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Benthic animal communities in Lapland streams

A field study with particular reference
to Ephemeroptera, Plecoptera, Trichoptera
and Diptera Simuliidae

OIKOS SUPPLEMENTUM 10 (1968)

Benthic animal communities in Lapland streams

A field study with particular reference to Ephemeroptera, Plecoptera, Trichoptera and Diptera Simuliidae

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MUNKSGAARD – COPENHAGEN

Trykt hos Andelsbogtrykkeriet i Odense
1968

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1. Introduction

1.1. Background – the exploitation of Lapland rivers for hydroelectric purpose

During the past 25 years the rate of exploitation of water systems in northern Sweden for hydroelectric purpose has been rapidly increasing. Today only very few large river systems remain intact. One of these is Vindelälven in central Swedish Lapland. About 1960, however, plans were presented for the regulation also of this river. The need for a documentation of the biological and other conditions before the river was altered was appreciated by conservation authorities, and in 1961 the author was asked to carry out a preliminary faunistical survey in the upper parts of the river system which were at that time judged to be the most important ones and also to be in greatest danger of exploitation.

It soon became evident that a more extensive investigation of the animal communities of the river was desirable. The area was found to be suitable for such work which was started in 1962.

1.2. Objectives and delimitation of the investigation

The primary purposes were to describe and analyse the qualitative and quantitative composition of the benthic animal communities in relation to the environmental conditions and to evaluate the significance of the population movements known to occur in the running waters.

The extent of the investigation was circumscribed in the following ways: 1) the choice of localities was restricted to those with fast current and bottom substrate consisting mainly of large stones; 2) only shallow bottom areas were sampled; 3) no attempt was made to study the hyporheal community (Schwoerbel 1964), the investigation being explicitly directed towards the "stone fauna"; 4) the sampling technique employed was not designed to catch the youngest larval and nymphal stages (<2–3 mm); 5) the winged stages of the amphibiotic insects will be discussed in another context; 6) the study consisted entirely of field work, because of the need rapidly to ascertain the prevailing ecological conditions in view of impending exploitation and because of the distance from the study area to the nearest ecological laboratory; 7) although all animals, within the limits set by the sampling technique, were sampled, the main interest was attached to the mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera) and blackflies (Diptera Simuliidae) which together comprised by far the greatest part of the standing crop of the localities studied.

1.3. The field work

The field work covered about 10 months distributed as follows: 1961, 16–31/7 (faunistic survey); 1962, 14–28/7, 1–22/8, 3–8/10; 1963, 7/6–13/8, 12–17/11; 1964, 4/5–18/9; 1965, 13/7–23/8; 1966, 8–10/6, 29/9–2/10.

1.4. Previous zoo-ecological work in Lapland streams

Apart from pure faunistic inventories only a few zoological studies have been devoted to the lotic biotopes and their inhabitants in Lapland. The first analytical investigation covering a variety of such biotopes and different systematic groups was that by Brinck and Wingstrand (1949, 1951). Lately a number of studies on running and/or still water biotopes have appeared particularly by Müller (1953 et seq.). Fishery biologists have conducted extensive ecological work but chiefly in lakes; some recent important contributions are those by Grimås and Nilsson (1965) and Grimås (1967). Monographs by Brinck (1949) and Carlsson (1962), although not restricted to Lapland, contain much useful information concerning Plecoptera and Simuliidae, respectively.

1.5. Taxonomical and nomenclatorial remarks

The taxonomy and nomenclature follows Limnofauna Europaea (Illies 1967) with a very few exceptions.

Brekke (1938, 1965) considered that *Ameletus alpinus* Bgtn. was a synonym of *A. inopinatus* Etn., and this is accepted. Further, it was shown by Brinck and Müller-Liebenau (1965) that what was previously called *Baetis bioculatus* L. should bear the name *B. fuscatus* L. Illies (1967) merged this species with *B. scambus* Etn. This conclusion is provisionally accepted, pending a thorough revision. In addition, I have also merged *Metretopus alter* Bgtn. and *Parameletus minor* Bgtn. with *M. borealis* Etn. and *P. chelifer* Bgtn., respectively. However, these two species form a negligible part of the total material.

Finally, the generic name *Synafophora* was rejected for what is here called *Glossosoma intermedium* (*Mystrophora intermedia*) Klap.

It was impossible to distinguish between the larvae of *Apatania stigmatella* Zett. and *A. wallengreni* McL. With regard to their different flight-periods (Ulfstrand 1968: Tab. 3) it was possible to refer most larvae to either species. This is the only case where "indirect" determination was resorted to. In all other cases specific identifications were founded on morphological criteria.

1.6. Terminological remarks

Many ecological terms have been used so loosely that their meaning has become lost in the process. "Biocenosis" and "zoocenosis" are, in the author's opinion, examples of this unfortunate development, and they will not be used in this paper. Some other terms were, however, unavoidable, and their usage in this paper will be explained here. For general terminologal discussions, see e.g. Allee et al. (1955), Odum (1959, 1963), Andrewartha (1965) and Clark et al. (1967).

The term *biotope* is used for a part of the environment within which some important factors vary within certain limits. What factors are important, and what amplitude they may have within a biotope depends on the animals under consideration.

The running waters of Lapland have a great many important properties in common, and can therefore under certain conditions be regarded as constituting one biotope. In a detailed analysis, however, endless numbers of biotopes may be defined within any small stream. Biotopes may, therefore, be conceived on different scales, and sometimes it is useful to add the prefixes macro- and micro- to indicate what scale one is using. Such considerations have led to the erection of elaborate hierarchic biotope systems with a corresponding terminology (Albrecht 1953, Steffan 1965).

All species and individuals inhabiting a biotope make up a *community*. Similar definitions were employed by Backlund (1945) and Brinck (1949). Since all the localities in the study area from which the benthic samples were taken may be regarded as representing one biotope, all the animals inhabiting the whole series of localities represent one community. Furthermore, if the environmental factors are examined in detail and the biotope accordingly subdivided, the community is consequently broken up into several subcommunities. It is therefore justified to state that the present contribution deals with the animal community of Lapland streams; but it is not contradictory to say, for example, that outlet communities differ from those found at other sites in the rivers, since it is understood that it is subcommunities that are being referred to.

All the individuals and species of a given major taxon (family, order etc.) inhabiting a biotope make up a *zoome* (cf. Brinck 1949). It seems to make for clarity not to employ the term community in this context. *Population* is used to denote the total number of individuals present of one species only.

All species making up a community are

bound to have a great many properties in common. For example, all members of the community of Lapland streams have to be able to survive a long period of darkness and low water temperature. At the same time, they have to differ in certain respects, in order not to interfere with each other's conditions of existence (De Bach 1966, Berthélemy 1967). The continuous coexistence of two or more species proves that they are able to survive in each other's presence; but the use of the word community in this paper does not imply that all species are dependent on each other (Dice 1952, Illies 1961 a).

A biotope, as the term is used here, is inhabited by a community, whose members have many common features, as well as some distinctive ones. A *habitat*, on the other hand, is the totality of all sites where a given species regularly dwells (cf. Macan 1963).

2. Environmental conditions

2.1. Physiographical survey

2.1.1. Geographical position

The geographical position of the study area is shown on Fig. 1. The field work centred around the village of Ammarnäs (lat. 65°58′N, long. 16°12′E). The area is shown in further detail in Fig. 2, where the sampling localities and other features of interest are entered.

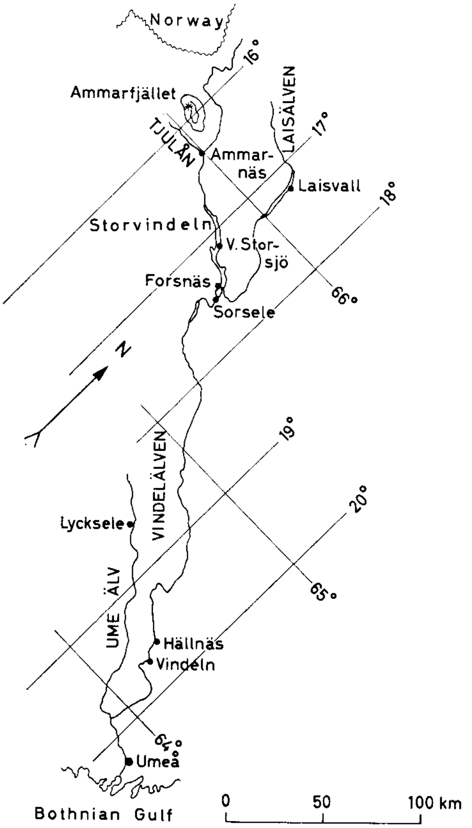

Fig. 1. Orienting map of the Vindelälven water system.

2.1.2. Topography

Vindelälven has its sources close to the Norwegian border at an altitude of approx. 1,000 m above sea level in the central part of the Scandinavian mountain chain. It rises as several streams winding over the mountain plateaux. Some 25 km from its sources it descends into the subalpine birch zone. Large stretches have only a very weak fall-gradient, so that the river takes the form of a series of elongated lake-like extensions, largely with soft substrates. About 12 km upstream of Ammarnäs the river becomes much more torrential. This continues until it falls into the lake Gautsträsk at Ammarnäs. Downstream of this lake there is a stretch of about 10 km of torrential rapids, followed by a long lake-like part, at the lower end of which the lowermost sampling locality is situated.

The tributary Tjulån (see Fig. 2) rises in the mountains to the west of Ammarnäs at an altitude of approx. 750 m. Several medium-sized streams drain into a lake known as Lilla Tjulträsk and unite in a delta in the western end of the lake. This lake drains into Stora Tjulträsk, at an altitude of 540 m. Stora Tjulträsk empties into Tjulån which in the course of about 10 km falls no less than 140 m before falling into Gautsträsk.

Both Gautsträsk and Stora Tjulträsk are

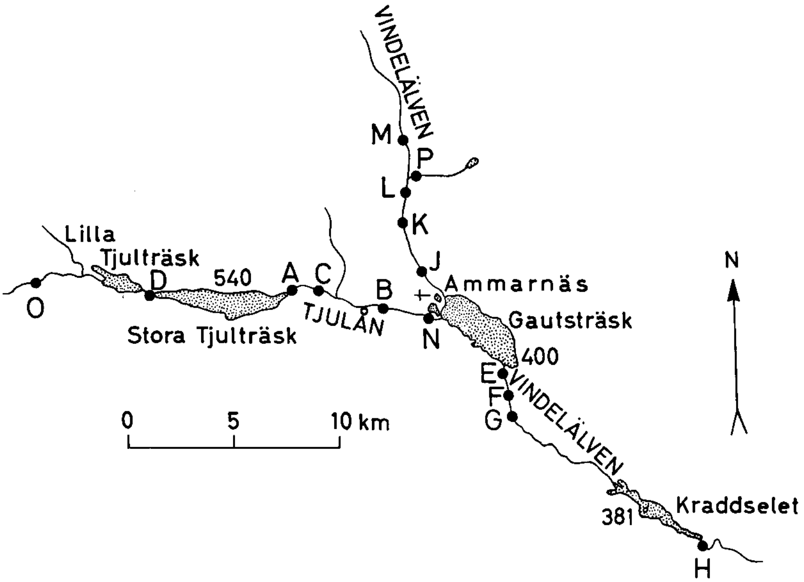

Fig. 2. Map of the Ammarnäs area. Letters refer to sampling localities. Figures show altitude in m above sea level.

very deep lakes with little emergent vegetation except in the western deltas. Lilla Tjulträsk, on the other hand, is extremely shallow, has a soft bottom and a dense carpet of submerse vegetation described by Wassén (1965).

From its source in the mountains to its mouth into the river Ume älv near the coast of the Bothnian gulf, Vindelälven traverses a distance of 444 km. Its total catchment area amounts to 12,655 km², of which half is upstream of Sorsele (Fig. 1). It is the eighth largest river in Sweden (Kungl. Vattenfallsstyrelsen 1962).

For a detailed description of the topography of the southern and central parts of the Scandinavian mountain chain, incl. the Ammarnäs area, see Rudberg (1954).

2.1.3. Geology

The study area lies almost entirely on a special geological formation called "the Ammarnäs complex of phyllite, greywacke and arkose" (Gavelin and Kulling 1955). Geologically it is part of the mountain chain proper. Within the whole catchment area of Vindelälven only very small areas of limestone and/or dolomite have so far been detected.

2.1.4. Air temperature, precipitation, snow cover

The nearest official meteorological station is Vindel-Storsjö (abbr. V. Storsjö in Fig. 1) about 45 km SE of Ammarnäs. The conditions at this place are probably sufficiently similar to those prevailing in the Ammarnäs area to provide an adequate description of the general climatic conditions. The correlation between the air temperatures as recorded on thermograph at Ammarnäs at 21 hr and at Vindel-Storsjö at 19 hr was very close indeed ($r = +0.97$). In absolute figures, the temperature at Ammarnäs was about 2° lower.

The air temperatures of 1962 to 1965 at Vindel-Storsjö are shown in Fig. 3. Hard frost regularly occurred from November to April. Only in June to September is frost irregular and usually mild. Temperature fluctuations from year to year in winter are of little importance for benthic animals, but during the rest of the year they may have a considerable effect. With regard to the sum-

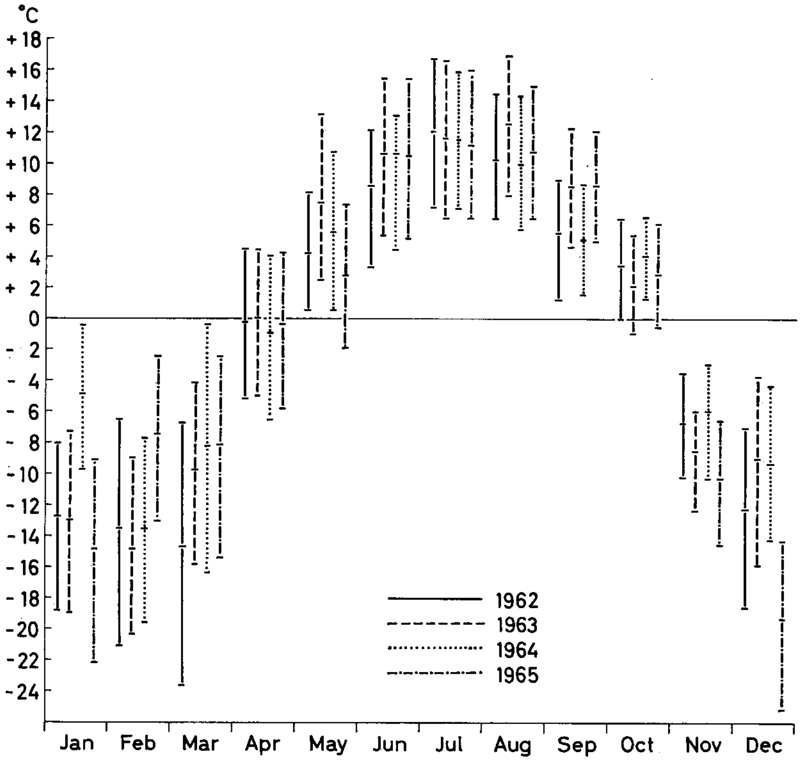

Fig. 3. Air temperature as reported from the official meteorological station at V. Storsjö (see Fig. 1). Upper cross-bar shows mean daily maximum, lower cross-bar mean daily minimum and middle cross-bar mean monthly temperature. Data from the Swedish Meteorological and Hydrological Institute.

mer half-year, 1963 was characterized by generally high air temperatures (May, August, September).

Average monthly precipitation in the years 1962 to 1965 at Vindel-Storsjö and Tjulträsk is shown in Fig. 4. The annual precipitation was, as expected, considerably higher at the latter, more westerly site (average 618 mm) than at the former (479 mm).

The duration of the snow cover at Vindel-Storsjö is shown in Fig. 5, from which it appears that the ground was snow-covered from early November to early May. In the vicinity of Ammarnäs, snow fields usually remained well into June, and in the surrounding mountains there are perennial snow fields and small glaciers.

2.1.5. Water temperature, ice conditions, flow

Water temperature was measured by the Swedish Meteorological and Hydrological Institute at Forsnäs (see Fig. 1). It was measured once a week with a mercury thermometer at a depth of approx. 1 m in slowly running water.

The annual course of the water temperature in 1962 to 1965 is shown in Fig. 6. Water temperature was consistently below +1° from November until late March. In April it was about +3°. The highest values, about +13°, were recorded in July and August. The very rapid rise in May and June is one of the most characteristic features of these northerly waters.

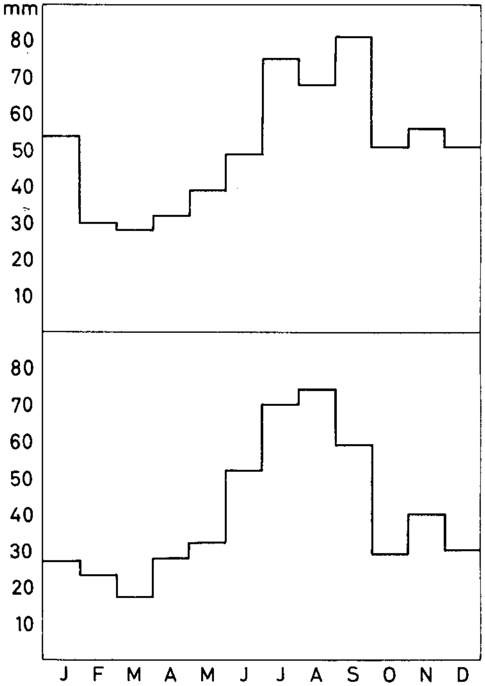

Fig. 4. Average monthly precipitation at Tjulträsk (upper graph) and V. Storsjö (lower graph) in 1962 to 1965. Data from the Swedish Meteorological and Hydrological Institute.

As with the air temperature, certain year-to-year differences were also found in the water temperature. It rose unusually early in 1963, but this was compensated by a considerable drop in June. The cooling was delayed in the autumns of 1963 and 1964 compared with the other two years.

Duration of ice cover is given in Fig. 7. In the three years for which comparison is possible, Lilla Tjulträsk became ice-free 5, 11, and 12 days earlier than Stora Tjulträsk, the lower of the two lakes in the river system. Considerable local differences are discernible from the graphs, whereas year-to-year differences were relatively small and desultory.

Some data on flow are assembled in Tab. 1. At the outlet of Vindelälven from Gautsträsk the flow was more than 13 m³/sec for 50% of the year; the corresponding figure for a point 15 km upstream of Gautsträsk in Vindelälven was 5.9 m³/sec and 3.0 m³/sec for a point in Tjulån. According to the useful stream classification employed by Brinck (1949) this places the lower part of Vindelälven in the category of "northern rivers", the upper parts of the same river make a borderline case between "northern rivers" and "northern streams", whereas Tjulån is a good example of the latter group.

Seasonal fluctuations are extremely great (Fig. 8). The highest flow, usually occurring in June, is about 100 times the lowest values which are found in the period preceeding the break-up of the ice. Daily fluctuations are also considerable (cf. § 9.4).

2.1.6. Vegetation

Vindelälven crosses the upper limit of coniferous forest approx. 15 km upstream of Ammarnäs, and Tjulån crosses it approx. 3 km downstream of its outlet from Stora Tjulträsk. Thus, most sampling localities were located in the high boreal coniferous zone (the taiga), while a few (A, D, O) were in the subalpine birch forest zone.

With the exception of the colonial diatom *Didymosphenia geminata*, macroscopic vegetation was very sparse or absent in lotic parts. Filamentous green algae were sometimes

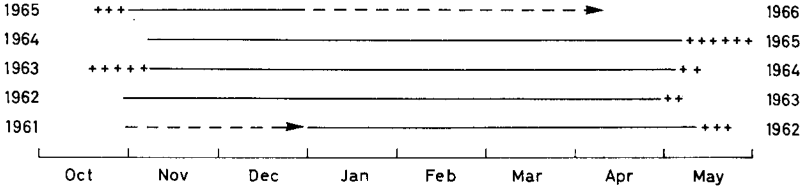

Fig. 5. Duration of snow cover at V. Storsjö. A line shows complete cover; crosses indicate partial cover; dashes followed by arrow indicate no information. Data from the Swedish Meteorological and Hydrobiological Institute.

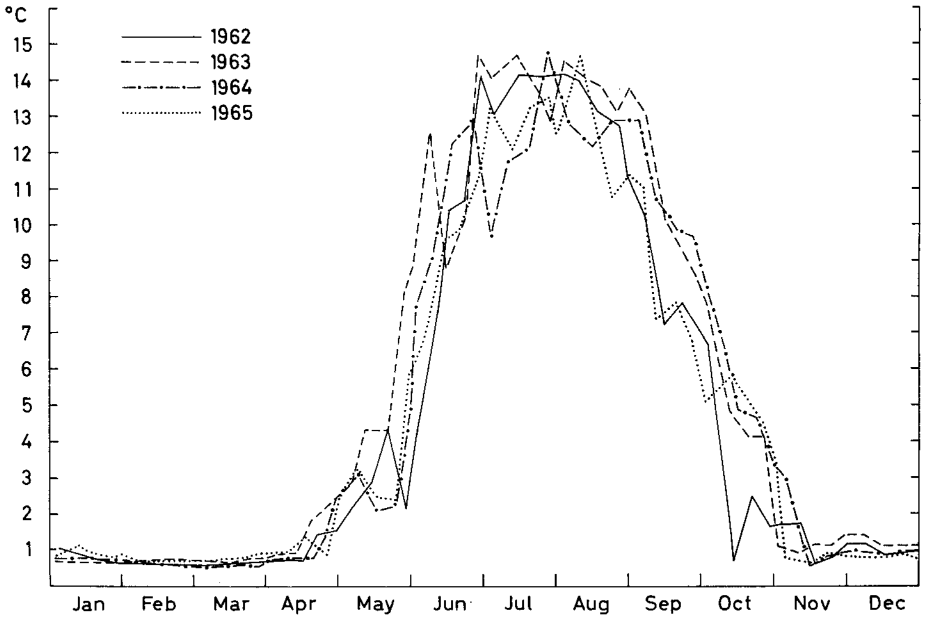

Fig. 6. Water temperature based on weekly measurements at the official hydrological station at Forsnäs near the outlet of the lake Storvindeln (Fig. 1). Data from the Swedish Meteorological and Hydrological Institute.

abundant at locs. E, F, G and H and occurred sparsely at loc. A. The emergent water vegetation of soft bottom river parts in calm reaches was not studied.

2.1.7. Human influence

The human population of the study area is very sparse. The village of Ammarnäs has

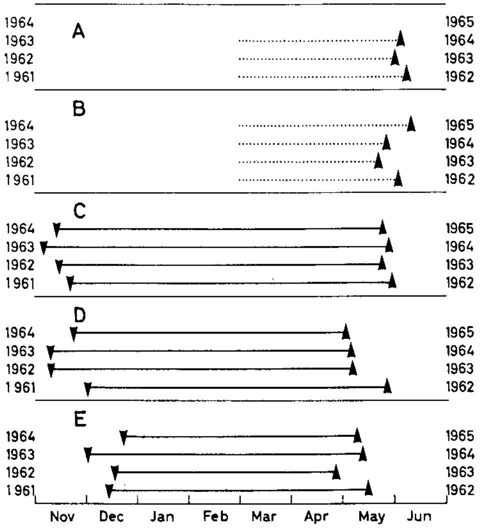

Fig. 7. Periods of ice cover. Downward arrow indicates beginning of ice cover, upward arrow the break-up of ice. A = Stora Tjulträsk, B = Lilla Tjulträsk, C = Tjulån at loc. N, D = Vindelälven at loc. E, E = Vindelälven at loc. H (cf. Fig. 2). Data from the Swedish Meteorological and Hydrological Institute.

Tab. 1. Water flow data from Vindelälven and Tjulån in m³/sec. Averages from 1925 to 1954. A = Vindelälven at the outlet from Gautsträsk, B = Vindelälven approx. 20 km upstream of Ammarnäs, C = Tjulån at the outlet from Stora Tjulträsk (cf. Fig. 2). Information supplied by Kungliga Vattenfallsstyrelsen (State Hydroelectricity Board).

	A	B	C
Extreme high flow	540	290	130
Average high flow	270	140	65
Average annual flow	33	15	7.8
Flow during 50% of year	13	5.9	3.0
Average low flow	3.0	1.5	0.9
Extreme low flow	1.5	0.8	0.4

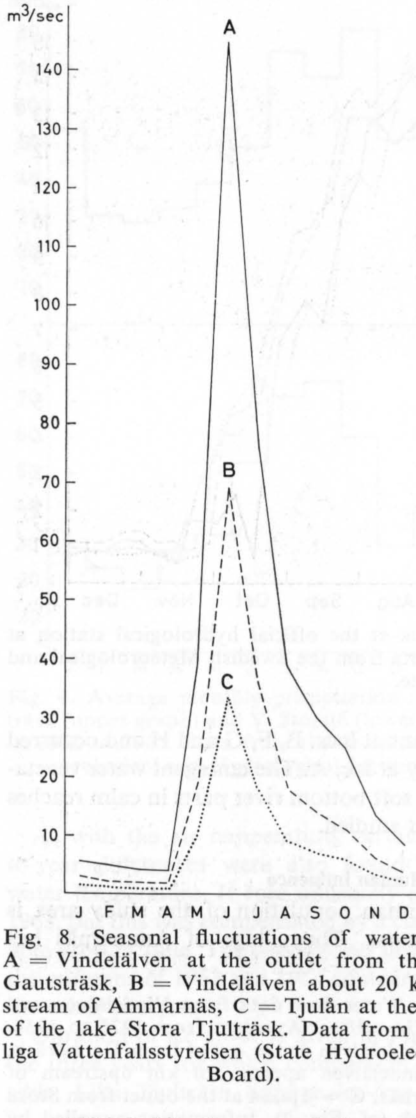

Fig. 8. Seasonal fluctuations of water flow. A = Vindelälven at the outlet from the lake Gautsträsk, B = Vindelälven about 20 km upstream of Ammarnäs, C = Tjulån at the outlet of the lake Stora Tjulträsk. Data from Kungliga Vattenfallsstyrelsen (State Hydroelectricity Board).

some 300 inhabitants many of whom are reindeer herdsmen and are absent from the village for at least half the year. Domestic effluents pass through a purification plant installed in 1963. Part of the sewage previously drained into a small pool in the village, and this pool is the only water body of the area showing signs of pollution. In general, the quantities of sewage are negligible in relation to the vast water volumes of the rivers.

Log-floating occurs to a limited extent. Small quantities of logs are dumped on the ice in winter and float downstream in spring. The amounts of bark deposited on the bottom are small and probably do not interfere with the ecological conditons in any way (cf. Müller 1962 a).

Locally the populations of *Salmo trutta* L., *Salvelinus alpinus* L. and perhaps *Thymallus thymallus* L. may be reduced because of intense sport angling.

Within the Ammarnäs area the rivers and streams may be regarded as unchanged by technical exploitation and pollution, apart from the diffuse global air pollution. There are very few places in Europe of which this may be said.

2.2. Description of sampling localities

2.2.1. Location and general features of the localities

Most of the benthic samples were taken from ten localities, the positions of which are shown in Fig. 2. A small number of samples were taken from five additional localities (C, F, G, J, M) which are entered on the map but will not be described in further detail.

Loc. A (Fig. 9). Tjulån, at the outlet of Stora Tjulträsk (alt. 540 m). Most of the river is very shallow, with a somewhat deeper central channel. At normal summer flow, the depth nowhere exceeds 100 cm. Very dense carpet of *Didymosphenia ge-*

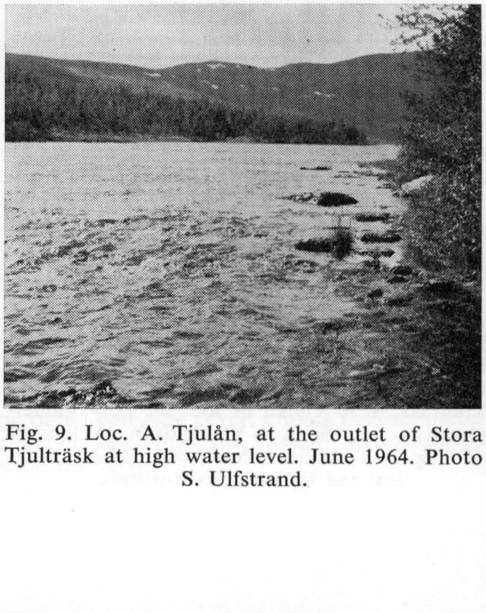

Fig. 9. Loc. A. Tjulån, at the outlet of Stora Tjulträsk at high water level. June 1964. Photo S. Ulfstrand.

minata in central channel, otherwise only scattered tufts. Small amounts of filamentous green algae and water moss near the shores. Some large boulders protrude above the water. Surroundings: dense, rich birch forests.

Loc. B (Fig. 10). – Tjulån, about 3 km upstream of Ammarnäs. Strong current, relatively uniform over considerable areas. Scattered tufts of *D. geminata*, very little moss and no green algae. Surroundings: partly meadows cropped for hay, partly mixed forest.

Loc. D (Fig. 11). – In the river connecting Lilla and Stora Tjulträsk. Most of the stream is very deep and slow-flowing, but at the sampling locality there is a short zone of faster current. Lenitic biotopes near by, and a small brook from the mountain side flows into the stream immediately below the sampling site. Small tufts of moss, otherwise no macroscopic vegetation. Surroundings: rich birch forest, willow thickets, some marshland.

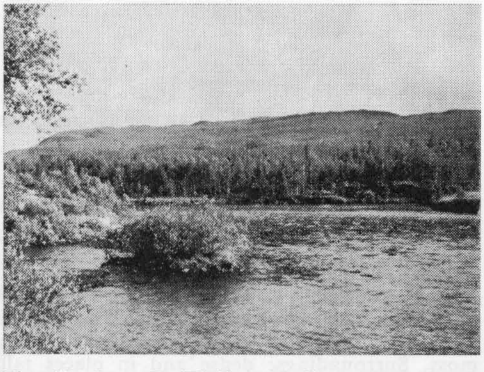

Fig. 10. Loc. B. Tjulån. Medium water level. July 1965. Photo S. Ulfstrand.

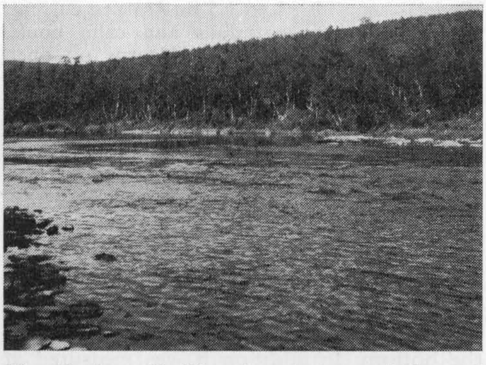

Fig. 11. Loc. D. The river between Lilla and Stora Tjulträsk at moderately high water level. June 1964. Photo S. Ulfstrand.

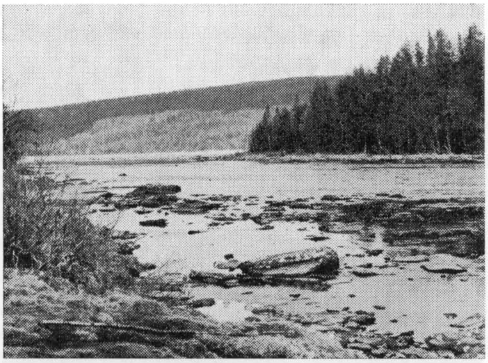

Fig. 12. Loc. E. The outlet of Vindelälven from Gautsträsk. Very low water level. May 1964. Photo S. Ulfstrand.

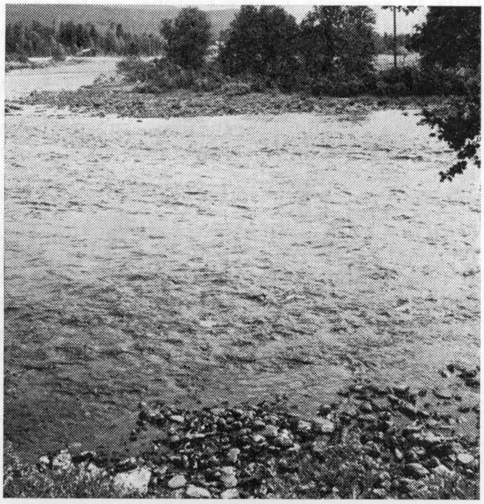

Fig. 13. Loc. H. Vindelälven. Medium water level. July 1965. Photo S. Ulfstrand.

Loc. E (Fig. 12). – Vindelälven at the outlet of Gautsträsk. Resembles loc. A although on a larger scale. Very large boulders protrude above water making current conditions extraordinarily variable; these boulders become almost submerged at extreme spring flow. A narrow deep zone in the middle, where the stones are covered by *D. geminata*, which also occurs in the shallower areas, although less densely. Filamentous green algae often plentiful. Surroundings: mixed forest, mainly conifers.

Loc. H (Fig. 13). – Situated at the downstream end of a long lake-like river extension in Vindelälven. Current even and strong, no emergent boulders. Much moss and green algae, very

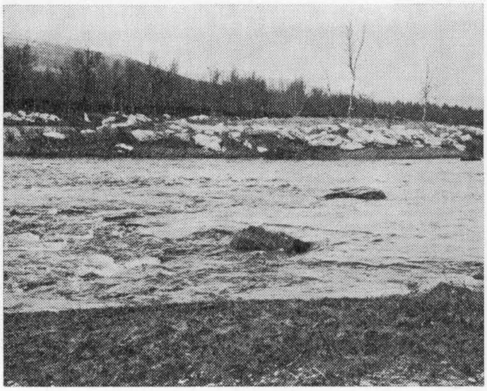

Fig. 14. Loc. K. Vindelälven. Extremely high water level. May 1964. Photo S. Ulfstrand.

little *D. geminata*. Lenitic biotopes nearby. Surroundings: open hay fields, some farmsteads, coniferous forest.

Loc. K (Fig. 14). – In Vindelälven, about 4 km upstream of Ammarnäs. A very variable locality, with some soft bottom at the upper end and large boulders protruding above the water. Some moss, otherwise no visible vegetation. Surroundings: open poor mixed forest.

Loc. L. – Closely resembling the previous locality, with much sand between the stones. A small brook with loc. P flows into Vindelälven about 50 m upstream of this locality. Practically no water vegetation. Surroundings: same as previous locality.

Loc. N. – Tjulån, in the village of Ammarnäs. Closely similar to loc. B (q. v.).

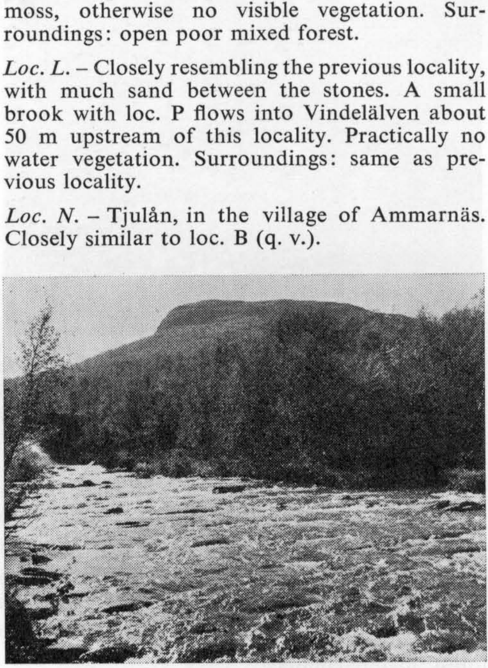

Fig. 15. Loc. O. Stream falling into Lilla Tjulträsk from the west. In the background the low fjeld Jenovardo, 885 m above sea level. Moderately high water level. June 1964. Photo S. Ulfstrand.

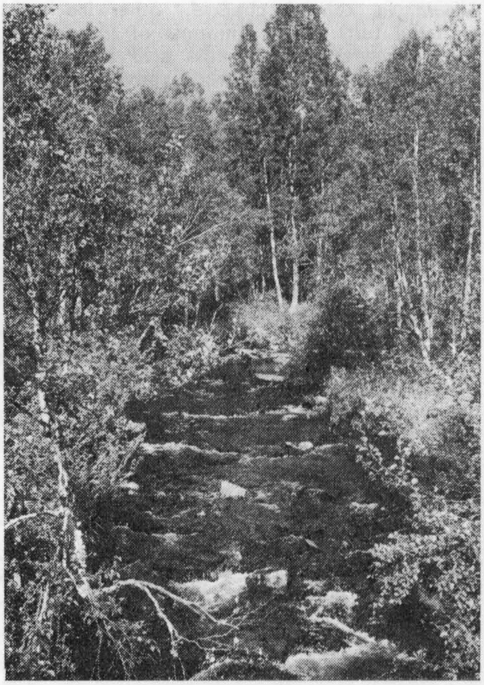

Fig. 16. Loc. P. Small stream falling into Vindelälven. Medium water level. July 1965. Photo S. Ulfstrand.

Loc. O (Fig. 15). – Sampling site located just below a waterfall in a stream flowing into Lilla Tjulträsk from the west. Stream uniformly shallow. A great deal of *D. geminata*, very little moss. Surroundings: dense and in places tall virgin birch forest.

Loc. P (Fig. 16). – A small brook falling into Vindelälven, width 1 to 1.5 m. Uneven current, many diminutive waterfalls and calm pools. Originates from several small tarns on open moorland in the birch zone. Much moss, no other visible aquatic vegetation. Surroundings: mixed forest with much birch, willow thickets along the brook, partly sheltering the stream from direct insolation.

2.2.2. Current

The current velocity was measured with an Ott propeller at depths of 10, 25 and 40 cm, the propeller always being held 5 cm above the bottom. In addition it was measured at the surface where the water was 40 cm deep. All values are averages of five readings, each

Tab. 2. Current velocity measurements from different stream localities in the Ammarnäs area. Each value represents the average of four measurements.

Loc.	June 1964				July 1962				August 1962			
	a	b	c	d	a	b	c	d	a	b	c	d
A	118	60	83	94	92	41	68	76	85	35	58	70
B	115	54	75	86	100	40	63	74	90	40	61	70
C	148	78	90	108	118	68	85	94	112	60	83	96
D	80	35	56	67	69	30	41	56	77	39	44	58
E	128	66	87	104	100	53	88	92	105	50	79	86
G	110	57	79	93	89	53	69	75	96	59	66	74
H	137	79	104	113	98	70	80	90	94	68	82	86
K	102	71	83	88	79	68	73	75	88	61	71	78
L	113	64	80	93	101	64	72	79	102	58	63	78
M	119	72	79	94	105	68	75	83	104	64	77	84
N	121	60	78	94	94	41	60	75	98	44	60	72
O[1]	100	65	81	90	88	48	57	69	74	40	53	59
P[1] [2]	64	35	41	–	66	37	43	–	58	33	39	–

a = water surface at 40 cm depth
b = 5 cm above bottom at 10 cm water depth
c = 5 cm above bottom at 25 cm water depth
d = 5 cm above bottom at 40 cm water depth

[1] Measurements refer to 1964 throughout.

[2] a, in this case at 25 cm water depth.

reading covering 60 sec. The data are collated in Tab. 2.

Such current measurements obviously have a limited direct relevance for the benthic animals most of which live in crevices between and under stones, in tufts of vegetation, or in other places where the full force of the current is mitigated. Even when moving over exposed stone surfaces they remain in the lowermost water layer with much reduced current speed (Ambühl 1959, 1962, Jaag and Ambühl 1962). Yet the rough measurements are of importance, since they indicate the sedimentation conditions which directly influence the life conditions of the animals. Macan (1961 b) found it difficult to explain why some species are restricted to calm parts of the stream, considering that animals are generally able to avoid the current force in the fast-running parts. Part of the explanation may lie in the different sedimentation conditions; a detritus consumer probably finds a richer food supply where the current is slower (cf. § 10).

