stones. Even in places where the substrate is obviously very unstable, *B. lapponicus* is often numerous. Its flattened body form approaching that of a heptageniid mayfly may be an important adaptation to this kind of substrate.

High blackfly SC values were not recorded at sites with low current velocities. In two cases, high SC values of both blackflies and mayflies coincided. At sites 17 and 18, extremely low SC values of both groups were found, probably because the substrate chiefly consisted of sand.

It is interesting to note that sites 7 and 8 were rated almost identical in terms of environmental features and yet no. 7 harboured large quantities of both blackflies and stoneflies, while no. 8 held very small quantities of both taxa. Sites 5 and 6, on the other hand, although being only approx. 40 cm from each other, were characterized by highly different current, depth and substrate conditions. No. 5 produced practically no blackfly larvae but an abundance of mayflies, while the opposite was true for no. 6.

Loc. 4. 29 July. 28 samples. Fig. 8.

This stream had a steeper fall gradient than the previous one, which, however, it resembled in many

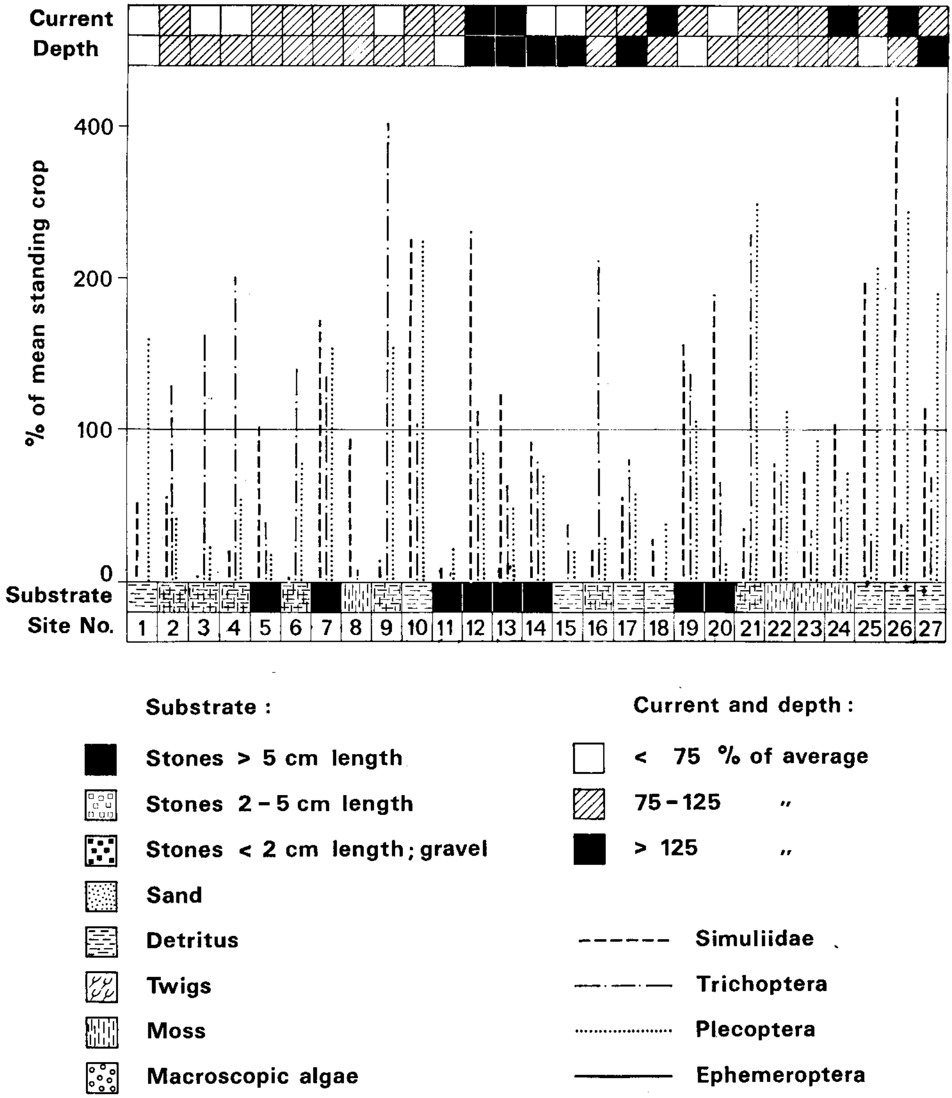


Fig. 5. Loc. 7. Standing crop values at 27 sites expressed as per cent of mean standing crop in relation to certain environmental features.

	Mean standing crop, mg per 2000 cm²	Standard deviation	Standard error of the mean, ±
Total	249	161	31
Plecoptera	68	58	11
Trichoptera	55	50	10
Simuliidae	105	111	21