Current speed as such probably has a limited direct influence on the life conditions of the animals but is of great importance because of its indirect effects (substrate, oxygen etc., cf. § 4.2; see also Scherer 1965 a, Eriksen 1966, Cummins 1966, Thorup 1966).

As is apparent from the table, all localities were characterized by swift current. Locs. D and P had somewhat lower values than the rest. The water is "rushing" rather than "streaming", in the sense of Ruttner (1963). Notwithstanding the variations, all localities were evidently within the same ecological category (cf. Nielsen 1950, Ruttner op. cit.). Within each locality, current conditions were extremely variable. Velocity measurements frequently varied between 0 and 175 cm/sec at points only about 1 m apart.

2.2.3. Substrate, including organic deposits

The present study primarily concerns the animal community of the large stones in fast current (§ 1.2). In the sampling, stones less than 6 cm along their longest axis were not removed, as a substrate consisting of so small stones was considered to constitute a different environment, and stones larger than 35 cm were for practical reasons ignored. Within this size range, the aim was to remove stones without bias.

Tab. 3. Average stone dimensions based on random sample of 100 stones from each of the localities from the Ammarnäs area. Stone surface area estimated as maximal length × maximal breadth (standard area).

Loc.	Average stone surface (cm^2)	Thickness (cm)	Surface area / thickness
A....	185	3.6	51.4
B.....	161	3.9	41.3
D....	153	4.1	37.3
E.....	237	3.0	79.0
G....	203	3.4	59.7
H....	172	3.8	45.3
K....	198	3.9	50.8
L.....	188	3.5	53.7
M....	227	3.5	64.9
N....	150	3.7	40.5
O....	223	3.6	61.9
P.....	187	3.2	58.4

Three measurements were taken of every stone from which animals were collected: greatest length, greatest breadth, and greatest thickness. By multiplying the first two values, one gets an estimate of the bottom surface area represented by that particular stone. Of course, the measurement is very rough, but yet has proved adequate for comparative purposes (cf. Müller 1953, Dittmar 1955 a, b, Schwoerbel 1966). Areas measured in this way will be referred to as *standard areas.*

The average stone standard area at each locality is shown in Tab. 3. In spite of certain local differences the localities belong to a similar general type, indicating the continuous or periodic operation of swift current. According to Cummins' (1962) classification the substrate may be called "cobble" and is referable to class −6 or −7 in his scale.

The shape of the stones is described as thickness in relation to standard area. It may be seen from the table that particularly flat stones were found at loc. E and the roundest ones at locs. D, N and B.

The amounts of finer inorganic and organic matter were assessed as follows. A portable pump was fitted with a 4 m inlet pipe, diameter 5 cm, with a funnel attachment with a distal diameter of 22.5 cm. The opening of the funnel was covered with a wire-grid with mesh-size approx. 2 cm. In action the funnel was moved over the bottom like a vacuum-cleaner for 4 min, covering a semicircle with the pump in the centre. The area sampled in this way can be considered as constant. The material sucked into the pump was collected first in a silt separator fitted on the inlet pipe and then in a nylon gauze bag (mesh-size 145 μ) through which the outlet water was filtered.

The separated material was preserved and later analysed for organic and inorganic components. The preservative fluid was decanted, the sample dried at 105° for 24 hr, and the residue weighed. After ignition at 500° in a muffle oven it was reweighed.

The finer fractions of bottom substrate consisted of several categories: 1) relatively coarse inorganic material not normally moved by the water such as gravel and packed sand in sheltered sites, 2) fine silt of mixed organic and inorganic origin deposited at falling flow and eroded at high flow, 3) organic debris (detritus), mainly remnants of vascular plants from the terrestrial vegetation. All these kinds of substrate were obtained in the pump.

In Tab. 4 the amounts of finer inorganic and organic fractions as well as the size distribution of inorganic particles based on samples taken in August 1965 are shown.

Tab. 4. Amounts of inorganic material (dry weight) and inorganic particle size distribution at different localities. Based on suction pump samples from August 1965. Each figure is average of four samples.

			Percent weight distribution on particle size classes		
Loc.	Organic (g/m^2)	Inorganic (g/m^2)	>2mm	2–0.2mm	<0.2mm
A..	3.7	197	78	16	6
B...	1.6	86	80	19	1
D..	4.7	140	63	23	14
E...	4.9	94	77	20	3
H..	3.6	99	85	15	0
K..	4.8	131	87	12	1
L...	1.8	210	80	17	3
N..	2.2	89	76	22	2
O..	4.9	133	91	9	0
P...	6.8	173	74	20	6

Four samples were taken on each site at depths varying from 10 to 40 cm. Certain local differences emerge from the data. Thus, locs. B, E, H and N have low figures for inorganic matter (sand, etc.) in comparison with locs. A, L and P. There is a group of localities with comparatively high organic values, viz. D, E, K, O and particularly P, whereas locs. B, L and N had very low values. With respect to particle size, loc. D had a markedly higher proportion of fine matter than any other.

In November 1963 and on several occasions in 1964 a rough estimate of the amounts of coarse detritus (vegetable debris) was obtained using the pump as described above. Organic material was separated from inorganic material by repeated flotation. When all visible inorganic particles had been removed, the organic matter was dried for 10 min in the open air (not exposed to sun) and then weighed with an accuracy of 1 g. Four such samples were taken on each occasion and averages calculated. The result is set forth in Fig. 17, from which may be seen that locs. P, E and A had relatively high values. Great amounts were obtained in May, i.e. before the annual melting spate had started. Quantities sank generally during summer, and there was again a very considerable increase in autumn due to leaf-fall. Obviously, a large part of the detritus derived from the leaves remained throughout winter.

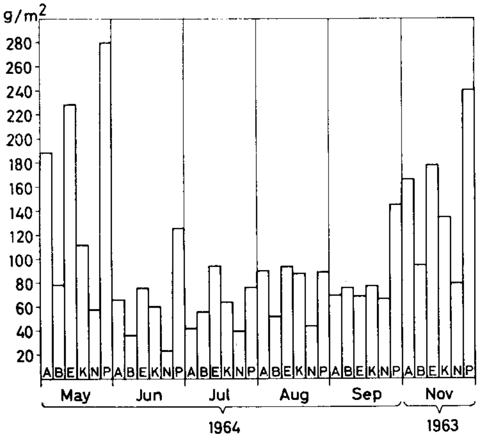

Fig. 17. Seasonal fluctuations of amounts of coarse detritus on the stream bottom, based on suction pump samples. Letters at column bases refer to localities.

2.2.4. Periphyton

The periphyton vegetation, mainly diatoms, is an important food source for benthic animals. Without aiming at accurate measurements, a simple technique was employed to obtain comparative figures from different localities.

A stone was removed from the bottom and rinsed without rubbing. A fairly smooth surface on its upper side was chosen and delimited by a rubber ring. The surface was first rubbed with a fine paint brush and then with a stiffer brush. The material brushed off was collected in a jar containing water and later filtered. Macroscopically visible inorganic particles were removed. The residue was carefully transferred to a crucible and dried at 105°, weighed, ignited and reweighed, so as to obtain the dry-weight of the organic matter. – A more elaborate but basically similar method was described by Cummins (1966).

The samples were taken in August 1965 and the results are shown in Tab. 5. The lake outlets as well as locs. D and P were characterized by relatively large amounts of periphyton. The high figures at the outlets may partly be the result of drifting plankton becoming stuck in the periphyton (cf. Chandler 1937).

Tab. 5. Periphyton in mg/dm^2 dry weight sampled in August 1965 as described in text. Values should be regarded as relative rather than absolute.

Loc.	Number of stones	Average amount of periphyton
A	4	13.6
B.	4	2.0
D	2	16.8
E.	4	19.8
H	4	22.2
K	2	4.7
N	4	5.3
O	2	6.3
P.	5	15.0

Tab. 6. Undissolved organic and inorganic matter (mg/l) in water samples from localities in Vindelälven and Tjulån in different months 1964.

Locs.	May Org.	May Inorg.	June Org.	June Inorg.	July Org.	July Inorg.	September Org.	September Inorg.
B........	1.5	1.0	2.5	2.5	3.0	0.5	<0.5	<0.5
E........	1.0	1.5	3.0	<0.5	2.5	<0.5	0.5	0.5
J........	2.0	14.0	<0.5	1.0	<0.5	0.5	<0.5	1.0
N.......	–	–	1.5	0.5	–	–	–	–

2.2.5. Seston

The organic material drifting with the current may be divided into a macro-fraction consisting of mainly lotic benthic nymphs and larvae and a micro-fraction consisting of mainly lenitic planktonic organisms and suspended organic matter.

A number of samples were taken from different places in the rivers and analysed for total undissolved organic and inorganic content at the Laboratory of Water Chemistry, "Järven", Umeå. As shown in Tab. 6, the content of inorganic substance was rather constant except for a deviating sample from loc. J in May. The organic material occurred in larger quantities at locs. B and E than at J and in June and July as compared with May and September. These comparisons indicate the influence of lakes on river seston.

Local differences in amounts of net-plankton were roughly estimated through sampling with plankton-bags placed in the river for 15 min. All samples were taken at the same time of day (about 2 hr before sunset) to minimize the effect of the circadian rhythms. The bags were equipped with flow-meters, so that the volume of net-plankton could be related to the water volume filtered.

As is apparent from Tab. 7 locs. A and E had much larger amounts of net-plankton in summer than any other locality. Loc. H had also a relatively high value. Locs. B and N had lower summer peaks, which were synchronized with those at locs. A and E. At all these localities, lake plankton was prominent.

At locs. K, O and P, quantities of plankton were small and seasonal fluctuations almost absent. No larger lakes occur upstream of these places, at which the plankton obviously consisted mainly of river bottom species etc. (cf. Müller-Haeckel 1966, 1967).

Although not quantitatively studied, it was apparent that the composition of the catch was very different at for example locs. A and B. At the former site, it consisted of a great many planktonic crustaceans imbedded in a

Tab. 7. Volumetric estimate of net-plankton drift in rivers and streams in the Ammarnäs area. Mesh size 89 μ. Quantities expressed as mm^3/m^3 (= 10^{-3} $ml/10^3$ l).

Loc.	1964 May	June	July	August	September	1965 July
A............	1,100	14,200	19,600	3,300	1,500	26,000
B............	850	5,000	3,100	1,400	450	3,800
E............	1,000	14,500	23,600	3,900	1,000	20,500
H...........	1,400	10,100	6,300	2,200	700	4,700
K...........	700	800	600	650	550	950
N...........	700	2,300	1,900	800	600	1,300
O............	–	750	900	–	500	850
P............	800	650	550	350	700	950

mass of phytoplankton, at the latter site the amounts of phytoplankton were much reduced, whereas the zooplankton occurred in about the same quantities. This indicates a more rapid disappearance of phytoplankton along the river course.

In contrast to this observation Chandler (1937) noted that the rate of disappearance of phyto- and zooplankton was about the same. Apparently several factors may influence the fate of lacustrine plankton in streams, e.g. current, substrate type, amount of vegetation and removal by filter feeders, in the Ammarnäs area particularly blackfly larvae.

2.2.6. Water temperature and break-up of ice

The break-up of the ice was observed in part in 1964. It was found that Vindelälven upstream of Gautsträsk became ice-free about a fortnight later than below Gautsträsk; Tjulån became ice-free at the same time as the lower parts of Vindelälven. Small brooks, such as the one with loc. P, became open at a very early date. Locs. D and O were inaccessible at the time. The transition from almost complete ice-cover to almost free flow in the upper part of Vindelälven took place within about 12 hr.

Local temperature differences were studied by means of mercury-in-copper thermographs which incorporated a compensation device to eliminate the influence of air temperature on the readings. The sensitive bodies were placed on the bottom at 20 to 40 cm depth and protected from direct radiation by a brick tube. Care was taken not to impede the flow around them. The thermographs were weekly checked against first-class mercury thermometers. Readings could be made to 0.1°.

Five localities were selected to show a

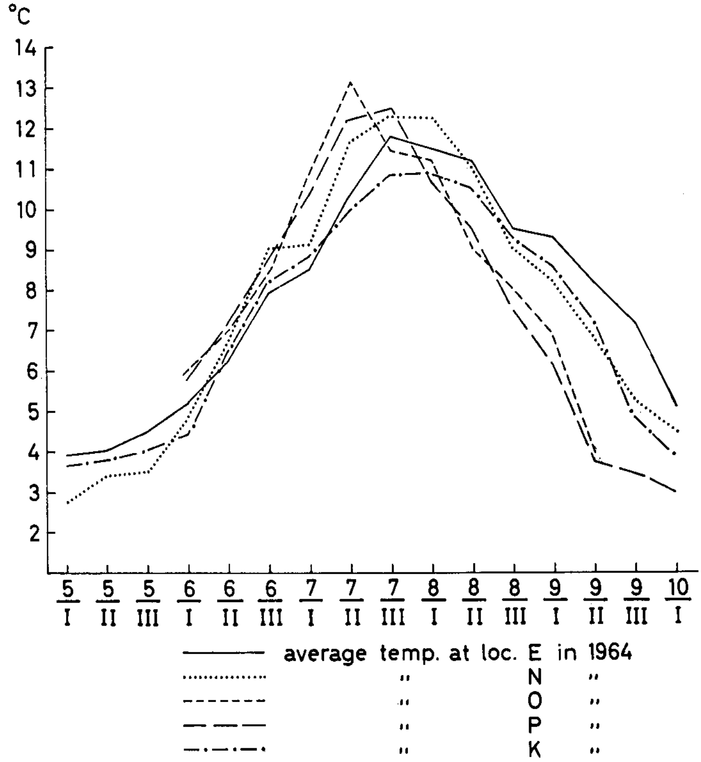

Fig. 18. Water temperature at five localities in the Ammarnäs area. Based on thermograph recordings. Averages for 10- or 11-day periods.

variety of conditions. Loc. E represents a lake outlet, and loc. K conditions in a large stream without a lake anywhere near it. Loc. N was intermediate, being almost 10 km below a lake. Locs. O and P were to represent the smaller streams. The former of these two streams ran over open heathland for most of its upper course, whilst the latter traversed partly sparse, partly dense forest.

The temperature curves (Fig. 18) disclose certain important local differences (cf. Schmitz 1954, Macan 1958 a, Edington 1966). The small streams heated up more rapidly and attained their annual peak earlier than the rivers; their peak was relatively high. On the other hand, they cooled off rapidly in autumn. Lakes exerted their maximal influence in autumn (Hrbácek and Straskraba 1966) through delaying the cooling of the downstream river stretch. Loc. K showed a particularly low temperature, whereas the highest temperature was recorded at loc. O, the highest locality situated in subalpine birch forest. This is probably due to the shallowness and the dark colour of the bottoms of the streams and small lakes on the plateau heathlands, from which its water derived. Around summer solstice, irradiation continues for 24 hr a day, and there is little or no vegetation to screen off the energy inflow. Elevated water temperatures in the uppermost parts of river systems were, although under rather different conditions, also observed by Müller (1954 a).

The curves are strongly smoothed, since they are based on average values deriving from 8 readings per 24-hr period and combined for 10-(11-)day periods. Average values for daily temperature amplitudes in corresponding periods are shown in Tab. 8. The stabilizing effect of large volume and of lacustrine influence is readily seen. The close contact between air and water in the torrential course of Tjulån resulted in comparatively large daily amplitudes. In June, all basins are full of melting water reducing local differences.

On several occasions water temperatures of above 16° have been measured in the Ammarnäs area, the maximum being 19.3° at loc. O in August 1963. Periods of water temperatures above 14° were, however, always of very short duration, only rarely covering 2 or 3 consecutive days. High air temperature is accompanied by increased snow-melting and thus does not necessarily result in markedly higher water temperatures. Moreover, the instability of the weather makes long spells of warm weather a rare occurrence.

2.2.7. Oxygen, pH, ionic composition

The oxygen content of the water was measured using standard Winkler method. A selection of representative values (compensated for altitude) are shown in Tab. 9. The river waters were usually more or less saturated with oxygen, and slight super-saturation was frequently recorded (cf. Lindroth 1957).

Very small local differences in $\varkappa$ and pH were established (Tab. 9). Conductivity was low, and pH about neutral.

Some results of water analyses performed by Dr. Th. Ahl, Uppsala, emphasize the ion poverty of the water. Only small differences between Vindelälven and Tjulån were noted (Tab. 10).

Tab. 8. Average daily water temperature amplitude per 10- or 11-day period at five stream localities in the Ammarnäs area.

Period: Loc.	5/I	5/II	5/III	6/I	6/II	6/III	7/I	7/II	7/III	8/I	8/II	8/III	9/I	9/II	9/III
E.......	0.1	0.1	0.2	0.1	0.2	0.1	0.4	0.7	0.4	0.1	0.4	0.4	0.2	0.1	0.2
N......	1.5	1.2	1.4	2.0	2.0	1.7	1.6	1.1	1.0	0.7	1.3	1.1	0.5	0.5	0.6
O.......	1.2	1.8	1.8	2.9	2.7	2.9	1.9	2.8	2.5	3.0	2.2	1.7	2.0	2.3	1.9
P.......	2.1	2.0	2.3	2.6	2.3	2.3	2.0	2.4	1.9	1.7	1.9	2.0	1.5	2.2	1.8
K......	0.6	0.8	0.7	0.7	0.7	1.2	1.5	1.6	2.0	1.4	2.0	0.8	0.4	0.3	0.5

Tab. 9. O_2 (% saturation), $\varkappa$ (S_{18}) and pH from different stream localities in the Ammarnäs area.

	15/6	15–18 hr		16/7	14–18 hr		11/8	14–16 hr		9/9	14–16 hr	
	O_2(%)	S_{18}	pH	O_2(%)	S_{18}	pH	O_2(%)	S_{18}	pH	O_2(%)	S_{18}	pH
A........	106	35.0	7.1	100	38.0	7.2	105	39.7	7.3	94	41.8	7.4
B........	98	33.5	7.0	108	34.7	7.0	112	35.0	7.0	99	31.9	7.1
D.......	94	40.8	7.4	–	–	–	100	45.9	7.5	89	50.3	7.3
E........	101	38.5	7.4	102	36.3	7.5	94	42.2	6.9	–	–	–
H.......	–	–	–	96	40.4	7.3	90	47.3	7.1	–	–	–
K.......	–	–	–	95	40.5	6.9	–	–	–	102	42.4	6.9
N.......	109	31.9	7.0	100	30.2	6.9	108	30.5	6.9	103	31.7	7.1
O........	–	–	–	–	–	–	105	48.8	6.9	94	52.5	7.3
P........	–	–	–	88	32.2	6.8	–	–	–	90	36.8	7.0

Tab. 10. Ionic composition (mg/l) at two stations in Vindelälven and Tjulån, respectively, according to data from early July 1965 (Th. Ahl, in litt.).

	pH	S_{18}	Ca	Mg	Na	K	HCO_3	SO_4	Cl	Total P	NO_3-N
Vindelälven, near loc. J.	6.90	56.3	4.1	0.8	1.2	0.5	21.1	3.3	1.3	0.003	0.040
Tjulån, near .... loc. B.	7.20	48.4	3.9	0.6	1.0	0.3	19.6	1.8	0.5	0.005	0.031

Tab. 11. Ionic composition (mg/l) at some sites in the upper Tjulån system according to Wassén (1965). Samples nos. 1 and 4 were taken near the shore at the western end of the lake, nos. 2 and 5 in the middle of the lake.

	pH	S_{18}	Ca	Mg	Na	K	HCO_3	SO_4	Cl	Total P
1. Lilla Tjulträsk 20/3/1964 .	8.5	73.6	12.7	1.5	0.8	0.6	44	5.1	1.0	0.0036
2. Same site and date	7.9	86.0	13.5	2.4	1.2	0.8	55	6.5	1.4	0.0028
3. Stora Tjulträsk, same date	8.4	64.1	9.9	1.6	1.0	0.8	36	4.7	1.4	0.0049
4. Lilla Tjulträsk, 26/7/1964.	6.8	25.8	3.7	0.7	1.2	0.8	14.6	3.1	0.6	–
5. Same site and date	7.2	29.6	4.5	1.1	0.7	0.4	17.6	2.6	0.6	–
6. Near loc. O, 24/7/1964...	7.5	76.5	–	–	–	–	–	–	–	–
7. Another stream W of Lilla Tjulträsk, same date	7.1	22.0	–	–	–	–	–	–	–	–
8. Stora Tjulträsk, 26/7/1964	7.4	41.1	–	–	–	–	–	–	–	–

Wassén (1965) presented some data for Stora and Lilla Tjulträsk and the streams flowing into the latter from the west (cf. Fig. 2). His values indicate higher conductivity values in winter, but his summer data fitted well with those obtained by me (Tab. 11).

Although chemical conditions affect the composition and abundance of benthic animals, either directly or indirectly via the vegetation (cf. Slack 1955, Armitage 1958), local differences within the Ammarnäs were probably too small to have any impact on the animal communities.

2.2.8. Recapitulation

Certain environmental factors were so uniform at all sampling sites that they cannot

Tab. 12. Recapitulation and amplification of certain environmental factors at the sampling localities in streams and rivers in the Ammarnäs area.

	A	B	C	D	E	F	G	H	J	K	L	M	N	O	P
Distance from upstream lake	0	7 km	2 km	0.5 km	0	1.5 km	2.5 km	0[1]	none	none	none	none	10 km	8 km	2–4 km[2]
Width (at normal summer flow)	20 m	20 m	10 m	10–15 m	50 m	40 m	30 m	50–60 m	30 m	30 m	25 m	35 m	20 m	10 m	1–2.5 m
Macrovegetation (aquatic)															
Didymosphenia geminata	much	some	little	little	much	much	much	little	none	none	none	none	little	some	none
mosses	much	little	little	some	some	some	some	much	some	much	much	little	little	some	very much
green algae	some	none	none	none	some	some	some	much	none	none	none	none	none	none	none
Tree vegetation	birch	mixed	birch	birch	coniferous	coniferous	coniferous	coniferous[3]	mixed	mixed	mixed	mixed	mixed[3]	birch	mixed
Current	fast	fast	fast	slow	fast	fast	fast	fast	fast	fast	fast	fast	fast	fast	slow
Stone size	average	small	average	small	large	average	average	small	average	average	average	large	small	large	average
Stone form	normal	rounded	normal	rounded	flat	flat	normal	rounded	normal	normal	normal	flat	rounded	flat	normal
Stone surface structure	rough	smooth	smooth	smooth	rough	rough	rough	smooth	rough	smooth	rough	rough	smooth	rough	rough
Amount of finer inorganic material	much	little	–	average	little	–	–	little	–	much	much	–	little	much	much
Amount of organic deposits	average	little	–	much	average	–	–	average	–	much	little	–	little	much	much
Periphyton	much	little	–	much	much	–	–	much	–	little	–	–	little	little	much
Break-up of ice	early	early	–	?	early	early	early	early	late	late	late	late	early	?	early
Freezing	late	early	–	?	late	late	late	late	early	early	early	early	early	?	early
Seston															
zooplankton	very much	much	–	–	very much	–	–	much	–	little	little	–	moderate	little	little
phytoplankton	very much	little	–	–	very much	–	–	much	–	little	little	–	little	little	little

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[1] A lake-like river extension (Swedish: sel), rather than a true lake.

[2] Several small tarns.

[3] Also hay-fields.

give rise to local differences in the animal communities. In addition to factors described above, light may be cited as such a factor. Except loc. P which was somewhat shaded, all localities were exposed to direct irradiation (cf. Scherer 1965 a, b, Hughes 1966 a, b).

The size of the water courses from which the samples were taken varied from a large river (locs. E, H, K, L) to a quite small brook (locs. O and still more, P) and included also a medium-sized stream (locs. A, B, N, D). Two localities were at lake outlets (A, E) and one at the downstream end of a lake-like river extension (H). Some localities were relatively uniform, for example H, N and O, others markedly variable, such as K and L.

The current was everywhere swift and the substrate accordingly composed of large stones with variable amounts of inorganic and organic matter in sheltered places. Periphyton and seston were particularly abundant at lake outlets, sometimes also at other localities.

Temperature conditions varied with the size of the stream and the distance from upstream lakes. Not only the temperature as such, but also the seasonal fluctuations were locally different.

Several important environmental factors are summarized in Tab. 12, which includes information also concerning some less readily quantified factors not discussed previously.

Some environmental factors are obviously dependent on others. Sometimes the parallellism is very close, for instance between current and substrate. The intricate interaction between factors is a circumstance that must be constantly kept in mind (cf. § 10). Another important feature of Lapland streams is that many factors vary within very small bottom areas (Ulfstrand 1967). Furthermore, there are many important similarities in respect of various environmental conditions between localities that superficially look very dissimilar (cf. § 3.4.3).

3. Qualitative composition and species density of the community and some zoogeographical comments

3.1. Introduction

As a basis for the analytical work a species list was compiled using the samples described in § 5 (cf. Macan 1963). Only species obtained in the benthic samples were included in the list, because records of imagines from the shore do not prove that the species is a member of the lotic community. A rough evaluation of the status of the listed species will also be made.

In this section a number of interesting cases of restricted local distribution within the study area will also be discussed, and special attention will be paid to the question of ecological segregation and interspecific interference.

3.2. Qualitative efficiency of the sampling method

The sampling method will be described and evaluated in §§ 5.2 et seqq. In this context we are interested in assessing its efficiency only from a qualitative viewpoint.

A number of localities which had been

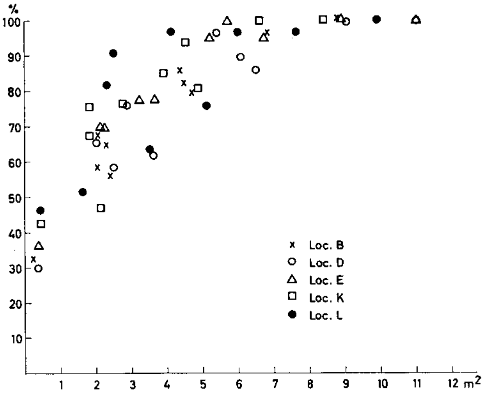

Fig. 19. Cumulative number of species recorded from each of five localities expressed as percentage of total number plotted against standard area sampled.

Tab. 13. Qualitative composition of the benthic community at the different sampling localities. tera, Trichoptera and Diptera Simuliidae, see § 3.7. Expla-

	A	B	D	E	H	K	L	N	O	P	Dominance index	Zoogeographical category
Ephemeroptera												
Siphlonurus sp.[1]	A	–	D	A	A	–	A	A	–	–	26	3
Ameletus inopinatus Etn.	I	D	S	D	D	S	I	D	A	S	98	3
Parameletus chelifer Bgtn.	–	–	–	–	–	–	–	A	–	–	2	1
Baetis fuscatus L.[2]	I	D	A	I	I	S	D	D	I	I	78	3
B. lapponicus Bgtn.	I	S	A	I	I	S	S	I	D	I	62	1
B. macani Kimm.	D	–	A	D	A	–	–	–	–	–	36	1
B. pumilus Burm.	I	S	I	I	I	S	I	S	I	I	52	3
B. rhodani Pict.	D	D	D	D	I	D	D	D	D	D	148	3
B. subalpinus Bgtn.	D	S	I	D	I	D	D	D	S	S	112	1
Centroptilum luteolum Müll.	–	A	A	–	–	–	–	–	–	–	4	3
Metretopus borealis Etn.	–	–	I	I	A	A	I	A	–	–	18	2
Ecdyonurus joernensis Bgtn.	S	A	A	S	I	–	A	A	I	A	34	1
Heptagenia dalecarlica Bgtn.	I	S	D	I	S	S	D	S	D	D	104	1
H. fuscogrisea Retz.	–	–	A	–	–	–	–	–	–	–	2	3
H. sulphurea Müll.	S	I	A	D	S	–	A	I	–	–	44	3
Leptophlebia marginata L.	–	–	A	–	–	–	–	–	–	–	2	3
Paraleptophlebia sp.[3]	–	–	–	A	A	–	–	–	–	–	4	1
Ephemerella aurivillii Bgtn.	D	D	S	D	D	D	S	D	I	D	132	2[10]
E. mucronata Bgtn.	–	–	I	I	S	S	I	–	–	–	28	2[11]
Plecoptera												
Brachyptera risi Mort.	–	I	D	–	–	I	I	A	I	I	38	3
Taeniopteryx nebulosa L.[4]	D	D	I	D	I	S	I	D	–	A	86	3
Amphinemura borealis Mort.	S	S	D	A	D	S	S	S	–	–	74	2
A. standfussi Ris	I	A	I	S	I	I	A	A	I	I	38	3
A. sulcicollis Steph.	A	A	S	A	I	I	A	I	A	S	38	3
Nemoura arctica Esb.-P.	–	–	–	–	–	A	–	–	–	–	2	1
N. avicularis Mort.	–	–	–	–	–	A	A	–	–	–	4	3
N. cinerea Retz.	–	A	A	A	–	A	–	A	I	I	18	3
Nemurella picteti Klap.	–	–	–	–	–	–	–	A	–	A	4	3
Protonemura meyeri Pict.	–	A	I	–	A	D	I	A	I	D	50	3
Leuctra digitata Kemp.	–	–	I	–	–	A	A	–	I	S	20	2
L. fusca L.	D	D	D	D	D	D	D	D	S	I	140	3
L. hippopus Kemp.	S	D	I	A	–	D	S	D	D	D	102	3
L. nigra Ol.	–	–	A	–	–	–	A	–	–	–	4	3
Capnia atra Mort.[4]	I	I	A	S	I	I	I	I	A	–	36	2
C. pygmaea Zett.[4]	–	–	–	–	–	A	A	I	–	–	8	1

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[1] Mainly *S. lacustris* Etn., according to records of imagines.

[2] For taxonomy, see § 1.5.

[3] Only *P. strandii* Etn. recorded from the area.

[4] Probably under-represented because of early flight-period.

[5] Possibly a very small proportion of *Rh. obliterata* McL. included, according to records of imagines.

[6] Only *H. nevae* Kol. identified from within the area.

[7] *A. stigmatella* Zett. and *A. wallengreni* McL., the former very widely spread, the latter apparently of more restricted local distribution. Possibly a few *A. zonella* Zett. included, particularly at lake outlets, according to records of imagines.

Letters and dominance index explained in text (§ 3.3). For other taxa than Ephemeroptera, Plecop-
nation of zoogeographical categories is found in § 3.6.

	A	B	D	E	H	K	L	N	O	P	Dominance index	Zoogeographical category
Capnopsis schilleri Rost.	–	A	A	–	–	I	–	–	A	A	12	2
Arcynopteryx compacta McL.	–	A	S	–	–	A	–	–	–	–	12	2
Diura bicaudata L.	D	A	D	D	I	–	–	–	–	–	54	2
D. nanseni Kemp.	D	D	D	D	D	D	D	D	D	D	160	1
Isoperla grammatica Poda	D	D	S	D	S	D	I	D	A	I	106	3
I. obscura Zett.	A	–	–	D	S	A	–	A	–	–	30	3
Dinocras cephalotes Curt.	–	–	–	–	–	–	A	–	D	A	20	3
Chloroperla burmeisteri Pict.	–	–	I	–	–	S	I	A	I	D	38	2
Trichoptera												
Rhyacophila nubila Zett.[5]	D	D	S	D	D	D	D	D	D	D	152	3
Glossosoma intermedium Klap.	–	D	–	–	–	–	–	D	–	–	32	2[12]
Philopotamus montanus Don.	–	–	–	–	–	–	A	–	D	D	34	3
Arctopsyche ladogensis Kol.	–	–	–	D	S	S	I	I	–	–	40	2[13]
Hydropsyche sp.[6]	–	–	–	A	A	–	A	–	–	D	22	2[13]
Plectrocnemia conspersa Curt.	A	A	–	–	–	A	I	–	–	D	26	3
Polycentropus flavomaculatus Pict.	S	D	D	D	I	D	I	S	I	–	92	3
Apatania spp.[7]	D	D	I	S	S	I	I	D	–	–	76	2[14]
Potamophylax stellatus Curt.	D	D	D	D	S	I	I	D	I	S	108	3
Silo pallipes Fabr.	–	A	–	–	–	–	–	A	–	–	4	3
Athripsodes sp.[8]	S	A	I	S	S	A	–	A	–	–	34	–
Diptera Simuliidae												
Helodon ferrugineus Wahlb.	–	D	S	–	–	S	S	I	D	I	64	–
Prosimulium hirtipes Fries	–	D	I	D	A	D	S	D	D	D	110	–
Cnephia fuscipes Fries[9]	I	D	S	I	D	S	D	S	I	D	100	–
C. lapponica End.	–	–	–	D	–	–	–	–	–	–	16	–
C. tredecimata Edw.	D	–	–	I	A	–	–	–	–	–	22	–
C. trigonia Ldstr.	I	A	–	S	A	–	–	A	–	–	18	–
Eusimulium aureum Fries	–	–	A	–	–	A	I	I	A	A	16	–
E. bicorne Dor. & Rubz.	–	A	I	A	A	A	A	A	A	–	18	–
E. latipes Mg.	A	I	I	A	A	S	S	S	I	S	50	–
Schönbaueria annulitarsis Zett.	D	I	I	D	S	I	I	S	S	–	72	–
Gnus forsi Carlss.	S	D	D	I	I	S	I	I	S	A	74	–
Odagmia monticola Fried.	I	S	I	A	D	D	D	S	D	D	106	–
O. ornata Mg.	–	I	I	A	I	S	A	–	I	D	44	–
Simulium argyreatum Mg.	S	–	A	D	A	–	–	–	–	–	28	–
S. truncatum Ldstr.	D	S	S	D	D	–	A	I	A	A	74	–

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[8] Several species known from area; imagines of *A. nigronervosus* Retz. taken in largest numbers.

[9] A few *C. pallipes* Fries possibly included. Not supported from records of imagines.

[10] Including the Baltic provinces.

[11] Including the southwestern parts of U.S.S.R.

[12] A disjunct distribution. Inadequate information?

[13] Not south of the Baltic.

[14] *A. stigmatella*: not south of the Baltic; *A. wallengreni*: not south of the Baltic on the continent, but occurs in the British Isles.

sampled on almost the same date in 1962 to 1965 were selected. As described below (§ 5.2), from June 1964 onwards, subsamples were kept separately. Through different combinations of samples and subsamples and the corresponding species lists, it was possible to follow the increase of number of species recorded in relation to standard area covered. Although a species list almost never becomes definitive, because of the addition of accidentals, an asymptotic flattening of the curve would indicate that the list was approaching completeness.

Provisionally using the final number of species recorded as 100%, the addition to the species lists was plotted against standard area in Fig. 19. At a standard area of about 6 m^2 only small increments occurred and even with much less sampling the percentages were so high that all regular and relatively common species were likely to be included. At 0.5 m^2 standard area between 30 and 50% of all the species had been obtained, indicating that such a comparatively small sample will secure practically all the dominant species (cf. Needham and Usinger 1956). Sampling efficiency was virtually the same at the different localities.

It can therefore be assumed that the extent of the samples was adequate for a qualitative analysis of the community.

3.3. Survey of species composition

For each of the ten localities described in § 2.2.1, a list was made of every mayfly, stonefly, caddisfly and blackfly species obtained in the benthic samples, and these lists are combined in Tab. 13. A classification of the species with respect to their status in the community was attempted as follows.

The tables showing the percentual composition of the standing crop of the major taxa (Tabs. 19 to 28) formed the basis for the classification. This information was supplemented by general experience concerning the status of the species gained in the course of the field work. This was particularly necessary to provide an adequate picture of the status of the scarcer species. Four categories were designed, viz.:

dominant species – D: species making up a large proportion (at least 25%) of the total standing crop of the zoome (Ephemeroptera, Plecoptera, Trichoptera, Diptera Simuliidae) during some part of the year;

subdominant species – S: species making up at least 10% of the zoome; species only occasionally making up more than 25% were also placed in this group;

incidental species – I: scarce species of more or less regular occurrence;

accidental species – A: species recorded on one or a few occasions, or if more often, in single individuals only.

Categories D and S comprise characteristic species of a given locality, usually completing their entire life cycle at the site. Category I includes species of variable status (cf. below), whilst the species of category A probably belong to some other biotope and make only a transient appearance in the sampling locality.

To facilitate a survey, a dominance index was calculated by giving the above symbols numerical values, viz. D = 16, S = 8, I = 4 and A = 2. By adding up the figures for all the localities, an overall impression is gained of the status of the species in the community. These indices are given in Tab. 13.

It should be mentioned that a proportion of the caddisfly and blackfly larvae could not be specifically identified.

On the basis of these indices, the species were classified in dominance groups as indicated in Tab. 14. Five species, viz. *Baetis rhodani*, *Ephemerella aurivillii*, *Leuctra fusca*, *Diura nanseni* and *Rhycophila nubila* were the most dominant members of the community.

A source of error is that if a species has a very early flight-period, it is likely to be under-represented as it was most catchable at times when sampling was impossible. This probably gave rise to reduced indices for e.g. *Taeniopteryx nebulosa* and *Capnia atra*. If a species with an early flight-period undergoes most of its growth already in the preceeding summer or autumn, it will not be under-represented to the same extent (e.g. *Glossosoma intermedium*).

A low index may depend on various reasons. Some species are widely but thinly distributed, e.g. *Amphinemura standfussi*,

Tab. 14. Grouping of the species in dominance classes based on dominance index figures of Tab. 13.

Index: 42–80	82–120	122–160
Baetis fuscatus *B. lapponicus* *B. pumilus* *Heptagenia sulphurea*	*Ameletus inopinatus* *Baetis subalpinus* *Heptagenia dalecarlica*	*Baetis rhodani* *Ephemerella aurivillii*
Amphinemura borealis *Protonemura meyeri* *Diura bicaudata*	*Taeniopteryx nebulosa* *Leuctra hippopus* *Isoperla grammatica*	*Leuctra fusca* *Diura nanseni*
Apatania spp.	*Polycentropus flavomaculatus* *Potamophylax stellatus*	*Rhyacophila nubila*
Helodon ferrugineus *Eusimulium latipes* *Schönbaueria annulitarsis* *Gnus forsi* *Odagmia ornata* *Simulium truncatum*	*Prosimulium hirtipes* *Cnephia fuscipes* *Odagmia monticola*	

A. sulcicollis, *Eusimulium bicorne*. Others are restricted to only one or a few localities where they may be highly dominant, e.g. *Dinocras cephalotes* at loc. O, *Plectrocnemia conspersa* at loc. P and *Cnephia lapponica* at loc. E. Some species belong to lenitic biotopes, or to other lotic biotopes than the types represented in the samples but invade the sampling localities with a certain regularity, e.g. *Baetis macani*, *Ecdyonurus joernensis*, *Metretopus borealis*, *Nemoura avicularis*, *N. cinerea*, *Arcynopteryx compacta*.

No blackfly species could be included in the highest dominance class, because these were usually abundant either at outlets or at other localities, but not at both (§ 3.5.2).

3.4. Species density

3.4.1. At the localities in the Ammarnäs area

The numbers of species of mayflies, stoneflies, caddisflies and blackflies found at each locality are shown in Tab. 15. Whether these groups are combined or each is regarded separately, inter-locality differences were rather small. There is no apparent correlation between stream size and species number. Even the smallest water courses seemed to be above the size limit regarded as inimical to the perpetual existence of benthic populations by Hynes (1941) and Berthélemy (1966). Nor were there any differences between outlet localities and the others.

3.4.2. Comparison with other regions

In Tab. 16 the species density at the localities in the Ammarnäs area is compared with that in other parts of Europe. Such comparisons have to be made with great care, because there will inevitably be differences in methods and extent of the sampling work, in the criteria on which species were included in the local list, etc. In the examples used in Tab. 16, all the biotopes are of rhithron type (§ 4.2) and are comparatively unaffected by human activities (exception: Mauch 1963). Comparison had to be limited to mayflies and stoneflies.