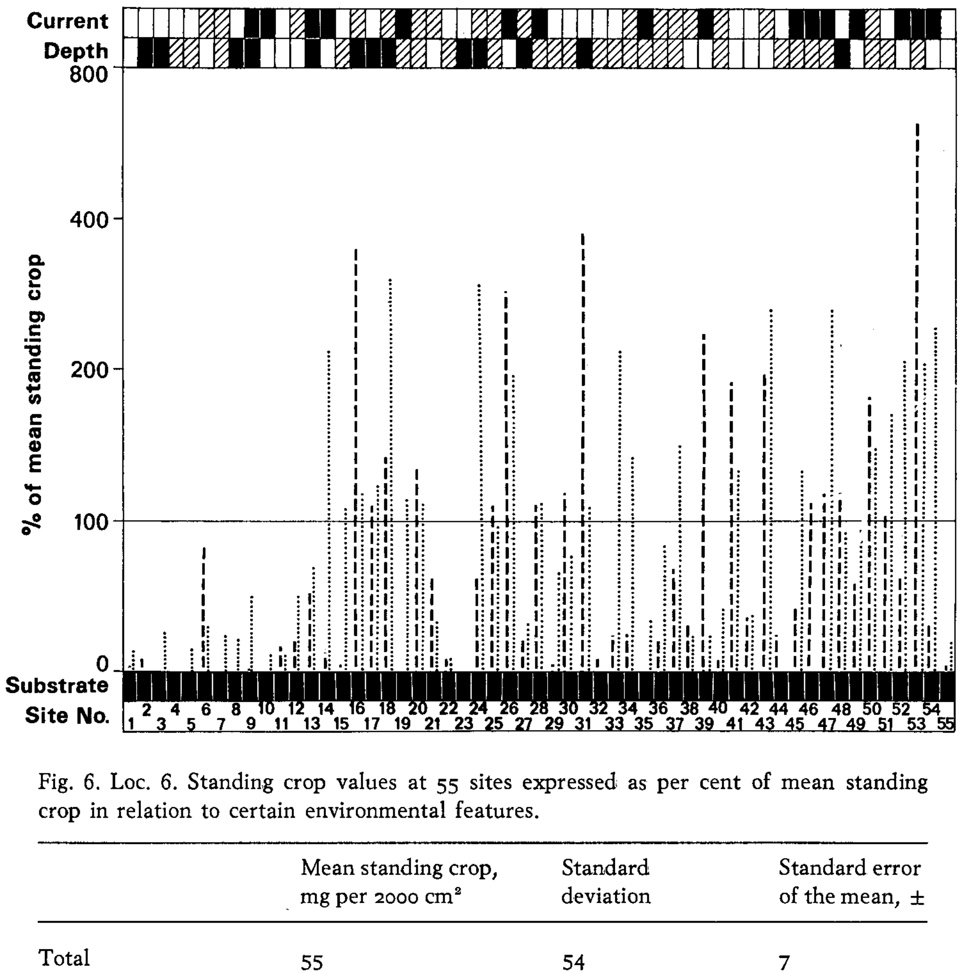


Fig. 6. Loc. 6. Standing crop values at 55 sites expressed as per cent of mean standing crop in relation to certain environmental features.

	Mean standing crop, mg per 2000 cm²	Standard deviation	Standard error of the mean, ±
Total	55	54	7
Plecoptera	25	22	3
Simuliidae	28	40	5

respects. The average TSC value was 242 mg/2000 cm^2 = approx. 1.2 g/m^2. About two thirds of the TSC consisted of blackflies, while stoneflies and mayflies rather equally shared the last third. A few *Rhyacophila nubila* larvae and pupae were the only caddisflies. The lower TSC of this locality in comparison with loc. 4 was chiefly due to the lower blackfly SC; this difference was not made up for by a relatively larger stonefly SC.

Ameletus inopinatus and *Baetis lapponicus* were the dominant mayfly species, at some sites also *B. rhodani*. The preference of *B. lapponicus* for smaller-sized and less stable substrate, as mentioned previously, is confirmed by large numbers of this species at, for example, sites 4 and 23. Usually this species shuns places with sand and other finer fractions filling the crevices between stones and rocks. It is therefore not surprising that the high mayfly SC at site 21, which had this sort of substrate, mainly consisted of *A. inopinatus* which is a "swimming" rather than a "creeping" mayfly.

Blackflies, as usual, were particularly abundant at sites with rapid current. They avoided sites with sand and moss.

Detritus seems to favour high numbers of stoneflies, among which, in terms of weight, *Isoperla grammatica* and *I. obscura* were dominant. Their preference for detritus-rich sites presumably depends on the abundance in the litter deposits of chironomid larvae on which these stoneflies prey (Brinck, 1949).

None of the sites showed high SC values for all

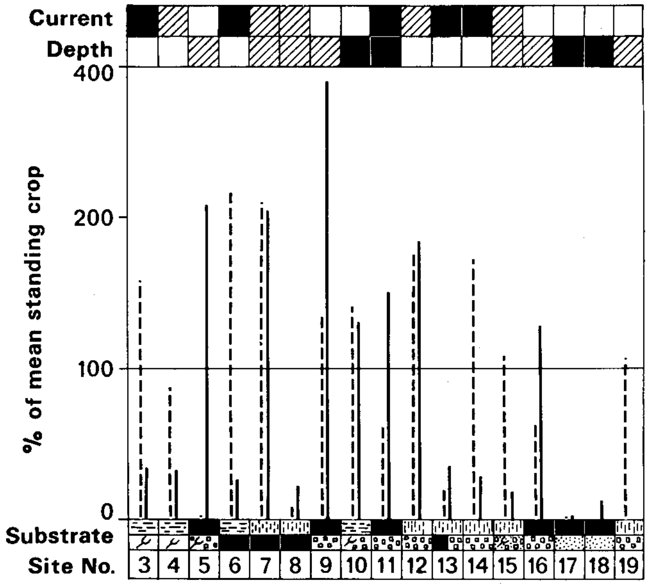


Fig. 7. Loc. 12. Standing crop values at 17 sites expressed as per cent of mean standing crop in relation to certain environmental features.

	Mean standing crop, mg per 2000 cm^2	Standard deviation	Standard error of the mean, ±
Total	431	300	73
Ephemeroptera	84	87	21
Simuliidae	340	267	65

three taxa. Wherever high values of two taxa coincided, the combination was mayflies and stoneflies. Blackflies, thus, seemed to diverge from both groups in terms of microdistribution pattern.

Loc. 11. 18 July. 20 samples. Fig. 9.

At the downstream end of the stretch examined there was a tunnel under a road. Four samples were taken within it, where they received only a dim light, while another two were taken so close to the upstream entrance that they received more light, but by no means as much as fully exposed sites. Inside the tunnel and some distance upstream of it the substrate consisted largely of naked stones. Further upstream, moss, detritus and an abundance of slimy algae were evident.

The average TSC amounted to 328 mg/2000 cm^2 = approx. 1.6 g/m^2. Some 60 per cent consisted of blackflies, while mayflies made up 17 per cent, caddisflies 8 per cent and stoneflies 2 per cent. The dominant mayfly species was *Baetis rhodani*, with *B. lapponicus* in the second place. *B. muticus* and *B. fuscatus* were scarce. *Rhyacophila nubila* was the most prominent caddisfly, but some specimens of *Potamophylax cingulatus, Plectrocnemia conspersa* and *Apatania stigmatella* were also obtained. *Amphinemura standfussi* and *Leuctra fusca* were the stoneflies most often obtained, but the nymphs were too small to influence weight measurements appreciably.