The compilation shows that the species density in the Ammarnäs area was about the same as found generally in western and central Europe, and only in certain mountainous regions with pronounced endemism (cf. Illies 1967) were distinctly larger numbers of species recorded.

It may therefore be concluded that the streams of northern Scandinavia possess a rich variety of niches and that climatical conditions generally are not adverse for mayflies and stoneflies. Certain major taxa prominent in more southerly areas, such as Turbellaria, Oligochaeta, Mollusca and Coleoptera, are on the contrary sparsely represented in northern

Tab. 15. Number of species recorded at the different stream localities in the Ammarnäs area. The letters D, S, I and A refer to dominance categories as explained in § 3.3.

	Locs.	A	B	D	E	H	K	L	N	O	P	Average
Ephemeroptera	D	4	4	3	6	2	3	4	5	3	4	3.8
	S.......	2	4	2	1	2	6	2	2	1	1	2.3
	I.......	5	1	4	6	7	–	4	2	4	4	3.7
	A	1	2	8	2	4	1	3	4	1	–	2.6
	Total ...	12	11	17	15	15	10	13	13	9	9	12.4
Plecoptera	D	6	5	5	6	3	5	2	5	3	4	4.4
	S.......	1	1	3	2	2	3	2	1	1	2	1.8
	I.......	2	2	5	–	5	5	6	3	6	5	3.9
	A	2	7	4	4	1	7	7	7	4	4	4.7
	Total ...	11	15	17	12	11	20	17	16	14	15	14.8
Trichoptera	D	3	5	3	4	1	2	1	4	2	4	2.9
	S.......	2	–	–	2	4	1	–	1	–	1	1.1
	I.......	–	–	2	–	1	2	5	1	2	–	1.3
	A	1	3	–	1	1	2	2	2	–	–	1.2
	Total ...	6	8	5	7	7	7	8	8	4	5	6.5
Diptera Simuliidae	D	3	4	1	5	3	2	2	1	3	4	2.8
	S.......	2	2	4	1	1	5	3	4	2	1	2.5
	I.......	3	3	5	3	2	1	3	4	3	1	2.8
	A	1	2	2	4	6	2	3	1	4	3	2.8
	Total ...	9	11	12	13	12	10	11	10	12	9	10.9
Grand total ...		38	45	51	47	45	47	49	47	39	38	44.6

Tab. 16. Number of species found in rhithron (except Mauch 1963) biotopes of different European regions compared with the number recorded in the Ammarnäs area.

Area	Ephemeroptera	Plecoptera	Authority	Remark
Wales.................	8	9	Jones (1948)	Several small streams
England..............	–	16	Mackereth (1957)	Small stream
Wales.................	12	19	Hynes (1961)	Small stream
England..............	9	14	Macan (1963)	Small stream
Central Germany......	10	10	Illies (1952a)	Small stream
Central Germany......	22	27	Dittmar (1955a)	Small stream
Germany (Moselle)	11	8	Mauch (1963)	Large river, partly polluted
The Pyrenees, France...	–	31	Berthélemy (1966)	Medium-sized river, only one station
The Carpathians, Poland	6	16	Kamler (1965)	Medium-sized river
The Carpathians, Poland	21	40	Sowa (1965)	Medium-sized river
Swedish Lapland:				
total study area......	19	24		River, large stream and small stream
Vindelälven (locs. E, H, K, L)..	15	23		River
Tjulån (locs. A, B, N)	15	19		Large stream
Locs. D and O	17	19		Medium-sized streams
Loc. P	9	15		Small stream

Scandinavia. This may depend, not on the prevalent ecological conditions, but on historical circumstances.

3.4.3. Biotope differentiation and amplitude in habitat requirements

Brinck (1949) and Brinck and Froehlich (1960) pointed out that certain stoneflies inhabit a considerably larger variety of habitats in the north than farther south. One explanation is that the differences between superficially widely different biotope types are relatively small in the north. Several circumstances contribute to reducing the ecological differentiation between, for instance, lake and river in the north. The low temperature and the rapid exchange of the water in part due to the large altitude gradients in many running waters bring about a very high oxygen content in the lakes as well as in the streams. Species which in the south are restricted to running water because of high oxygen requirements may in the north penetrate into the lakes.

The sampling localities in the Ammarnäs area were inhabited, regularly or irregularly, by no less than 24 of the 35 (Brinck 1949, Illies 1953 a) stonefly species found in Sweden. Such an accurate proportion cannot be given for the mayflies, but it is likely that the species obtained make up a very large part of the whole Swedish fauna. This high species density is probably related to a combination of the reduced biotope differentiation and the extended habitat range of many species.

3.5. Ecological differences between species

3.5.1. Introduction

A great many species were found at all or nearly all of the sampling localities. This applies not only to those in the highest dominance category, but also to many with lower dominance indices (Tab. 13). Others, however, showed different types of range restrictions indicating special ecological requirements. Of particular interest are cases of ecological segregation between species. These questions will be discussed in the following; a certain amount of speculation will be unavoidable in this connection.

3.5.2. The lake outlet community

In respect of certain environmental factors, the lake outlets were found to deviate from other localities. This particularly concerns the supply of food in the form of lacustrine seston and the temperature conditions (§§ 2.2.5 and 2.2.6).

Certain blackfly species are characteristic of the outlets. Elsewhere they occur in small numbers only, if at all. Good examples are *Cnephia lapponica* (only at loc. E), *C. tredecimata* (mainly at loc. A), *C. trigonia*, *Schönbaueria annulitarsis*, *Simulium truncatum* and *S. argyreatum*. The well-known abundance of blackflies at lake outlets is certainly related to food supply (cf. Knöpp 1952, Müller 1955, 1956, 1962 b, Illies 1957, Carlsson 1962, 1967, Cushing 1963). It is more remarkable that certain blackfly species definitely avoided the outlets, or were at least sparse or irregular at these sites. This applies to *Helodon ferrugineus*, *Prosimulium hirtipes*, *Cnephia fuscipes*, all *Eusimulium* spp., *Gnus forsi* (not invariably) and *Odagmia ornata*, in part also to *Odagmia monticola*. The populations of these species were never anything like so numerous as those of the outlet species (cf. § 7.4). In the absence of upstream lakes they were obviously restricted to a much poorer food supply, above all drifting benthic algae. Morphologically they reveal no fundamentally different feeding specialisations.

Among the mayflies, stoneflies and caddisflies, hardly any species was as distinctly dependent on outlet conditions as several of the blackflies. Therefore, only in the last-mentioned group is it legitimate to speak of a particular outlet zoome.

Heptagenia sulphurea revealed a distinct preference for the lake outlets, where it was usually more numerous than its close relative *H. dalecarlica*, which in turn was more numerous at the other localities. *H. sulphurea* was probably favoured by the elevated autumn water temperatures at lake outlets which permitted a more rapid growth of the nymphs (Ulfstrand 1968).

On the other hand, *Baetis fuscatus* and *B. lapponicus* as well as *Brachyptera risi* were practically absent from the lake outlets. Nevertheless, the outlet communities differed qualitatively from other communities only in respect of the blackfly zoome.

3.5.3. Stream size

A number of species were much more abundant in, or even restricted to, the smaller water courses, of which loc. P was the best example. This applies to *Amphinemura sulcicollis*, *Leuctra hippopus*, *L. digitata*, *Dinocras cephalotes*, *Plectrocnemia conspersa*, *Hydropsyche* sp. and *Philopotamus montanus*. Conversely, certain species tended to avoid, or be sparse in, these smaller streams, viz. *Amphinemura borealis*, *Leuctra fusca*, *Isoperla obscura*, *Arctopsyche ladogensis*, *Polycentropus flavomaculatus* and both *Apatania* spp. In most cases the distinction was not absolute. Macan (1961 b, 1962 a, b) discussed similar circumstances and attached a considerable importance to the biotic factor (cf. the following section).

Glossosoma intermedium was found to be unusually restricted; its larvae and pupae were never obtained outside locs. B and N. They were usually found on rounded stones with a smooth surface; a kind of unstable substrate that was particularly widespread at these localities. It is believed that this factor was the most important, but this cannot be shown conclusively from the present data. The significance of substrate stability has been discussed by Hynes (1941) and Scott (1958).

3.5.4. Ecological segregation

Coexisting species are usually segregated ecologically. This generally accepted principle has been discussed for lotic communities or zoomes by Ide (1935), Illies (1952 b, 1961 a, b), Botosaneanu (1960), Macan (1962 a, 1963), Berthélemy (1966, 1967) and Sheldon and Jewett (1967). For a recent survey, see also De Bach (1966). The ways in which segregation is affected are various and include differences in habitat preferences, in the timing of the reproductive season or other phases of the life cycle, in feeding habits or in activity rhythm patterns (e.g. Schmidt and Müller 1967).

Closely related species, e.g. members of the same genus, may have evolved in different environments and have aquired, through natural selection, different ecological attributes. If two such species establish contact after a change in distribution, they can coexist if their ecological adaptations have become sufficiently divergent, i.e., if they occupy different ecological niches. If their differences are less marked, some kind of interspecific interference will occur. This may lead to displacement of either species, being in some respect inferior to the other. Natural selection may, however, force either or both species in the direction of increased divergence, leading to a relationship between the two species that allows them to coexist. In this way, convergence of initially divergent species is also prevented.

These general considerations no doubt apply also to the insect groups with which we are here concerned. However, the situation is obscured by the fact that many aquatic insect species possess a surprisingly great local or regional ecological variability.

According to Brinck and Wingstrand (1951), Brinck and Froehlich (1960) and Brinck (personal communication), *Diura nanseni*, *D. bicaudata* and *Arcynopteryx compacta* occur together in large numbers in the lake Virihaure situated in a high mountain area in northern Lapland. This is in striking contrast to the situation in the Ammarnäs area, where these three species are almost totally segregated, *D. bicaudata* being almost entirely restricted to lakes, *D. nanseni* to rivers and streams and *A. compacta* to water above the altitudinal range of the study area, within which *A. compacta* was only a scarce accidental.

Setipalpian stoneflies were discussed in this respect by Hynes (1952) and Macan (1962 b, 1963). *D. bicaudata* in Britain inhabits high altitude streams, being replaced at lower levels by *Perlodes microcephala* Mort. On the Isle of Man the latter is absent, and here *D. bicaudata* descends to sea level. Hynes interpreted this in terms of competitive displacement to which Macan agreed.

It is very possible that such cases are often the result of interspecific interference. But the local variability displayed by the Lapland setipalpians indicates that other factors also influence the interspecific relationships, which may be different in different regions.

Surveying the species list from the Ammarnäs area, one finds that congeneric species are often well segregated ecologically. As their phylogeny and earlier distribution patterns are unknown, it is impossible to say whether these differences have evolved as response to interspecific relationships in communities closely similar to the present ones, or whether they arose under profoundly different conditions.

Before citing some examples, it should be pointed out that congeneric species are not invariably similar ecologically; but this is so frequently the case that it may be used as a working hypothesis.

Six *Baetis* spp. are represented in the benthic samples. *B. macani* is mainly a lenitic species and thus deviates from the rest. The other five species may be subdivided in two groups with respect to nymphal morphology and locomotory pattern. One group consists of *B. rhodani*, *B. fuscatus*, and *B. subalpinus*, whose nymphs are good swimmers and often take to swimming around when kept in an aquarium. The most intense growth periods of *B. fuscatus* and *B. subalpinus* occur in July and August, i.e. during and shortly after the flight-period of *B. rhodani*. The maximal growth of the two first-mentioned species, thus, is undergone when the nymphal population of the last-mentioned species is at its lowest level. *B. fuscatus* and *B. subalpinus* have several distinctive features too, as was revealed in the drift and colonization studies (§§ 8 and 9). The three species of this group, thus, were in part segregated in various ways.

The other group consists of *B. lapponicus* and *B. fuscatus*, which, when observed in the laboratory, were seen to swim only reluctantly and – when forced to do so – with considerable effort. They seem to be adapted to crawling on and in the substrate, rather than swimming. Between themselves, they differ strikingly, for *B. pumilus* is laterally, *B. lapponicus* dorsoventrally compressed.

No other mayfly genus was represented by so many species.

The two *Ephemerella* spp. differ in habitat requirements and life cycle pattern (Ulfstrand 1968), whereas *Heptagenia sulphurea* and *H. dalecarlica* overlap considerably, but the latter has a much wider local distribution range. Other heptageniids were restricted to lenitic biotopes.

To the above discussion of setipalpian stoneflies it may be added that the habitats and flight-periods of *Isoperla grammatica* and *I. obscura* overlapped widely, the former having a much wider local distribution range. Svensson (1966) found a clear segregation between *I. grammatica* and *I. difformis* Klap. in his study area in northeastern Sweden.

Among the filipalpians, the three *Amphinemura* spp. were temporally segregated, *A. standfussi* being later than the others, as well as spatially, *A. borealis* preferring larger and *A. sulcicollis* smaller streams. The position of *Protonemura meyeri* is uncertain. The four *Leuctra* spp. also differed, *L. nigra* being rare in the present biotopes and primarily inhabiting very small brooks, *L. hippopus* being early and most abundant in relatively small streams, where it was succeeded by *L. digitata*, and *L. fusca* being later than any other stonefly species.

Spatial segregation also occurs in the caddisflies. The large rivers and streams are inhabited by *Arctopsyche ladogensis* and *Polycentropus flavomaculatus*, whereas the small streams (loc. P) constituted the preferred habitats of *Hydropsyche* sp. and *Plectrocnemia conspersa*. The life cycles of the two *Apatania* spp. were completely asynchronous.

Superficially at least, blackflies seem to be an usually homogeneous group in their larval ecology. As discussed in § 3.5.2, some species were restricted to or much more abundant at lake outlets than elsewhere, and at the outlets there was a tendency to temporal succession. But it also occurred that dense larval populations of more than one species were present simultaneously, a situation challenging further study.

The many cases of interspecific segregation of ecologically similar species and the scarcity of cases of apparently effective overlapping suggest that interspecific interference is an important determinant of the community composition. At the same time, the example of the setipalpian stoneflies emphasizes that other factors affect the efficacy of interspecific interference in producing segregation. In some biotopes, two or more species can coexist, in other biotopes they cannot.

In recently disturbed biotopes, communities have not had time to return to a steady state, and it is therefore not unexpected that cases of interspecific ecological overlapping are said to be more numerous in such biotopes (cf. Dittmar 1955 a).

3.6. Zoogeographical aspects

In many cases the zoogeographical discussion is seriously impeded by inadequate taxonomic and faunistic information. Only the stoneflies are wellknown in these respects. Their zoogeography has been discussed by Brinck (1949), Illies (1953 b, 1955, 1965) and others. The distribution of blackflies is poorly known in spite of Rubzow's (1959/64) great monograph, and many new species are being described in this family. There are also serious gaps in our knowledge of the mayflies and caddisflies, although Illies (1967) compiled a great deal of previously scattered information.

A zoogeographical classification of the species is attempted in Tab. 13 (right-hand column). Three categories were distinguished, viz. 1) species having a distinctly northeasterly distribution, being absent from western and central Europe, 2) species of the same general character as group 1, but having outposts in central and western Europe, 3) widely distributed species in western Europe, often predominantly southerly.

Some of the species in category 2 were so placed because their continuous range extends into east-central Europe (both *Ephemerella* spp.), others because they have some scattered outposts in the central European mountains, as discussed in great detail by Illies.

From Tab. 17 it is seen that a proportionately larger number of mayflies than of the other two major taxa were referable to group 1. No caddisfly belonged to that group. A general northeasterly predominance of mayflies is, thus, very obvious. Stoneflies have many species in group 2. Caddisflies, evidently, differed profoundly from the other two groups from the zoogeographical standpoint.

No correlation between zoogeographical category and preference for lotic as compared with lenitic biotopes can be found. Nor is there any correlation between zoogeographical affinity and dominance.

Tab. 17. Distribution of mayfly, stonefly and caddisfly species on zoogeographical groups. The classification of each species may be seen in Tab. 13. Group 1 = distinctly northeasterly species absent from western Europe, 2 = basically northeasterly species having a smaller or larger number of outposts in central and/or western Europe, 3 = widespread species in western Europe, often predominantly southerly.

Taxon	Zoogeographical group 1	2	3	Total
Ephemeroptera...	7	3	9	19
Plecoptera.......	3	7	14	24
Trichoptera......	–	5	6	11
Total...........	10	15	29	54

3.7. Other major taxa

Although mayflies, stoneflies, caddisflies and blackflies form the subject of this investigation, other groups will be briefly mentioned. In the samples all macroscopically visible animals were included, but apart from the four major taxa mentioned, only Diptera Chironomidae were at all numerous and regular.

The sponge *Spongilla lacustris* L. was sometimes numerous, especially at loc. D. Nematodes were regularly obtained, but never in large quantities. Among the molluscs, *Radix peregra* Müll. was by far the most numerous species, whereas *Gyraulus acronicus* Fér. was much more local and sparse. *Pisidium* sp. were only sporadically obtained.

Oligochaetes were numerous at some localities. The tufts of *Didymosphenia geminata* were inhabited by large numbers of enchytraeids, and lumbricids were not seldom obtained near the shore.

At the lake outlets and at loc. D, *Gammaracanthus lacustris* Sars was frequent. The only abundant species of Coleoptera was *Elmis aenea* P. Müll., particularly at locs. D, K and L. The only other species ever found was *Oreodytes alpinus* Payk. (determined by Dr. B.-O. Landin).

Dipteran larvae (other than blackflies) were often abundant. Chironomids and ceratopogonids were the most numerous groups, but in *D. geminata* and moss, empidid larvae were also abundant. Particularly in early spring samples, tipulid larvae were often prominent.

Finally, the bryozoan *Fredericella sultana* Blb. (determined by Dr. B. Hyltén-Cavallius) was obtained in a few samples.

Generally speaking, the animal community was completely dominated by insects. This is generally true of lotic biotopes in this part of the world (cf. Lillehammer 1966 for Norway).

4. Characterization and classification of lotic biotopes and their animal communities

4.1. Introduction

For descriptive purposes it would be useful to have a practical classification of running water biotopes and their animal communities, and several attempts have recently been made in this direction, particularly by Illies (1961 b, 1962) and Illies and Botosaneanu (1963). No distinction is generally made between the problems of biotope and community classification, although it would seem natural to use environmental conditions for the fomer and faunistic composition for the latter purpose.

4.2. Biotope classification

Illies (1961 b) divided the running water biotopes into two categories called *rhithron* and *potamon*, each with several subdivisions that will not concern us. He made use of several environmental conditions and took account of latitudinal differences.

The environmental criteria of Illies permit the inclusion of all the present localities into the rhithron category. Thus, the annual temperature amplitude in the water was less than 20° (Figs. 6 and 18), current was rapid (Tab. 2) and oxygen content high (Tab. 9). The Ammarnäs localities were not situated very near to where the streams rise, nor is the water volume small, but these divergences were anticipated and explained in Illies's scheme.

Environmental factors are the basis for the delimitation of biotopes (§ 1.6). The question then arises: What environmental factor has the most direct influence on the life conditions of the benthic species of lotic biotopes? The answer to this question is of considerable importance for a biotope classification.

Current and substrate (s.l.) are inseparable factors. Temperature is largely an independent variable, although the speed and turbulence of the current affects the contact between air and water and accordingly the heat transfer from one to the other. Oxygen conditions are influenced by current and temperature, as well as by biotic factors (cf. Edwards 1962), although not usually in the rhithron. These must be considered the most important environmental factors for the rhithron community. The reactions of animals to these factors may be modified by still other factors, such as light and CO_2-content (Scherer 1965 a, b).

Substrate, in the wide sense, undoubtedly has a very direct effect on the life conditions of a great many benthic animals. In particular the detritus and periphyton are major food sources for most species; much of the detritus is allochthonous (Hynes 1963, Darnell 1964, Minshall 1967). Some special groups such as blackfly larvae and net-spinning caddisflies feed mainly on seston, but also for these species the substrate plays a fundamental role (Carlsson 1967). At the same time it is clear that these groups are more directly dependent on current conditions than others (Phillipson 1957, Carlsson 1962, Edington 1965, Harrod 1965). In addition, the community has its share of predators.

The direct effect of current speed on the life conditions of the benthic community has frequently been overrated. Many workers, however, emphasize the fact that animals are able to live in a stream without being really in contact with the current (Nielsen 1950, Macan 1961 b, Ambühl 1961), because of the stratification of current velocity as well as their own ethological and morphological adaptations (cf. Ambühl 1959, 1961, Pleskot 1962, Jaag and Ambühl 1962, Bournaud 1963, Scherer 1965 a, b). I am therefore inclined to agree with e.g. Thorup (1966) that current is less advisable for biotope classification. This is not to underestimate the effect of catastrophic spates which have been known seriously to deplete benthic populations (Maitland 1966). Nor is this to underestimate the effects of current on oxygen availability (Berg 1948, Ambühl 1961, Ruttner 1963). However, from this viewpoint there is an important distinction between no current at all and the presence of current, whereas great differences in current velocity are frequently of minor significance (Philipson 1954, Zahner 1959). Only where the current becomes very strong, the water falling rapidly over rocks, a distinctive community is found (but not in Lapland) which to a large extent is determined by the current. The speed range within which differences are of minor significance is, however, so wide that current speed as such is not very suitable for classification of lotic biotopes.

There are, therefore, many reasons for primarily making use of the substrate (s.l.) for this purpose, as suggested by Moon (1939), Linduska (1942), Cummins (1962, 1964, 1966), and Thorup (1966). The correlation between certain "Zoozönosen" and definable substrate types was pointed out by Schmitz (1957), and Scherer (1965 a) in a penetrating analysis arrives at a similar conclusion. Substrate is determined by the interaction of erosion and sedimentation (cf. Johansson 1963). It has certain practical advantages as a classification criterion. Because the condition of the substrate is the result of processes which have acted over a period of time, it nicely reflects the life conditions in a particular biotope. Moreover, it is fairly readily observed and measured.

4.3. Community classification

Faunistic criteria have been frequently employed to characterize biotopes. This inevitably leads to difficulties.

Illies (1961 b) enumerated a number of taxa which he alleged characterize the rhithron and potamon biotope types. The families Leptophlebiidae and Nemouridae were, for example, said to characterize rhithron biotopes. In northern Scandinavia, all members of the former family except probably *Paraleptophlebia strandii* Etn. and about half those of the latter are restricted to lenitic biotopes. Similarly among Heptageniidae, only *Heptagenia dalecarlica* can be said in the Ammarnäs area to characterize rhithron conditions, but *H. sulphurea* is very euryoecious and the rest are lenitic. Conversely, the families Perlodidae and Perlidae are stated to characterize potamon conditions, but many members of these families occur in distinctly rhithron environments in Lapland.

Attempts by Berthélemy (1961, 1966) and Minckley (1963) to adopt faunistic criteria in their respective study areas in southern Europe and North America were largely unsuccessful.

The "fish zones" of central European hydrobiologists are not recognizable in Lapland (Müller 1968).

Faunistic criteria, then, are not generally useful outside a restricted geographic region. Environmental factors should be used to characterize environmental subdivisions (biotopes), while faunistic criteria should be used to characterize faunistic subdivisions (communities). On these premises, a generally valid biotope classification may be possible, but community classifications, based on characteristic species or species constellations (cf. Berg 1948), will generally have only regional applicability.

5. Quantitative composition of the benthic community in terms of standing crop

5.1. Introduction

Most of the quantitative studies on lotic biotopes and their communities differ markedly from the present contribution. Usually they have been devoted to much smaller watercourses (Illies 1952, Albrecht 1953, Dittmar 1955 a, Macan 1957 a, b, Hynes 1961), they have rarely included lenitic parts (exceptions: Knöpp 1952, Müller 1955, 1956), or, if concerned with larger streams, these have been of potamon character (Berg 1948, Mauch 1963). Many papers have contained data on only a few systematic groups, or have not attempted analysis at the specific level.

Much of the work on rhithron biotopes and their communities has been summarized by Albrecht (1959), Macan (1961 a, 1962 b, 1963) and Cummins (1966).

The quantities of animals inhabiting a stream bottom area may be expressed as numbers of individuals per unit area or weight per unit area.

As described below, the technique employed did not permit the sampling of very small organisms. Their absence from the samples may not be wholly due to the imperfections of the sampling method, but also to different microhabitat preferences of the youngest stages of many species (cf. Schwoerbel 1964). In other words, for certain periods, nymphs or larvae a species may be absent from the biotopes included in the present sampling programme. Small nymphs and larvae make up a very large portion of the population in terms of numbers of individuals, but a very much smaller portion in terms of weight per unit area (cf. Jónasson 1955, Macan 1958 b, Maitland 1965). If the quantitative composition of the community is studied in terms of weight, then the error introduced will be less than if numbers are used (cf. Maitland 1964). Therefore, the main presentation of the community will be in terms of standing crop data while, for special purposes, a short survey of population density figures will be given in § 6.

5.2. Sampling technique

When taking a sample the worker moved upstream, removing stones from the bottom and placing them in a bucket. A bag-formed net with 18 meshes/cm was held immediately downstream of the stone to be removed, the lower rim of the net (85 × 65 cm) being pressed firmly against the bottom. Animals releasing their hold of the stones were carried into the net by the current. Variable amounts of vegetable debris and finer inorganic particles also accumulated in the net. After a certain number of stones had been collected, the net and the contents of the bucket were carefully searched for all macroscopic animals. Usually many more animals were found in the net than clinging to the stones. Finally, the stones were brushed over some water which was subsequently sieved through the net; tufts of vegetation and clumps of debris were parted and searched. The animals were transferred to 70% ethanol.

After the animals had been removed, all stones were measured to the nearest cm as described in § 2.2.3. By this means an approximate measurement of the area sampled (standard area) was obtained, adequate for comparative purposes (cf. Schräder 1932, Müller 1953, Dittmar 1955 b, Schwoerbel 1966).

In 1962, 1963 and May 1964 each bucket of stones originated from one of three depth classes, viz. 5 to 15 cm, 15 to 25 cm and 25 to 40 cm. Approximately the same number stones was taken from each depth class, so that there would be no bias in relation to depth within the range sampled. All animals from a given depth class were pooled, so that each sample resulted in three jars of animals.

From June 1964 onwards, each bucket was filled with stones from all three depth classes in approximately equal numbers, and the animals contained in each bucket-full of stones were kept separately. Thus each sampling occasion yielded up to 10 subsamples of strictly comparable origin, permitting a statistical analysis. Otherwise the sampling technique was not modified.

5.3. Discussion of the sampling procedure

Five essentially different sampling methods have been employed for running water studies, as is apparent from the useful reviews by Albrecht (1959) and Cummins (1966).

Cylinders have found a wide usage, and it was initially planned to make use of a sampling cylinder in the present study. In spite of several modifications, however, the results were conspicuously unsatisfactory. It proved impossible to press the lower rim into the coarse substrate, and large quantities of water and animals were observed to escape beneath it, even when the smoothest bottom areas were chosen. Cylinders were therefore discarded.

Shovels of various designs have also been widely used, but were assumed to be impracticable in the present context. Either all big stones would have to have been avoided, or the shovel would have been so large that it would not have been possible to operate it single-handed.

Various net methods have been used by many workers. For this study the Schräder method was adopted and found to work with reasonable efficiency. It is imperative to have a net downstream of the stones to be removed in view of the effect of the current on animals abandoning the stones. Caddisfly and blackfly pupae, however, usually remained in situ, to a considerable extent also blackfly larvae.

The Surber sampler may be considered as a variation of the net method. A frame is attached to the front of the net delineating an exact sampling area. This method was not employed because in view of the extreme patchiness of the environmental conditions and that of the microdistribution of the populations, it was considered more expedient to remove one stone at a time in a random fashion, so that as many microbiotopes are represented in the sample as possible. The length of each sampling locality was 30 to 50 m. Certain workers have refrained from removing the stones and have contented themselves with violently disturbing the substrate in front of a net, for instance by means of a standardized number of kicks (Hynes 1961, Morgan and Egglishaw 1965). However certain groups will be largely missed, if the stones are not removed.

Another method consists of introducing trays containing some natural substrate removing them after a period of time and collecting the animals which have settled in the trays (Moon 1940, Wene and Wickliff 1940, Linduska 1942, Carlsson 1962, Egglishaw 1964, Kajak 1964 (in lenitic biotopes), Lillehammer 1964, Waters 1964). Most of these workers have of course been aware that this is a method of field experimentation, not of sampling, since the implanted trays constitute an artifact (cf. § 9).

Recently Cummins (1966) suggested a photographic method, which has not yet been tried in the field.

A weakness with the net methods is that mesh-size has a great effect on the composition of the catch (Jónasson 1955, Macan 1958 b). With too small meshes, clogging occurs almost immediately, deflecting the current and leading to unsatisfactory results. If the meshes are too large, many small animals escape, so that a compromise has to be struck. In addition, handling the net requires practice. Slight tilting of the net in relation to current direction will bring about the loss of many animals already in the net or being transported towards it. Before the sampling on which the present results are based was commenced, the author worked for some time with the express purpose of obtaining practice and in order to standardize the procedure.

5.4. Weighing procedure

Before being weighed, the animals were immersed in distilled water for about 30 min and then left to dry on a filter paper, until no liquid was visible on their surface. Most samples were weighed on an analytical balance permitting readings to 0.1 mg, but the large blackfly samples were weighed on a coarser balance to 10 mg. Cases of caddisfly larvae and pupae were removed, but molluscs were weighed in their shells.

5.5. Statistical evaluation of the standing crop data

For all samples of mayflies, stoneflies and caddisflies taken in June 1964 and later, mean values and the standard error of the means were estimated (Tabs. 19 to 28). This parameter was chosen because, given the mean and the number of subsamples (Tab. 18), the significance of any difference may be determined using Student's *t*-test.

It was empirically found that when two mean SC values differed by a factor >2, the difference was usually significant at a level of $P < 0.05$. A slightly higher factor was required in the caddisflies, a slightly lower one in the mayflies and stoneflies.

The distribution of blackfly larvae over the stream floor was so clumped that statistical analysis was not justified. Yet most differences to be discussed were so large and consistent that their existence is beyond question.

Standard error of the means could not be estimated in the material from before June 1964, because of the treatment of the samples (§ 5.2). It may be assumed, however, that the differences in this material are equally significant, since the sampling procedure was identical.

5.6. Extent and presentation of the material

The ten localities at which the main samples were taken were described in § 2.2. Their positions are shown in Fig. 2. The dates of sampling are shown in Tab. 18, which also includes data on the extent of each sample in terms of standard area (calculated as described in § 2.2.3) and the number of subsamples comprised in the sample. A total of 13,378 stones were examined and their total standard area amounted to approx. 250 m².

The primary data for each locality are set forth in Figs. 20 to 29 showing the share of mayflies, stoneflies, caddisflies, blackflies and "other taxa" in the total standing crop (TSC) as well as TSC in g/m². In Tabs. 19 to 28, the four major taxa mentioned are analysed on the species level.

Tab. 18. The quantitative benthic samples. A survey of their distribution in time, extent in terms of standard area sampled and division on subsamples.

Loc.	Year	Date	Numbers of stones	Standard area (m^2)	Numbers of subsamples
A	1962	15/7	108	2.01	3
		2/8	124	2.36	3
		5/10	56	1.23	3
	1963	18/6	80	1.89	3
		18/7	117	2.23	3
		8/8	95	1.82	3
	1964	13/5	129	2.60	3
		5/6	133	2.87	9
		16/7	88	1.60	6
		13/8	77	1.46	9
		11/9	74	1.57	9
	1965	16/7	118	2.12	9
		6/8	131	2.41	9
			1330	26.17	
B	1962	16/7	76	1.30	3
		8/8	159	2.43	3
	1963	12/6	100	1.64	3
		20/7	109	1.83	3
		7/8	116	2.28	3
		13/11	139	2.32	3
	1964	10/5	172	2.85	3
		1/6	148	2.33	9
		12/7	63	1.01	3
		11/8	133	2.07	8
		4/9	98	1.64	6
	1965	17/7	108	1.89	8
		11/8	129	2.06	9
			1550	25.65	
D	1962	17/7	267	3.92	3
		3/8	175	2.85	3
	1963	17/6	154	2.56	3
		12/7	152	2.59	3
		6/8	222	3.57	3
	1964	11/6	204	3.34	8
		24/7	144	2.30	7
		24/8	151	2.54	8
		16/9	113	1.80	6
	1965	19/7	163	2.46	9
		18/8	120	2.02	8
			1865	29.95	

Loc.	Year	Date	Numbers of stones	Standard area (m²)	Numbers of subsamples
E	1962	18/7	120	3.16	3
		4/8	147	3.29	3
		4/10	91	2.19	3
	1963	11/6	100	2.37	3
		11/7	148	3.63	3
		2/8	127	3.38	3
		14/11	89	2.54	3
	1964	9/5	173	4.06	2
		8/6	88	2.02	6
		21/7	92	2.11	6
		17/8	87	2.09	7
		13/9	120	2.93	8
	1965	20/7	104	2.22	7
		10/8	116	2.66	7
			1602	38.65	
H	1962	20/7	143	2.91	3
		9/8	93	1.60	3
		4/10	52	0.93	3
	1963	10/6	96	1.59	3
		17/7	138	2.44	3
		5/8	115	1.96	3
	1964	19/5	94	1.47	3
		12/6	101	1.77	6
		22/7	75	1.18	5
		14/8	88	1.43	6
		15/9	55	1.06	6
	1965	17/7	115	1.88	7
		11/8	114	1.75	7
			1279	21.97	
K	1962	21/7	144	2.73	3
		6/8	161	2.85	3
		6/10	47	0.96	3
	1963	14/6	112	2.24	3
		14/7	110	2.10	3
		3/8	86	1.84	3
		14/11	169	3.44	2
	1964	18/5	125	2.55	2
		3/6	166	3.17	9
		18/7	84	1.82	6
		27/8	49	1.05	6
		17/9	74	1.59	8
	1965	15/7	91	1.79	8
		7/8	99	2.00	9
			1517	30.13	
L	1962	23/7	160	3.51	3
		7/8	142	2.71	3
	1963	9/7	78	1.61	3
		4/8	101	1.92	3
		16/11	137	2.88	2
	1964	7/6	107	1.94	6
		20/7	126	2.53	8
		12/8	74	1.52	7
		12/9	90	1.78	7
	1965	14/7	116	2.26	9
		9/8	89	1.67	6
			1220	24.33	
N	1962	24/7	200	3.35	3
		8/8	177	2.60	3
		5/10	66	0.95	3
	1963	12/6	138	2.11	3
		22/7	135	2.08	3
		9/8	186	2.83	3
		15/11	108	1.69	2
	1964	11/5	64	0.95	2
		21/5	142	2.06	3
		6/6	153	2.24	10
		13/7	48	0.82	6
		10/8	102	1.42	7
		14/9	122	1.80	8
	1965	18/7	148	2.17	9
		13/8	156	2.24	9
			1945	29.31	
O	1963	16/7	86	1.68	3
		1/8	128	2.41	3
	1964	2/6	74	1.38	6
		23/7	120	2.39	10
		6/9	89	1.93	7
	1965	27/7	110	2.58	10
			607	12.37	
P	1964	23/5	69	1.35	4
		7/6	60	1.26	4
		10/7	51	1.14	4
		12/8	53	1.10	4
		7/9	77	1.41	4
	1965	14/7	89	1.73	4
		16/8	64	1.29	4
			463	9.28	

Total number of stones, all ten localities: 13378
Total standard area, all ten localities(m²): 248.31

5.7. Standing crop of the localities

5.7.1. Loc. A (Fig. 20, Tab. 19)

TSC was found to vary between 1.9 (May 1964) and 128 (July 1964) g/m². The highest values derived from July and August, when TSC was usually about 30 g/m², with exception for August 1963 (3.9 g/m²) and July 1964 (128 g/m²). These high TSC values were almost entirely due to the mass development of blackfly larvae and pupae, which made up 97.8% of TSC in July 1964.

Mayflies reached their highest percentual share in June 1964 and October 1962; the absolute value was highest on the former occasion. Mayflies were practically absent in May 1964 (cf. § 7.3). The high SC one month

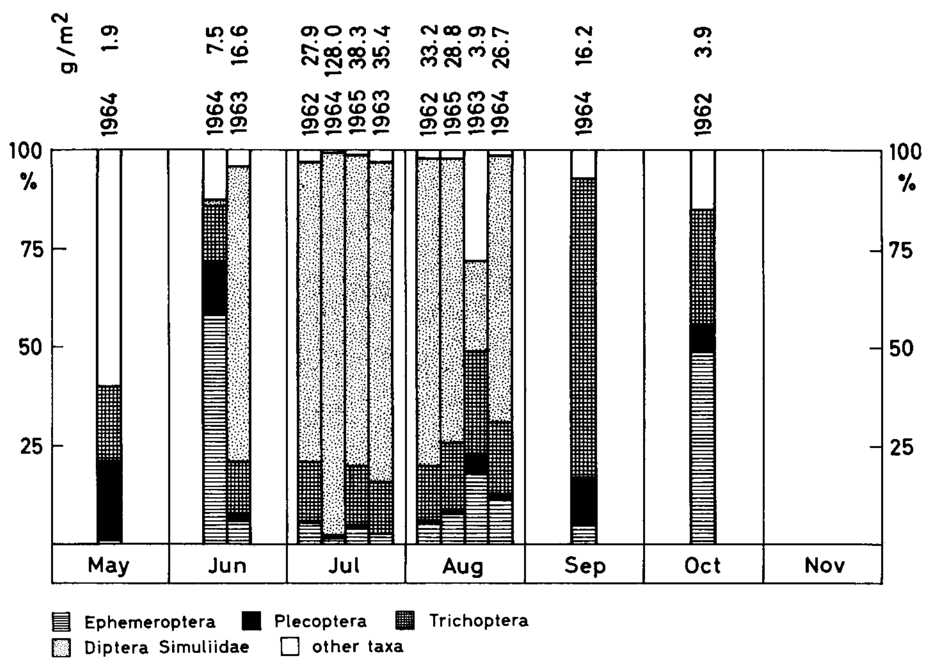

Fig. 20. Loc. A. Percentual composition of the standing crop. Total standing crop values are shown above the graph.

later was caused by *Ephemerella aurivillii* which also dominated in June 1963. In July *Heptagenia sulphurea* and *Baetis macani* were in many places dominant, and were succeeded in August by *B. subalpinus*; unidentified small *Baetis* nymphs were also numerous in this month. In September and October, *E. aurivillii* was again the dominant species.

Stoneflies made up an insignificant portion of TSC at all times except early spring and autumn. Both relatively and absolutely they were particularly poorly represented in July and August. In May, *Diura nanseni* was the dominant species followed by *Isoperla grammatica*, which was dominant in June. The low summer stonefly SC values reflected small quantities of several species. In autumn, *D. nanseni* again became numerous and was co-dominant with *Taeniopteryx nebulosa*.

Caddisflies were often important at loc. A. In September 1964, caddisflies made up $^3/_4$ of the TSC. Usually *Rhyacophila nubila* was the dominant species, but in June *Potamophylax stellatus* and *Apatania* sp. were also important. It is not known why *Rh. nubila* was absent in May.

In May only egg-masses of blackflies were found. In June small larvae of the genus *Cnephia* abounded; they were presumably *C. tredecimata*. The July SC was usually dominated by *Schönbaueria annulitarsis*, which was succeeded by *Simulium truncatum* in August, at which time *S. argyreatum* was also important. After the end of August there were no traces of blackflies except in the form of egg-masses.