Sample sites with much algae, at times with moss as well, yielded low TSC values. If coarse debris, such as twigs, was also present, values tended to rise. Algal growth seemed particularly unfavourable for the blackflies.

Inside the tunnel, blackfly larvae and pupae were obtained in moderate quantities. At these sites, mayflies were scarce. At the first site so close to the tunnel entrance that it was reached by much light, by far the densest blackfly population of all sites at this locality was found. Whether this had

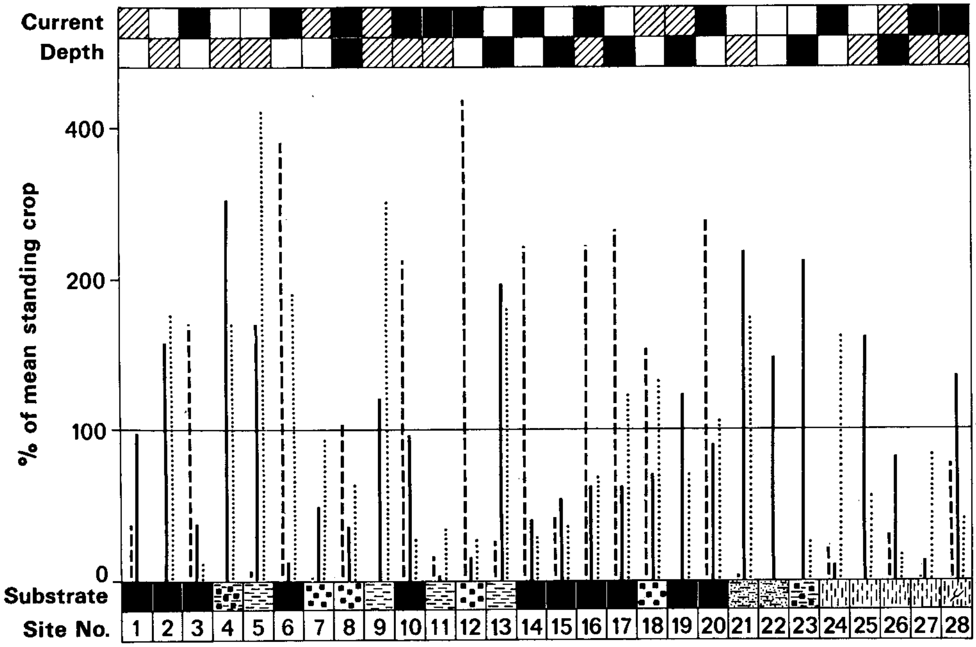


Fig. 8. Loc. 4. Standing crop values at 28 sites expressed as per cent of mean standing crop in relation to certain environmental features.

	Mean standing crop, mg per 2000 cm²	Standard deviation	Standard error of the mean, ±
Total	111	62	16
Ephemeroptera	38	27	7
Plecoptera	12	14	4
Simuliidae	56	69	17

something to do with the tunnel and its light-screening effect is impossible to decide. Also the mayflies were above the average at the sites near the tunnel entrance.

The ratio between *Baetis lapponicus* and *B. rhodani* changed along the stream course. The former species was more abundant than, or at least as abundant as, the latter species inside and just outside the tunnel, where, significantly, the substrate consisted of naked stones and was clearly unstable. Further upstream, where litter and algae became prominent, *B. rhodani* was the dominant species. The highest mayfly SC, which was found at site 17, consisted entirely of *B. rhodani.*

Rhyacophila nubila larvae of different sizes showed a tendency of having different microdistribution patterns within the stream section examined. Larger larvae as well as pupae were found chiefly at the uppermost nine sites, smaller larvae at the lower ones. A similar situation was indicated at loc. 2 (q.v.).

Site 5 was the only one with high SC values for both blackflies and mayflies. Otherwise, these two taxa were well separated. Site 5 was situated close to the upstream end of the road tunnel, as discussed above.

Loc. 2. 21 July. 23 samples. Fig. 10.

As pointed out in the locality descriptions, this locality resembled the preceding one, but the stream was rather smaller. Detritus, moss and algae were plentiful at most sites, only five of which were classified as being dominated by naked stones. The average TSC was 263 mg/2000 cm² = approx. 1.3 g/m². About half the TSC was composed of blackflies, one third of mayflies, 12 per

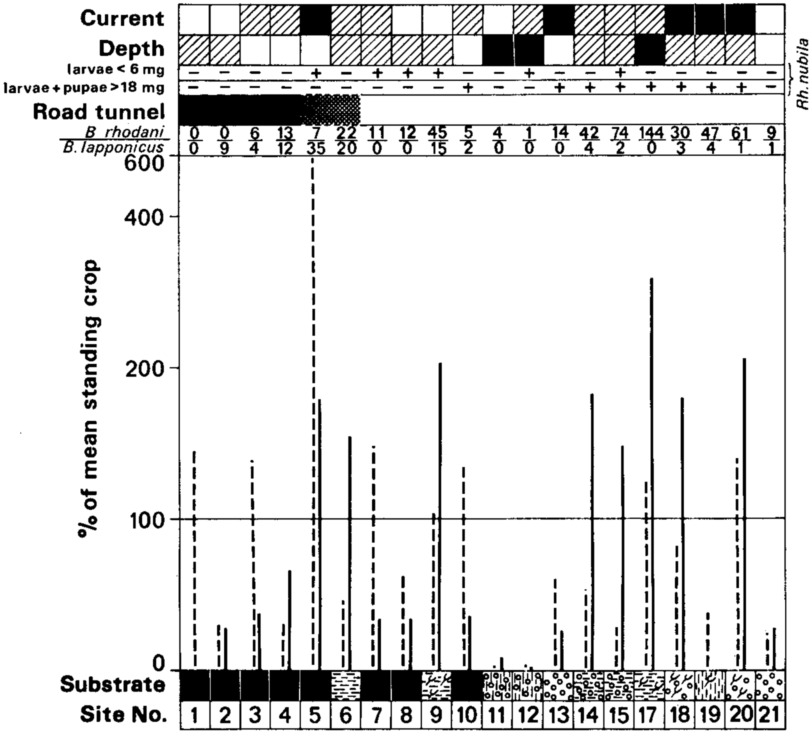


Fig. 9. Loc. 11. Standing crop values at 20 sites expressed as per cent of mean standing crop in relation to certain environmental features.