In the impoverished May sample, tipulid larvae made up a large proportion of TSC. Gastropods (usually *Radix peregra* but sometimes *Gyraulus acronicus*) were relatively important in autumn. Chironomids made up a small but comparatively constant element. A few heavy lumbricids were sometimes obtained, while the vicinity of the lake explains the presence of *Gammaracanthus lacustris*.

Tab. 19. Percentual composition of the standing crop at loc. A. When SC < 0.1 g/m^2, no percentages are given. When SC > 0.1 g/m^2, only species representing at least 10% of the SC are included.

	May		June		July		August		September		October	
Ephemeroptera												
1962	–		–		*E. aurivillii* *H. sulphurea* 1.5 g/m^2	75 10	*B. subalpinus* *Baetis* sp. *H. sulphurea* 1.7 g/m^2	45 24 12	–		*E. aurivillii* *H. sulphurea* 1.9 g/m^2	78 14
1963	–		*E. aurivillii* *H. sulphurea* 0.9 g/m^2	71 14	*B. macani* *H. sulphurea* *E. aurivillii* 1.0 g/m^2	42 17 11	*B. subalpinus* *Ecd. joernensis* 0.7 g/m^2	66 15	–		–	
1964	*A. inopinatus* *E. aurivillii* *B. rhodani* 0.02 g/m^2		*E. aurivillii* 4.4 ± 0.6 g/m^2	96	*B. macani* *H. sulphurea* *E. aurivillii* *Siphlonurus* sp. 2.0 ± 0.3 g/m^2	24 23 16 15	*B. subalpinus* 3.1 ± 0.5 g/m^2	83	*E. aurivillii* *H. sulphurea* 0.9 ± 0.2 g/m^2	55 31	–	
1965	–		–		*H. sulphurea* *B. macani* *H. dalecarlica* *E. aurivillii* 1.9 ± 0.3 g/m^2	28 18 14 11	*B. subalpinus* *Baetis* sp. *B. macani* 2.3 ± 0.4 g/m^2	46 17 13	–		–	
Plecoptera												
1962	–		–		*D. nanseni* *A. borealis* *L. fusca* 0.04 g/m^2		*L. fusca* *D. nanseni* 0.09 g/m^2	85 14	–		*T. nebulosa* *D. nanseni* 0.3 g/m^2	54 45
1963	–		*I. grammatica* 0.3 g/m^2	97	*D. nanseni* *L. fusca* *A. standfussi* 0.02 g/m^2		*D. nanseni* *L. fusca* *D. bicaudata* 0.2 g/m^2	53 30 18	–		–	
1964	*D. nanseni* *I. grammatica* 0.4 g/m^2	47 37	*I. grammatica* *L. hippopus* *D. nanseni* *D. bicaudata* 1.0 ± 0.2 g/m^2	36 27 23 12	*A. borealis* 0.02 g/m^2		*D. nanseni* *D. bicaudata* 0.4 ± 0.09 g/m^2	66 29	*D. nanseni* *D. bicaudata* 2.0 ± 0.3 g/m^2	71 27	–	

1965	–		–		*L. fusca* *A. borealis* *D. nanseni* 0.06 g/m^2		*D. nanseni* *D. bicaudata* *L. fusca* 0.4 ± 0.08 g/m^2	51 26 17	–		–	
Trichoptera												
1962	–		–		*P. stellatus* *Rh. nubila* 4.3 g/m^2	55 32	*Rh. nubila* 5.1 g/m^2	93	–		*Rh. nubila* *P. flavomaculatus* 1.1 g/m^2	86 14
1963	–		*Rh. nubila* *P. stellatus* 2.2 g/m^2	51 40	*Rh. nubila* Limnephilinae sp. 4.6 g/m^2	75 23	*Rh. nubila* Limnephilinae sp. *P. flavomaculatus* 1.0 g/m^2	67 17 15	–		–	
1964	*P. stellatus* *Athripsodes* sp. 0.4 g/m^2	87 10	*Apatania* sp. *Rh. nubila* *P. stellatus* 1.1 ± 0.2 g/m^2	36 35 22	*Rh. nubila* *Pl. conspersa* 0.7 ± 0.2 g/m^2	79 17	*Rh. nubila* 4.9 ± 0.8 g/m^2	96	*Rh. nubila* 12.1 ± 2.0 g/m^2	98	–	
1965	–		–		*Rh. nubila* Limnephilinae sp. *P. stellatus* 5.8 ± 1.3 g/m^2	52 24 16	*Rh. nubila* Limnephilinae sp. 5.0 ± 0.9 g/m^2	80 13	–		–	
Simuliidae												
1962	–		–		*C. tredecimata* *Sch. annulitarsis* 21.4 g/m^2	57 17	*Sch. annulitarsis* *S. truncatum* 25.5 g/m^2	82 10	–		*Odagmia* sp. 0.001 g/m^2	
1963	–		*Cnephia* sp. 12.6 g/m^2	98	*Sch. annulitarsis* *S. truncatum* 28.8 g/m^2	68 13	*S. argyreatum* *S. truncatum* *Sch. annulitarsis* 0.9 g/m^2	38 37 24	–		–	
1964	0		*Cnephia* sp. 0.1 g/m^2	92	*C. tredecimata* *G. forsi* *Sch. annulitarsis* *Cnephia* sp. 125.1 g/m^2	31 27 19 11	*S. truncatum* *S. argyreatum* *Sch. annulitarsis* 17.9 g/m^2	49 29 22	*S. truncatum* *S. argyreatum* *Sch. annulitarsis* 0.02 g/m^2		–	
1965	–		–		*Sch. annulitarsis* *S. truncatum* 38.3 g/m^2	69 11	*S. truncatum* *S. argyreatum* *Sch. annulitarsis* 20.7 g/m^2	47 22 22	–		–	

Tab. 20. Percentual composition of the standing crop at loc. B. See Tab. 19.

	May		June		July		August		September		November	
Ephemeroptera												
1962	–		–		*B. rhodani* 2.2 g/m²	69	*H. dalecarlica* *B. fuscatus* *B. subalpinus* 0.9 g/m²	38 23 16	–		–	
1963	–		*B. rhodani* *E. aurivillii* 2.5 g/m²	65 28	*B. rhodani* *B. pumilus* *B. fuscatus* *B. lapponicus* 0.9 g/m²	47 13 12 11	*B. fuscatus* *H. dalecarlica* *B. subalpinus* 0.7 g/m²	32 30 27	–		*E. aurivillii* *B. rhodani* *H. dalecarlica* 2.1 g/m²	50 34 14
1964	*E. aurivillii* *A. inopinatus* *B. rhodani* *H. dalecarlica* 0.6 g/m²	36 23 22 18	*E. aurivillii* *B. rhodani* *H. dalecarlica* 2.9 ± 0.4 g/m²	46 43 10	*B. rhodani* *E. aurivillii* 5.7 ± 0.9 g/m²	65 28	*B. fuscatus* *B. subalpinus* *B. rhodani* 2.3 ± 0.4 g/m²	37 30 11	*B. fuscatus* *E. aurivillii* *B. subalpinus* *H. dalecarlica* 1.6 ± 0.3 g/m²	35 27 16 15	–	
1965	–		–		*B. rhodani* *E. aurivillii* *B. pumilus* 3.3 ± 0.7 g/m²	56 14 11	*B. fuscatus* *B. subalpinus* *B. rhodani* *H. dalecarlica* 1.1 ± 0.2 g/m²	38 27 12 11	–		–	
Plecoptera												
1962	–		–		*I. grammatica* *A. borealis* *L. fusca* *D. nanseni* 0.06 g/m²		*D. nanseni* *L. fusca* 0.2 g/m²	56 44	–		–	
1963	–		*I. grammatica* *L. hippopus* *B. risi* 0.3 g/m²	52 25 22	*I. grammatica* *L. fusca* *A. borealis* *D. nanseni* 0.08 g/m²		*D. nanseni* *L. fusca* 0.2 g/m²	68 32	–		*D. nanseni* *T. nebulosa* 1.4 g/m²	69 29
1964	*D. nanseni* 1.1 g/m²	82	*D. nanseni* *I. grammatica* *L. hippopus* 1.9 ± 0.4 g/m²	73 13 12	*A. borealis* *I. grammatica* 0.5 ± 0.1 g/m²	71 28	*D. nanseni* *L. fusca* 0.4 ± 0.09 g/m²	55 40	*D. nanseni* 1.3 ± 0.3 g/m²	94	–	

1965	–		–		*D. nanseni* *L. fusca* *A. borealis* *I. grammatica* 0.2 ± 0.04 g/m²	32 31 23 13	*D. nanseni* *L. fusca* 0.4 ± 0.09 g/m²	69 31	– –			
Trichoptera												
1962	–		–		*Rh. nubila* *Apatania* sp. 1.4 g/m²	85 15	*Rh. nubila* Limnephilinae sp. 0.6 g/m²	79 12	–		–	
1963	–		*P. stellatus* *Rh. nubila* *P. flavomaculatus* 2.3 g/m²	52 31 16	*Rh. nubila* *P. stellatus* 0.8 g/m²	70 21	*Rh. nubila* *P. flavomaculatus* 0.4 g/m²	70 24	–		*Rh. nubila* *G. intermedium* *P. flavomaculatus* 1.0 g/m²	56 17 15
1964	*G. intermedium* *Rh. nubila* 0.5 g/m²	64 28	*G. intermedium* *P. stellatus* *Rh. nubila* 0.5 ± 0.1 g/m²	44 34 10	*Rh. nubila* *Apatania* sp. 2.1 ± 0.5 g/m²	85 15	*Rh. nubila* 4.0 ± 1.0 g/m²	96	*Rh. nubila* *P. flavomaculatus* 0.7 ± 0.2 g/m²	67 28	–	
1965	–		–		*Rh. nubila* 1.6 ± 0.4 g/m²	82	*Rh. nubila* Limnephilinae sp. *Apatania* sp. 1.1 ± 0.2 g/m²	65 20 13	–		–	
Simuliidae												
1962	–		–		*C. fuscipes* *H. ferrugineus* *G. forsi* 0.2 g/m²	33 24 23	*S. truncatum* 0.007 g/m²		–		–	
1963	–		*P. hirtipes* *Cnephia* sp. *H. ferrugineus* 0.5 g/m²	60 26 10	*Cnephia* sp. *S. truncatum* *Sch. annulitarsis* 0.01 g/m²		*O. monticola* 0.02 g/m²		–		*O. monticola* 0.02 g/m²	
1964	*P. hirtipes* 0.05 g/m²		*P. hirtipes* *O. ornata* 0.5 g/m²	86 13	*H. ferrugineus* *G. forsi* *Cnephia* sp. *C. fuscipes* 4.4 g/m²	47 18 17 13	*S. truncatum* *O. monticola* 0.06 g/m²		*O. ornata* 0.002 g/m²		–	
1965	–		–		*H. ferrugineus* *Eus. latipes* *Sch. annulitarsis* 0.09 g/m²		*O. monticola* 0.01 g/m²		–		–	

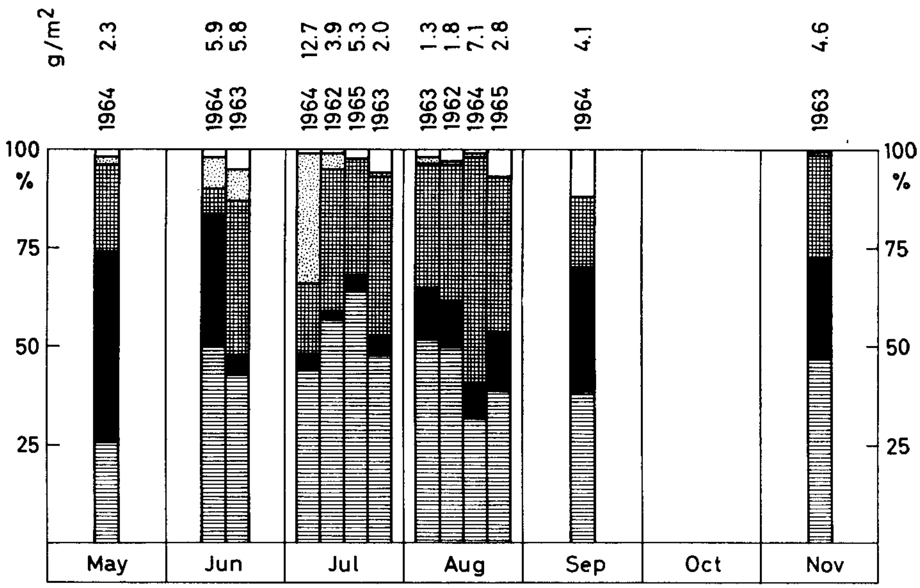

Fig. 21. Loc. B. Percentual composition of the standing crop. For explanation, see Fig. 20.

5.7.2. Loc. B (Fig. 21, Tab. 20)

TSC values were at a much lower level in summer than at loc. A, seasonal differences being almost non-existent. Another palpable difference is the relative insignificance of blackflies.

Mayflies were the most important group at loc. B, where they made up 25 to 65% of TSC. The highest absolute value was recorded in July 1964, followed by that of the same month in 1965. Low figures were usually found in August and May. The dominant species in May and June were *Ephemerella aurivillii*, *Baetis rhodani* and *Ameletus inopinatus*. In July the first and the last of these had vanished, and *B. rhodani* dominated alone. *B. fuscatus*, *B. pumilus* and *B. lapponicus* sometimes occurred in considerable quantities in that month, but the first-mentioned of these three became more important in August, when *Heptagenia dalecarlica* and *B. subalpinus* were also prominent. Later in the year *B. rhodani* and *E. aurivillii* became once more common, but not *Ameletus inopinatus*.

Stoneflies reached their highest relative and absolute values in spring and autumn. In all months except July, *Diura nanseni* was very important. Other prominent species were *Isoperla grammatica* and *Leuctra fusca*. In November, *Taeniopteryx nebulosa* and *D. nanseni* comprised the entire SC.

Caddisflies fluctuated irregularly, but usually achieved a high figure in August. In May and June, *Glossosoma intermedium* and *Potamophylax stellatus* were dominant. For the rest of the year, *Rhyacophila nubila* was dominant. *G. intermedium* became important again in late autumn.

As mentioned above, blackfly larvae were far less abundant at loc. B than at loc. A. They were numerous only in June when *Prosimulium hirtipes* and *Cnephia* sp. (almost certainly *C. fuscipes*) were the main species. *Helodon ferrugineus* and *Odagmia ornata* were also of some importance, emphasizing the qualitative difference between the two localities. In July, values generally dropped, but in 1964 they remained high. Later only scattered specimens, often of *Simulium truncatum*, were recorded, whereas a certain number of *Odagmia* spp. larvae were found in late autumn.

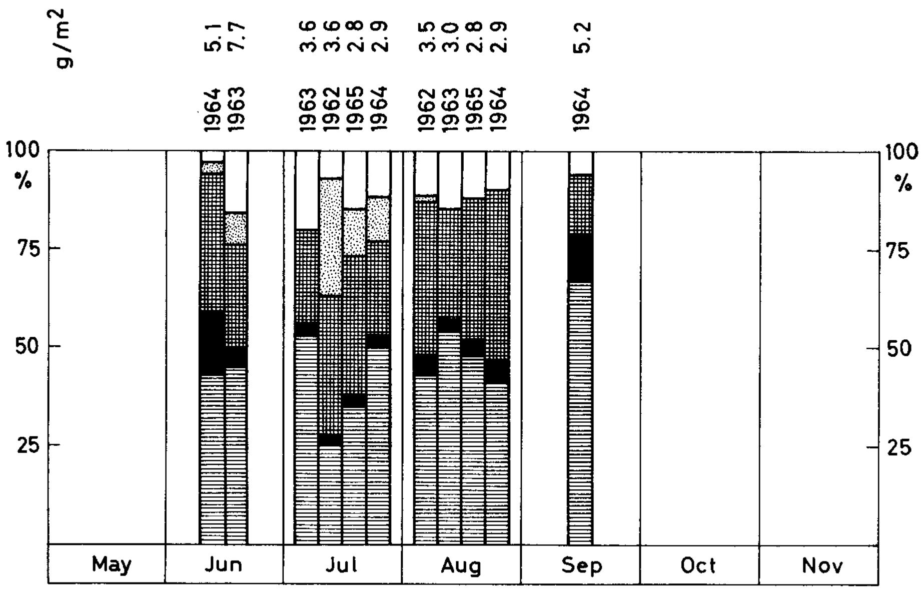

Fig. 22. Loc. D. Percentual composition of the standing crop. For explanation, see Fig. 20.

5.7.3. Loc. D (Fig. 22, Tab. 21)

Like loc. B, seasonal fluctuations at loc. D were of small extent in terms of TSC. Unfortunately this locality was inaccessible in May, October and November.

Mayflies were very important and usually responsible for about half the TSC. In June, four species were about equally abundant, viz. *Ameletus inopinatus*, *Ephemerella aurivillii*, *Baetis rhodani* and *Heptagenia dalecarlica*. By July the first two species had vanished. The other two species were dominant throughout the rest of the year. A considerable number of species were found in small quantities, among which *Baetis pumilus* and *Metretopus borealis* were most frequent.

Stoneflies comprised only a small portion of the TSC. Their relative share was higher in spring and autumn than in summer. There was a frequent invasion of species deriving from the nearby lake, particularly *Diura bicaudata*, and also of *Arcynopteryx compacta* from at little stream falling into the main stream near the sampling site. Early in the year, *Brachyptera risi* was relatively numerous.

Loc. D differed from the rest in the relatively low dominance of *Rhyacophila nubila*; it was replaced by *Polycentropus flavomaculatus*, unidentified limnephilins and, early in the season, *Potamophylax stellatus*.

Blackflies were present in appreciable quantities only in July and, to a much lesser extent, in June. *Gnus forsi*, *Cnephia fuscipes* and *Helodon ferrugineus* were particularly important.

Oligochaetes had a larger share of TSC than at most sites. Occasional high values were due to a few heavy lumbricids. As a result of the proximity of lenitic biotopes, *Gammaracanthus lacustris* was frequently recorded.

5.7.4. Loc. E (Fig. 23, Tab. 22)

This locality resembled loc. A, although with some clear distinctions. The chief similarity was the predominance of blackflies in summer and the consequently large seasonal fluctuations in TSC. Spring values were remarkably low.

The composition and fluctuations of the mayfly zoome were similar to those described for loc. A. Because of the proximity to the

Tab. 21. Percentual composition of the standing crop at loc. D. See Tab. 19.

	June		July		August		September	
Ephemeroptera								
1962	–		*B. rhodani*	65	*B. rhodani*	51	–	
			H. dalecarlica	17	*H. dalecarlica*	36		
			0.9 g/m^2		1.5 g/m^2			
1963	*A. inopinatus*	27	*Siphlonurus* sp.	44	*H. dalecarlica*	38	–	
	E. aurivillii	26	*H. dalecarlica*	21	*Siphlonurus* sp.	24		
	B. rhodani	23	*B. rhodani*	17	*B. rhodani*	12		
	H. dalecarlica	18	1.9 g/m^2		1.6 g/m^2			
	3.4 g/m^2							
1964	*E. aurivillii*	28	*B. rhodani*	69	*H. dalecarlica*	74	*H. dalecarlica*	72
	B. rhodani	28	*H. dalecarlica*	22	*B. rhodani*	17	*B. rhodani*	19
	H. dalecarlica	24	2.7 ± 0.6 g/m^2		1.2 ± 0.2 g/m^2		3.5 ± 0.6 g/m^2	
	A. inopinatus	16						
	2.2 ± 0.4 g/m^2							
1965	–		*B. rhodani*	49	*H. dalecarlica*	53	–	
			H. dalecarlica	30	*Siphlonurus* sp.	16		
			E. aurivillii	13	*B. rhodani*	14		
			1.0 ± 0.2 g/m^2		1.3 ± 0.3 g/m^2			
Plecoptera								
1962	–		*D. nanseni*		*D. nanseni*	55	–	
			A. borealis		*A. sulcicollis*	23		
			A. sulcicollis		*L. fusca*	17		
			0.08 g/m^2		0.2 g/m^2			
1963	*D. bicaudata*	48	*L. fusca*	77	*L. fusca*	60	–	
	A. compacta	24	*I. grammatica*	14	*D. nanseni*	40		
	B. risi	22	0.1 g/m^2		0.09 g/m^2			
	0.3 g/m^2							
1964	*D. bicaudata*	39	*L. fusca*	37	*D. nanseni*	67	*D. nanseni*	70
	B. risi	22	*D. nanseni*	33	*L. fusca*	19	*I. grammatica*	12
	A. compacta	16	*L. digitata*	12	0.2 ± 0.04 g/m^2		0.6 ± 0.1 g/m^2	
	I. grammatica	14	0.1 ± 0.03 g/m^2					
	0.8 ± 0.1 g/m^2							

1965	–		*D. nanseni* *D. bicaudata* *L. fusca* *A. sulcicollis* 0.06 g/m²		*L. fusca* *D. nanseni* *A. standfussi* 0.1 ± 0.02 g/m²	48 29 24	–	
Trichoptera								
1962	–		*P. stellatus* *P. flavomaculatus* *Rh. nubila* 1.3 g/m²	52 24 17	*P. flavomaculatus* *Rh. nubila* 1.3 g/m²	50 41	–	
1963	*P. stellatus* *Rh. nubila* 2.0 g/m²	79 10	Limnephilinae sp. *P. flavomaculatus* *Rh. nubila* 0.8 g/m²	41 38 19	Limnephilinae sp. *P. flavomaculatus* *Rh. nubila* 0.9 g/m²	52 32 16	–	
1964	*P. stellatus* 1.8 ± 0.4 g/m²	95	*Rh. nubila* *P. flavomaculatus* 1.3 ± 0.4 g/m²	57 40	*P. flavomaculatus* *Rh. nubila* 1.3 ± 0.4 g/m²	68 29	*P. flavomaculatus* 0.8 ± 0.2 g/m²	84
1965	–		*P. flavomaculatus* *Rh. nubila* 1.0 ± 0.2 g/m²	63 34	*Rh. nubila* Limnephilinae sp. *P. flavomaculatus* 1.0 ± 0.3 g/m²	63 20 11	–	
Simuliidae								
1962	–		*G. forsi* *C. fuscipes* *H. ferrugineus* 1.1 g/m²	53 21 17	*S. truncatum* 0.5 g/m²	91	–	
1963	*Cnephia* sp. *H. ferrugineus* *G. forsi* 0.5 g/m²	50 24 12	*Eusimulium* sp. *G. forsi* 0.008 g/m²		0		–	
1964	*P. hirtipes* 0.2 g/m²	85	*H. ferrugineus* *G. forsi* 0.6 g/m²	39 31	*Eusimulium* sp. 0.002 g/m²		*O. monticola* *Eusimulium* sp. 0.006 g/m²	
1965	–		*C. fuscipes* *H. ferrugineus* 0.3 g/m²	41 37	*O. monticola* *Eusimulium* sp. 0.003 g/m²		–	

Tab. 22. Percentual composition of the standing crop at loc. E. See Tab. 19.

	May		June		July		August		September		October		November	
Ephemeroptera														
1962	–		–		*Baetis* sp. *B. macani* 0.7 g/m^2	52 28	*B. subalpinus* *H. sulphurea* 2.0 g/m^2	44 37	–		*H. sulphurea* *E. aurivillii* 0.9 g/m^2	48 43	–	
1963	–		*A. inopinatus* 0.04 g/m^2		*B. macani* *H. sulphurea* 2.3 g/m^2	63 22	*B. subalpinus* *Ecd. joernensis* *B. macani* *H. dalecarlica* *H. sulphurea* 0.4 g/m^2	25 23 19 14 13	–		–		*E. aurivillii* *B. rhodani* *H. sulphurea* 2.3 g/m^2	55 30 13
1964	*B. rhodani* *A. inopinatus* *E. aurivillii* 0.4 g/m^2	48 24 23	*B. rhodani* *A. inopinatus* 0.4 $\pm$ 0.07 g/m^2	52 41	*B. macani* 1.0 $\pm$ 0.2 g/m^2	81	*B. subalpinus* *Ecd. joernensis* 2.8 $\pm$ 0.5 g/m^2	74 11	*E. aurivillii* 1.4 $\pm$ 0.3 g/m^2	74	–		–	
1965	–		–		*B. macani* *H. sulphurea* 0.9 $\pm$ 0.2 g/m^2	55 24	*B. subalpinus* *H. sulphurea* 1.5 $\pm$ 0.3 g/m^2	32 25	–		–		–	
Plecoptera														
1962	–		–		*I. obscura* *A. sulcicollis* 0.06 g/m^2		*D. nanseni* *I. obscura* *L. fusca* 0.1 g/m^2	41 32 24	–		*D. nanseni* *T. nebulosa* 0.1 g/m^2	72 24	–	
1963	–		*D. nanseni* 0.2 g/m^2	96	*I. obscura* 0.2 g/m^2	98	*D. nanseni* *A. sulcicollis* *L. fusca* 0.03 g/m^2		–		–		*T. nebulosa* *D. nanseni* 2.2 g/m^2	85 11
1964	*D. nanseni* *C. atra* *D. bicaudata* 0.3 g/m^2	60 16 10	*D. nanseni* *I. grammatica* 0.4 $\pm$ 0.09 g/m^2	65 16	*I. grammatica* *I. obscura* 0.04 g/m^2		*D. nanseni* *L. fusca* 0.3 $\pm$ 0.06 g/m^2	77 15	*D. nanseni* *T. nebulosa* *L. fusca* 0.9 $\pm$ 0.2 g/m^2	63 17 11	–		–	
1965	–		–		*I. grammatica* *I. obscura* *A. standfussi* 0.04 g/m^2		*D. nanseni* *L. fusca* 0.2 $\pm$ 0.04 g/m^2	64 29	–		–		–	

Trichoptera														
1962	–		–		*Rh. nubila* Limnephil. sp. 2.4 g/m²	70 25	*A. ladogensis* *Rh. nubila* Limnephil. sp. 3.9 g/m²	47 38 15	–		*A. ladogensis* *Rh. nubila* 1.0 g/m²	59 34	–	
1963	–		Limnephil. sp. 0.006 g/m²		*Rh. nubila* *A. ladogensis* Limnephil. sp. 1.0 g/m²	53 26 13	*Rh. nubila* Limnephil. sp. 1.1 g/m²	59 32	–		–		*A. ladogensis* *P. flavomacul.* 4.7 g/m²	76 13
1964	*Athripsodes* sp. *A. ladogensis* 0.3 g/m²	84 16	*A. ladogensis* Limnephil. sp. 0.3 ± 0.08 g/m²	59 32	Limnephil. sp. *Rh. nubila* 0.6 ± 0.1 g/m²	51 49	*Rh. nubila* 4.3 ± 1.3 g/m²	92	*Rh. nubila* 2.9 ± 0.9 g/m²	88	–		–	
1965	–		–		*A. ladogensis* *Rh. nubila* Limnephil. sp. 1.8 ± 0.4 g/m²	41 39 16	*Rh. nubila* 2.3 ± 0.8 g/m²	84	–		–		–	
Simuliidae														
1962	–		–		*C. lapponica* 57.7 g/m²	67	*S. truncatum* *S. argyreatum* *Sch. annulitarsis* 1.9 g/m²	52 22 18	–		0		–	
1963	–		*P. hirtipes* *Cnephia* sp. 0.5 g/m²	54 42	*S. truncatum* *Sch. annulitarsis* 9.9 g/m²	58 26	*S. truncatum* 0.2 g/m²	99	–		–		0	
1964	0		*P. hirtipes* *Cnephia* sp. *G. forsi* 1.0 g/m²	47 21 11	*Sch. annulitarsis* *S. truncatum* *C. trigonia* *C. lapponica* 35.3 g/m²	30 23 16 15	*S. truncatum* 4.4 g/m²	98	*S. truncatum* 0.001 g/m²		–		–	
1965	–		–		*Sch. annulitarsis* *C. trigonia* *S. truncatum* *C. lapponica* 12.9 g/m²	37 21 17 15	*S. truncatum* *S. argyreatum* 0.7 g/m²	83 17	–		–		–	

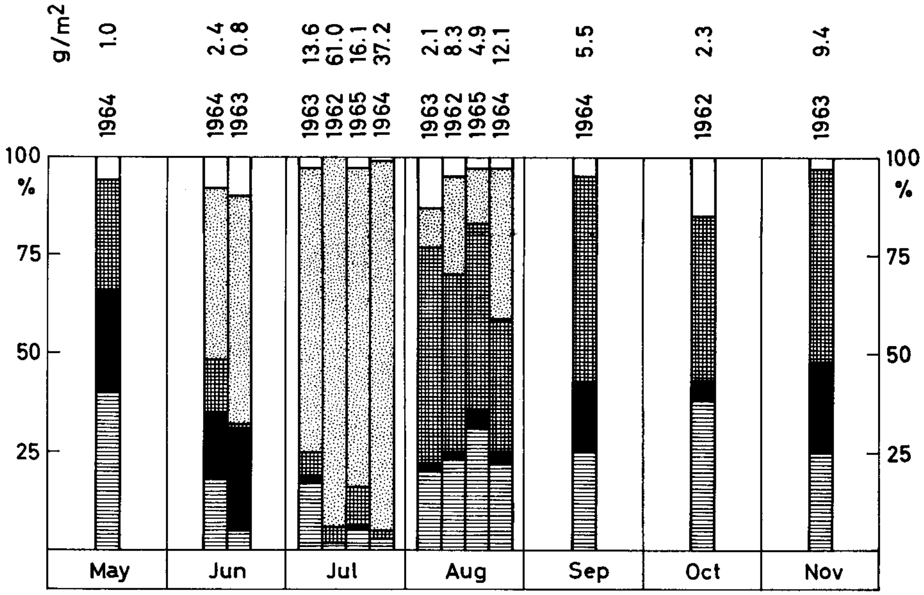

Fig. 23. Loc. E. Percentual composition of the standing crop.
For explanation, see Fig. 20.

lake, *Baetis macani* was important in summer. The stonefly pattern also resembled that found at loc. A. The very high SC value recorded in November was due mainly to *Taeniopteryx nebulosa.* A difference from loc. A was the presence of *Isoperla obscura.*

Except in October, the caddisfly SC tended to increase in the course of the year. A striking difference from loc. A was the presence of *Arctopsyche ladogensis.* Usually *Rhyacophila nubila* was the most important caddisfly species.

Again as in loc. A, there were no blackfly larvae at loc. E in May. The subsequent succession of species resembled in many respects that found at loc. A, but *Cnephia tredecimata* was replaced by *C. lapponica* at loc. E.

Among lacustrine species, *Gammaracanthus lacustris* was frequent at loc. E. Molluscs were of some significance, particularly in autumn, with *Radix peregra* dominating and *Gyraulus acronicus* playing a subordinate role.

5.7.5. Loc. H (Fig. 24, Tab. 23)

This locality was in many ways intermediate between the outlet and the non-outlet types. This is seen from the TSC figures. Judging from these for 1964, one would be inclined to group loc. H with locs. A and E, but from the data of the other years, one would rather place it with the non-outlet localities. In July 1964 there was a considerable peak of blackfly SC, which was without correspondence in the other years.

Mayflies were not so important as at locs. B and D. The highest absolute figures occurred in June 1963 and 1964 as well as in August and September 1964. The relative scarcity of *Baetis rhodani* was characteristic. The temporal succession of the species on the whole resembles that already described.

Diura nanseni was very dominant for most of the year. In May it was the only stonefly present in any numbers.

The bulk of the caddisfly SC consisted of *Rhyacophila nubila.* Sometimes *Arctopsyche ladogensis* was also important. Possibly a small proportion of the larvae belonged to *Rh. obliterata* McL., imagines of which were obtained in small numbers in a light-trap at this site.

The year-to-year differences of blackfly SC were extremely large. In June the dominant

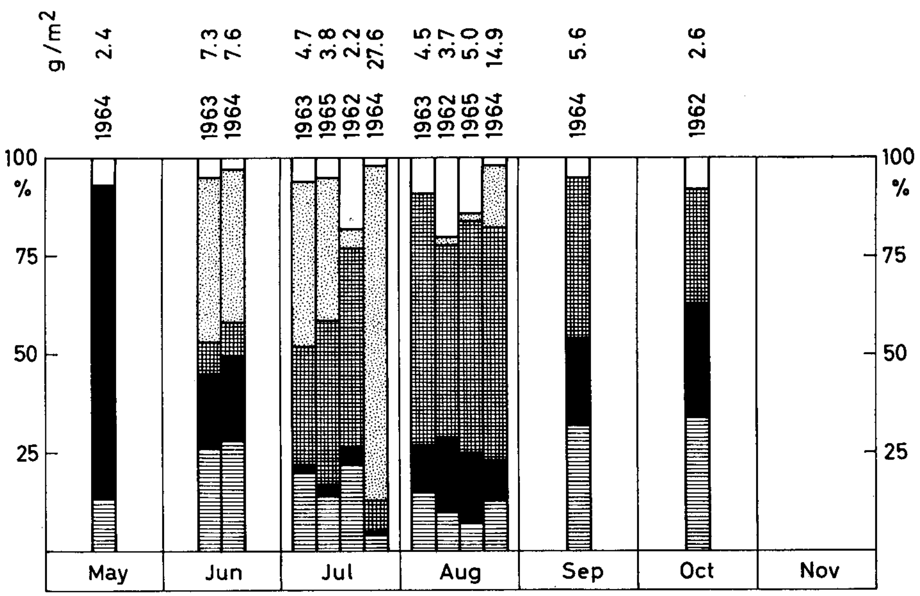

Fig. 24. Loc. H. Percentual composition of the standing crop. For explanation, see Fig. 20.

species was *Cnephia fuscipes* followed by *Gnus forsi*, thus two species of very secondary importance at the true outlet localities. In 1964, *C. fuscipes* dominated in July, but in the other years, when the SC values were lower, *S. truncatum* was dominant in this month. Thus, in 1964 when the seasonal fluctuations were of "lake outlet type", the dominant species was *C. fuscipes*, usually preferring non-outlets.

5.7.6. Loc. K (Fig. 25, Tab. 24)

This locality most closely resembled locs. B and D, TSC values being low and without noticeable seasonal fluctuations. A distinguishing feature was the relative importance of gastropods and oligochaetes.

Mayflies usually comprised between ½ and ⅓ of TSC. The sequence of species was similar to that repeatedly described above. There were scarcely any lenitic species present.

Stoneflies were as usual most important in spring and autumn. *Amphinemura borealis* and *Protonemura meyeri* were more important here than at most places. Among the caddisflies, *Rhyacophila nubila*, *Arctopsyche ladogensis* and *Polycentropus flavomaculatus* dominated.

Except in July 1964, blackfly SC was low. *Helodon ferrugineus*, *Eusimulium* spp. and *Odagmia* spp. were prominent. The peak in July 1964 was due to *Cnephia fuscipes*. Some larvae of the genera *Eusimulium* and *Odagmia* overwintered.

The relatively high SC of Coleoptera was almost exclusively due to *Elmis aenea*. Small numbers of lumbricids were frequently obtained, considerably affecting the TSC. The dominant gastropod was *Radix peregra*.

5.7.7. Loc. L (Fig. 26, Tab. 25)

This locality closely resembled the previous one, although oligochaetes and gastropods were much less important. A small brook falling into Vindelälven just above this locality explains the occasional findings of e.g. *Plectrocnemia conspersa* and *Dinocras cephalotes*. TSC was low and without obvious seasonal fluctuations.

Mayflies were important, *Ephemerella aurivillii* making up a large part of their SC in June and September. Stoneflies were relatively unimportant, while caddisflies were more

Tab. 23. Percentual composition of the standing crop at loc. H. See Tab. 19.

	May		June		July		August		September		October	
Ephemeroptera												
1962	–		–		*Baetis* sp. *H. dalecarlica* *B. rhodani* *B. fuscatus* 0.5 g/m^2	30 16 15 12	*B. subalpinus* *H. dalecarlica* 0.4 g/m^2	58 16	–		*E. aurivillii* *H. dalecarlica* 0.9 g/m^2	67 26
1963	–		*E. aurivillii* *A. inopinatus* 1.9 g/m^2	61 23	*B. macani* *H. sulphurea* *Siphlonurus* sp. *B. rhodani* 1.0 g/m^2	19 15 15 10	*H. dalecarlica* *B. subalpinus* 0.7 g/m^2	36 34	–		–	
1964	*E. aurivillii* *A. inopinatus* 0.3 g/m^2	67 30	*E. aurivillii* *A. inopinatus* *Siphlonurus* sp. *E. mucronata* 2.1 ± 0.3 g/m^2	48 13 11 10	*Baetis* sp. *H. dalecarlica* *B. lapponicus* 1.0 ± 0.2 g/m^2	40 20 14	*B. subalpinus* 1.9 ± 0.3 g/m^2	74	*E. aurivillii* *H. dalecarlica* 1.8 ± 0.3 g/m^2	82 16	–	
1965	–		–		*H. dalecarlica* *Baetis* sp. *B. subalpinus* *B. fuscatus* 0.5 ± 0.09 g/m^2	31 22 19 11	*B. subalpinus* *B. macani* 0.3 ± 0.06 g/m^2	44 24	–		–	
Plecoptera												
1962	–		–		*I. obscura* *L. fusca* *D. nanseni* 0.08 g/m^2		*D. nanseni* *L. fusca* *I. grammatica* 0.7 g/m^2	41 40 18	–		*D. nanseni* 0.8 g/m^2	98
1963	–		*D. nanseni* *D. bicaudata* 1.4 g/m^2	75 12	*I. obscura* *I. grammatica* *D. nanseni* 0.1 g/m^2	45 37 17	*D. nanseni* *L. fusca* 0.6 g/m^2	53 46	–		–	
1964	*D. nanseni* 1.9 g/m^2	93	*D. nanseni* *I. grammatica* *I. obscura* 1.7 ± 0.3 g/m^2	66 13 11	*I. grammatica* *D. nanseni* *L. fusca* 0.1 ± 0.02 g/m^2	46 22 18	*D. nanseni* *L. fusca* 1.5 ± 0.3 g/m^2	70 27	*D. nanseni* 1.3 ± 0.3 g/m^2	95	–	

1965	–	–		*I. grammatica* *D. nanseni* *L. fusca* *I. obscura* 0.1 ± 0.02 g/m^2	45 28 15 11	*D. nanseni* *L. fusca* 0.9 ± 0.1 g/m^2	46 36	–		–	
Trichoptera											
1962	–	–		*Rh. nubila* Limnephilinae sp. 1.1 g/m^2	72 20	*Rh. nubila* 1.8 g/m^2	94	–		*Rh. nubila* 0.8 g/m^2	97
1963	–	*P. stellatus* 0.6 g/m^2	100	*Rh. nubila* 1.4 g/m^2	80	*Rh. nubila* 2.9 g/m^2	98	–		–	
1964	0	*P. stellatus* *A. ladogensis* 0.7 ± 0.2 g/m^2	61 30	*Rh. nubila* 2.3 ± 0.5 g/m^2	99	*Rh. nubila* 8.6 ± 2.2 g/m^2	97	*Rh. nubila* 2.3 ± 0.6 g/m^2	86	–	
1965	–	–		*Rh. nubila* *A. ladogensis* 1.6 ± 0.3 g/m^2	61 27	*Rh. nubila* 2.9 ± 0.5 g/m^2	89	–		–	
Simuliidae											
1962	–	–		*S. truncatum* 0.1 g/m^2	87	*O. monticola* 0.05 g/m^2		–		0	
1963	–	*Cnephia* sp. *G. forsi* 3.0 g/m^2	79 13	*S. truncatum* *Sch. annulitarsis* 2.0 g/m^2	67 20	*O. monticola* 0.009 g/m^2		–		–	
1964	0	*Cnephia* sp. *C. fuscipes* *G. forsi* 2.9 g/m^2	49 28 14	*C. fuscipes* *S. truncatum* *Cnephia* sp. 23.6 g/m^2	36 30 20	*O. monticola* 2.6 g/m^2	95	*O. monticola* 0.003 g/m^2		–	
1965	–	–		*S. truncatum* *Sch. annulitarsis* *O. monticola* 1.4 g/m^2	67 20 13	*O. monticola* *O. ornata* 0.1 g/m^2	81 14	–		–	

Tab. 24. Percentual composition of the standing crop at loc. K. See Tab. 19.