	Mean standing crop, mg per 2000 cm^2	Standard deviation	Standard error of the mean, ±
Total	328	319	71
Ephemeroptera	55	51	11
Trichoptera	28	35	8
Simuliidae	234	294	66

cent of caddisflies and 4 per cent of stone-flies. *Baetis rhodani* was the clearly dominant mayfly species, followed by *B. lapponicus* and *B. macani.*

The five sites with mainly naked stones contained most of the blackflies which were relatively sparse at the other sites.

B. lapponicus and *B. macani* were differently distributed at the sampling sites. The former was dominant at the lower sites with little detritus, the latter at the upper sites with much more detritus. Generally speaking, *B. macani* is less tied to running water than any other Scandinavian *Baetis* species; in fact, it is frequently met with in purely lenitic environments.

The dominant stonefly species were *Leuctra fusca* and *Amphinemura standfussi*, both of which were most abundant at sites with much detritus.

The caddisfly population consisted chiefly of larvae and pupae of *Rhyacophila nubila*. As at loc. 11, there was a difference in the distribution pattern of different size classes. The lower sites contained only small larvae, the middle and upper ones only big larvae and pupae. At both localities, the small larvae were found chiefly at sites with little or no moss and detritus. The preference of the big larvae for sites rich in detritus may depend on the more abundant supply of prey organisms, as was argued for the predatory stoneflies at loc. 4.

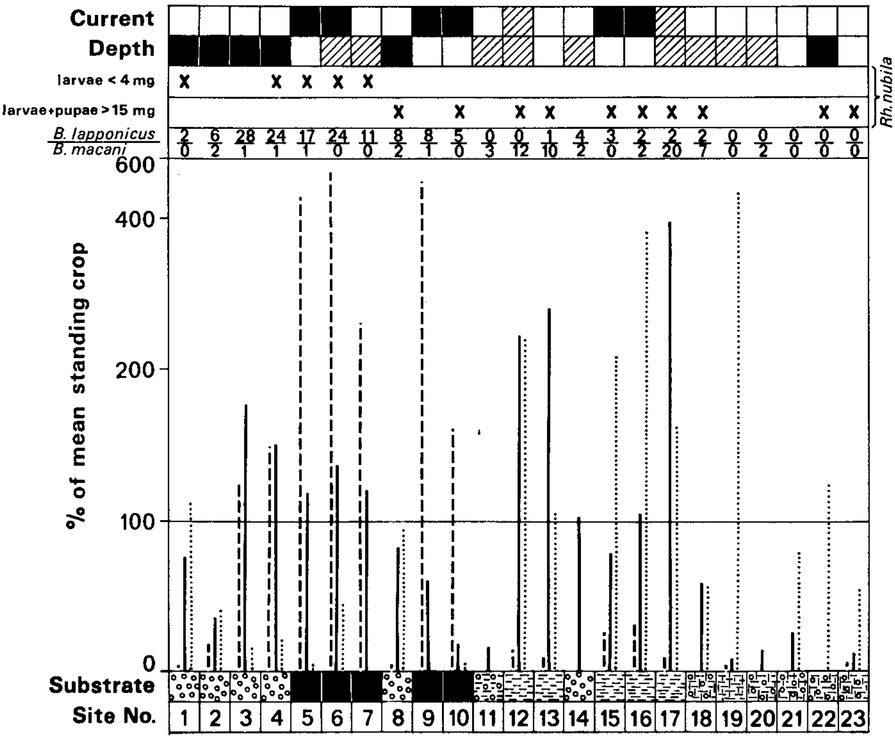


Fig. 10. Loc. 2. Standing crop values at 23 sites expressed as per cent of mean standing crop in relation to certain environmental features.

	Mean standing crop, mg per 2000 cm²	Standard deviation	Standard error of the mean, ±
Total	263	236	49
Ephemeroptera	88	87	18
Plecoptera	10	14	3
Trichoptera	33	49	10
Simuliidae	132	221	46

Larger-scale intrariverine differences

The sampling sites between which the differences have been examined in the previous paragraph were situated close to one another. It may be asked if and to what extent the intrariverine differences would increase with an increasing distance between sample sites (cf. Mackay, 1969). This question was examined at locs. 7, 12 and 4.

The procedure employed was the same as in the preceding section, only the distance between sample sites were in the order of tens or hundreds of meters and three Surber samples, rather than one, were taken at each site.

Loc. 7. 8 and 14 August, 12 samples; 12 October, 10 samples. Tab. 4.

On the two dates in August samples were taken at irregular distances from the mouth of the stream in Lake Satihaure (approx. 350 m below the stream section dealt with on p. 320) to the foot of Nieras (approx. 1400 m upstream of that section).

Standing crop values were very low throughout.

Table 4. Standing crop values along the stream course at loc. 7. Three Surber samples comprising in all 0.6 m² were taken at each site on each occasion.

Date	Distance from mouth (m)	TSC g/m²	Plecoptera SC g/m²	Epheme-roptera SC g/m²	Trichop-tera SC g/m²	Simuliidae SC g/m²	Comments
14/8	Lake shore	0	0	0	0	0	
14/8	10	0.05	0	0	0.05	0	
14/8	50	0.14	0.03	0	0.07	0.02	
14/8	250	0.27	<0.01	0	0.17	0.02	
8/8	350	0.16	0.10	0	0.04	0.02 }	At sites
8/8	550	0.62	0.27	0	0.05	0.26 }	for mapping
8/8	725	0.19	0.04	0	0.11	0.05	
8/8	925	0.29	0.02	0	0.04	0.24	
8/8	1100	0.19	0.08	0.06	0.04	0	
8/8	1250	0.04	0.01	0	0.02	0.01	
8/8	1275	0.22	0.02	<0.01	0.17	0	
8/8	1325	0.51	0.07	0.16	0.06	0	At the moun-
14/8	1425	0.03	0	0	0.01	0.02	tain slope
12/10	325	1.09	0.03	0	0.05	0	Mainly ti-
12/10	340	0.17	0.04	0	0.07	0	pulid larvae
12/10	360	0.03	0.01	0	0.01	0	
12/10	380	0.01	<0.01	0	<0.01	0	
12/10	400	0.26	0	0	0.22	0	
12/10	435	0.11	0.01	0	0.07	<0.01	
12/10	455	0.12	0	0	0.07	0	
12/10	475	0.04	0.01	0	0.03	0	
12/10	490	0.11	0.02	0	0.02	0	
12/10	520	0.10	0.01	0	0.08	0	

No trend of change along the stream course is apparent. No animals were taken in the sample from just outside the mouth of the stream, as might be expected, since Lake Satihaure is impounded and subject to abnormal water level fluctuations (cf. p. 318). These fluctuations probably make themselves felt for some distance upstream of the shoreline. The slightly elevated stonefly SC values at 350 and 550 m from the lake, i.e. close to where the more detailed study was carried out, was due to a locally restricted population of *Brachyptera risi.* Mayflies, mainly *Baetis lapponicus,* were found only at some of the uppermost sites. At 1425 m upstream from the lake, the site was characterized by such a steep gradient that the water partly fell through the air. There was very little substrate other than bedrock, so that the scarcity of animals was not surprising; only a few blackfly larvae and some pupae of *Apatania stigmatella* were obtained.

The October samples derive from a much shorter section of the stream. SC values are extremely low, apart from one site, where a relatively high value was caused by a few very big tipulid larvae.

It seems correct to conclude that no significant trend in terms of quantitative or qualitative community composition was discernible along the stream course examined.

Loc. 12. 11 and 12 August, 16 samples; 13 October, 7 samples. Tab. 5.

The lowermost sample was taken in a small bay just outside the mouth of the stream. In August, samples were scattered over a distance of approx. 250 m, and in October over approx. 75 m.

In the August sample series, TSC values tended to rise at the more upstream sites. This is due to increasing numbers of stoneflies, among which

Table 5. Standing crop values along the stream course at loc. 12. Three Surber samples comprising in all 0.6 m^2 were taken at each site on each occasion.

Date	Distance from mouth (m)	TSC g/m^2	Plecoptera SC g/m^2	Ephemeroptera SC g/m^2	Trichoptera SC g/m^2	Simuliidae SC g/m^2	Comments
11/8	−20	0.19	0	0.09	0.07	0	In shallow
	−2	0.14	0.03	0.09	0.02	0	bay
	0	0.10	0	0.09	0	<0.01	
	10	0.38	<0.01	0.08	0	0.29	
	30	0.24	<0.01	0.23	0	0	Location of
	40	0.36	0	0.28	0.01	0.04 }	sites for
	50	0.36	<0.01	0.35	0	0.01 }	detailed
	70	0.52	0.01	0.18	0	0.20	study
12/8	80	0.36	0.02	0.11	0	0.20	
	85	0.22	0.01	0.20	0	<0.01	
	100	0.32	0.02	0.23	0	0.03	
	125	0.22	0	0.20	0	0	
	145	0.86	0.03	0.38	0	0.37	
	150	0.37	0.05	0.09	0	0.06	
	175	0.87	0.02	0.20	0	0.51	
	200	1.28	0.07	0.27	0	0.77	
	210	0.32	0.03	0.10	0	0.20	
13/10	−10	0.03	<0.01	0	0	0	
	0	<0.01	0	0	<0.01	0	
	30	0.01	0.01	0	0	0	
	40	<0.01	<0.01	0	0	0	
	50	<0.01	<0.01	0	0	0	
	60	<0.01	<0.01	0	0	0	
	65	0.04	0.04	0	0	0	

Amphinemura standfussi dominated, and blackflies. Caddis larvae were obtained only outside the mouth of the stream and were *Potamophylax sp.* Mayfly SC values did not show any noticeable change along the stream, but the specific composition did change. Thus, at the lower sites, *Baetis rhodani* and *B. macani* were common, at the middle ones the former became scarce and the latter disappeared, while *B. lapponicus* became prevalent, and at the uppermost ones the last-mentioned species was practically the only one.

Hence a certain change along the stream course is discernible at this locality, although the distance covered was quite brief.

The October samples produced extremely few animals; those that were found were chiefly stoneflies, mainly *Nemoura cinerea*, but also a few *Arcynopteryx compacta, Diura nanseni* and *Brachyptera risi.*

Loc. 4. 6 and 7 August, 15 samples; 11 October, 11 samples. Tab. 6.

The present sample series was started at a distance of approx. 200 m upstream from where the microdistribution samples were taken, that is, about 275 m from the mouth of the stream. In August, samples were taken with such intervals that the uppermost ones were located above the tree line on the mountain moorland. The October series comprised a shorter section.

In the August series, the middle sites yielded higher values than the remainder of the sites. This was chiefly due to higher density of blackfly larvae. To a lesser extent, the same was the case for the other groups. The uppermost two sites were close to the source of the stream at a very steep slope. A small number of blackfly larvae were the only animals obtained there. They must rely for food on benthic algae appearing in the drift (Müller-

Table 6. Standing crop values along the stream course at loc. 4. Three Surber samples comprising in all 0.6 m² were taken at each site on each occasion.