	May	June	July	August	September	October	November
Ephemeroptera							
1962	–	–	*B. rhodani* 39 *B. pumilus* 17 *E. aurivillii* 15 *Baetis* sp. 10 0.6 g/m²	*B. subalpinus* 33 *H. dalecarlica* 30 *Baetis* sp. 24 0.4 g/m²	–	*E. aurivillii* 49 *H. dalecarlica* 31 *B. rhodani* 16 0.6 g/m²	–
1963	–	*E. aurivillii* 55 *B. rhodani* 24 1.1 g/m²	*B. rhodani* 42 *B. pumilus* 18 *E. aurivillii* 14 0.7 g/m²	*B. subalpinus* 48 *H. dalecarlica* 26 *B. fuscatus* 14 0.3 g/m²	–	–	*B. rhodani* 57 *E. aurivillii* 32 1.4 g/m²
1964	*E. aurivillii* 46 *H. dalecarlica* 22 *A. inopinatus* 16 *B. rhodani* 14 2.6 g/m²	*E. aurivillii* 51 *H. dalecarlica* 21 *B. rhodani* 12 2.6 ± 0.4 g/m²	*B. rhodani* 40 *H. dalecarlica* 27 *E. aurivillii* 22 2.6 ± 0.4 g/m²	*H. dalecarlica* 47 *B. subalpinus* 22 0.8 ± 0.1 g/m²	*H. dalecarlica* 47 *E. aurivillii* 25 *B. rhodani* 11 1.3 ± 0.2 g/m²	–	–
1965	–	–	*B. rhodani* 56 0.6 ± 0.1 g/m²	*H. dalecarlica* 38 *B. fuscatus* 26 *B. subalpinus* 21 0.7 ± 0.1 g/m²	–	–	–
Plecoptera							
1962	–	–	*A. borealis* *A. sulcicollis* *L. fusca* 0.08 g/m²	*P. meyeri* *D. nanseni* *L. fusca* 0.05 g/m²	–	*D. nanseni* 71 *P. meyeri* 16 *T. nebulosa* 12 0.1 g/m²	–
1963	–	*D. nanseni* *Chl. burmeisteri* *I. obscura* 0.06 g/m²	*A. borealis* *P. meyeri* 0.07 g/m²	*D. nanseni* *L. fusca* 0.07 g/m²	–	–	*D. nanseni* 61 *T. nebulosa* 19 *C. atra* 13 0.5 g/m²
1964	*D. nanseni* 88 1.5 g/m²	*D. nanseni* 71 0.5 ± 0.09 g/m²	*I. grammatica* 52 *A. borealis* 47 0.1 ± 0.02 g/m²	*D. nanseni* 67 *P. meyeri* 20 *L. fusca* 13 0.2 ± 0.03 g/m²	*D. nanseni* 90 0.6 ± 0.09 g/m²	–	–

1963	–	–	*A. borealis* 37 *I. grammatica* 32 *L. fusca* 13 0.1 ± 0.01 g/m²	*P. meyeri* *L. fusca* *D. nanseni* 0.07 g/m²	–	–	–
Trichoptera							
1962	–	–	*A. ladogensis* 39 *Rh. nubila* 25 *P. flavomaculat.* 22 Limnephil. sp. 14 0.6 g/m²	*Rh. nubila* 76 *P. flavomaculat.* 15 0.7 g/m²	–	*Rh. nubila* 47 *P. flavomaculat.* 46 0.5 g/m²	–
1963	–	*Rh. nubila* 78 *P. flavomaculat.* 22 0.6 g/m²	*P. flavomaculat.* 36 *A. ladogensis* 29 *Rh. nubila* 21 Limnephil. sp. 14 0.6 g/m²	*P. flavomaculat.* 52 *Rh. nubila* 48 0.8 g/m²	–	–	*A. ladogensis* 66 *Rh. nubila* 21 *P. flavomaculat.* 13 1.0 g/m²
1964	*P. flavomaculat.* 54 *Rh. nubila* 30 *A. ladogensis* 15 0.7 g/m²	*A. ladogensis* 49 *P. flavomaculat.* 23 *Rh. nubila* 18 0.9 ± 0.2 g/m²	*Rh. nubila* 62 *P. flavomaculat.* 25 *A. ladogensis* 11 0.7 ± 0.2 g/m²	*P. flavomaculat.* 51 *Rh. nubila* 49 0.8 ± 0.2 g/m²	*A. ladogensis* 62 *Rh. nubila* 22 *P. flavomaculat.* 12 2.9 ± 0.7 g/m²	–	–
1965	–	–	*A. ladogensis* 57 *Rh. nubila* 33 0.9 ± 0.3 g/m²	*Rh. nubila* 87 *A. ladogensis* 13 0.8 ± 0.2 g/m²	–	–	–
Simuliidae							
1962	–	–	*H. ferrugineus* *Eus. latipes* 0.02 g/m²	*Eus. latipes* *Eusimulium* sp. 0.007 g/m²	–	*Eus. latipes* *O. monticola* 0.008 g/m²	–
1963	–	*H. ferrugineus* 0.007 g/m²	*G. forsi* 34 *O. monticola* 26 Simuliidae sp. 17 *Cnephia* sp. 16 0.1 g/m²	*O. monticola* 0.02 g/m²	–	–	*O. monticola* *O. ornata* *Eusimulium* sp. 0.02 g/m²
1964	*O. monticola* *Prosimulium* sp. 0.03 g/m²	*O. monticola* *O. ornata* *P. hirtipes* 0.03 g/m²	*Cnephia* sp. 58 *H. ferrugineus* 28 1.2 g/m²	*O. monticola* *Eusimulium* sp. 0.007 g/m²	*O. monticola* *Eusimulium* sp. 0.007 g/m²	–	–
1965	–	–	*H. ferrugineus* *Eus. latipes* 0.04 g/m²	*O. monticola* *Eusimulium* sp. 0.01 g/m²	–	–	–

Tab. 25. Percentual composition of the standing crop at loc. L. See Tab. 19.

	June		July		August		September		November	
Ephemeroptera										
1962	–		*H. dalecarlica* *B. fuscatus* *B. rhodani* 0.5 g/m^2	34 17 15	*H. dalecarlica* *B. subalpinus* *Baetis* sp. 0.5 g/m^2	31 29 25	–		–	
1963	–		*B. rhodani* *E. aurivillii* *E. mucronata* 1.1 g/m^2	41 20 17	*H. dalecarlica* *B. subalpinus* 0.6 g/m^2	43 32	–		*B. rhodani* *E. aurivillii* *A. inopinatus* 0.7 g/m^2	53 28 13
1964	*E. aurivillii* *H. dalecarlica* *B. rhodani* 2.7 ± 0.4 g/m^2	55 17 11	*B. rhodani* *H. dalecarlica* *E. aurivillii* 2.2 ± 0.2 g/m^2	52 14 13	*B. subalpinus* *H. dalecarlica* 1.6 ± 0.3 g/m^2	58 25	*E. aurivillii* *B. rhodani* *H. dalecarlica* *Baetis* sp. 2.9 ± 0.4 g/m^2	33 26 19 16	–	
1965	–		*B. rhodani* *E. aurivillii* *H. dalecarlica* 1.0 ± 0.09 g/m^2	41 20 15	*H. dalecarlica* *B. subalpinus* 0.8 ± 0.09 g/m^2	37 30	–		–	
Plecoptera										
1962	–		*A. borealis* *D. nanseni* 0.02 g/m^2		*D. nanseni* *L. fusca* 0.04 g/m^2		–		–	
1963	–		*A. borealis* *L. fusca* *A. sulcicollis* 0.03 g/m^2		*D. nanseni* *L. fusca* 0.06 g/m^2		–		*T. nebulosa* *P. meyeri* *D. nanseni* 0.1 g/m^2	35 32 29
1964	*D. nanseni* *P. meyeri* 0.8 ± 0.1 g/m^2	62 17	*A. borealis* *L. digitata* *L. fusca* 0.02 g/m^2		*D. nanseni* 0.08 g/m^2		*D. nanseni* 0.4 ± 0.06 g/m^2	94	–	
1965	–		*A. borealis* *L. fusca* *D. nanseni* 0.02 g/m^2		*D. nanseni* *L. fusca* *A. standfussi* 0.08 g/m^2		–		–	

Trichoptera										
1962	–		*Rh. nubila* *Pl. conspersa* 0.6 g/m^2	89 11	*Rh. nubila* *A. ladogensis* 1.2 g/m^2	74 26	–		–	
1963	–		*Rh. nubila* *A. ladogensis* *P. flavomaculatus* 1.4 g/m^2	58 22 11	*Rh. nubila* 0.3 g/m^2	89	–		Limnephilinae sp. *Rh. nubila* 0.2 g/m^2	44 41
1964	*P. stellatus* *Rh. nubila* 1.6 ± 0.4 g/m^2	65 18	*Rh. nubila* *A. ladogensis* 2.8 ± 0.6 g/m^2	59 36	*Rh. nubila* *A. ladogensis* 1.9 ± 0.6 g/m^2	86 12	*A. ladogensis* *Rh. nubila* 1.8 ± 0.4 g/m^2	56 32	–	
1965	–		*Rh. nubila* *A. ladogensis* Limnephilinae sp. 1.4 ± 0.3 g/m^2	44 25 21	*Rh. nubila* *A. ladogensis* 1.0 ± 0.2 g/m^2	79 20	–		–	
Simuliidae										
1962	–		*Eus. latipes* 0.004 g/m^2		*O. monticola* *H. ferrugineus* *Eus. latipes* 0.01 g/m^2		–		–	
1963	–		*Sch. annulitarsis* *H. ferrugineus* *Eus. latipes* *Cnephia* sp. 0.2 g/m^2	28 25 15 14	*H. ferrugineus* *O. monticola* 0.05 g/m^2		–		*Eusimulium* sp. 0.006 g/m^2	
1964	*Cnephia* sp. *P. hirtipes* *Prosimulium* sp. 0.3 g/m^2	41 38 15	*Cnephia* sp. *C. fuscipes* *H. ferrugineus* 3.7 g/m^2	32 29 28	*H. ferrugineus* *O. monticola* *Eus. latipes* 0.06 g/m^2		*O. monticola* 0.04 g/m^2		–	
1965	–		*H. ferrugineus* *C. fuscipes* *G. forsi* *O. monticola* 0.2 g/m^2	27 17 16 15	*O. monticola* 0.02 g/m^2		–		–	

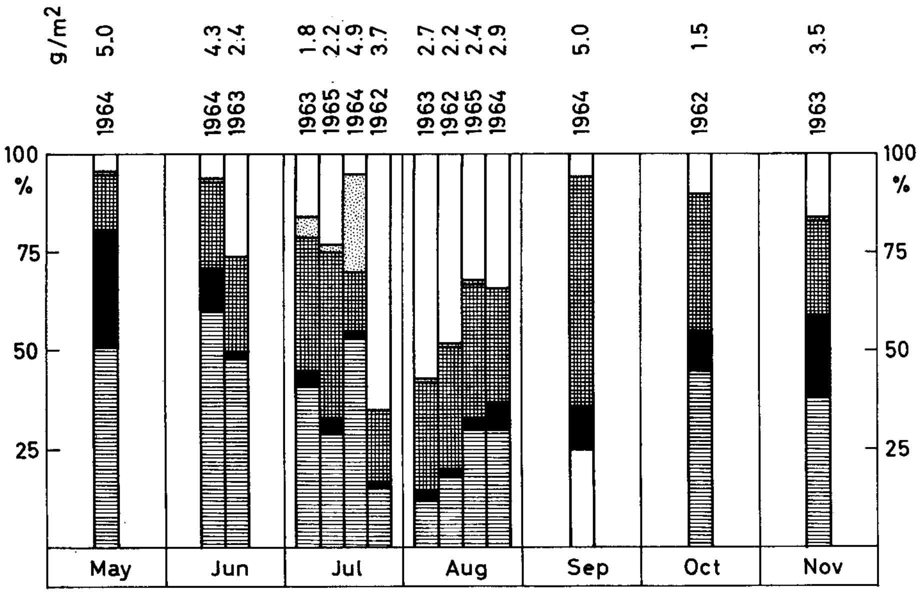

Fig. 25. Loc. K. Percentual composition of the standing crop.
For explanation, see Fig. 20.

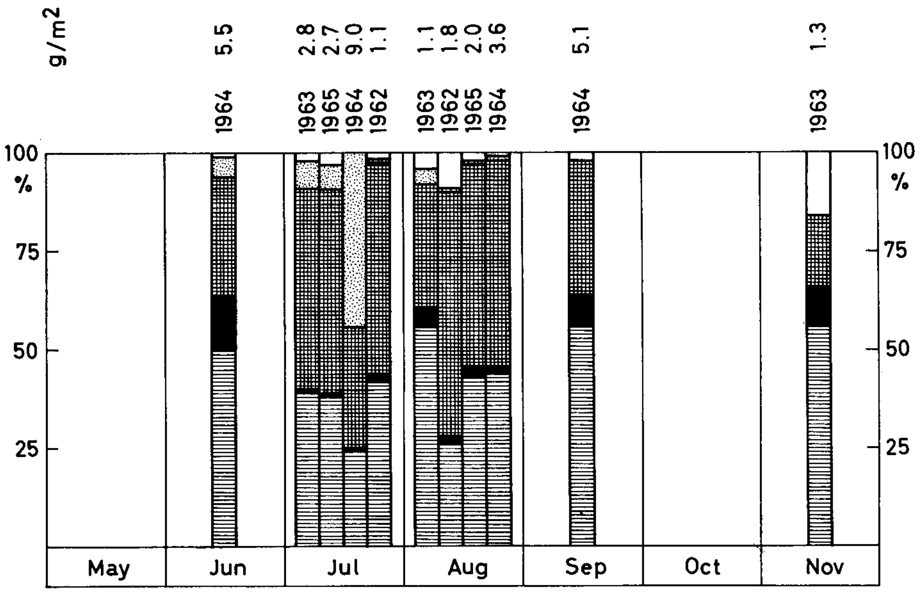

Fig. 26. Loc. L. Percentual composition of the standing crop.
For explanation, see Fig. 20.

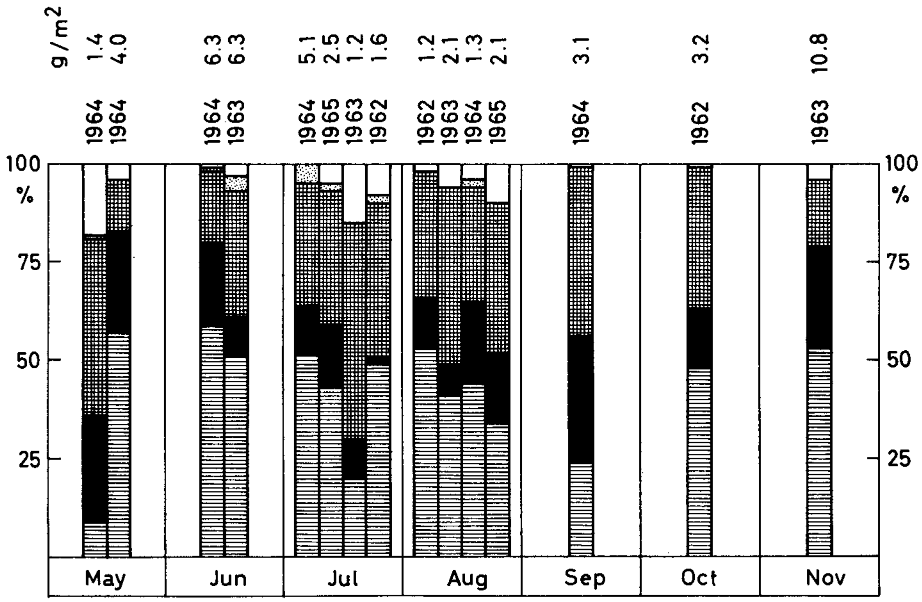

Fig. 27. Loc. N. Percentual composition of the standing crop. For explanation, see Fig. 20.

than usually prominent. *Rhycophila nubila* and *Arctopsyche ladogensis* were usually dominant, but in June, *Potamophylax stellatus* dominated.

In all years except 1964, blackflies were relatively unimportant. *Prosimulium hirtipes* and *Cnephia* sp. (only *C. fuscipes* positively identified) were important in June and sometimes in July, when *Helodon ferrugineus*, *Schönbaueria annulitarsis* and *Gnus forsi* also occurred. Sparse populations of *Odagmia monticola* and *Eusimulium* sp. probably hibernated as larvae.

5.7.8. Loc. N (Fig. 27, Tab. 26)

This was also a locality with low and relatively stable TSC, very like loc. B in particular. The highest TSC was recorded in November 1963.

Absolute values of mayfly SC were highest early and late in the year. The seasonal succession was similar to that at loc. B. Stoneflies were relatively important. In late autumn, *Taeniopteryx nebulosa* was very prominent. Among the caddisflies, *Glossosoma intermedium* and *Potamophylax stellatus* dominated in May and June. From July onwards, *Rhyacophila nubila* was usually the most important species, but was sometimes surpassed by *Potamophylax stellatus* and *Apatania* sp. (almost certainly *A. stigmatella*, cf. § 1.5). On one occasion, *Arctopsyche ladogensis* larvae were obtained in some numbers; this was the only locality in Tjulån where this species occurred. The absence of *G. intermedium* from the November sample is inexplicable.

Blackfly larvae were sparse at all times. In spring *Prosimulium hirtipes* dominated, succeeded by *Cnephia* sp. (only *C. fuscipes* positively identified); the relatively high SC of July 1964 was due to this species.

5.7.9. Loc. O (Fig. 28, Tab. 27)

This locality most closely resembled locs. B and N, but with important differences. There were no significant seasonal TSC fluctuations.

Among the mayflies, *Baetis rhodani* and *Heptagenia dalecarlica* dominated. At no other place was *B. lapponicus* as important as here, whereas *B. fuscatus* and *B. subalpinus* were of little importance.

Tab. 26. Percentual composition of the standing crop at loc. N. See Tab. 19.

	May	June	July	August	September	October	November
Ephemeroptera							
1962	–	–	*H. dalecarlica* 33 *B. rhodani* 32 *B. lapponicus* 14 *B. pumilus* 13 0.8 g/m²	*H. dalecarlica* 54 *B. subalpinus* 19 *B. fuscatus* 13 0.6 g/m²	–	*H. dalecarlica* 52 *E. aurivillii* 41 1.5 g/m²	–
1963	–	*E. aurivillii* 43 *B. rhodani* 36 *A. inopinatus* 15 3.2 g/m²	*H. dalecarlica* 31 *B. fuscatus* 19 *E. aurivillii* 17 0.2 g/m²	*H. dalecarlica* 46 *B. fuscatus* 39 0.8 g/m	–	–	*B. rhodani* 49 *E. aurivillii* 30 *H. dalecarlica* 20 5.7 g/m²
1964	I: *A. inopinatus* 88 0.1 g/m² II: *A. inopinatus* 72 *E. aurivillii* 17 2.2 g/m²	*A. inopinatus* 43 *B. rhodani* 31 *E. aurivillii* 11 3.7 ± 0.8 g/m²	*B. rhodani* 57 *E. aurivillii* 18 *A. inopinatus* 15 2.6 ± 0.6 g/m²	*B. fuscatus* 48 *B. rhodani* 24 0.6 ± 0.09 g/m²	*H. dalecarlica* 50 *E. aurivillii* 24 0.7 ± 0.1 g/m²	–	–
1965	–	–	*B. rhodani* 29 *E. aurivillii* 25 *B. fuscatus* 23 *H. dalecarlica* 13 1.1 ± 0.2 g/m²	*H. dalecarlica* 42 *B. fuscatus* 42 0.7 ± 0.08 g/m²	–	–	–
Plecoptera							
1962	–	–	*L. fusca* *D. nanseni* *A. sulcicollis* *A. borealis* 0.03 g/m²	*D. nanseni* 63 *L. fusca* 36 0.2 g/m²	–	*D. nanseni* 91 0.5 g/m²	–
1963	–	*I. grammatica* 54 *D. nanseni* 41 0.6 g/m²	*I. grammatica* 74 *L. fusca* 11 0.1 g/m²	*D. nanseni* 81 *L. fusca* 19 0.2 g/m²	–	–	*D. nanseni* 60 *T. nebulosa* 39 2.8 g/m²
1964	I: *D. nanseni* 98 0.4 g/m² II: *D. nanseni* 79 1.1 g/m²	*D. nanseni* 82 *I. grammatica* 15 1.3 ± 0.3 g/m²	*I. grammatica* 44 *D. nanseni* 28 *A. borealis* 22 0.6 ± 0.08 g/m²	*D. nanseni* 71 *L. fusca* 29 0.3 ± 0.05 g/m²	*D. nanseni* 100 1.0 ± 0.2 g/m²	–	–
1965	–	–	*I. grammatica* 51 *D. nanseni* 23 *L. fusca* 12 0.4 ± 0.07 g/m²	*D. nanseni* 63 *L. fusca* 34 0.4 ± 0.05 g/m²	–	–	–

1962	–	–	*A. ladogensis* 56 *Apatania* sp. 21 *Rh. nubila* 11 0.6 g/m²	*Rh. nubila* 81 *Apatania* sp. 11 0.4 g/m²	–	*G. intermedium* 82 1.2 g/m²	–
1963	–	*P. stellatus* 33 *G. intermedium* 24 Limnephil. sp. 21 *Rh. nubila* 13 2.1 g/m²	*P. stellatus* 67 *Rh. nubila* 14 *P. flavomaculat.* 12 0.6 g/m²	*Rh. nubila* 35 *A. ladogensis* 24 *G. intermedium* 17 *Apatania* sp. 14 0.9 g/m²	–	–	*A. ladogensis* 43 *Rh. nubila* 32 Limnephil. sp. 21 2.0 g/m²
1964	I: *G. intermedium* 100 0.6 g/m² II: *P. stellatus* 59 *G. intermedium* 27 0.5 g/m²	*G. intermedium* 58 *P. stellatus* 34 1.1 ± 0.3 g/m²	*Apatania* sp. 62 *P. stellatus* 20 *Rh. nubila* 13 1.6 ± 0.4 g/m²	*Apatania* sp. 49 *Rh. nubila* 26 *P. flavomaculat.* 22 0.4 ± 0.09 g/m²	*G. intermedium* 63 *Rh. nubila* 29 1.3 ± 0.4 g/m²	–	–
1965	–	–	*Rh. nubila* 49 *P. stellatus* 44 0.9 ± 0.3 g/m²	*Rh. nubila* 49 *Apatania* sp. 25 Limnephil. sp. 17 0.8 ± 0.2 g/m²	–	–	–
Simuliidae							
1962	–	–	*Sch. annulitarsis* *S. truncatum* *H. ferrugineus* *Eus. latipes* 0.03 g/m²	*S. truncatum* 0.002 g/m²	–	0	–
1963	–	*P. hirtipes* 68 *Cnephia* sp. 18 0.2 g/m²	*Sch. annulitarsis* 0.001 g/m²	*O. monticola* 0.007 g/m²	–	–	*O. monticola* 0.002 g/m²
1964	I: *P. hirtipes* 0.007 g/m² II: *P. hirtipes* 0.002 g/m²	*P. hirtipes* *Cnephia* sp. 0.07 g/m²	*C. fuscipes* 33 *H. ferrugineus* 22 *G. forsi* 14 *Eusimulium* sp. 12 *Eus. latipes* 11 0.2 g/m²	*C. fuscipes* *S. truncatum* 0.03 g/m²	*O. monticola* 0.006 g/m²	–	–
1965	–	–	*Eus. latipes* *Sch. annulitarsis* 0.04 g/m²	*O. monticola* 0.005 g/m²	–	–	–

Tab. 27. Percentual composition of the standing crop at loc. O. See Tab. 19.

	June		July		August		September	
Ephemeroptera								
1963	–		*B. rhodani*	59	*B. rhodani*	39	–	
			H. dalecarlica	22	*H. dalecarlica*	34		
			B. lapponicus	17	*B. subalpinus*	19		
			0.6 g/m^2		0.3 g/m^2			
1964	*H. dalecarlica*	45	*B. rhodani*	48	–		*H. dalecarlica*	49
	B. rhodani	38	*B. lapponicus*	31			*B. rhodani*	23
	1.2 $\pm$ 0.2 g/m^2		*H. dalecarlica*	15			*Baetis* sp.	15
			3.5 $\pm$ 0.6 g/m^2				2.6 $\pm$ 0.4 g/m^2	
1965	–		*B. rhodani*	41	–		–	
			H. dalecarlica	40				
			B. lapponicus	13				
			1.7 $\pm$ 0.2 g/m^2					
Plecoptera								
1963	–		*D. cephalotes*	99	*D. cephalotes*	91	–	
			0.8 g/m^2		0.2 g/m^2			
1964	*D. cephalotes*	56	*D. cephalotes*	96	–		*D. cephalotes*	84
	L. hippopus	14	2.0 $\pm$ 0.5 g/m^2				*D. nanseni*	13
	B. risi	10					2.3 $\pm$ 0.4 g/m^2	
	1.7 $\pm$ 0.2 g/m^2							
1965	–		*D. cephalotes*	91	–		–	
			1.4 $\pm$ 0.3 g/m^2					

Trichoptera								
1963	–		*Rh. nubila* *Ph. montanus* *P. flavomaculatus* 0.2 g/m²	50 40 10	*Ph. montanus* *Rh. nubila* 0.4 g/m²	65 35	–	
1964	*Rh. nubila* *Ph. montanus* 1.6 ± 0.5 g/m²	50 45	*Rh. nubila* 2.0 ± 0.5 g/m²	90	–		*Ph. montanus* *Rh. nubila* 2.2 ± 0.5 g/m²	50 48
1965	–		*Rh. nubila* *Ph. montanus* 1.6 ± 0.4 g/m²	75 20	–		–	
Simuliidae								
1963	–		*H. ferrugineus* *Sch. annulitarsis* 0.07 g/m²		*O. monticola* *Cnephia* sp. 0.02 g/m²		–	
1964	*P. hirtipes* 1.4 g/m²	97	*H. ferrugineus* *G. forsi* *Cnephia* sp. 0.3 g/m²	39 17 15	–		*O. monticola* 0.2 g/m²	87
1965	–		*C. fuscipes* *H. ferrugineus* *G. forsi* 0.2 g/m²	26 24 17	–		–	

Tab. 28. Percentual composition of the standing crop at loc. P. See Tab. 19.

	May		June		July		August		September	
Ephemeroptera										
1964	*E. aurivillii*	68	*E. aurivillii*	71	*B. rhodani*	64	*B. subalpinus*	72	*E. aurivillii*	48
	H. dalecarlica	30	*A. inopinatus*	14	*H. dalecarlica*	14	*H. dalecarlica*	12	*Baetis* sp.	18
	2.1 g/m²		*H. dalecarlica*	10	3.5 ± 0.4 g/m²		*E. aurivillii*	10	*H. dalecarlica*	17
			1.6 ± 0.2 g/m²				1.7 ± 0.2 g/m²		*B. rhodani*	14
									2.5 ± 0.4 g/m²	
1965	–		–		*B. rhodani*	61	*B. subalpinus*	46	–	
					H. dalecarlica	13	*E. aurivillii*	22		
					B. pumilus	11	*H. dalecarlica*	19		
					E. aurivillii	10	1.2 ± 0.1 g/m			
					2.9 ± 0.4 g/m²					
Plecoptera										
1964	*D. nanseni*	41	*A. sulcicollis*	20	*D. nanseni*	55	*D. nanseni*	45	*D. nanseni*	82
	L. hippopus	37	*Chl. burmeisteri*	17	*I. grammatica*	26	*P. meyeri*	27	*P. meyeri*	15
	2.7 g/m²		*P. meyeri*	16	0.2 ± 0.03 g/m²		*L. digitata*	23	1.1 ± 0.2 g/m²	
			D. nanseni	15			0.4 ± 0.05 g/m²			
			B. risi	13						
			0.5 ± 0.08 g/m²							
1965	–		–		*D. nanseni*	38	*D. nanseni*	45	–	
					L. digitata	29	*L. digitata*	16		
					I. grammatica	25	*A. standfussi*	11		
					0.1 ± 0.02 g/m²		*I. grammatica*	10		
							0.4 ± 0.04 g/m²			

Trichoptera										
1964	*P. stellatus*	51	*Rh. nubila*	63	*Rh. nubila*	76	*Rh. nubila*	47	*Rh. nubila*	36
	Rh. nubila	37	*P. stellatus*	19	*Pl. conspersa*	16	*Hydropsyche* sp.	24	*Pl. conspersa*	30
	Pl. conspersa	11	*Pl. conspersa*	18	1.6 ± 0.3 g/m^2		*Pl. conspersa*	15	*Ph. montanus*	18
	2.6 g/m^2		1.9 ± 0.5 g/m^2				*Ph. montanus*	14	*Hydropsyche* sp.	14
							2.7 ± 0.6 g/m^2		6.1 ± 1.1 g/m^2	
1965	–		–		*Rh. nubila*	79	*Rh. nubila*	58	–	
					Pl. conspersa	17	*Pl. conspersa*	20		
					1.8 ± 0.4 g/m^2		*Hydropsyche* sp.	11		
							3.0 ± 0.6 g/m^2			
Simuliidae										
1964	*O. monticola*	50	*P. hirtipes*	71	*C. fuscipes*	98	*O. monticola*	43	*O. monticola*	
	P. hirtipes	36	*C. fuscipes*	26	8.9 g/m^2		*Eus. latipes*	34	*O. ornata*	
	O. ornata	12	0.7 g/m^2				0.2 g/m^2		*Eusimulium* sp.	
	0.3 g/m^2								0.07 g/m^2	
1965	–		–		*C. fuscipes*	77	*O. monticola*	40	–	
					H. ferrugineus	12	*Eus. latipes*	23		
					3.1 g/m^2		*Eusimulium* sp.	13		
							H. ferrugineus	12		
							C. fuscipes	10		
							0.1 g/m^2			

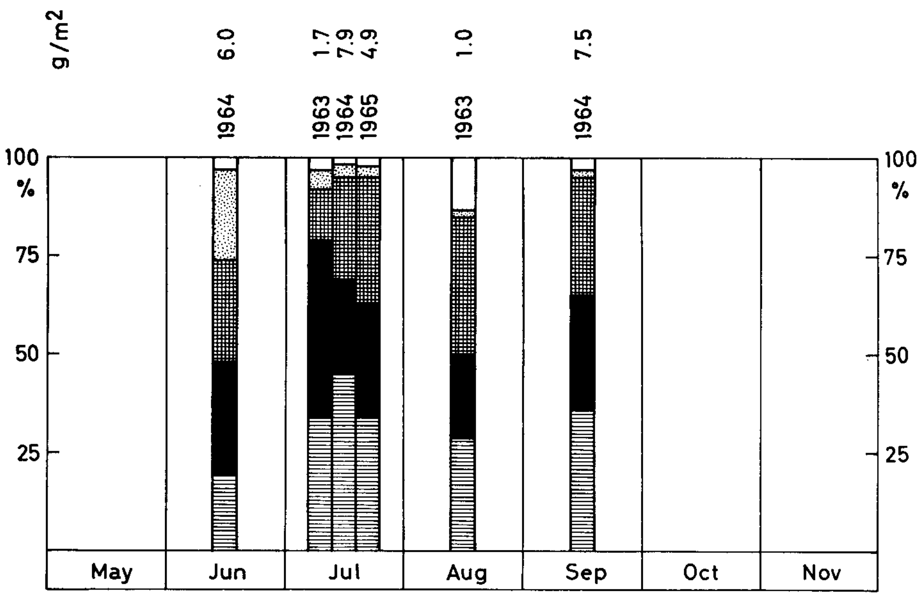

Fig. 28. Loc. O. Percentual composition of the standing crop. For explanation, see Fig. 20.

The most characteristic feature of loc. O was the abundance of *Dinocras cephalotes*. Most samples were totally dominated by this species as far as stoneflies are concerned.

Rhyacophila nubila was the dominant caddisfly but in autumn was surpassed by *Philopotamus montanus* – a species restricted to locs. O and P.

A conspicuous difference from other localities described above was the absence of *Simulium truncatum* and *Schönbaueria annulitarsis*. Dominant blackfly species were *Prosimulium hirtipes*, *Cnephia fuscipes*, *Helodon ferrugineus* and *Gnus forsi*. Seasonal changes in blackfly SC were exceptionally small at loc. O.

5.7.10. Loc. P (Fig. 29, Tab. 28)

This locality was in a much smaller water course than any other, but was most similar to loc. O. Blackflies were comparatively important for a non-outlet locality.

The proportion of mayflies was relatively low and stable. It differed from loc. O in that *Baetis lapponicus* was replaced by *B. pumilus* as a dominant species.

Except in the May sample, stoneflies made up a very small proportion of TSC. In May, *Diura nanseni* and *Leuctra hippopus* were the dominant species. In June, the composition was very unusual, consisting of *Amphinemura sulcicollis*, *Protonemura meyeri* and *Chloroperla burmeisteri*. Later, *Leuctra digitata* was of some importance, while *L. fusca* was scarce. There were two records of small nymphs of *Dinocras cephalotes*, indicating a resident population higher up in the stream.

In May and June, *Potamophylax stellatus* dominated among the caddisflies, but *Rhyacophila nubila* and *Plectrocnemia conspersa* were also common. The last-mentioned species was not regularly obtained at any other locality; interestingly *Polycentropus flavomaculatus*, its ecological counterpart, was absent (cf. § 3.5.4). Similarly, *Arctopsyche ladogensis* was replaced by *Hydropsyche* sp. (only *H. nevae* Kol. identified from the study area).

The high blackfly SC in July was due to

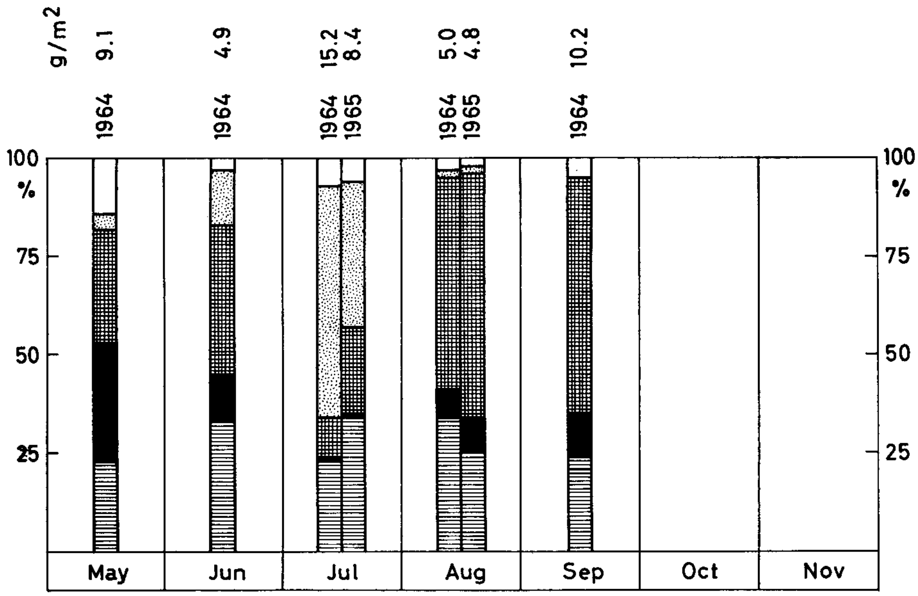

Fig. 29. Loc. P. Percentual composition of the standing crop. For explanation, see Fig. 20.

Cnephia fuscipes, which was preceeded by *Prosimulium hirtipes* and succeeded by *Odagmia monticola*. *O. monticola* and *O. ornata* hibernated as larvae in the stream. As at loc. O, seasonal fluctuations of blackfly SC were not particularly violent at loc. P. A certain number of larvae spent the winter in the benthos, which is in contrast to the outlets and most other localities in the main river. Again like loc. O, this locality was not inhabited by *Schönbaueria annulitarsis* and *Simulium truncatum*.

5.8. Local differences of standing crop and of its seasonal cycle

As is apparent from the above descriptions there are important differences between the lake outlet localities (A, E and to some extent H) and the others. A closer analysis will be made here, on the basis of the data from 1964 supplemented with those from October 1962 and November 1963.

As may be seen in Fig. 30, local differences of TSC were relatively unimportant in May, June, October and November. In July and August, the outlets had much larger TSC values than the other localities, and in September this was so for loc. A but not for locs. E and H.

The less extensive information from 1963 confirms this result (Fig. 31). In this year the distinctiveness of the outlets disappeared as early as in August but had, on the other hand, developed in June.

In Fig. 32 the situation of the blackflies in the two locality types is compared. A very clear peak in July extending into August occurs at the outlets. When that part composed of blackflies is subtracted from the TSC, the differences between outlets and the others are seen practically to disappear. Loc. A did show a fairly high TSC value even after this subtraction, which was due to a high caddisfly SC, particularly *Rhyacophila nubila* and *Potamophylax stellatus*. These are active feeders. The net-spinning caddisflies did not occur in particularly large quantities at the outlets.

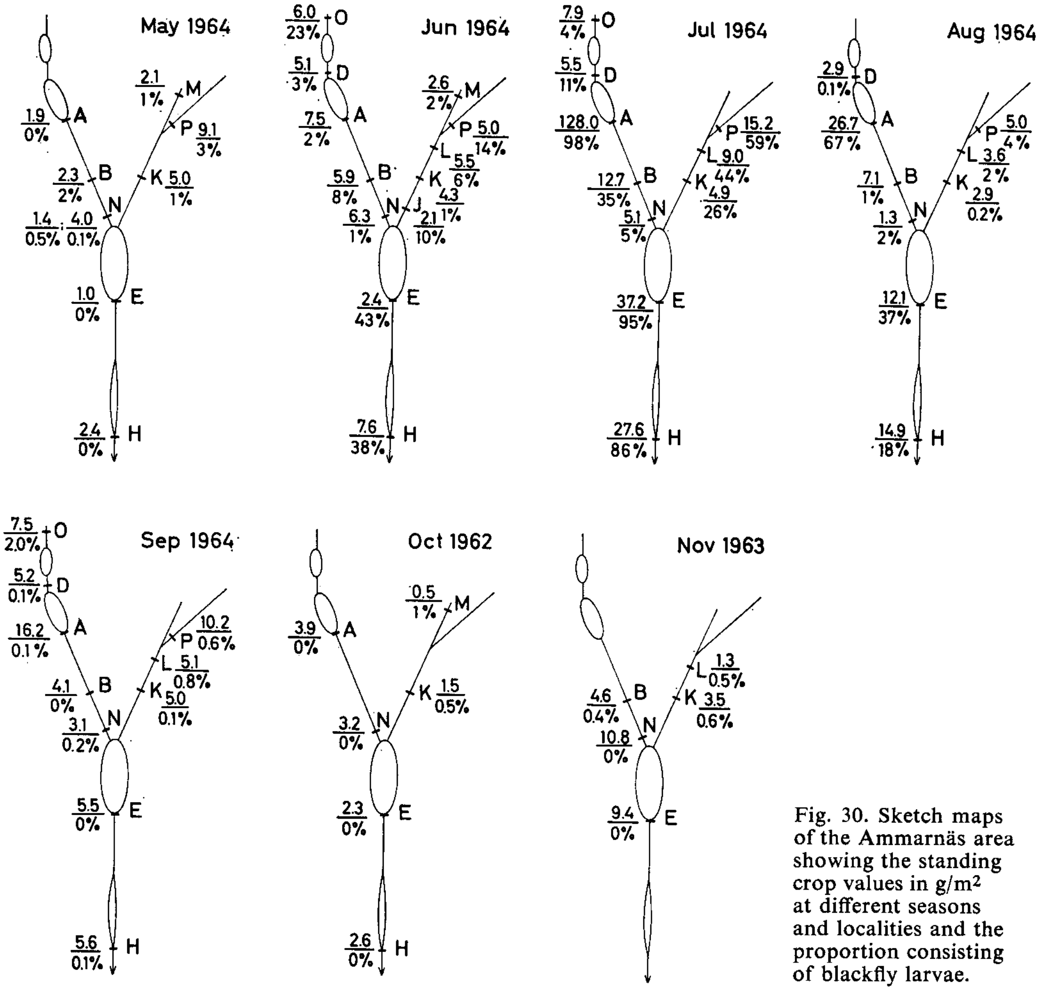

Fig. 30. Sketch maps of the Ammarnäs area showing the standing crop values in g/m² at different seasons and localities and the proportion consisting of blackfly larvae.