Date	Distance from mouth (m)	TSC g/m²	Plecoptera SC g/m²	Epheme-roptera SC g/m²	Trichop-tera SC g/m²	Simuliidae SC g/m²	Comments
6/8	250	0.29	0.01	0.01	0.03	0.17	Mixed forest
	350	0.40	0.05	0.08	0.07	0.18	Mixed forest
	450	0.54	0.07	0.03	0.01	0.35	Mixed forest
	550	0.36	0.08	0.04	0.10	0.14	Mixed forest
	650	0.34	0.06	0.16	0.04	0.08	Mainly birch forest
	850	0.74	0.08	0.06	0.06	0.54	Birch forest
	1050	0.66	0.09	0.08	0.05	0.44	Birch forest
7/8	1350	0.77	0.06	0.14	0.05	0.52	Sparse birches
	1450	0.64	0.15	0.04	0.36	0.02	Sparse birches
	1650	0.40	0.09	0.07	0.21	0.03	Birch scrub only
	1850	0.22	<0.01	0.07	0.02	0.04	Moorland
	2150	0.32	0.06	0.06	0.03	0.07	Moorland
	2450	0.14	0.03	0.02	0.06	0.04	Moorland
	2850	0.19	0	0	0	0.19	Moorland, steep slope
	2900	0.05	0	0	0	0.05	Ditto, at stream scarce
11/10	75	0.26	0.06	0	0	0	Mixed forest
	75	0.11	0.11	<0.01	0	0	Mixed forest
	95	0.30	0.08	0	0	0	Mixed forest
	95	0.09	0.09	0	0	0	Mixed forest
	115	0.03	0.02	<0.01	0	0	Mixed forest
	115	0.02	0.02	0	0	0	Mixed forest
	135	0.02	0.01	<0.01	0	0	Mixed forest
	155	0.05	0.05	0	0	0	Mixed forest
	160	0.03	0	0	0.03	0	Mixed forest
	165	0.05	0.02	<0.01	0.01	0	Mixed forest
	165	0.11	0.05	0.01	0.04	0	Mixed forest

Haeckel, 1970) and produced locally. The relatively high values of caddisfly SC at the middle sites were due to the presence of larvae and pupae of *Rhyacophila nubila*.

Amphinemura standfussi was regularly met with up to and including the site at 1350 m but further upstream was replaced by *Nemoura cinerea* and *N. arctica*. Among the mayflies, *Ameletus inopinatus*, *Baetis rhodani* and *B. lapponicus* were regularly obtained. The first-mentioned species was the only mayfly at 1850, 2150, and 2450 m, but was absent or only occasionally found at the lower sites, where *B. rhodani* was dominant. *Apatania stigmatella* occurred all along the stream, while, as mentioned above, *Rh. nubila* was concentrated to the middle sites.

In October, as usual, TSC values were low. *Diura nanseni* was the most numerous stonefly and *Baetis rhodani* the only mayfly. A few caddis larvae (*A. stigmatella* and *Rh. nubila*) were also taken.

Short-time changes of standing crop values and of species composition

Method

At loc. 4, 16 of the 28 sites sampled on 29 July (see p. 323) were again sampled on 1 August, i.e. three days later, in order to examine whether the "losses" from our sampling work had been rapidly compensated for and whether the community composition would change within such a short period.

Results

A comparison between the values obtained at the 16 sites on the two occasions shows that the TSC had dropped from 278 to 111 mg/2000 cm^2, the blackfly SC from 202 to 56, and the stonefly SC from 32 to 12, while the mayfly SC had risen from 21 to 38 mg/2000 cm^2. All these differences in terms of average standing crop are significant at between the 0.05 and 0.01 levels.

Judging from the SC values, the mayflies obviously had recolonized the sites completely and more than that. There is a statistically significant correlation between site SC values on the occasions ($r = +0.50$, $t = 2.13$, $P < 0.05$). Thus, the pattern of SC distribution remained the same. With respect to species composition, however, a certain change had taken place, there being proportionately fewer *A. inopinatus* in relation to *B. lapponicus* on the second occasion, but this difference was not quite significant ($\chi^2 = 2.8$). Yet it probably explains why the increase was less in terms of SC than in number of individuals, *B. lapponicus* being a considerably smaller and lighter animal than *A. inopinatus*.

The second series of samples, as mentioned above, yielded a significantly lower average SC value for the stoneflies than the first series. However, it does not follow that the recolonization process had been inadequate to make up for the losses. An alternative possibility is, of course, that some important species on the first occasion had abandoned the sample sites before the second, for example, because of emergence. That this was the case is demonstrated by the fact that a significant change in species composition had taken place: *Isoperla* (*grammatica* + *obscura*) had decreased and *Amphinemura standfussi* had increased ($\chi^2 = 5.5$, $P < 0.05$), while a small number of *Leuctra fusca* nymphs did not influence the figures appreciably. *A. standfussi* is a smallspecies, and many nymphs were young, while *Isoperla spp.* are fairly big species, the nymphs of which were close to emergence. Consequently, the drop in SC value became considerable, although total numbers remained fairly similar. The species composition having changed, the distribution of SC values over the sites may be expected to change as well. This was found to be true to such an extent that a significant negative correlation between the values on the two occasions was found ($r = -0.57$, $t = 2.60$, $P < 0.05$).

Since the blackfly larvae were not identified to species, no similar analysis is feasible in this group. There was a significant positive correlation between site SC values on the two occasions ($r = +0.52$, $t = 2.28$, $P < 0.05$).

Drift and colonization in relation to benthic standing crop

In the manner described before (p. 317), drift samples were taken at all the main localities. We do not have information on the total flow volume of these streams. The quantity filtered in our drift trap was a very small fraction of the whole volume but it is believed that differences in the volume filtered roughly reflected differences of flow volume of the whole stream. The results are shown in Tab. 7, where for comparison relevant data are presented about the density of benthic population at about the same date as the drift samples were taken. The differences in estimates of benthic numbers due to different sampling methods should be kept in mind (see p. 315).

The benthic community at loc. 7 consisted mainly of stoneflies, blackflies and caddisflies. The drift was comparatively small. In particular the caddisflies did not participate very much. The dominant species of this group was *Apatania stigmatella,* which has been known to occur numerously in drift elsewhere, the larvae having discarded their cases before joining the drifting fraction (Ulfstrand, 1968).

At loc. 6 the drift reflected the composition of the benthic community rather accurately. Caddisflies were so scarce on the bottom that their absence in the drift samples is hardly surprising. The first day yielded a lot more blackflies than the following day. This was the

Table 7. Drift rates, benthic population densities, and colonization of trays implanted in the stream bed at six localities.

Loc.	Drift Inds./24 hrs (excl. pupae)						Benthos Inds./m² (excl. pupae)						Colonization Inds./m²/72 hrs (excl. pupae)				
	Date	m³/24 hrs	Eph.	Plec.	Trich.	Sim.	Date	Method	Eph.	Plec.	Trich.	Sim.	Date	Eph.	Plec.	Trich.	Sim.
7	19/7	173	0	5	0	3	15/7	ST	0	63	12	65	19–22/7	0	22	9	25
	20/7	173	0	7	0	0	16/7	AST	10	341	90	410	19–22/7	2	2	24	2
	21/7	128	0	4	1	2	—	—	—	—	—	—	19–22/7	2	0	13	2
	22/7	112	1	4	5	4											
6	15/7	120	0	12	0	42	13/7	ST	0	33	2	46	16–19/7	0	5	5	0
	16/7	173	0	5	0	8	13/7	AST	0	80	7	292	16–19/7	0	0	5	0
	17/7	184	0	4	0	4	—	—	—	—	—	—	16–19/7	0	7	0	35
	18/7	346	0	1	0	6											
12	15/8	173	144	5	0	12	11–12/8	ST	139	6	>1	61					
	16/8	144	294	12	0	13											
	17/8	146	100	11	1	14											
4	31/7	137	7	1	0	16	6/8	ST	16	17	2	74	30/7–2/8	20	0	0	11
	1/8	79	65	13	2	20	—	—	—	—	—	—	30/7–2/8	7	5	0	5
	2/8	69	67	4	0	28											
	3/8	103	20	33	0	56											
	4/8	144	9	19	0	48											
	5/8	216	12	26	3	16											
	6/8	—	7	17	0	0											
	9/8	192	39	20	0	4											
	10/8	173	46	40	3	0											
	11/8	216	52	9	0	4											
	13/8	108	11	6	0	0											
	14/8	108	10	13	2	0											
2	27/7	127	5	0	0	4	25/7	ST	51	5	6	152	25–28/7	31	4	2	109
	28/7	160	4	5	1	5	—	—	—	—	—	—	25–28/7	2	8	11	27
	29/7	173	7	9	1	8	—	—	—	—	—	—	28–30/7	38	2	0	2
	30/7	149	15	33	0	8	—	—	—	—	—	—	28–30/7	8	5	0	222
11	23/7	192	28	5	1	5	19/7	AST	363	70	18	500					
	24/7	173	20	3	4	4											
	26/7	127	33	2	0	3											

day with the least flow volume measured at this locality.

At loc. 12 the benthic community was at the time dominated by an abundance of mayflies, and these insects were also very numerous in the drift. In proportion the blackflies were less numerous in the drift. Other components were so scarce in the benthic community that they were not to be expected in the drift.

A comparatively long series of drift samples were taken at loc. 4. The results illustrate the very considerable day-to-day variations of drift rates. Another important aspect is the poor correlation between the daily variations of different species or other taxa. Thus, in this particular case, the three dominant groups showed unsynchronized fluctuations. The mayflies were especially abundant in two periods, viz. 1 to 3 August and 9 to 11 August. The stoneflies were taken in largest quantities on 3 to 10 August, and were numerous on several occasions when the mayflies were particularly few, namely 4 to 6 August. Finally, the blackflies were very numerous during the first half of the sampling period, later dwindling to almost zero. It is important to point out that, in none of these cases, there is any obvious relationship between drifting numbers and flow volume filtered; as mentioned above, the volume filtered is roughly proportional to the whole flow volume of the stream. Numbers obtained in the drift appear comparatively high at this locality compared with the rest.

At loc. 2, a notable feature is the relatively high number of stoneflies in the drift in comparison with the low benthic populations, but here as at the preceding locality daily variations were of a considerable magnitude.

At loc. 11, finally, remarkably few blackflies were obtained in the drift, although the benthic population was dense.

To study the rate of colonization, trays were implanted on the bottom. They contained stones from the surroundings which had been carefully rinsed from all macroscopic animals before being put in the trays. As has been shown elsewhere (Ulfstrand, 1968) the process of colonization reaches equilibrium after a certain period but rarely so rapidly as within the three days during which the trays were exposed in these cases. The trays were placed so that animals could not crawl but had to swim or drift into them. There are several obvious cases of discrepancy between the proportions found in the drift samples and those in the colonization trays. For example, very few caddisflies were obtained in the drift at locs. 7 and 6, but still quite a few had colonized the trays. In other words, the constellation of environmental features offered in the trays was particularly attractive for the caddisflies. There are more examples of the same kind to be found in the table. Considering the shallowness of the stream and the turbulence of its water, the possibility that the drift tube provided a biased sample of the drifting fraction may safely be rejected.

Discussion

Limits of distribution within the study area and zoogeographical characterization of the fauna

Inspection of Table 1 reveals that many species were found at only a few localities within the study area and that in some cases these localities were concentrated to either the western or the eastern part of it. This suggests that the limits of distribution for these species ran through the area surveyed by us.

Among the mayflies, *Ameletus inopinatus* and *Baetis lapponicus* were found in the more westerly localities, while *B. muticus, B. fuscatus* and *B. subalpinus* were found in the easterly ones. *B. rhodani* was absent from the two most westerly and "alpine" localities. For the other species there are too few records to define any distribution patterns.

Many of the stoneflies appear to have a very wide distribution within the study area, but *Brachyptera risi, Nemoura arctica, Capnia atra, Capnopsis schilleri* and *Acrynopteryx compacta* seem to be more abundant in the west. It is a possible source of error that different flight periods in different parts of the area might distort the picture; this is particularly likely to be a major error for the stoneflies which, broadly speaking, tend to have early flight periods. For example, the scattered records of *Taeniopteryx nebulosa* cannot be used for assessing the local distribution of this species. It may be argued that this would apply also the other species. For *B. risi,* however, it is unlikely to be true since, at the localities where this species was obtained, it occurred in abundant populations of nymphs of varying size. To some extent, the same applies also to *Nemoura arctica*. However, for the capniids the picture may be influenced by local differences of their flight periods. *Amphinemura sulcicollis, Leuctra digitata* and *L. fusca* appear to have an easterly distribution within the study area.