The lacustrine organic matter entering the river to a certain extent becomes attached to the bottom and periphyton. It may then be utilized by bottom feeding animals for which the seston is unavailable. Only the blackfly larvae exploit the seston in a large scale. The restricted occurrence of certain blackfly species at the outlets (§ 3.5.2) probably reflects this special adaptation to the nutritional conditions prevailing at these sites.

The TSC values at outlets and non-outlets at the time of peak development of the blackfly zoome at the former sites are compared in Tab. 29. The TSC at the outlets was usually about 10 to 20 times higher than at the non-outlets, the differences being smaller and less regular in Vindelälven than in Tjulån.

The outlets differed from the other localities not only in absolute TSC levels but also with respect of their seasonal variations. Outlets are characterized by extremely pronounced TSC peaks in July, whereas seasonal fluctuations at the non-outlets are barely discernible: sometimes there was even a slightly lower TSC in summer.

The outlet communities of northern Scan-

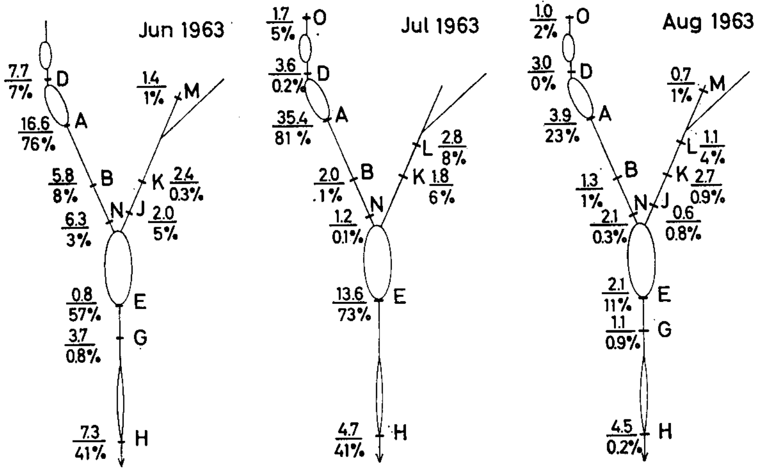

Fig. 31. Sketch maps of the Ammarnäs area showing the standing crop values] in g/m² in June, July and August 1963 and the proportion consisting of blackfly larvae.

dinavia have been studied by Müller (1954 a, 1955, 1956, 1962 b) and Illies (1957). In many respects, the results of the present investigation agree with those found by these workers, for example in terms of TSC and the ratio between outlet and non-outlet TSC values. The specific composition, however, in part differed. Müller and Illies found a considerable quantity of net-spinning caddisfly larvae at their outlet localities; the most abundant species in their areas, *Neureclipsis bimaculata* L., has never been recorded from the Ammarnäs area. For mayflies, stoneflies and caddisflies, Illies (op. cit.) found no qualitative difference between outlets and non-outlets, as in the Ammarnäs area, where, however, certain blackfly species were found to characterize outlet communities (cf. § 5.7.2).

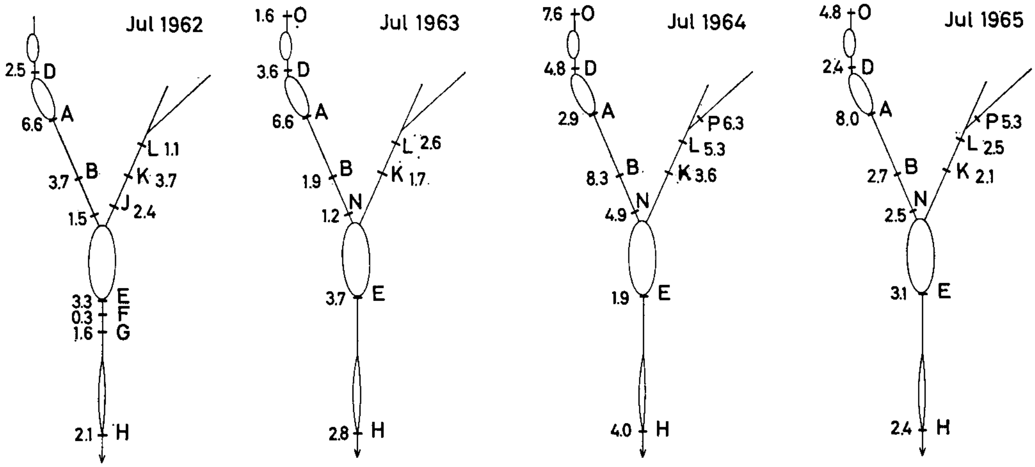

Fig. 32. Sketch maps of the Ammarnäs area showing the standing crop values for mayflies, stoneflies and caddisflies but without the blackflies in July 1962 to 1965.

Tab. 29. Standing crop at the non-outlet localities expressed as percentage of the quantity at the outlets in Tjulån (locs. A, B, N) and Vindelälven (locs. M, L, K, J, E, F, G) in July and August 1962 to 1965. See Fig. 2.

Loc.	July 1962		July 1963		July 1964		July 1965	
	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%
A	27.9	100	35.4	100	128.0	100	38.3	100
B	3.9	14	2.0	6	12.7	10	5.3	14
N	1.6	6	1.2	3	5.1	4	2.5	7
L	1.1	2	2.8	21	9.0	24	2.7	17
K	3.7	6	1.8	13	4.9	13	2.2	14
J	2.4	4	–	–	–	–	–	–
E	61.0	100	13.6	100	37.2	100	16.1	100
F	0.8	1	–	–	–	–	–	–
G	1.7	3	–	–	–	–	–	–
	August 1962		August 1963		August 1964		August 1965	
A	33.2	100	3.9	100	26.7	100	28.8	100
B	1.8	5	1.3	33	7.1	27	2.8	10
N	1.2	4	2.1	54	1.3	5	2.1	7
M	1.8	22	0.7	33	–	–	–	–
L	1.8	22	1.1	52	3.6	30	2.0	41
K	2.2	27	2.7	129	2.9	24	2.4	49
J	2.2	27	0.6	29	–	–	–	–
E	8.3	100	2.1	100	12.1	100	4.9	100
F	1.4	17	–	–	–	–	–	–
G	2.5	30	1.1	52	–	–	–	–

5.9. Year-to-year differences in standing crop

Year-to-year comparisons were possible for June, July and August (Tabs. 30 to 32).

Differences were assessed in two ways. As stated above (§ 5.5), if an SC value is about twice another, the difference may be assumed to be significant. In the three tables, values that are more than twice any other value for the same month and locality are printed in bold-type, those that are less than half any other value in italicized type. Exceptions were made when either or both values in a comparison was less than 0.1 g/m^2; such low values are less reliable and were therefore omitted.

Moreover, the SC values for each month and locality were ranked in order of decreasing size, and the ranking figures summed for each year. The lower the total score, the higher the relative SC quantities.

It is found that the SC values for July and August 1964 were distinctly higher than in any other year for practically all major taxa. Otherwise, year-to-year fluctuations were much less obvious, although low values were particularly frequent in 1963. In June 1964, stoneflies showed higher SC values than in the same month 1963, but for the other three groups this was not the case.

It might be expected that blackflies would differ from mayflies, stoneflies and caddisflies because, in the main, they have a very different life cycle. Most blackfly species spend much of the year as eggs, and these animals are presumably protected from a great many vicissitudes to which animals with long nymphal/larval periods are exposed. Yet the blackflies showed close parallellism with the other groups.

In some cases year-to-year differences may be due to different timing of the life cycles

Tab. 30. Annual differences in June of standing crop values for mayflies, stoneflies, caddisflies and blackflies. When one value was at least twice the other value for the same locality, the higher value was printed bold-face and the lower one in italics. When either was lower than 0.1 g/m², no typographical demarcation was used.

Loc.		Ephemeroptera		Plecoptera		Trichoptera		Simuliidae	
		1963	1964	1963	1964	1963	1964	1963	1964
A	SC	*0.9*	**4.4**	*0.3*	**1.0**	**2.2**	*1.1*	**12.6**	*0.1*
	rank......	2	1	2	1	1	2	1	2
B	SC	2.5	2.9	*0.3*	**1.9**	**2.3**	*0.5*	0.5	0.5
	rank......	2	1	2	1	1	2	1	1
D	SC	3.4	2.2	*0.3*	**0.8**	2.0	1.8	**0.5**	*0.2*
	rank......	1	2	2	1	1	2	1	2
E	SC	0.04	0.4	*0.2*	**0.4**	0.006	0.3	*0.5*	**1.0**
	rank......	2	1	2	1	2	1	2	1
H	SC	1.9	2.1	1.4	1.7	0.6	0.7	3.0	2.9
	rank......	2	1	2	1	2	1	1	2
J	SC	1.1	0.8	0.02	0.1	0.6	0.5	*0.1*	**0.2**
	rank......	1	2	2	1	1	2	2	1
K	SC	*1.1*	**2.6**	0.06	0.5	0.6	0.9	0.007	0.03
	rank......	2	1	2	1	2	1	2	1
M	SC	1.0	1.8	0.02	0.4	0.3	0.3	0.02	0.05
	rank......	2	1	2	1	1	1	2	1
N	SC	3.2	3.7	*0.6*	**1.3**	2.1	1.1	0.2	0.07
	rank......	2	1	2	1	1	2	1	2
Total score		16	11	18	9	12	14	13	13

affecting the result of the sampling. This probably explains some of the fluctuations in the blackflies, which would be particularly sensitive to this sort of disturbance because of their compressed life cycle. This is not the whole explanation though.

Too few years were studied to allow a more detailed analysis of the year-to-year fluctuations. However, apart from a few exceptions, the four major taxa did tend to vary in a parallel manner. One of the few features common to a majority of the species is that their flight-periods are restricted to a short period of the year, approximately from the middle of July to the end of August (Ulfstrand 1968: Tab. 3). During this time most species undergo their adult life. At this time another whole complex of factors are encountered which affect survival.

Large-scale year-to-year fluctuations in benthic communities were found by Allen (1951), who was able to correlate them with spate frequency, and by Macan (1962 a) who also found long-term trends which were presumably the result of human disturbance.

5.10. Regional comparisons

Any comparison between different workers' results will suffer from the partial incompatibility of their methods (cf. Cummins 1966). But despite this, some conclusions may be drawn from such comparisons – with due circumspection. Albrecht (1959) has published a useful review of precisely this problem. It will therefore suffice to compare the present results with those compiled by her. She listed standing crop values from a number of rhithron biotopes, and it is obvious that the data from the Ammarnäs area fall well in line with the other records, although they are, on the whole, a little low. Some papers published after Albrecht's review show no particular divergencies (Ökland 1963, Maitland 1965, 1966, Lillehammer 1966). Müller's (1953) results from the high boreal zone of northern Sweden are strikingly similar to mine.

Large rivers of potamon character often yield much higher TSC values, in many cases because of an abundance of mussels (e.g. Berg 1948).

Tab. 31. Annual differences in July of standing crop values for mayflies, stoneflies, caddisflies and blackflies. Values more than twice any other value for the same locality are printed bold-face, those lower than half any other value in italics. Values were ranked from 1 to 4, and rank values were added up to a "total score" (bottom row).

		1962	1963	1964	1965	1962	1963	1964	1965	1962	1963	1964	1965	1962	1963	1964	1965
Loc.		Ephemeroptera				Plecoptera				Trichoptera				Simuliidae			
A	SC....	1.5	1.0	2.0	1.9	0.04	0.02	0.02	0.06	4.3	4.6	*0.7*	5.8	21.4	28.8	**125.1**	38.3
	rank...	3	4	1	2	2	3	3	1	3	2	4	1	4	3	1	2
B	SC....	2.2	*0.9*	5.7	3.3	0.06	0.08	**0.5**	0.2	1.4	0.8	2.1	1.6	0.2	0.01	**4.4**	0.09
	rank...	3	4	1	2	4	3	1	2	3	4	1	2	2	4	1	3
D	SC....	0.9	1.9	2.7	1.0	0.08	0.1	0.1	0.06	1.3	0.8	1.3	1.0	1.1	0.008	0.6	0.3
	rank...	4	2	1	3	3	1	1	4	1	4	1	3	1	4	2	3
E	SC....	0.7	**2.3**	1.0	0.9	0.06	0.2	0.04	0.04	2.4	1.0	0.6	1.8	57.7	9.9	35.3	12.9
	rank...	4	1	2	3	2	1	3	3	1	3	4	2	1	4	2	3
H	SC....	0.5	1.0	1.0	0.5	0.08	0.1	0.1	0.1	1.1	1.4	2.3	1.6	*0.1*	2.0	**23.6**	1.4
	rank...	3	1	1	3	4	1	1	1	4	3	1	2	4	2	1	3
K	SC....	0.6	0.7	**2.6**	0.6	0.08	0.07	0.1	0.1	0.6	0.6	0.7	0.9	0.02	0.1	**1.2**	0.04
	rank...	3	2	1	3	3	4	1	1	3	3	2	1	4	2	1	3
L	SC....	0.5	1.1	**2.2**	1.0	0.02	0.03	0.02	0.02	0.6	1.4	2.8	1.4	0.004	0.2	**3.7**	0.2
	rank...	4	2	1	3	2	1	2	2	4	2	1	2	4	2	1	2
N	SC....	0.8	*0.2*	**2.6**	1.1	0.03	0.1	0.6	0.4	0.6	0.6	1.6	0.9	0.03	0.001	0.2	0.04
	rank...	3	4	1	2	4	3	1	2	3	3	1	2	3	4	1	2
Total score..		27	20	9	21	24	17	13	16	22	24	15	15	23	25	10	21

Tab. 32. Annual differences in August of standing crop values, as in Tab. 31 (q. v. for explanation).

Loc.		Ephemeroptera				Plecoptera				Trichoptera				Simuliidae			
		1962	1963	1964	1965	1962	1963	1964	1965	1962	1963	1964	1965	1962	1963	1964	1965
A	SC....	1.7	*0.7*	3.1	2.3	0.09	0.2	0.4	0.4	5.1	*1.0*	4.9	5.0	25.5	*0.9*	17.9	20.7
	rank...	3	4	1	2	4	3	1	1	1	4	3	2	1	4	3	2
B	SC....	0.9	0.7	**2.3**	1.1	0.2	0.2	0.6	0.4	0.6	0.4	**4.0**	1.1	0.007	0.02	0.06	0.01
	rank...	3	4	1	2	3	3	1	2	3	4	1	2	4	2	1	3
D	SC....	1.5	1.6	1.2	1.3	0.2	0.09	0.2	0.1	1.3	0.9	1.3	1.0	0.05	0	0.002	0.003
	rank...	2	1	4	3	1	4	1	3	1	4	1	3	1	4	3	2
E	SC....	2.0	*0.4*	2.8	1.5	0.1	0.03	0.3	0.2	3.9	*1.1*	4.3	2.3	1.9	*0.2*	**4.4**	0.7
	rank...	2	4	1	3	3	4	1	2	2	4	1	3	2	4	1	3
H	SC....	0.4	0.7	**1.9**	0.3	0.7	0.6	1.5	0.9	1.8	2.9	**8.6**	2.9	0.05	0.009	**2.6**	0.1
	rank...	3	2	1	4	3	4	1	2	4	2	1	2	3	4	1	2
K	SC....	0.4	0.3	0.8	0.7	0.05	0.07	0.2	0.07	0.7	0.8	0.8	0.8	0.007	0.02	0.007	0.01
	rank...	3	4	1	2	4	2	1	2	4	1	1	1	3	1	3	2
L	SC....	0.5	0.6	**1.6**	0.8	0.04	0.06	0.08	0.08	1.2	*0.3*	1.9	1.0	0.01	0.05	0.006	0.02
	rank...	4	3	1	2	4	3	1	1	2	4	1	3	4	2	1	3
N	SC....	0.6	0.8	0.6	0.7	0.2	0.2	0.3	0.4	0.4	0.9	0.4	0.8	0.002	0.007	0.03	0.005
	rank...	3	1	3	2	3	3	2	1	3	1	3	2	4	2	1	3
Total score..		23	23	13	20	25	26	9	14	20	24	12	18	22	23	14	20

Tab. 33. The composition of the benthic communities at locs. A, B and N in Tjulån in terms of numbers of individuals per m² standard area.

Locality:	A							B							N							
Year:	1964					1965		1964					1965		1964						1965	
Month:	May	June	July	Aug.	Sep.	July	Aug.	May	June	July	Aug.	Sep.	July	Aug.	May	May	June	Jul.	Aug.	Sep.	Jul.	Aug.
Siphlonurus sp. . .	1	–	28	–	–	19	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
A. inopinatus. . . .	–	2	–	–	–	–	–	20	2	2	–	–	–	–	13	462	408	71	–	–	3	–
B. fuscatus.	–	–	41	6	–	14	9	–	–	–	498	278	88	233	–	–	–	–	242	21	179	200
B. lapponicus. . . .	–	–	9	–	–	30	–	–	–	–	66	–	73	3	–	–	–	8	4	–	16	5
B. macani	–	–	218	5	–	129	129	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
B. pumilus	–	6	33	9	–	28	20	–	–	43	56	24	102	17	–	–	4	50	30	4	28	5
B. rhodani	1	8	–	9	6	28	–	60	313	746	85	29	348	61	–	35	304	266	37	29	60	48
B. subalpinus. . . .	–	–	60	593	4	75	266	–	–	–	319	69	–	100	–	–	–	–	16	14	–	6
Baetis sp.	–	–	58	230	19	87	448	24	19	12	288	110	–	79	–	18	268	46	66	68	–	33
H. dalecarlica . . .	–	6	31	3	4	58	18	9	18	10	8	15	10	19	–	13	20	15	24	29	8	46
H. sulphurea	–	10	20	39	33	33	22	–	2	–	–	–	–	–	–	–	1	–	1	–	1	2
Ecd. joernensis . .	–	–	7	16	8	6	8	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
E. aurivillii	1	351	63	17	221	51	83	27	90	78	26	313	18	16	–	26	20	20	8	65	40	24
Others	–	–	–	–	–	–	1	1	–	–	–	–	–	–	6	–	–	5	–	–	–	1
Total	3	383	568	927	295	558	1004	141	444	891	1347	838	639	528	19	554	1025	482	428	230	335	371

B. risi	–	–	–	–	–	–	–	10	1	–	–	–	–	–	–	–	–	–	–	–	–	–
T. nebulosa	–	–	–	–	20	–	–	–	–	–	–	2	–	–	–	–	–	–	–	4	–	–
A. borealis	–	4	4	–	–	6	–	–	1	100	–	–	18	–	–	27	1	55	–	–	4	–
L. fusca	–	–	–	8	3	6	30	–	–	2	115	6	23	44	–	–	–	2	29	–	22	20
L. hippopus	8	72	–	–	–	–	–	5	60	–	–	–	–	–	4	18	6	–	–	–	–	–
C. atra	2	4	–	–	–	–	–	5	–	–	–	–	–	–	–	3	–	–	–	–	–	–
D. bicaudata	1	4	–	20	27	–	21	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
D. nanseni	8	8	–	55	121	6	64	33	57	–	214	366	6	128	17	39	35	5	173	188	2	153
I. grammatica	14	31	–	–	–	–	–	3	33	4	1	–	1	–	–	11	23	29	–	–	12	–
Others	–	1	–	1	–	–	12	3	–	–	4	2	–	–	–	6	2	3	–	–	4	3
Total	33	124	4	84	171	18	127	59	153	106	334	376	48	172	21	104	67	94	202	192	44	176
Rh. nubila	–	17	29	135	508	118	108	14	4	109	153	110	118	38	–	2	6	8	2	18	28	20
G. intermedium	–	–	–	–	–	–	–	35	22	–	–	3	–	–	48	15	49	–	9	107	–	12
P. flavomaculatus	–	5	–	10	20	11	6	3	2	–	20	12	8	1	–	3	–	12	17	4	–	5
Apatania sp.	4	95	39	3	3	171	54	3	2	106	2	15	18	44	–	–	2	188	56	12	10	27
P. stellatus	4	3	–	–	–	14	–	–	3	–	–	–	2	–	–	4	9	4	–	–	8	–
Limnephilinae	–	–	–	–	–	19	11	–	–	–	–	1	–	6	–	–	–	–	–	1	–	6
Athripsodes sp.	2	1	–	1	8	6	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Others	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total	10	121	72	149	539	339	183	55	33	215	175	141	146	89	48	24	66	212	84	142	46	70
Simuliidae	–	856	67655	7266	10	18018	7760	25	309	1014	37	2	65	9	3	2	131	110	15	5	28	6
Grand total	46	2484	68299	8426	1015	18933	9074	280	939	2226	1893	1357	898	798	91	684	1289	898	729	569	453	623

Rhithron biotopes all over Europe, thus, seem to contain TSC of approximately similar levels. There is of course no definite relationship between productivity and standing crop. It is quite possible that potamon biotopes with very high TSC may have a rather low productivity. It is also likely that in productivity, the Lapland rhithron streams would compare more unfavourably with more southerly ones, where many species are able to produce two or more generations per year (e.g. Illies 1952, Dittmar 1955 a, Macan 1963, Ulfstrand 1968).

Finally, it can be observed that the general similarities between standing crop data obtained by different workers in different areas attest to the practicability of benthic sampling in rhithron biotopes.

6. Quantitative composition of the benthic community in terms of population densities

6.1. Introduction

The advantage of studying community composition in terms of standing crops rather than numbers of individuals was pointed out in § 5.1. However as a background to an analysis of the relationships between population movements and resident benthic populations it was found necessary to obtain some information of numbers of individuals present (cf. § 8.7). These studies were restricted to Tjulån, i.e. locs. A, B and N and to the years 1964 and 1965.

When a species is represented by large numbers of small nymphs/larvae, the population density is likely to be strongly underestimated. And even when a population consists only of large nymphs/larvae, the estimates will be conservative.

Mayflies, stoneflies and caddisflies from locs. A, B and N were directly counted; blackflies at locs. B and N were also counted but at loc. A had to estimated from weighing subsamples and counting the individuals, after which the numbers included in the whole sample could be calculated. Numbers of caddisflies and blackflies include pupae.

6.2. Population densities

In Tab. 33 the results of these counts are presented. The numbers of individuals of all major taxa combined at loc. A fluctuated between 70,000 and 46 ind/m^2. The poverty of the community in May was remarkable, as was the rapid increase in the ensuing period. In June to August, blackflies comprised the vast majority.

The amplitude of fluctuations was much smaller at locs. B and N. But apart from blackfly larvae, population densities were at least as high at these sites as at loc. A. The density of mayflies sometimes rose to over 1,000 ind/m^2, that of stoneflies and caddisflies to 300 ind/m^2, although the last-mentioned group on one occasion at loc. A achieved a figure of 500 ind/m^2.

The great difference between the outlet and the other two sites is as apparent in these terms as in terms of standing crop (cf. §§ 5.7.1, 5.7.2 and 5.7.8).

6.3. Total numbers of blackfly larvae/pupae at loc. A at maximum development

It is possible to arrive at a rough estimate of the total number of blackfly larvae present at loc. A in July 1964, when numbers were at their peak.

The distribution of the blackfly larvae at and near sampling loc. A was examined in some detail. The central deepest part of the stream could not be sampled extensively, but it was possible to observe that blackfly density was very much lower there than in the shallower waters. This was probably because of the dense carpet of *Didymosphenia geminata* covering this central channel, which was approximately 5 m wide. Along each shore was a zone of more favourable conditions, also about 5 m in width on each side. From where the lotic conditions start, similar densities as those found in the samples prevailed for a distance of approx. 40 m. In the next 50 m of stream blackfly density was less and was estimated at about 25% of that found at the sampling locality proper. Below this, the nature of the stream changed abruptly, and blackflies were almost absent.

Thus, in an area of 2 × 40 × 5 m = 400 m^2 there were ca 67,000 ind/m^2; in the downstream area of 2 × 50 × 5 m = 500 m^2 there was an estimated density of ca 16,000 ind/m^2; the few larvae in the deep zone being disregarded. The total number of blackfly larvae and pupae at the outlet of Tjulån from Stora Tjulträsk in July 1964 was thus in the order of 35 × 10^6 individuals, concentrated to an area of ca 900 m^2.

7. Standing crop changes, population movements and production

7.1. Introduction

As is apparent from §§ 5 and 6 both standing crop and population density frequently changed drastically between consecutive samples.

In theory, the productivity of a population or a community may be estimated from data on weight increase, divided by time. However this is rarely possible in practice, since standing crop is influenced by many other factors, such as immigration, emigration, mortality, etc.

Jónasson (1955), Hynes (1961) and others have commented upon the extreme difficulty of estimating productivity in running water communities. The heterogeneity of the substrate, the continuous accrual of newly hatched nymphs and the variety and variability of life cycles are some of the obstacles. But in many of these discussions, the influence of population movements is neglected. Studies of the productivity in springs have in some cases met with considerable success (Odum 1957, Teal 1957). One of the reasons for this is probably that population movements (apart from emergence of amphibiotic insects) are of relatively small extent; however Müller, Kureck and Müller-Haeckel (1963) found that ground-water animals may move into and out of a spring in a circadian rhythm.

In the present section some striking standing crop changes will be discussed in terms of population movements and productivity. But first there is need for a definition of some terms.

7.2. Definition of productivity and production

Very different meanings have been attached to these terms by different workers (Macfadyen 1948, 1957, Thienemann 1955, Odum 1963, Davis 1963, Westlake 1965, Steemann Nielsen 1965/66).

In this paper, the term productivity denotes the rate of weight accumulation by a population, by a zoome or by a community (cf. Spet 1965), whereas production is the accumulated result of such a process. In amphibiotic insects, productivity ceases when the insects emerge, and total production is the total weight of all the individuals immediately before emergence.

Accurate production and productivity measurements are practically impossible in lotic biotopes; a number of errors that occur will be discussed below. Considering the absence of any such data from northern Europe, however, even rough estimates may be of interest.

7.3. Population movements and standing crop changes

It is unnecessary to examine every standing crop change established in § 5, as something about the background of such changes may be learnt from a few characteristic examples.

In May 1964 practically no mayflies were present at loc. A (§ 5.7.1), but some three weeks later a large quantity was obtained, representing an SC of 4.4 g/m^2 (Tab. 19). This large increase was almost entirely due to *Ephemerella aurivillii* whose density rose from

1 to 351 ind/m^2 (Tab. 33). At this season the nymphs of this species are large and approaching emergence (Ulfstrand 1968). It was therefore out of the question that they might have been overlooked on the first occasion, or have dwelt in the hyporheal biotope: they were plainly too large for either alternative. Furthermore, ephemerellid nymphs are extremely poor swimmers, and crawl slowly and deliberately, so that long-range upstream transfers are ruled out. Finally they could not invade the place from upstream, since it was a lake outlet and the species does not live in lakes. There seems to remain just one possibility, that of transverse movement across the stream bed. Probably the nymphs spend winter in the middle of the river to avoid being stranded at low flow. It seems reasonable to assume that they spread out again after the break-up of the ice prior to their emergence. No other explanation of this enormous increase of *E. aurivillii* is forthcoming.

Another example is taken from loc. N (§ 5.7.8). Two samples were taken in May 1964 with ten days' interval. In this period the mayfly SC rose from 0.1 to 2.2 g/m^2 (Tab. 26). On both occasions the dominant species was *Ameletus inopinatus* which increased from 13 to 462 ind/m^2 (Tab. 33). This species, in contrast to *E. aurivillii*, is a deft swimmer, so that upstream movements cannot be ruled out, although downstream or transverse movements are perhaps more likely. In any case, a population movement rather than local weight accumulation evidently brought about the change.

Numerous SC changes seem impossible to explain in any other terms than population movements. Sometimes it is possible to suggest how these movements take place. The conclusion is that many SC increases are not due to local productivity and that SC values cannot be used for productivity estimates in the biotopes under consideration. The only way of estimating productivity and production would be encompass a stretch of river between two lakes, but this is as yet impossible. However, because of a series of favourable circumstances it is possible to make an approximate assessment of blackfly productivity at the lake outlets.

7.4. Productivity and production in blackfly zoomes at lake outlets

7.4.1. Some sources of error

Because of their rapid life cycle, synchronized hatching and emergence and dense populations the blackflies are comparatively suitable for productivity estimates. Moreover, population movements may be largely ignored, for there is no downstream invasion from the lake and obviously little if any upstream movement, so that the only effect of movements is the downstream drift reducing the apparent productivity. With regard to the large numbers of resident animals and the relatively moderate occurrence of drift farther downstream this factor was probably only of minor significance.

In addition to downstream drift, there are some factors causing the productivity estimates to be too low, e.g. larval and pupal mortality and emergence.

While it is as yet impossible to appreciate the quantitative significance of these errors, they all tend to reduce the estimated values which are consequently very conservative.

7.4.2. Blackfly productivity and production at loc. A

In June 1963, *Schönbaueria annulitarsis* was not found at loc. A but in July its SC was 19.5 g/m^2. The productivity in this time span was then 0.65 g/m^2/day.

In 1964, there were no blackflies at all in May and very few in June. In July, however, total blackfly SC amounted to not less than 125 g/m^2, representing a productivity between the two sampling occasions of 3 g/m^2/day. The species involved were *Cnephia* sp. (mainly *C. tredecimata*) with 60.5 g/m^2 = 1.48 g/m^2/day, *Sch. annulitarsis* with 23.9 g/m^2 = 0.58 g/m^2/day, and *Gnus forsi* with 34.3 g/m^2 = 0.81 g/m^2/day. Between July and August, the SC of *Simulium truncatum* increased at a rate of 0.19 g/m^2/day.

7.4.3. Blackfly productivity at loc. E

Between June and July 1963, total increase of blackfly SC occurred at a rate of 0.3 g/m^2/day. In 1964, no blackflies were present in May and very few in June. The productivity of *Cnephia* spp. between June and July amounted to 0.35 g/m^2/day. The corresponding values for *Schönbaueria annulitarsis* and *Simulium truncatum* were 0.24 and 0.19 g/m^2/day, respectively.

7.4.4. Blackfly productivity and production at loc. A in relation to food supply

To my knowledge the productivity of the blackfly zoome at loc. A in 1964 surpasses anything previously found in rhithron biotopes. This raises the question of how much organic matter transported with the water was available for this tremendous aggregation.

The SC value in July 1964 was the mean of six subsamples covering in all 1.6 m^2. As discussed in § 5.3, stones making up a sample were removed at random within the locality and represented a variety of microbiotopes. They were taken in three different water depth classes in approximately equal proportions. The six subsamples yielded the following SC values: 78, 109, 126, 139, 139, and 159 g/m^2.

In § 6.3, the distribution of the blackfly larvae at the outlet of Tjulån from Stora Tjulträsk was discussed. Making the same assumptions as in that section, the total SC of the blackflies at the outlet in July 1964 was estimated to be 65 kg. This amount was formed in the interval since the preceeding sample which yielded almost no blackfly SC at all. Thus the overall productivity in this period was about 1.6 kg/24 hr.

As is well known, blackfly larvae ingest suspended matter, without distinct preferences as long as the particles are of a certain size (e.g. Rubzow 1959/64, Williams et al. 1961, Carlsson 1962).

According to data from Kungl. Vattenfallsstyrelsen (in litt.) the flow in Tjulån in late June 1964 amounted to ca 25 m^3/sec, corresponding to 2.16×10^6 m^3/24 hr. As shown in Tab. 6, the water contained, on average, about 2 mg/l undissolved organic substance at that time (as measured *below* the blackfly aggregation). This corresponds to 2 g/m^3 and 4,320 kg/24 hr.

Naturally not all the organic matter transported with the current is available for the blackfly larvae, and of the part ingested only a fraction may be utilized for growth (e.g. Lindeman 1942, Teal 1957). However, the total quantity of organic matter passing the blackfly aggregation in one 24-hr period was about 2,700 times larger than the total daily weight increase within the latter, so that the food basis for the productivity seems quite adequate.

The productivity fell sharply after mid-July. It may be assumed that annual blackfly production at the lake outlet was in the order of 100 kg per year. The surface area of river bottom on which this was achieved may be estimated at roughly 100 m^2. The food for this aggregation of animals was drawn from the whole lake. A great part of the production was removed from the stream as winged insects, but a small fraction was returned in the form of eggs.

8. Drift in relation to benthic populations

8.1. Introduction

Drift, in this context, is the downstream transport of benthic organisms in a river. This has for some time been recognized as an important feature of lotic life. It has been especially studied with respect to its circadian rhythm (summarized by Müller 1966; see also Waters 1962 b, Lehmann 1967). A number of investigations have dealt with drift as a component of population ecology (Müller 1954 a, b, c, 1956, Waters 1962 b, 1964, 1965, 1966, Elliott 1965 a, b, 1967 a, b, Lehmann 1967, Dimond 1967, Elliott and Minshall 1968). It is mainly with this latter problem we are concerned.

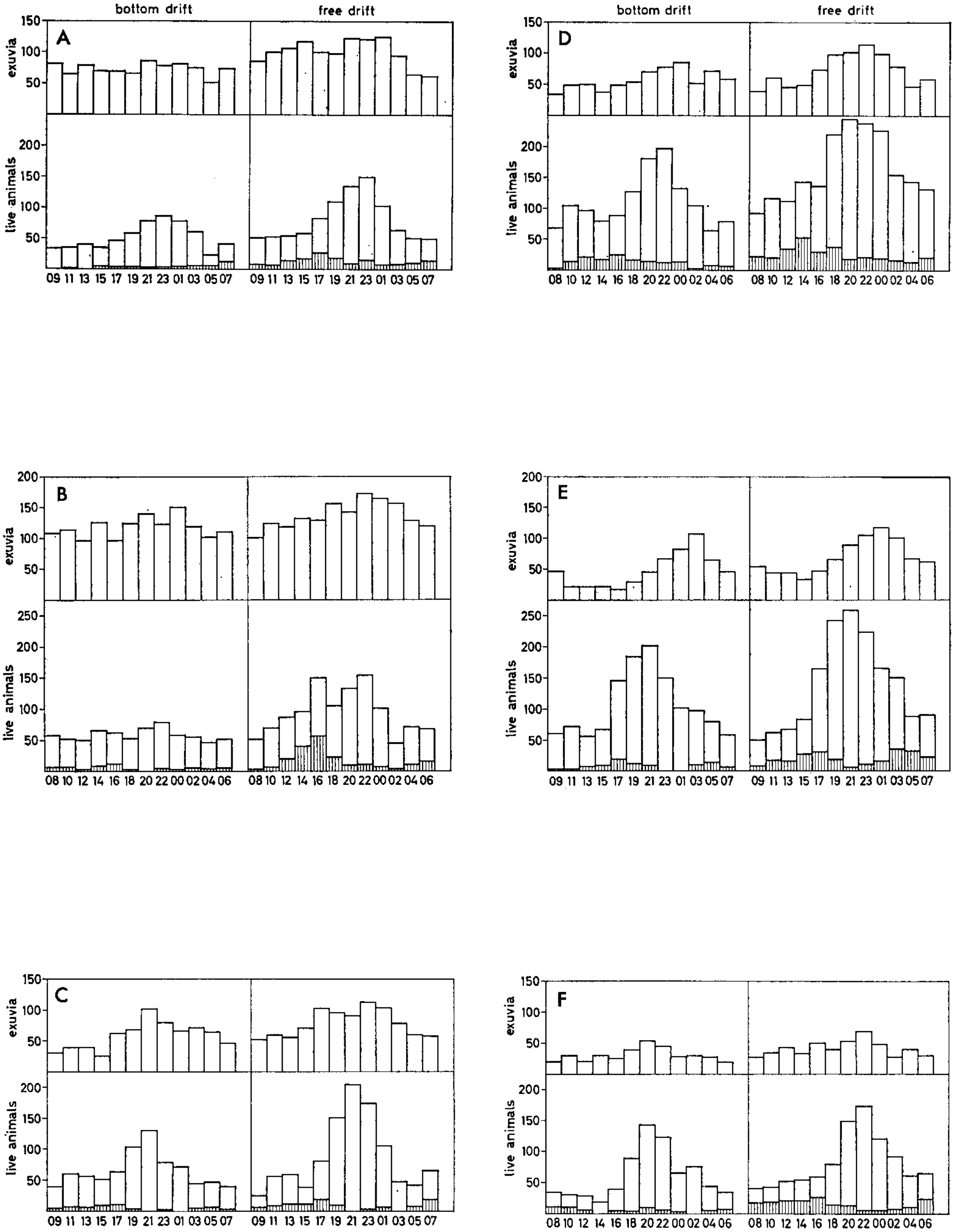

Fig. 33. Total numbers of drifting animals obtained during the first 30 min of each 2-hr period showing the circadian rhythm of the bottom and free drift of live animals and exuvia. The streaked parts indicate the proportion of imagines. Letters A to F refer to sampling series I to VI, respectively.

Tab. 34. Total number of live animals (the imagines having been subtracted) and exuvia in the nocturnal and diurnal drift, as defined in the text (§ 8.3). χ^2 values above 3.84 are significant on the <0.05 level, those above 10.83 at the <0.001 level.

	Bottom drift				Free drift			
Series	Nocturnal	Diurnal	Total	χ^2	Nocturnal	Diurnal	Total	χ^2
				Live animals				
I	382	187	569	66.02	560	247	807	120.48
II	345	294	639	3.90	547	378	925	30.48
III	742	431	1173	81.86	1102	554	1656	181.34
IV	468	259	727	59.42	728	227	955	261.50
V	831	353	1184	192.98	1088	322	1410	416.14
VI	515	147	662	204.56	624	185	809	236.84
				Exuvia				
I	457	420	877	1.64	663	536	1199	13.24
II	757	651	1408	7.98	916	719	1635	23.96
III	408	275	683	26.26	536	323	859	53.26
IV	450	248	698	58.46	587	359	946	54.96
V	345	220	565	28.04	520	301	821	58.88
VI	224	148	372	15.52	282	226	508	6.18

8.2. Methods and material

Drift was sampled using plankton bags modified to withstand the swift current of Lapland streams. They were fitted with flow-meters for the immediate reading of the amounts of water sampled. The entrance diameter was 16 cm, the bags ca 95 cm long, and mesh-size 145 µ. Samplers intended for obtaining the drift in the water near the bottom were placed on the substrate and fastened with metal rods. Drift in the upper water layers was sampled in nets tied to a rope hung over the stream.

Six series each covering 24 hr were taken at loc. N. Parallel samples in the upper and lower water layers were drawn. Henceforth these fractions will be referred to as *free* and *bottom drift*, respectively. Animals riding on the water surface were largely missed. Samples were taken during the first 30 min of each 2-hr period.