Both *Apatania spp.* seem to be more abundant in the west, although the apparent absence of *A. stigmatella* from the three most easterly localities may be due to the less extensive sampling of these streams. *Micrasema sp.* was also found only in the west. *Rhyacophila nubila* was not found in the westernmost localities. However, our caddisfly collection is too small to permit any elaboration.

It is well-known that a gradual change in species composition takes place from the lowland towards the mountains in northern Scandinavia. The point we wish to make is rather that the study area was clearly outside the zone within which southerly fauna elements are met with. This is in contrast to the corresponding parts of River Vindelälven area, situated roughly 200 km to the southwest, where a remarkable blending of southerly and northerly elements was recorded (Ulfstrand, 1968). In SSNP, the species not ascending into the mountain streams proper are not southerly but rather easterly, zoogeographically speaking.

Species numbers and standing crop values

It may be asked if differences in SC values are correlated with differences in species numbers. Since the blackflies were not analysed to species, we have to restrict the comparison to the stoneflies, mayflies and caddisflies. The SC values of the July samples (ST) shown in Tab. 2 correspond to the following number of species: loc. 7, 6 spp.; loc. 6, 3 spp.; loc. 12, 5 spp.; loc. 4, 6 spp.; loc. 2, 9 spp.; and loc. 11, 7 spp. The last mentioned locality was the one deviating most clearly in terms of TSC value, but it did not possess an appreciably higher number of species than the rest. The SC values obtained through AST sampling correspond to the following number of species: loc. 7, 6 spp.; loc. 6, 2 spp.; loc. 11, 11 spp. The last mentioned locality was intermediate in terms of SC but had by far the highest number of species. Hence there is no close agreement in this case either, although the very low TSC at loc. 6 was combined with a very low number of species.

The comparison of course is made difficult by the fact that the blackflies that are very important in terms of weight cannot be included. However, it seems nevertheless legitimate to say that there was no consistent relationship between species numbers and standing crop values at the localities examined in this study.

Brachyptera risi at locs. 6 and 7

As mentioned initially, a great deal of faunistical work has been devoted to the aquatic insects of northern Sweden over the past ten to fifteen years. This allows the assertion that it is extremely unusual to find a stream in which *Brachyptera risi* is the dominant stonefly species, as was the case at locs. 6 and 7. At the former, there were no other stonefly species at all. Usually *B. risi* belongs to the scarcer species (see Ulfstrand, 1968), although it has a very wide distribution (Brinck, 1949).

Another feature is also notable, namely the fact that large numbers of *B. risi* nymphs were found as late as mid-July to mid-August. The general situation is that *B. risi* is among the early stoneflies, although some species which emerge at the break-up of the ice are still earlier (for example, *Taeniopteryx nebulosa* and *Capnia atra*).

One may speculate if these two circumstances, viz. (1) the rarely encountered predominance of *B. risi* in the community, and (2) the unusual life cycle of the species at this locality, are interrelated phenomena. It is conceivable that the populations of *B. risi* elsewhere are kept low because of interference from other members of the lotic community. In other words, some biotic factor may preclude the growth of the *B. risi* nymphs during the part of the year during which the nutritional conditions are optimal for a species specialized on grazing periphytic algae (Brinck, 1949). At locs. 6 and 7, *B. risi*, being relieved from its hypothetical competitors, gets the opportunity of utilizing the summer for growth and therefore occurs in uncommonly flourishing populations.

Madsen (1968, 1969) found that *B. risi* preferred to live on top of the stones of the stream bottom, that is where epilithic algae are abundant. Moreover he established that the species was reluctant to enter detritus accumulations present on the stream bottom. Madsen showed that *B. risi* displays an abnormal kind of behaviour when held in aquaria without water movements and suggests that its dependence on current explains its avoidance of the litter deposits. While this is probably true, it may not be the whole truth. It is mentioned by Madsen that inside the accumulations another stonefly species, viz. *Nemoura flexuosa* Aub., is abundant. Biotic interaction may possibly contribute to the resource partitioning demonstrated by these two species. In our localities in Lapland, *B. risi* was frequent also at sites with abundant detritus. However, this does not prove that biotic factors prevented *B. risi* from inhabiting detritus deposits in the Danish streams studied by Madsen, for other factors, such as temperature and oxygen supply, may be decisive for the ability of *B. risi* to live in detritus accumulations in Lapland.

We have little factual information to support one or the other hypothesis but wish to point out the great interest attached to a species like *B. risi,* which in most places is sparse but locally is found in abundance. The places where it occurs usually are on the "extreme" side, and this contributes to the impression that *B. risi* is a species with great difficulties to resist biotic interferences in species-rich communities (cf Grant & Mackay, 1969; Ulfstrand, 1969).

Summary

The benthic communities of some streams in Stora Sjöfallet National Park in Swedish Lapland were found to be comparatively species-poor, being made up of northerly, easterly and widely distributed forms but no southerly elements. Standing crop values in Lapland streams tend to be lower than further south with the exception for lake outlets. Certain localities damaged by hydroelectric impoundments were found to be practically devoid of benthic animal life.

Although relatively few species made up the communities, small-scale differences of standing crop values were very considerable. In some cases, a correlation between standing crop values and certain environmental features could be assessed. The possible significance of biotic interactions is underlined, particularly in connexion with the stonefly *Brachyptera risi,* which seems particularly to thrive at localities where the community is particularly species-poor. The mosaic distribution of different abiotic factors at a stream bottom, not least the substrate and the current, leads to a corresponding pattern of standing crop distribution, enforced perhaps by interspecific interactions.

Drift is an integral phenomenon of lotic communities. It involves rapid redistribution of populations within a stream. While a drifting animal is obviously unable to choose where to strike the bottom, it reacts to unfavourable conditions through re-entering the drift, so that, for example, on an experimental tray implanted on the bottom, a set of species, for which the conditions are favourable, is obtained after a certain period. Daily differences of drift rates were apparently not correlated with water flow fluctuations and were frequently completely unsynchronized between different taxa. This emphasizes the complicated interplay of abiotic and biotic factors govering the drift rates of the different species.

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