8.3. Circadian rhythm

The circadian rhythm in drift is illustrated in Fig. 33. The material deriving from the six samples was divided into live animals and exuvia; the live animals were subdivided into benthic organisms and winged insects, and these latter will not be discussed further. Free and bottom drift were kept separate.

Exuvia exhibited less pronounced circadian rhythm than live animals. The 24-hr period was divided into two parts, one from 17.00 to 04.00 hr and the other from 05.00 to 16.00 hr. The former included the hours of reduced light intensity or darkness and was considered as "night", the latter as "day". Using equal division between night and day as a null hypothesis, deviation from this was tested with χ^2 analysis, and the result is shown in Tab. 34. The difference between night and day drift was significant in all cases except for exuvia in bottom drift, series I.

The χ^2 values indicate that rhythm was more distinct in August and September than in June and July. Since the light factor has been conclusively shown to be of paramount importance for the circadian drift rhythm (Müller 1966), this is according to expectation. At the same time, the existence of a circadian rhythm around midsummer is not surprising, for even if darkness is absent at this latitude for a period around summer solstice, there is a great difference between day and night light intensity, and these differences are strengthened under the water surface. Cf. Remmert (1965) and Kureck (1966).

For live animals, χ^2 values were consistently higher in the free than in the bottom drift.

A closer analysis of circadian rhythm is

Tab. 35. Total numbers of drifting animals obtained in the bottom and free drift samplers, respectively.

	I				II				III	
	Bottom	Free	Total	χ^2	Bottom	Free	Total	χ^2	Bottom	Free
Volume sampled (m^3):	300	420			384	480			324	432
Live animals										
A. inopinatus	129	127	256	7.77	95	87	182	4.36		
B. fuscatus										
B. lapponicus									27	49
B. pumilus									39	22
B. rhodani	49	35	84	9.60	60	109	169	5.39	36	62
Baetis sp.	85	110	195	0.34	94	293	387	63.67	37	85
E. aurivillii	31	9	40	20.05						
A. borealis					42	47	89	0.18	25	23
L. fusca										
L. hippopus	33	37	70	0.94						
C. atra	23	42	65	1.01						
D. nanseni	18	16	34	1.94	17	11	28	3.64		
I. grammatica					29	32	61	0.27		
Rh. nubila										
G. intermedium										
A. stigmatella									46	80
Apatania sp.					18	7	25	7.95		
Simuliidae	31	153	184	47.26	28	48	76	1.92	253	276
Chironomidae	157	252	409	1.70	203	248	451	0.09	686	1032
Other benthic	13	26	39	0.95	53	43	96	4.22	24	27
Total	569	807	1376		639	925	1564		1173	1656
Exuvia										
Ephemeroptera	230	362	592	2.01	353	438	791	0.05	426	467
Plecoptera					16	26	42	0.86		
Trichoptera					20	26	46	0		
Simuliidae					92	104	196	0.52	91	138
Chironomidae	423	527	950	3.16	927	1041	1968	5.56	154	240
Other benthic	224	310	534	0.01					12	14
Total	877	1199	2076		1408	1635	3043		683	789

beyond the scope of this study, but it may be mentioned that differences between species were present (Waters 1962 a, Müller 1966, Anderson 1967).

8.4. Vertical distribution of drifting live animals and exuvia

In order to apply the results of the samplings to the whole water volume, possible deviations from random distribution of the drifting animals in the water have to be assessed. The animals drifting on the surface (winged insects) were not studied.

As a null hypothesis it was assumed that the numbers of animals in the bottom and free drift samplers were proportional to the water volume passing through them: a larger volume was usually filtered in the free drift sampler.

In Tab. 35 the total number of animals obtained in the two samplers are set forth. The information is condensed in Tab. 36, where all cases of significant deviations from expected distribution are listed. These made up only a minority, so that most often animals were normally scattered within the flow. *Ephemerella aurivillii* was over-represented in the bottom drift on all three occasions when it was at all numerous. All five cases of significant deviation concerning exuvia revealed a

Significant deviations from expected distribution between the two drift fractions are listed in Tab. 36.

		IV				V				VI			
Total	χ^2	Bottom	Free	Total	χ^2	Bottom	Free	Total	χ^2	Bottom	Free	Total	χ^2
		216	288			240	336			240	324		
		52	95	147	1.39	149	210	359	0.01	49	96	145	2.85
76	1.93												
61	11.33												
98	1.50					54	57	111	2.37	87	74	161	11.32
122	7.54	83	134	217	0.30	143	134	277	11.66	54	67	121	0.86
						133	143	276	4.83	82	67	149	12.24
48	1.35												
		129	123	252	12.95	96	115	211	1.25				
		99	150	249	0.02	151	181	332	2.09	106	84	190	17.05
										43	62	105	0
		15	14	29	1.28					70	111	181	0.37
										22	49	71	2.86
126	2.08	32	39	71	0.94	46	71	117	0.31				
529	5.22	136	160	296	4.57	67	99	166	0.10				
1718	5.95	114	171	285	0	330	385	715	5.90	128	162	290	1.43
51	3.20	67	69	136	5.19	15	15	30	0.53	21	37	58	0.64
2829		727	955	1682		1184	1410	2594		662	809	1471	
893	8.46	226	295	521	2.60	99	171	270	2.97	128	186	314	0
229	0.87	224	249	453	4.86	25	30	55	0.30				
394	2.33	223	381	604	2.49	428	598	1026	0	160	263	423	1.66
26	0.16	25	21	46	4.47	15	22	37	0	84	59	143	19.60
1472		698	946	1644		565	821	1386		372	508	880	

certain over-representation in the bottom drift. Evidently exuvia were drifting entirely passively, and their distribution may be taken as an indication of how passively drifting small objects with a specific gravity near 1 would behave in the flow. This implies that over-representation in the free drift sampler would indicate some sort of "activity" on the part of the drifters, and this fits in with the finding (§ 8.3) that free drift was more rhythmic than bottom drift. On the other hand, it is difficult to see how blackfly and midge larvae could influence their course in the stream; but the mucous threads trailing behind blackfly larvae might confer special properties to these animals.

8.5. Quantities of drifting animals

8.5.1. Calculation of flow volumes in different water layers

Since certain differences between the free and bottom drift fractions were found, it was necessary to take account of this in the calculation of the total drift.

The bottom drift sampler was assumed to yield a representative sample for the lowermost 20 cm of water, and the free drift sampler for the rest of the flow. Total flow on the sampling days could be computed on the basis of measurements carried out by Kungl. Vattenfallsstyrelsen (in litt.).

Since the two samplers were identical, the differences between the water volumes sampled

Tab. 36. Significant deviations from expected distribution in bottom and free drift fractions. Roman numerals refer to sampling series. Asterisks show conventional probability levels.

Live animals	More in bottom drift	More in free drift
Live animals		
A. inopinatus	I**	II*
B. pumilus	III***	
B. rhodani	I** VI***	II*
Baetis sp.	V***	II*** III***
E. aurivillii	I*** V* VI***	
L. fusca	IV***	
D. nanseni	VI***	
Apatania sp.	II**	
Simuliidae	III* IV*	I***
Chironomidae	V***	III*
"Other benthic"	II* IV*	
Exuvia		
Ephemeroptera	III**	
Simuliidae	IV*	
Chironomidae	II*	
"Other benthic"	IV* VI***	

by each were due mainly to differences in current speed of the different water layers. The ratio between the volumes was therefore taken as reflecting the ratio between the current speeds.

It was furthermore necessary to estimate how much of the total flow passed in the upper and how much in the lower layers, the limit being put at 20 cm above the bottom. This was calculated geometrically, assuming that the cross-section of the stream was triangular. Width and largest depth were known, and hence the area of the cross-section of the entire flow and of the flow of the upper layers could be calculated; by subtraction that of the lower layer was obtained. In fact the cross-section of the stream was nearly triangular at the sampling site (loc. N). The results of these calculations are given in Tab. 37.

8.5.2. Calculation of the density of drifting animals and exuvia and their total numbers

In Tab. 38 the density of drifting animals and exuvia in the upper and lower water layers is shown. As is seen in the bottom rows, the differences in animal density were comparatively small between sampling occasions, when all systematic groups were combined, a partial exception being series V. The density of live animals varied between 190 and 493 and that of exuvia between 155 and 367 per 100 m^3.

On the basis of these figures total drift per 24-hr period may be estimated (Tab. 39). The result will be related to the corresponding benthic populations in § 8.9.

There were obviously large differences between species in drifting frequency. Some abundant species took practically no part at all on the sampling occasions, e.g. *Heptagenia sulphurea* and *H. dalecarlica*, *Baetis subalpinus* and *Potamophylax stellatus*. The few *Glossosoma intermedium* larvae found in the drift were usually without their cases as was found also by Waters (1962 b); a larger proportion of the *Apatania* larvae were in cases.

8.6. Relationship between total flow and total drift

Elliott (1967 b) established that drift quantity rose with flow volume, and this was confirmed

Tab. 37. Flow volumes of the different water layers in Tjulån as defined and calculated in § 8.5.1.

Series	Date	Total flow 10^6 m^3/24 hr	Ratio current speed bottom: free	Ratio section area bottom: free	Flow (10^6 m^3/24 hr) bottom	free
I	28–29/5	3.8	5:7	6:19	0.7	3.1
II	15–16/6	4.8	4:5	1:4	0.8	4.0
III	14–15/7	2.2	3:4	29:71	0.5	1.7
IV	27–28/7	1.4	3:4	31:69	0.35	1.05
V	15–16/8	0.6	5:7	17:33	0.15	0.45
VI	11–12/9	1.5	20:27	3:7	0.4	1.1

Tab. 38. Density of drifting live animals and exuvia in Tjulån expressed as ind/100 m³. Values are averages for an entire 24-hr period. In the lowermost rows also scarcer species and higher taxa are included.

	I		II		III		IV		V		VI	
	Bottom	Free	Bottom	Free	Bottom	Free	Bottom	Free	Bottom	Free	Bottom	Free
Live animals												
A. inopinatus	43	30	25	18								
B. fuscatus							24	33	62	62	20	30
B. lapponicus					8	11						
B. pumilus					12	5						
B. rhodani	16	8	16	23	11	14			22	17	36	23
Baetis sp.	28	26	24	61	12	20	38	47	60	40	22	21
E. aurivillii	10	2							55	43	34	21
A. borealis			11	10	8	5						
L. fusca							60	43	40	34		
L. hippopus	11	9										
D. nanseni	6	4	4	2			46	52	63	54	44	26
I. grammatica											18	19
Rh. nubila							7	5			29	34
A. stigmatella					14	19	15	14	19	21		
Apatania sp.			5	1								
Simuliidae	10	36	7	10	78	64	63	56	28	29		
Chironomidae	52	60	53	52	212	239	53	59	137	115	53	50
Exuvia												
Ephemeroptera	77	86	92	99	131	108	105	102	41	51	53	57
Plecoptera			4	5								
Trichoptera			5	5								
Simuliidae			24	22	28	32	104	86	10	9		
Chironomidae	141	125	241	217	48	56	103	132	178	178	67	81
Total live	190	192	166	193	362	383	337	332	493	420	276	250
Total exuvia	292	285	367	341	211	183	323	328	235	244	155	157

in the present material (Fig. 34). The correlation was quite close for both live animals and exuvia, although one value referring to the former category fell outside the pattern. The regression line was steeper for the exuvia than for the live animals. The relationship was not linear under conditions of very low flow.

8.7. Size distribution of drifting animals compared with benthic populations

8.7.1. Introductory remarks and methods

The composition of the drifting fraction has on several occasions been found to differ from that of the benthic population in terms

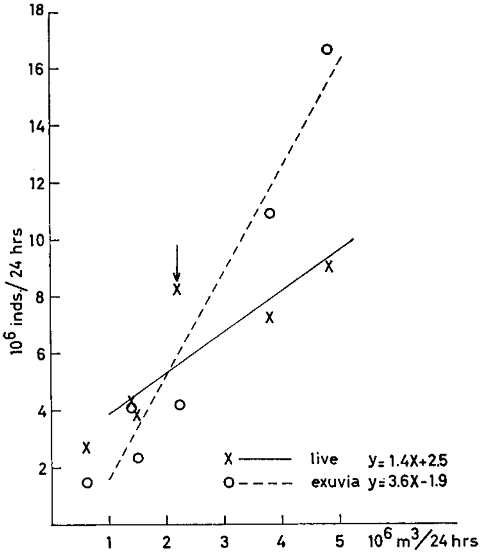

Fig. 34. Total drift per 24 hr of live animals and exuvia, respectively, plotted against total flow volume per 24 hr. The regression ceases to be linear at low flow volumes. The deviating value marked by an arrow was included in the equations.

Tab. 39. Total numbers of animals drifting

	I		II	
	Bottom	Free	Bottom	Free
Live animals				
A. inopinatus	301,000	930,000	200,000	720,000
B. fuscatus				
B. lapponicus				
B. pumilus				
B. rhodani	112,000	248,000	128,000	920,000
Baetis sp.	196,000	806,000	192,000	2,440,000
E. aurivillii	70,000	62,000		
A. borealis			88,000	400,000
L. fusca				
L. hippopus	77,000	279,000		
D. nanseni	42,000	124,000	32,000	80,000
I. grammatica				
Rh. nubila				
A. stigmatella				
Apatania sp.			40,000	40,000
Simuliidae	70,000	1,116,000	56,000	400,000
Chironomidae	364,000	1,860,000	424,000	2,080,000
Exuvia				
Ephemeroptera	539,000	2,666,000	736,000	3,960,000
Plecoptera			32,000	200,000
Trichoptera			40,000	200,000
Simuliidae			192,000	880,000
Chironomidae	987,000	3,875,000	1,928,000	8,680,000
Total live	1,330,000	5,952,000	1,328,000	7,720,000
	7,282,000		9,048,000	
Total exuvia	2,044,000	8,835,000	2,936,000	13,640,000
	10,879,000		16,576,000	

of age classes, sex, pathological conditions, etc. (Müller 1966, Lehmann 1967).

It is of obvious importance for the interpretation of drift to know whether a whole population is uniformly affected, or whether certain parts are particularly involved. As pointed out above, the drift samples would include anything down to newly hatched organisms. A larger proportion of small nymphs/larvae in the drift than in the benthos cannot be taken to show that small larvae drift in higher frequency than the older stages. Conversely similar size distribution in the drift and benthic samples does not prove that the latter were accurate, although it may suggest that this is so.

A large material of nymphs and larvae were studied to assess the life cycles of the main benthic species (Ulfstrand 1968). Additional measurements were carried out to supplement those results. The absolute values have little interest in the present context where we are mainly interested in tracing possible differences.

Drift samples were compared with the benthic samples nearest in time. Since there were no benthic samples from a time close to drift series II and IV, these are omitted. Benthic samples from locs. B and N were used; drift samples were from the latter site.

8.7.2. Specific comparisons

The relevant information is condensed in Tab. 40. In 14 out of 19 comparisons, there was no statistically significant difference between the size distribution in the drift and benthic samples.

In *Ameletus inopinatus* and *Baetis fuscatus* past the sampling point in Tjulån per 24 hr.

III		IV		V		VI	
Bottom	Free	Bottom	Free	Bottom	Free	Bottom	Free
		55,200	346,500	93,000	279,000	80,000	330,000
40,000	187,000						
60,000	85,000						
55,000	238,000			33,000	76,500	144,000	253,000
60,000	340,000	87,400	493,500	90,000	180,000	88,000	231,000
				82,500	193,500	136,000	231,000
40,000	85,000						
		138,000	451,500	60,000	153,000		
		105,800	546,000	94,500	243,000	176,000	286,000
						72,000	209,000
		16,100	52,500			116,000	374,000
70,000	323,000	34,500	147,000	28,500	94,500		
390,000	1,088,000	144,900	588,000	42,000	130,500		
1,060,000	4,063,000	121,900	619,500	205,500	517,500	212,000	550,000
655,000	1,836,000	241,500	1,071,000	61,500	229,500	212,000	627,000
140,000	544,000	239,500	903,000	15,000	40,500		
240,000	952,000	236,900	1,386,000	267,000	801,000	268,000	891,000
1,810,000	6,511,000	775,100	3,486,000	739,500	1,890,000	1,104,000	2,750,000
8,321,000		4,261,100		2,629,500		3,854,000	
1,055,000	3,111,000	742,900	3,444,000	352,500	1,098,000	620,000	1,727,000
4,166,000		4,186,900		1,450,500		2,347,000	

the largest nymphs (of 10 and 7 to 8 mm size, respectively) were over-represented in comparison with slightly smaller nymphs.

In *Ephemerella aurivillii* and *Diura nanseni* (two cases) the smallest size classes were strongly over-represented in the drift, showing that these had been, as suspected, missed in the benthic sampling.

It seems extremely unlikely that the differences found in *A. inopinatus* and *B. fuscatus* were due to defective benthic sampling. Instead, it is probable that the largest nymphs approaching emergence were more frequently taking part in drift than those having a longer time left in the benthic environment. Increasing drift rates before emergence have been found in various mayfly species by Macan (1957 a), Waters (1965) and Müller (1966).

The numerous cases of agreement between drift and benthic samples suggest that the benthic samples were representative of the benthic populations except in periods when very small nymphs/larvae were present in large numbers.

8.8. Proportion of resident benthic populations participating in drift

Here the drift density (Tab. 38) is related to the population density on the bottom of the species concerned (Tab. 33). For an estimate of the latter parameter average values from locs. B and N were used. To transform the data on drift density per unit volume to drift density per unit area an estimate of river depth had to be made. Errors in this estimate can only marginally influence the result. The

Tab. 40. Size distribution of the animals obtained in the drift samples compared with that of the benthic population in Tjulån. Asterisks denote conventional probability levels.

	series	Drift n	Benthos n	χ^2	df	P
A. inopinatus	I	386	176	14.53	5	<0.01**
B. fuscatus	V	398	211	18.86	5	<0.01**
	VI	312	151	5.15	3	>0.10
B. pumilus	III	143	101	1.27	4	>0.80
B. rhodani	I	120	70	8.20	5	>0.10
	III	81	89	2.85	4	>0.50
	V	197	57	3.78	3	>0.20
	VI	80	80	1.97	3	>0.50
E. aurivillii	I	105	93	4.11	2	>0.10
	V	245	41	51.81	3	<0.001***
	VI	213	154	4.80	3	>0.10
A. borealis	III	71	61	7.28	3	>0.05
L. fusca	V	134	59	1.63	3	>0.50
D. nanseni	I	212	69	0.62	3	>0.80
	V	218	118	139.66	4	<0.001***
	VI	102	139	19.46	4	<0.001***
Rh. nubila	VI	72	37	7.36	5	>0.10
A. stigmatella	III	62	43	0.52	4	>0.95
	V	79	50	0.29	3	>0.95

number of drifting animals was taken as the average between the free and bottom drift densities. Cases where unsatisfactory benthic sampling was disclosed in the preceeding section are omitted, so that 16 cases remain.

From Tab. 41 it can be seen that the fraction of the benthic populations taking part in the drift at any given moment was in the order of 0.05%. Three values were somewhat different, viz. for *Leuctra fusca*, *Apatania stigmatella* and *Rhyacophila nubila*, and one deviated more strongly, viz. for *Baetis rhodani*.

The only comparable calculations seem to be those by Elliott (1965 a, 1967 b). In the earlier publication based on an investigation of a Norwegian mountain stream, Elliott found a percentage of the same order as the one I have found, but in his later paper dealing with an English stream, it was about 50 times lower. Further studies will show whether regional differences occur that might explain this discrepancy (cf. Bailey 1966).

8.9. Total drift and total benthic populations

The significance of drift cannot be judged from values such as those presented in the preceeding section, where the time dimension is ignored. It is more pertinent to compare the total drift quantity past a given point with the total benthic populations occurring upstream of the sampling site. The total numbers of animals drifting past loc. N per 24 hr was shown in Tab. 39.

In order to obtain a rough estimate of the total populations resident in Tjulån (above loc. N) the population density figures of Tab. 33 may be used (averages from locs. B and N). The question then arises: For how large areas of bottom can these samples be regarded as representative?

A large part of Tjulån is distinctly uniform. Current is fast, and there are virtually no pools of stagnant water. Variability within locs. B and N apparently represents a large part of the variability of the river as a whole. However, about 8 km upstream from loc. N, the character of the river changes abruptly, and above this point there are very few places where the animals occurring in the drift can derive from. This is known from some samples taken within this river stretch in 1962 (loc. C). An exception may be the blackfly aggregation at the lake outlet (loc. A) from

Tab. 41. Calculation of the proportion of the benthic populations participating in the drift movement at any given moment. The result is an average for a whole 24-hr period.

	Series	Drift ind/100 m^3	Average water depth m	A drift, ind/m^2 bottom area	B population density ind/m^2	$\frac{A}{B} \cdot 100$ %
A inopinatus	I	36.5	0.5	0.18	435[1]	0.041
B. fuscatus	V . . .	62	0.25	0.16	370	0.043
	VI. . .	25	0.35	0.09	150	0.060
B. pumilus	III . .	8.5	0.4	0.03	47	0.064
B. rhodani	I	12	0.5	0.06	242	0.025
	III . .	12.5	0.4	0.05	506	0.010
	V . . .	19.5	0.25	0.05	61	0.082
	VI. . .	29.5	0.35	0.10	29	0.345
E. aurivillii	I	6	0.5	0.03	57	0.053
	VI. . .	27.5	0.35	0.10	189	0.053
A. borealis	III . .	6.5	0.4	0.03	78	0.038
L. fusca	V . . .	37	0.25	0.09	72	0.125
D. nanseni	I	5	0.5	0.03	47	0.064
Rh. nubila	VI. . .	31.5	0.35	0.11	64	0.172
A. stigmatella	III . .	16.5	0.4	0.07	147	0.048
	V . . .	20	0.25	0.05	29	0.172

[1] Based on sampling only at loc. N.

which a portion of the drifting larvae obtained at loc. N might derive. But the first 8 km, where the overwhelming majority of the populations involved reside, are fairly uniform.

Although, as mentioned in § 6.3, there was a considerable difference between the conditions in mid-stream (where *Didymosphenia geminata* was abundant) and along the shorelines at loc. A, this was much less pronounced further downstream in the stretch with which we are concerned here. *D. geminata* occurred

Tab. 42. Total numbers of animals drifting past the sampling point in relation to total benthic populations in Tjulån.

	Series	Width of river m	Total bottom area m^2	Population density ind/m^2	A Total resident population 10^6 ind	B Total drift per 24 hrs. 10^6 ind	$\frac{B}{A} \cdot 100$ %
B. fuscatus	V . . .	15	120,000	370	44.4	0.37	0.83
	VI. . .	18	144,000	150	21.6	0.41	1.90
B. pumilus	III . .	20	160,000	47	7.5	0.145	1.93
B. rhodani	I	25	200,000	242	48.4	0.36	0.74
	III . .	20	160,000	506	81.0	0.29	0.36
	V . . .	15	120,000	61	7.3	0.11	1.51
E. aurivillii	I	25	200,000	57	11.4	0.13	1.14
	VI. . .	18	144,000	189	27.2	0.37	1.36
A. borealis	III . .	20	160,000	78	12.5	0.125	1.00
L. fusca	V . . .	15	120,000	72	8.6	0.21	2.44
D. nanseni	I	25	200,000	47	9.4	0.17	1.81
Rh. nubila	VI. . .	18	144,000	64	9.2	0.49	5.33
A. stigmatella	III . .	20	160,000	147	23.5	0.39	1.66
	V . . .	15	120,000	29	3.5	0.12	3.43

in scattered tufts in all depth conditions in this lower part of the river. Therefore it seems justified to regard the benthic samples as representative for the whole river breadth, including the (proportionately small) zone of water too deep for sampling.

Thus, the samples from locs. B and N will be accepted as representative of the species composition and population density in the whole Tjulån up to a point 8 km above the drift sampling point (loc. N).

Of the original 19 cases, three were omitted earlier because of apparently unpresentative benthic sampling. *Ameletus inopinatus* also has to be omitted from the present discussion as its distribution was particularly uneven and could not be determined solely on the basis of the benthic samples from locs. B and N. Moreover, the ratio between drifting *Baetis rhodani* in series VI and the corresponding population density indicates that the latter was not adequately assessed. Thus 14 cases remain for the present purpose.

Total drift quantities and corresponding estimates of total upstream benthic populations and the ratio between these values are shown in Tab. 42. In eight out of the 14 cases the proportion of the benthic population drifting past the sampling point was between 1 and 2%; three were lower than 1% and three higher than 2%. The concentration of values to between 1 and 2% indicates this to be the most typical situation under conditions prevailing. Since the benthic samples were under- rather than over-estimates, the percentages are on the whole probably on the high side.

This fraction represents a definite loss to the populations, as some 100 m downstream from loc. N the river enters the delta in the lake Gautsträsk and an almost total mortality of the drifting animals must be expected in that unsuitable environment (Dendy 1944).

8.10. Population decrease at varying emigration rates

In Fig. 35 the effect on a population of a daily emigration amounting to 0.5, 1, 2 and 4% is examined. At an emigration rate of 1% per day, about $^2/_3$ of the population still remain after 50 days, and at 2% almost half the population. This covers most or the whole of the nymphal period in many benthic species, e.g. *Baetis* spp., let alone the much shorter periods of intense growth and drift. For species which spend long periods as relatively large nymphs/larvae, such as *Ephemerella aurivillii*, *Diura nanseni* and *Rhyacophila nubila*, it has to be assumed that any one population does not participate in drift to any extent for more than part of its total life cycle; this is borne out by the scarcity of these species in several of the sampling series (Tab. 39).

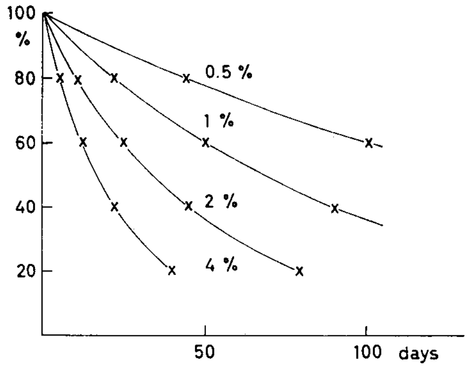

Fig. 35. The process of population decrease at varying daily loss rates.

There are factors operating to compensate for the losses. A certain upstream movement may be of importance for nymphal/larval populations of more agile species; in many animals without a winged stage considerable upstream movements have been found (Steinmann 1913, Lehmann 1967). It may be doubted, however, if such movements have a particularly great significance under the special environmental conditions in a large torrential stream. Further, the estimates of emigration percentage were probably somewhat too high. But it is evident that populations undergoing reduction of this magnitude will have to adopt some effective means of upstream movements in some life stage, as found in many stream-dwelling insects (cf. § 11).

9. Colonization of implanted trays

9.1. Introduction

Many standing crop changes were found to be due to population movements (§ 7.3). In § 8 the motility of many benthic populations was further discussed. A small part of the drifting animals are transported out from the river and perish in the downstream lake, others are destroyed in violent collisions with the bottom, or are eaten by fishes etc. But most individuals evidently return safely to the bottom (cf. § 11). Several questions arise in this context: To what extent are the animals capable of choosing their new place of residence, and what factors influence their choice? How fast does colonization of an implanted substrate proceed? In other words: How soon do immigration into and emigration out of such a new place come into balance? It was further desirable to check previous findings on micro-habitat preference in certain species (Ulfstrand 1967). Hence a number of field experiments were conducted to analyze these problems.

9.2. Methods

The technique of implanting artificial bottoms in a river or a lake (§ 5.3) was first employed by Moon (1940) and Wene and Wickliff (1940). In the present study wooden trays of dimensions 96 × 58 cm and with rims 8 cm high were covered on their inner sides with a cloth having ca 20 meshes/cm. The cloth swelled slightly in water, so that after a couple of hours' submersion water poured through it only slowly. Even tiny mayfly and stonefly nymphs were unable to get through. The wooden bottom had several holes to facilitate draining when the tray was lifted out off the water. The substrate (see below) and the cloth were carefully searched for macroscopic animals, after the trays had been drained and carried to the shore. Other animals than mayflies, stoneflies and caddisflies were ignored in these studies.

When not otherwise stated, the substrate placed in the trays consisted of stones from the surrounding river bottom that had been rinsed from macroscopic animals. Tufts of vegetation were removed, if present. The standard area of the stones was measured as described in § 5.2. Their total standard area was permitted to vary between 2,200 and 2,900 cm^2 per tray. It was examined whether differences of standard area within this range had any effect on the number of animals settling in the trays. The correlation coefficient was, however, -0.04 for mayflies and $+0.16$ for stoneflies which was far from significant ($P > 0.8$ and $P > 0.2$, respectively). Therefore, the standard area of the substrate was considered to be a constant.

The trays were placed on stones on the bottom. Because of their high rims, animals could enter the trays only by swimming and drifting. The trays were tilted slightly towards the current to improve the stability.

All figures indicate number of individuals per tray.

9.3. Circadian rhythm

As colonization was assumed to be connected with drift and as this phenomenon shows a circadian rhythm, it was an expected result that colonization was also rhythmical (Tab. 43).

Eight or six trays were exposed on the river bed, their animal colonizers being collected each morning and evening. The differences between diurnal and nocturnal (§ 8.3) colonization were tested by χ^2 analysis.

The first series did not reveal any rhythm, but in the two later series rhythm was pronounced. Two species, viz. *Baetis pumilus* and *Capnia* sp., however rather scarce, had no rhythm in any series. The general absence of rhythm in the first series is explained by the fact that the former species made up a considerable proportion of the colonization on that occasion.

Tab. 43. The colonization of experimental trays placed on the bottom of Tjulån, divided on the night (approx. between 18 and 07 hr) and the day (between 07 and 18 hr).
n = night, d = day.

Locality	N				B						N			
Period	29–31/7 1965				14–17/8 1965						20–22/8 1964			
Exposure	n	d	n	d	n	d	n	d	n	d	n	d	n	d
Number of trays	8	8	8	8	8	8	8	8	8	8	6	6	6	6
A. inopinatus	–	–	–	–	–	–	–	–	–	–	1	–	–	1
B. fuscatus	3	6	6	5	117	60	158	88	132	68	117	61	151	65
B. lapponicus	–	–	–	3	2	2	3	–	1	–	–	–	–	–
B. pumilus	10	15	17	14	3	–	6	3	2	3	3	27	18	10
B. rhodani	2	1	5	4	5	4	9	6	9	4	18	2	58	9
B. subalpinus	–	–	–	–	–	1	3	3	2	–	–	–	–	3
Baetis sp.	–	1	–	2	3	1	8	1	11	–	70	30	64	60
Ecd. joernensis	–	–	–	–	–	–	–	–	–	–	–	–	1	–
H. dalecarlica	–	–	–	–	1	–	–	–	–	–	–	1	2	1
E. aurivillii	1	–	–	–	4	3	9	1	13	1	58	33	55	47
Total Ephemeroptera	16	23	28	28	135	71	196	102	170	76	267	154	349	196
	$\chi^2 = 0.52$ P$\sim$0.50					$\chi^2 = 84.7$		P < 0.001			$\chi^2 = 73.2$		P < 0.001	
T. nebulosa	–	–	–	–	–	–	–	1	–	1	3	1	1	–
A. standfussi	–	1	–	1	–	–	–	–	–	–	2	1	–	–
L. fusca	7	4	17	3	6	1	6	–	2	1	6	4	16	7
Capnia sp.	–	–	–	–	–	–	–	–	1	–	2	5	3	11
D. nanseni	–	1	2	2	6	4	13	1	13	1	60	30	49	29
Total Plecoptera	7	6	19	6	12	5	19	2	16	3	73	41	69	48
	$\chi^2 = 2.58$ P$\sim$0.10					$\chi^2 = 23.2$		P < 0.001			$\chi^2 = 12.7$		P < 0.001	
Rh. nubila	1	–	–	–	–	–	–	–	–	–	5	–	11	6
P. flavomaculatus	–	–	–	–	–	–	–	–	–	–	3	–	3	4
A. stigmatella	2	8	–	2	–	–	–	–	–	–	–	–	3	1
Total Trichoptera	3	8	0	2	0	0	0	0	0	0	8	0	17	11
Grand total	26	37	47	36	147	76	215	104	186	79	348	195	435	255

9.4. Rate of colonization and flow volume

As was seen in § 8.6, total drift was proportional to total flow. Here the daily rate of colonization is related to fluctuations in flow.

For this purpose eight trays were placed in a rapidly flowing part of the river, and their animal colonizers collected each morning for 18 consecutive days. Both depth and current increased at rising flow, and vice versa.

A close correlation was found between flow volume and colonization rate of mayflies and stoneflies: for mayflies, $r = +0.32$, $f = 16$, $t = 8.76$, $P < 0.001$; for stoneflies, $r = +0.74$, $f = 16$, $t = 23.22$, $P < 0.001$ (Tab. 44, Fig. 36).

From Fig. 36 it is seen that colonization was largest shortly after peak flow, when the water was beginning to recede. This indicates that the strength of the current was not the sole factor initiating the drift. Rather it may be suggested that increased activity as a consequence of receding water level gives rise to drifting in certain species.

9.5. Field experiments on colonization under different environmental conditions

9.5.1. Current

Three series of experiments were carried out to examine the influence of current on the specific composition of the colonization. In such cases, trays have to be exposed for so long that the animals have the opportunity to react to prevailing conditions. Animals evidently may happen to settle in unsuitable

Tab. 44. The daily colonization of eight experimental trays placed on the bottom of Tjulån, August to September, 1964. The trays were removed each morning, the animals collected and the trays replaced in the river.

	August															September		
Date	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3
B. fuscatus	33	43	20	37	59	69	78	71	99	28	50	121	90	20	29	46	77	72
B. lapponicus	6	–	4	10	4	–	1	18	17	7	14	18	10	1	–	1	13	12
B. pumilus	3	5	2	3	–	1	1	13	27	5	29	19	5	–	4	1	9	17
B. rhodani	9	6	12	12	6	8	13	29	48	11	46	54	47	33	29	66	89	119
B. subalpinus	1	–	–	2	–	–	–	–	2	–	1	–	4	4	5	5	8	3
Baetis sp.	7	9	12	11	4	8	10	10	13	17	18	26	21	31	19	42	79	102
E. aurivillii	4	9	11	5	4	9	10	6	7	11	13	13	6	2	9	11	14	12
Other Ephemeroptera	3	–	3	5	–	1	–	–	–	4	–	–	3	2	1	–	1	4
Total	66	72	64	85	77	96	113	147	213	83	171	251	186	93	95	172	290	341
T. nebulosa	–	–	–	–	–	–	1	–	–	6	3	2	–	9	12	3	3	4
L. fusca	5	10	9	3	4	7	5	16	10	–	18	21	8	5	7	9	18	16
Capnia sp.	–	–	–	–	5	13	19	14	7	2	18	10	4	29	28	20	14	10
D. nanseni	1	3	2	2	4	6	–	11	17	5	17	25	10	12	9	39	57	51
Other Plecoptera	1	–	–	2	–	–	–	–	2	–	–	–	1	–	–	–	–	–
Total	7	13	11	7	13	26	25	41	36	13	56	58	23	55	56	71	92	81
Trichoptera	4	12	7	5	4	10	8	3	8	13	7	7	6	13	5	3	4	7
Grand total	77	97	82	97	94	132	146	191	257	109	234	316	215	161	156	246	386	429

microbiotopes and will probably depart at an early opportunity. After some days, therefore, the proportion of accidental settlers in a tray will probably decrease.

Since the number of animals passing over a given bottom area is proportional to flow volume (and this is proportional to the current speed, if depth is constant), many more animals have an opportunity to settle in a tray exposed to fast current than in one over which the water flows more slowly, regardless of their preferences.

As a null hypothesis it was therefore assumed that the ratio between the numbers of animals in different sets of trays would be the same as the ratio between current speeds over the respective trays. If a species prefers fast current, it would be found in larger numbers than expected in trays with a fast current and in lower numbers in trays with a slow current. The significance of such deviations was examined by means of χ^2 tests.

In these experiments eight trays were placed in each of two or three current classes. The trays were invariably placed at a depth of ca 25 cm, and the current speed was measured over each tray at a depth of ca 10 cm. Ve-

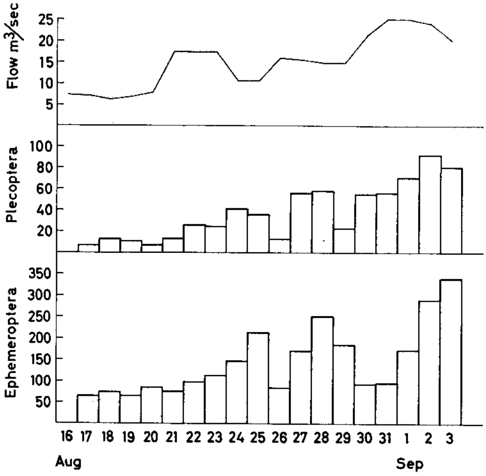

Fig. 36. Daily colonization of eight experimental trays placed on the river bottom in relation to flow volume in m^3/sec.

Tab. 45. The colonization of experimental trays exposed to different current conditions in Tjulån. Asterisks denote conventional probability levels.

Period	14–20/7 1965			15–21/8 1965				13–20/8 1965			
Current cm/sec...	120	42		108	51	12		102	48	10	
Rel. current speed	2.85:1		χ^2	9:4.25:1			χ^2	10.2:4.8:1			χ^2
B. fuscatus	28	7	0.59	156	70	11	2.37	238	66	7	23.50***
B. lapponicus	36	19	2.40	–	–	–		–	–	–	
B. pumilus	29	19	5.44*	–	–	–		–	–	–	
B. rhodani	84	12	9.14**	99	32	6	5.24	106	53	20	7.94*
B. subalpinus	–	–		28	45	36	100.72***	68	59	41	97.65***
Baetis sp.	49	28	4.32*	47	37	42	134.64***	21	33	25	100.20***
H. dalecarlica ...	15	12	4.82*	–	–	–		12	10	5	3.97
E. aurivillii	59	22	0.07	69	33	12	1.49	88	52	16	5.35
A. borealis	48	16	0.08	–	–	–		–	–	–	
L. fusca	47	29	5.50*	48	58	20	36.77***	46	35	22	49.25***
D. nanseni	66	8	8.57**	79	45	5	3.12	75	20	4	6.29*
I. grammatica ...	–	–		7	17	10	28.08***	–	–	–	
Rh. nubila	37	9	1.01	41	12	2	2.83	38	8	8	1.08
A. stigmatella ...	22	17	6.59*(*)	16	16	7	7.51**	62	34	24	35.03***

locities are given as averages for measurements over all eight trays.

It is seen from Tab. 45 that certain species were randomly distributed over the two sets of trays. But many species deviated significantly from the assumption. In the first series, *Baetis rhodani* and *Diura nanseni* were more numerous in the fast current, whereas the reverse was true for *Baetis pumilus*, *Baetis* sp., *Leuctra fusca*, *Apatania stigmatella* and *Heptagenia dalecarlica*. In the second series, no species was over-represented in the swift current, while *Baetis subalpinus*, *Baetis* sp., *Leuctra fusca*, *Isoperla grammatica* and *Apatania stigmatella* were significantly over-represented in the slower current. In the third series, *Baetis fuscatus*, *B. rhodani* and *Diura nanseni* were over-represented in the fast current, while the reverse applied to *Baetis subalpinus*, *Baetis* sp., *Leuctra fusca* and *Apatania stigmatella*.

The agreement between the three series is close. No species reversed its preference, although some varied between random distribution and preference in one direction. Usually, there is also close agreement between these results and those found for the same species by a different method (Ulfstrand 1967).

Probably a great proportion of the unidentified *Baetis* sp. nymphs belonged to *B. rhodani*. This species evidently changes its preference during its development (cf. Ulfstrand op. cit.).

It is obvious from these results that current has a distinct influence on the microhabitat selection of several species. This is, however, not so say that the effect was a direct one. It may well be exerted via sedimentation conditions.

9.5.2. Water depth

In four series 8 trays were placed at different water depths under similar current conditions. Flow volume was approximately proportional to water depth in these cases, as had to be taken account of when formulating the null hypothesis. Thus, it was assumed that the number of animals in the different sets of trays would be proportional to water depth, and the significance of deviations from this assumption was examined by χ^2 tests. But in no case was there any significant deviation from expected distribution (Tab. 46). Therefore χ^2 values were omitted from the table.

Thus within the range covered by these experiments, water depth had no decisive influence on the habitat selection of the species involved.

Tab. 46. The colonization of experimental trays exposed to different water depths in Tjulån. The numbers of animals were expected to be proportional to the flow volume, in this case = the depth. No significant deviation from such a distribution was found.

Locality	N		B		B		B	
Period (1965)	18–22/7		28/7–2/8		4–10/8		6–12/8	
Depth cm	30	10	40	15	40	10	30	20
Relative depth	3:1		2.67:1		4:1		1.5:1	
Average current cm/sec	88		70		69		83	
B. fuscatus	46	18	213	72	198	38	164	112
B. lapponicus	18	8	12	7	–	–	–	–
B. pumilus	14	10	36	16	–	–	–	–
B. rhodani	28	9	58	14	88	26	106	73
B. subalpinus	–	–	14	7	20	7	22	16
Baetis sp.	98	36	196	69	94	19	86	69
H. dalecarlica	24	10	28	9	17	4	30	25
E. aurivillii	77	20	100	34	133	40	111	72
L. fusca	66	21	112	50	100	28	75	46
D. nanseni	24	7	68	19	58	18	39	25
Rh. nubila	–	–	10	6	15	5	6	6
A. stigmatella	37	16	50	28	33	13	33	23

9.5.3. Stone size

Two series were conducted using stones of different dimensions. The number of stones was very different in the different trays, from three to four in those with the biggest stones to ca 650 in those with the smallest stones. It is evident that the total stone surface area was much larger in the trays with the smaller stones. The number of animals immigrating into the different trays may be assumed to be equal, since each tray covered the same bottom area; and this assumption was used as a null hypothesis, deviations from which were examined by χ^2 analysis. All trays were placed under similar current and depth conditions.

The results show that the different size of the stones in the trays had an influence on the composition of the colonization (Tab. 47). In most cases species were over-represented in the trays with larger stones; exceptions being *Diura nanseni* and *Ephemerella aurivillii* which showed no discrimination, *Baetis subalpinus* which was indifferent in one of the series, and *Baetis* sp. which preferred the smaller stones.

If the separate χ^2 values are examined, it is found that small differences usually prevailed between the two coarsest substrate fractions and between the two smallest ones. The most important division seems to be between the two intermediate fractions. However *Baetis* sp. distinctly preferred the smallest fraction in comparison with the next smallest.

These results ought to be interpreted with some caution, because the current conditions in the trays were probably to some extent modified by the substrate; these two factors generally are difficult to separate (cf. Ulfstrand 1967 and § 4.2).

9.5.4. Periphyton supply

As was mentioned previously (Ulfstrand op. cit.) and will be further discussed in § 10, food seems to exert a strong influence on microhabitat selection (microdistribution) in many species. This was illustrated by the following experiment.

From a nearby quarry, stones of all sizes could be obtained. These had recently been blasted from the solid rock and had not yet attracted any noticeable periphytic growth. Such stones of the same general size as those usually used in these experiments were compared with stones from the river bottom covered by dense periphyton. Eight trays with stones of each kind were used.

Tab. 47. The colonization of experimental trays containing substrate of different dimension.

Average length cm	2.5	6	18	36	χ^2
Number of stones	ca 650	ca 100	10	3	
Number of trays	4	4	4	4	
Loc. N 18–23/8 1965					
B. fuscatus	19	23	88	76	20.94+16.17+24.92+11.08 = 73.11***
B. rhodani	5	9	36	40	14.09+ 8.52+ 7.35+12.57 = 42.53***
B. subalpinus	10	16	17	13	1.14+ 0.29+ 0.64+ 0.07 = 2.14
Baetis sp.	39	26	12	12	13.14+ 0.73+ 4.55+ 4.55 = 22.97***
H. dalecarlica	–	6	10	9	3.00+ 2.67+ 1.50 = 7.17*
E. aurivillii	28	24	17	21	1.09+ 0.04+ 1.57+ 0.17 = 2.87
L. fusca	–	5	31	21	18.89+20.64+ 3.50 = 43.03***
D. nanseni	8	14	19	13	2.57+ 0 + 1.79+ 0.07 = 4.43
Rh. nubila	1	2	10	16	8.64+ 1.29+11.57 = 21.50***
A. stigmatella	–	3	13	13	8.64+ 5.14+ 5.14 = 18.92***
Loc. B 17–23/8 1965					
B. fuscatus	12	44	92	80	35.53+ 2.96+21.49+ 9.28 = 69.26***
B. rhodani	6	12	38	32	11.64+ 4.55+11.64+ 4.55 = 32.38***
B. subalpinus	4	14	19	21	8.07+ 0.07+ 1.07+ 2.40 = 11.61**
Baetis sp.	29	21	13	7	6.72+ 0.50+ 1.39+ 6.72 = 15.33**
H. dalecarlica	–	–	8	8	
E. aurivillii	26	36	33	30	0.81+ 0.81+ 0.13+ 0.03 = 1.78
L. fusca	2	–	19	23	18.18+ 5.82+13.09 = 37.09***
D. nanseni	10	12	12	19	0.69+ 0.08+ 0.08+ 2.77 = 3.62
Rh. nubila	–	1	11	15	12.07+ 2.29+ 9.14 = 23.50***
A. stigmatella	–	2	11	17	12.25+ 4.50+10.13 = 26.88***

As seen in Tab. 48, *Baetis fuscatus* and *B. rhodani* showed a clear preference for the bottom stones, as was the case also in *Apatania stigmatella*. Questionable preference for the river bottom stones was shown in a few more cases, whereas many species were neutral. Probably the periphyton was important as food for the species showing preference for the bottom stones; the other species probably, under conditions prevailing, were feeding on other matter. Using a similar technique Egglishaw (1964) showed the preference for

Tab. 48. The colonization of trays containing stones from a quarry, i.e. without periphytic vegetation, and stones from the river bottom.

Locality	B			N		
	24–28/8 1964			12–17/8 1965		
Period	Stones from Quarry	Stones from River	χ^2	Stones from Quarry	Stones from River	χ^2
B. fuscatus	46	121	33.68***	23	53	11.84***
B. rhodani	18	61	23.40***	9	22	5.46*
B. subalpinus	10	17	1.82	11	20	2.62
Baetis sp.	36	46	1.25	47	37	1.20
H. dalecarlica	8	18	3.84	5	11	2.26
E. aurivillii	22	38	4.26*	20	32	2.76
L. fusca	19	34	4.24*	13	20	1.48
D. nanseni	17	19	0.12	12	13	0.04
Rh. nubila	6	7	0.08	6	4	0.40
A. stigmatella	9	21	4.80*	15	33	6.76**

Tab. 49. The colonization process in Tjulån.

			Number of animals per tray									
Period	Days	Trays	*Baetis fuscatus*	*Baetis lapponicus*	*Baetis pumilus*	*Baetis rhodani*	*Baetis* sp.	*Ephemerella aurivillii*	Ephemeroptera Total	*Leuctra fusca*	*Diura nanseni*	Plecoptera Total
Loc. N 1964 Series I												
11–12/8 ..	1	6	41	1	1	5	12	1	61	1	2	3
11–13/8 ..	2	6	67	1	–	7	17	4	96	1	5	6
11–15/8 ..	4	6	91	3	1	10	30	6	141	1	11	12
10–15/8 ..	5	6	122	–	4	6	25	13	170	2	20	22
7–15/8 ..	8	5	128	1	4	4	30	18	185	2	17	19
28/7–10/8.	13	6	154	1	7	4	15	10	191	10	24	34
28/7–15/8.	18	5	128	–	7	5	22	18	180	6	29	35
Loc. N 1965 Series II												
16–17/7 ..	1	6	–	–	2	7	–	1	10	–	–	0
15–17/7 ..	2	6	–	–	5	9	–	1	15	–	–	0
16–20/7 ..	4	5	–	2	9	12	1	5	29	1	1	2
16–22/7 ..	6	5	–	2	7	19	1	3	32	1	1	2
16–25/7 ..	9	6	1	9	6	21	4	5	46	7	3	10
15–28/7 ..	13	4	4	5	14	23	3	1	50	13	8	21
17/7–1/8..	15	6	10	9	14	29	2	–	64	10	7	17
17/7–4/8..	18	6	24	6	10	30	4	1	75	13	9	22
15/7–4/8..	20	5	22	8	12	30	4	3	79	13	12	25
Loc. B 1965 Series III												
20–21/7 ..	1	6	8	2	2	4	7	4	27	1	4	5
20–23/7 ..	3	6	19	4	3	12	16	9	63	5	13	18
20–26/7 ..	6	6	25	7	4	18	24	10	88	10	18	28
18–26/7 ..	8	6	28	9	5	20	34	9	105	12	24	36
18–29/7 ..	11	5	30	7	5	23	30	7	102	12	22	34
18–31/7 ..	13	6	25	11	5	21	37	7	106	11	17	28
18/7–2/8..	15	5	28	13	2	18	32	12	105	13	13	26
Loc. L 1964 Series IV												
4–6/9	2	5	4	–	–	10	11	5	30	1	7	8
4–8/9	4	5	5	–	–	19	13	11	48	4	13	17
1–8/9	7	5	7	–	–	24	13	18	62	3	19	22
1–10/9 ...	9	5	6	–	–	33	21	22	82	3	21	24
1–11/9 ...	10	4	2	–	1	30	17	26	76	7	20	27
30/8–11/9.	12	4	4	–	–	27	27	22	80	4	17	21
27/8–11/9.	15	5	2	–	–	25	24	20	71	2	25	27

detritus-rich substrate in certain benthic species.

9.6. The colonization process

9.6.1. Introduction

Long-term colonization experiments were difficult to conduct because of the violently fluctuating flow. Four series – many more were attempted – could be satisfactorily concluded.

Even when flow changes did not ruin the experiments, various environmental factors changed in the course of the experiments which lasted for 2 to 3 weeks. Equally important, the drifting intensity of certain populations may change during an experimental series. Thus, during series II, *Leuctra fusca* and *Baetis fuscatus* suddenly occurred in larger numbers than before.

It may be assumed that drifting animals come into contact with the experimental trays

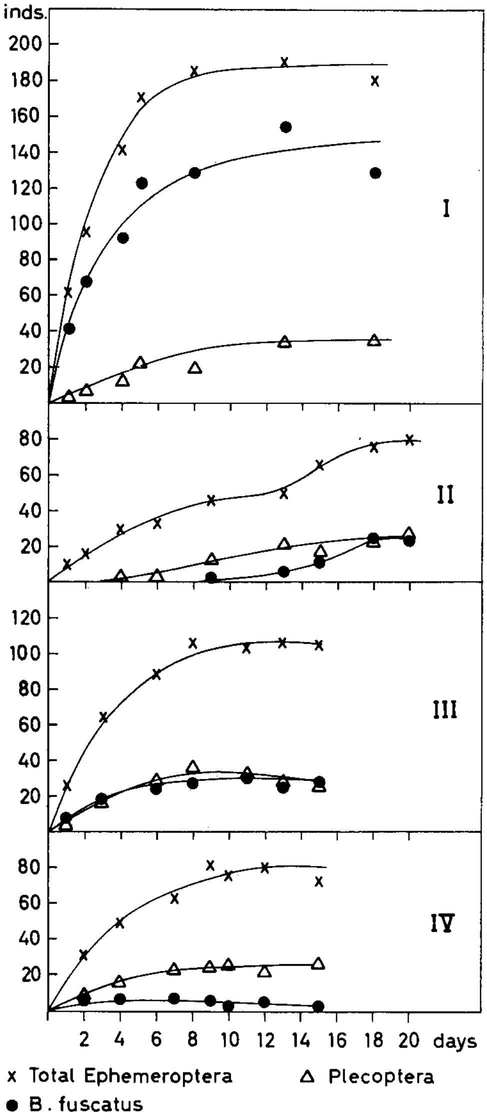

Fig. 37. The colonization process. Number of individuals per experimental tray plotted against period of exposure on the stream bottom.

in a random manner. Some settle, others continue immediately or after a period of time. Differences in environmental conditions influence the resulting composition of the colonization; some factors were discussed in § 9.5. Since the numbers of individuals in the trays stabilized after a certain time, colonization evidently is the result of two processes, viz. immigration into and emigration out of the trays, the latter process being influenced by the environmental factors prevailing in the trays.

9.6.2. Results of four colonization series

In Tab. 49 and Fig. 37, the colonization process in the four completed series is shown. Only the abundant species were taken into account. As is seen from the graphs, numbers rose at first but after a period of about 8 days, little further change occurred. The pattern is very clear in series I, III and IV and is discernible also in series II, if the sudden change in the occurrence of *Baetis fuscatus* and *Leuctra fusca* in the middle of the period is allowed for.

9.6.3. Discussion

The colonization pattern described in the previous section (Fig. 37, Tab. 49) may be interpreted as A) a density independent or B) a density dependent process.

A) *A constant rate of immigration into and a constant percentual rate of emigration out of the trays per time unit.* – It is evident that the immigration into the trays occurs in a random fashion. The consequences of constant daily percentual emigration for the colonization process were hypothetically examined by drawing curves for 5, 10, 25 and 50% daily emigration (Fig. 38). A comparison between these hypothetical curves and the empirical ones in Fig. 37 demonstrates that the best fit is with the 25% curve. A similar figure is obtained from the following consideration: After the balance has been reached, immigration and emigration are obviously compensating each other. But immigration may be assumed to occur in a constant rate. From Fig. 37 it may be seen that the first day's colonization amounted to approx. $\frac{1}{4}$ to $\frac{1}{3}$ of the final density level. The first day's colonization may be assumed to reflect the daily colonization also in the following days, and it then follows that the emigration has to be of the same magnitude, viz. $\frac{1}{4}$ to $\frac{1}{3}$ of the total colonization

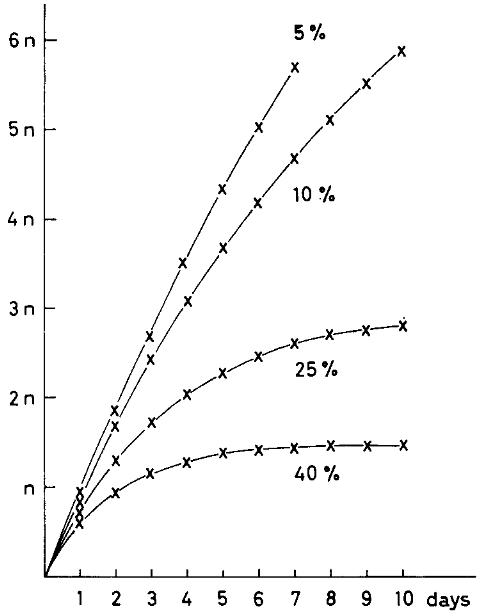

Fig. 38. Theoretical curves showing the colonization process assuming a constant number (*n*) of immigrating individuals per 24 hr period and a constant rate of emigration per 24 hr period.

present. This model presupposes that, of the animals immigrating into the trays in the first day of first few days, a great proportion stay for some time. If the rate of emigration in the first few days is high, the process would not lead to the empirically found results.

B) *A constant rate of immigration into and a density dependent rate of emigration out of the trays per time unit.* – The observed colonization process will also occur, if the percentual rate of emigration per day rises with increased colonization density. In this case, it is not possible to estimate the percentages, because the percentual emigration in the first few days may be anything from relatively low (viz. if a large proportion of the immigrating individuals remain for some time) to very high (viz. if the majority of the immigrating individuals emigrate after a very short time).

It is important to realize that the colonization process observed may be the result of density independent movements. On the data available, however, it is not possible to decide which of the two models is closest to the real conditions; they are not mutually exclusive. This question will be further discussed in § 11.

9.7. Colonization and natural bottom community

Three series of experiments were carried out to examine to what extent the composition of the colonizers differed from the natural community on the surrounding river bed. The comparison could not be quantitative, since it was impossible strictly to compare the standard area represented by the benthic sample with the area of the tray bottom and the substrate placed in the tray. Differences will therefore be shown in terms of percentual species composition.

The result is shown in Tab. 50 from which all scarce species have been omitted. In series I, agreement between the natural community and the colonization was comparatively close, except for *Ephemerella aurivillii.* In the other two series, there were large differences. In both cases, *Baetis fuscatus* was more abundant in the natural community than in the trays, while the opposite was true for *B. lapponicus.* The relative frequencies of *Leuctra fusca* and *Diura nanseni* were reversed in the two samples.

The trays were exposed for six days, that is, for such a period that the colonization had reached, or was near, the stable phase (cf. § 9.6).

The considerable differences between the colonization and the natural bottom community indicate that the trays represented a rather unusual configuration of factors, although each separate factor was within the range of naturally occurring variability. The results support the view that experimental trays implanted on the river bottom provide only an approximate picture of the qualitative and quantitative composition of the natural benthic community. This of course does not detract from the usefulness of the technique in the study of population movements, habitat preferences, etc.

Tab. 50. Comparison between the natural bottom community in Tjulån and the composition of the colonization in four trays (series I, II, and III) exposed on the river bottom.

	Loc. N				Loc. N				Loc. B			
	Ser. I		Benthos		Ser. II		Benthos		Ser. III		Benthos	
	Ind.	%	Ind.	%	Ind.	%	Ind.	%	Ind.	%	Ind.	%
B. fuscatus ..	128	71	242	63	22	28	200	63	28	27	233	57
B. lapponicus	–	–	4	1	8	10	5	2	13	12	3	1
B. pumilus ..	7	4	30	8	12	15	5	2	2	2	17	4
B. rhodani ..	5	3	37	10	30	38	48	15	18	17	61	15
Baetis sp....	22	12	66	17	4	5	33	10	32	30	79	19
E. aurivillii..	18	10	8	2	3	4	24	8	12	11	16	4
	180		387		79		315		105		409	
L. fusca	6	17	29	14	13	52	20	12	13	50	44	26
D. nanseni..	29	83	173	86	12	48	153	88	13	50	128	74
	35		202		25		173		26		172	

9.8. Decolonization as a response to changed environmental conditions

In northern Scandinavian rivers, flow fluctuations are very common and violent, even from day to day (cf. Figs. 8 and 36), exposing the benthic populations to obvious dangers. One is the possibility of being swept away by a spate. Under such circumstances, a great many animals will probably be transported out of their suitable environments and perish. An equally great danger is that of being stranded by the receding water. Any reaction reducing this risk would confer a selective advantage on its possessor.

Four experimental series were carried out to simulate the conditions in rapidly receding water. Eighteen trays in each series were placed on the river floor as described above and exposed to colonization under favourable conditions for seven days. After this time six of the trays were dragged slowly and carefully over the bottom into shallower and slower-flowing water, 5 to 10 m from the original position. Another group of six trays were dragged about the same distance but were replaced in the same conditions as they had been previously exposed to. The last six trays were brought ashore and their colonizers collected. After another two days, the twelve trays still on the bottom were removed and their contents collected.

The inhabitants of the six trays transferred to still water were exposed to a change that was thought to simulate the one experienced by benthic animals in a period of rapidly sinking water level. In these trays little immigration could occur, because very little water flowed over them; at the same time animals would have to swim actively out of them and could not be passively swept away. There was at least 6 cm of water above the rims of the trays, so that the animals were able to escape.

The colonization of the trays removed after six days was approximately similar to that found in those exposed for another two days after disturbance, and it was concluded that the disturbance did not lead to an appreciable evacuation of the trays. Therefore, the losses due to this reason from the trays transferred into still water were presumably also small.

Reduced current speed seems to be a very probable proximate stimulus for the animals to react to falling water level. If this is so, it is to be expected that the trays transferred to calm water would be abandoned by most of their inhabitants fairly quickly.

The results of these experiments are shown in Tab. 51. No statistical tests were attempted since it appears impossible to define expected values. Between the first two columns in each series, the differences are slight indicating

Tab. 51. Decolonization experiments in Tjulån. A = ind/tray after 7 days in fast current, B = ind/tray after 7 days in fast current, change of sites and another 2 days in fast current, C = after 7 days in fast current, change of sites and 2 days in almost still water.

	Loc. N Series I June–July 1964			Loc. N Series II July 1964			Loc. N Series III Aug. 1965			Loc. B Series IV Aug. 1965		
	A	B	C	A	B	C	A	B	C	A	B	C
A. inopinatus	28	26	5	17	16	2	–	2	–	–	–	–
B. fuscatus	–	–	–	–	–	–	29	34	11	55	59	10
B. lapponicus	–	–	–	12	12	9	9	13	8	1	–	1
B. pumilus	6	9	10	13	11	8	10	11	9	–	3	3
B. rhodani	88	77	22	56	65	17	12	14	3	17	19	4
B. subalpinus	–	–	–	–	–	–	8	11	6	16	9	4
Baetis sp.	16	12	10	10	14	14	24	30	20	42	44	28
H. dalecarlica	9	7	5	7	11	6	4	6	6	10	8	5
E. aurivillii	17	9	12	16	16	6	4	2	1	9	13	7
A. borealis	29	33	11	11	5	5	–	1	1	–	–	–
L. fusca	–	–	–	9	13	6	26	21	9	29	22	7
D. nanseni	18	14	2	8	6	1	3	5	1	9	10	1
I. grammatica	13	17	9	14	14	9	2	4	2	–	–	–
Rh. nubila	6	9	3	10	9	1	8	11	2	9	13	2
A. stigmatella	–	–	–	5	7	7	17	13	5	20	26	9

that the disturbance itself had little effect upon the colonization. The figures in the third column denoting the number of individuals present after two days in still water, are frequently much lower; in no case is there any significant increase. Evidently some species evacuated the trays much more quickly than others. Examples in series I were *Ameletus inopinatus*, *Amphinemura borealis* and *Diura nanseni*, in series II, *A. inopinatus*, *Baetis rhodani* and *Rhyacophila nubila*, in series III, *B. rhodani*, *B. fuscatus*, *Leuctra fusca*, *Apatania stigmatella* and *Rh. nubila*, and in series IV, *B. fuscatus*, *L. fusca*, *D. nanseni*, *A. stigmatella* and *Rh. nubila*. Certain species remained in the trays despite the changed conditions, viz. *Baetis lapponicus*, *B. pumilus*, *Baetis* sp. and *Heptagenia dalecarlica*. For some species the different experiments provided contradictory results, e.g. in *Ephemerella aurivillii* which largely abandoned the trays in series II but otherwise remained. This may indicate different reaction patterns in different life stages.

It seems natural that many species would evacuate the trays after these had been transferred to still water. Probably the other species did not receive sufficiently strong stimuli for emigration: they were still at a considerable water depth and in rather a favourable environment.

Sessile stages, such as blackfly pupae, are particularly vulnerable to changes of water level. Vast quantities of in situ desiccated blackfly pupae have sometimes been found at various places in Lapland, although not actually in the Ammarnäs area. Sprules (1947) found that mayfly nymphs reacted more quickly on flow fluctuations than caddisfly and blackfly larvae and that the latter were frequently exposed to desiccation at times of rapid recession of the water level.

10. Some interactions between microdistribution, food habits and life cycles

When reviewing the life conditions of the most important members of the benthic community of Lapland streams, the differences between species are seen to be very large. This fact is surprisingly often neglected in the literature where all too many generalizations about "the stream fauna" are to be found. The differences concern every aspect of the species' bionomics.

At the same time it is striking how different environmental conditions tend to occur in more or less fixed combinations (cf. Ulfstrand 1967). Substrate, in its wide sense, and current generally vary in a parallel fashion. Our understanding of the ecological functioning of the benthic community will benefit from a full recognition of the different reactions of species to factor combinations. Against this background the need for a new experimental approach becomes apparent. Only a few aspects of this involved subject can be considered here.

The microdistribution of a number of species belonging to the benthic community was examined in a previous paper (Ulfstrand 1967). Although the assessment of the factors involved was relatively rough, correlations between the factors (factor combinations) and the microdistribution patterns of many species could be established. It may be assumed that the relatively small qualitative differences of community composition between the sampling localities are due to different proportions of the microbiotopes at the localities in question. Similarly, in quantitative terms, standing crop and productivity will be strongly influenced by the microbiotopic pattern and the relative frequency of various microbiotope types (factor combinations). This has been repeatedly confirmed, particularly in studies concerning the relationship between substrate, animal community composition and standing crop (cf. Sprules 1947; vide Albrecht 1959 for compiled data).

These problems may be analysed in terms of such field data as may be obtained with the mapping method (Ulfstrand 1967). It should be pointed out however that this method will only yield an approximate picture of the single species' autecological attributes.

The basic importance of food for the microdistribution was underlined in my paper referred to above. Comparatively few workers have paid attention to the food factor in benthic ecology, among others Dittmar (1955 a), Scott (1958), Cummins (1964) and Buscemi (1966); and the significance of lacustrine products for benthic heterotrophs has been discussed by e.g. Knöpp (1952) and Müller (1954 b, c, 1956). Not only microdistribution but also standing crop and productivity are influenced by food availability.

In the benthic community, the seston feeders (blackfly larvae, net-spinning caddisfly larvae) and the predators (e.g. *Rhyacophila nubila, Diura nanseni*) constitute special categories and will be ignored in the following discussion. Most of the benthic species subsist on detritus (s. l.) and periphyton for food, and it is with these species we shall be primarily concerned. They will for short be referred to as detritus consumers and algal grazers, respectively.

Moon (1939) remarked that in a "young" stream, periphyton probably tends to be of relatively great importance but that, with the "ageing" of the stream, detritus will become gradually more and more important. With respect to the relatively great significance of periphyton in the young Lapland streams one is inclined to agree. However, even in this early stage the detritus may well be in absolute terms of greatest significance. The changes in the animal community at the upper birch forest limit, above which the amounts of detritus are presumably much less than below it, need to be studied. Perhaps the relative prominence of periphyton is another feature separating rhithron from potamon biotopes (§ 4.2).

Algae grow in greatest abundance on the upper surfaces of stones which are exposed to light and protected from sedimentation by fast current (Butcher 1949, Blum 1956). It follows that animals feeding on such algae are exposed to strong current. They seem to be able to cope with this difficulty in one (or perhaps sometimes both) of two ways. They may have evolved such ethological and morphological adaptations that they are able to withstand the force of the current or confine themselves to the lowermost water stratum with its reduced current speed (Nielsen 1950, Ambühl 1959, 1961). Alternatively they may compensate for the drift of part of their populations by upstream-oriented movement in the adult stage (amphibiotic insects); cf. Müller (1954 a, b, c), Roos (1957) and § 11.

Detritus is particularly abundant at places with a reduced current speed. But coarse detritus (vegetable debris) emanating from land may become anchored between stones in quite fast current. Animals exploiting such accumulations of detritus are also protected from the current by the substrate itself. Allochthonous detritus probably constitutes the most important food source in many parts of Lapland streams which thus represent exceptionally "open systems" (cf. Nelson and Scott 1962, Minckley 1963, Darnell 1964, Minshall 1967).

Both for the algal grazers and for the detritus consumers, the food is part of the substrate, so that analysis of a species' microdistribution indicates something of its feeding habits as well (Scott 1958, Egglishaw 1964, Sowa 1965). Nielsen (1942) found that the differences in habitats of various caddisfly species were reflected in different mouth-part morphology, and Décamps (1967) suggested that the larval cases of caddisfly species showed many adaptations to the microbiotopic environments to which the animals were exposed during feeding.

However, there is no sharp distinction between the algal grazers and the detritus consumers. Algal grazers are known to supplement their diet with detritus, and to some extent the reverse is probably also the case. Consequently, no absolute differences between microdistribution patterns of different species (based upon food preferences) can be expected.

When a species moves from one microbiotope to another within the benthos in the course of its development, a simultaneous change in feeding habits may occur (cf. Cummins 1964, Kownacka and Kownacki 1965, Ulfstrand 1967).

In a previous communication key references are given to the food habits of many of the most important taxa involved (Ulfstrand op. cit.). Only some essential data will be repeated here, with some additional information.

All the mayfly nymphs of importance in the community studied except *Ephemerella aurivillii* seem to exploit periphytic growth as the major food source, supplementing their diet from time to time with varying quantities of detritus (cf. Gajevskaja 1958, Minckley 1963). *E. aurivillii* is an omnivorous scavenger, possibly preferring higher plant material (both live and dead). The food of the youngest stages is generally unknown.

Filipalpian stonefly nymphs almost exclusively consume detritus and living higher plant material (Brinck 1949). Algae were found in very small quantities in the alimentary tracts of stoneflies. Nymphs of setipalpians prey upon small benthic animals but also ingest some detritus.

Cummins (1964) found that the larvae of two North American lotic limnephilins consumed vascular plant material, green algae and to some extent diatoms. This seems to hold for the whole subfamily (Nielsen 1942). *Glossosoma intermedium* has close relatives known to be algal grazers. Nielsen found that *Apatania muliebris* McL. also was primarily an algal grazer.

The seasonal changes in abundance of periphyton and detritus are not co-incident (cf. Chapman and Demory 1963). As shown in Fig. 17, detritus on the bottom was particularly plentiful after the autumnal leaf-fall. Much of it was flushed away by the following vernal spate. Nevertheless, considerable quantities remained throughout the year.

For many months each year, there is very little sunshine in Lapland, and this in combination with the thick ice and snow layer blacks out the stream bottom completely. The abundance of autotrophs is consequently evanescent with a distinct peak (or sometimes two) in summer (Butcher 1949, Blum 1956, Schmitz 1961, Müller-Haeckel 1967). A benthic species cannot therefore base its subsistence on algal consumption without either passing the dark months in quiescence, or switching to some other food source.

Against this background the timing of life cycles acquires additional significance.

Ulfstrand (1968) measured large numbers of nymphs/larvae, and these measurements supplemented with data on the flight-periods provided detailed information of the life cycles, especially the main growth periods, of many benthic species. The results will be briefly reviewed.

All *Baetis* spp. (except *B. rhodani*) and *Ephemerella mucronata* underwent a short period of rapid nymphal growth in summer. *B. rhodani* had distinct growth periods in late summer and autumn and again in spring and summer preceeding emergence. At some point, after a period of winter quiescence, growth was resumed. *Heptagenia dalecarlica, H. sulphurea* and *Ephemerella aurivillii* spent long periods as large nymphs but underwent their most intense growth in late summer and autumn. *Ameletus inopinatus* deviated in undergoing most of its growth under the ice.

The main growth periods of filipalpian stonefly species were more scattered over the year than was the case among the mayflies. Some species had their main growth periods in autumn and again in spring, others spent the winter as eggs or as quiescent small nymphs and underwent all their growth in spring, while a few grew in summer. However, apart from *Amphinemura standfussi* and *Leuctra fusca* in particular, filipalpian stoneflies grew little in July and August.

Among the caddisflies, *Apatania wallengreni* and *Potamophylax stellatus* grew mainly in winter and into early summer, *Apatania stigmatella* during July and August, and *Glossosoma intermedium* in August to October.

It is interesting that *A. stigmatella*, growing in summer, was found to prefer naked stones to detritus, and that *A. wallengreni*, growing in winter and spring, prefers detritus to naked stones (Ulfstrand 1967). Since preference for naked stones indicates disposition to algal grazing (cf. § 9.5.4), and preference for detritus that this is a basic food source, this is in line with the suggested relationship between food preference and life cycle pattern (see below).

The restricted growth period of blackflies at the lake outlets evidently represents an adaptation to the short season of maximum plankton productivity in the lakes (Cushing 1963, Maciolek 1966). The fact that a limited productivity occurs also under the ice does not invalidate this interpretation (cf. Rodhe 1955, Rodhe et al. 1966).

Thus, there seems to be a general correlation between the life cycle, especially the periods of intense growth, and food availability. Detritus consumers undergo intense growth at various season, but populations are generally low and growth retarded in the summer months, when detritus is scarcer than in any other season. Algal grazers, on the other hand, have their most intense growth periods concentrated to June–September, i.e. the season with most light and photosynthesis. There are a few apparent exceptions, e.g. *Ameletus inopinatus* and *Leuctra fusca*, and these call for further investigation.

Thus, in many of the benthic species in the biotopes studied, nutritional conditions seem to be of paramount significance for the life cycle patterns, but these are modified in many ways by several other factors, of which only temperature will be discussed here (see below).

The significance of the nutritional factor is particularly conspicuous in springs with more or less constant temperatures (cf. Nielsen 1942, Throup 1963). Hynes (1961) touched upon the possibility that the main reason for the location of growth periods of detritus consumers in streams to the winter months was the abundance of allochthonous detritus during that part of the year. From lenitic biotopes, Reynoldson and Young (1965) and Lellák (1965) have indicated possible relationships between food conditions and life cycle patterns.

The influence of temperature often makes itself manifest in the timing of the life cycle (cf. Ide 1935, Sprules 1947, Brinck 1949, Pleskot 1951, Macan 1961 b, 1962 b, Armitage 1961, Kamler 1965). However in several cases it has been shown to have surprisingly small effect (Macan 1960, 1961 b). The ability of many species to adapt to diverse temperature conditions is considerable: Thienemann (1950) and Botosaneanu (1960) have given many examples of populations of the same species inhabiting biotopes with widely different temperature régimes, sometimes within a restricted geographical area. However since populations are adapted to a restricted temperature range, correlations between the distribution range of a given species and this environmental parameter are not infrequently found.

Under the conditions prevailing in Lapland, the flight-period has to be confined to a season without ice and with a certain air temperature. Only in June to September are sharp frosts rare. Almost all species accordingly have their flight-periods located to this short period of the year. Within this period, inter-specific relationships may impose further restrictions on each species' flight-period (cf. Illies 1952 b, Macan 1958 c, Corbet 1964).

11. Significance of drift

Widely divergent opinions have been advanced concerning the nature of drift and, more particularly, its significance from the standpoint of population ecology. It is clear that if the distances traversed are so short that the individuals involved may rapidly return to their starting point, the process has little significance in this respect. But if the distances covered are more extensive and the probability of return small, the phenomenon acquires considerable significance.

In §§ 8.5 and 8.9, estimates of the total drift in Tjulån were presented. The numerical values were very high, and when related to the benthic populations inhabiting the stream, they permit the conclusion that drift was an important factor affecting population densities of many species. The fraction of the se populations passing the sampling site per 24-hr period was in the order of 1 to 2%; this was also the proportion of the populations drifting out of the suitable biotope per day. This represents a considerable loss (cf. Dendy 1944, Carlsson 1962).

The extent of the drift of benthic nymphs/larvae in Tjulån emphasizes the need for compensatory upstream movements (Müller 1954 a, b, c). In amphibiotic insects these are performed in the adult stage, particularly by egg-bearing females (Roos 1957). It may be assumed that in many species, the eggs are transported downstream for a more or less considerable distance before becoming attached to suitable substrate; a situation that will also require compensatory upstream movements in some stage of the species concerned (cf. Bernstein quoted from Müller 1966).

Elliott (1967 b) objected to the view that drift is a phenomenon of major significance for lotic populations, since he found that the proportion of the benthic populations participating in drift at any given moment was very small (cf. § 8.8) and that the drifting distances covered were short (cf. below). The first argument is found to be invalid when the time during which drift occurs is fully taken into account, and the latter argument reflects only local conditions. Elliott studied drift in a comparatively small and slow-flowing stream in which, moreover, a dense submerse vegetation acted as a sieve for the drifting animals.

Similarly, Lehmann (1967) in a careful study of *Gammarus pulex fossarum* Koch found that drift movements were generally of very restricted extent. His stream was also small and slow-running. In addition, *G. pulex* is entirely aquatic, and its ability of long-range upstream migration is limited in comparison with a winged insect (even one endowed with relatively weak flight powers) (cf. Steinmann 1913 for turbellarians).

This discussion emphasizes a point made

in § 10 that each species has to be regarded separately – there are so many differences between species that generalizations have to be very circumspectly qualified. There also seem to be considerable differences between different biotope types with regard to the extent of drifting.

The controversy whether drift is "active" or "passive" is partly semantic. The pronounced circadian rhythm of most species examined (§ 8.3; Müller 1966) and frequent over-representation in the drift of certain elements of the populations (§ 8.7; Müller op. cit.) suggest that the start of the drifting movements is by no means purely "accidental". At some time during the 24-hr cycle and, for example, in some age stages, individuals of certain species behave in such a way that the probability of their entering the drift increases. It may be that, at night, they enter microbiotopes that are characterized by strong current; or increased motility may lead to more interactions between individuals resulting in flight reactions. The animals may actually "allow" themselves to be carried into the current in response to some stimulus, a possibility that has yet to be demonstrated or excluded. The differential composition of the animal assemblage in experimental trays in different environmental conditions indicates that animals are more ready to abandon by drift certain places than others, according to specific preferences. Waters (1964) claimed that the density of one species influences the density of another species (even one belonging to a remote systematic group), and Dimond (1967) reported that, under certain circumstances, drift seems to be density dependent. Thus many factors may bring about the initiation of drift from an area.

There are, thus, many reasons for considering drift to be an active phenomenon. At the same time it is clear that the actual transport itself with the current is largely beyond the animals' control. Hence, it may be said that the beginning and the end of the drift involve the active participation of the individual, whereas the movement itself is passive (cf. § 8.4).

The finding by Elliott (1967 b) that drift quantities are correlated with flow volumes were confirmed by the present study (§ 9.4). Rising flow would be experienced by the animals, among other ways, as increased dynamic pressure on exposed sites, and this factor may by itself bring about increased drifting. Sudden spates are often accompanied by large-scale drifting, sometimes leading to considerable population loss (Maitland 1966). On the other hand it was found that drift maxima tended to come just after flow maxima. This may also be adduced as evidence against passivity. Certain factors seem to influence the distance covered by drifting animals. Although they are unable actively to move out of a fast current and make contact with the bottom, they are, because of the turbulence, frequently carried to the bottom. Many factors probably determine whether an animal having made contact with the substrate settles or returns to drift.

It should be kept in mind that when current velocity increases, not only will animals traverse longer distances per time unit, but also settling will become more difficult. Thus, even if the proportion of the benthic population departing from the bottom remains the same, there will be an increased rate of population loss due to animals drifting out of suitable biotopes.

There have been attempts, particularly by Waters (1961, 1962 b), to use drift rate measurements for estimating productivity. They have been criticized by Müller (1966), inter alia, for many reasons which need not be repeated here. Waters' (1962 b) analysis of incoming and outgoing drift in restricted riffle sections of a stream indicated, not the productivity so much as the rate of downstream transport of the populations studied.

The colonization of the experimental trays is of course closely connected with drift. As discussed in § 9.6.3, two models for the colonization process may be assumed. According to the first that assumes emigration rate to be density independent, it is possible to estimate the proportion of the benthic population taking part in drift per 24-hr period, and on the basis of data on drift quantities and population densities it is also possible to estimate the drifting distances. However there is another model, according to which emigration rate is assumed to be density dependent, and on the basis of this alternative no estimate can be made concerning drifting distances. This latter model leaves the possibility open that a very low proportion of the whole benthic population takes part in the drift and these individuals drift for very long distances; an extreme theoretical situation being that 1 to 2% take part and drift through the whole stream per 24-hr period.

Waters (1964) studied colonization in a somewhat different way. He exposed artificial bottoms for so long periods that maximum colonization had been attained. The animals were removed, and colonization was allowed to re-occur. The original colonization density, or 100% recolonization in Waters' terminology, was found after 4 to 10 days in *Baetis vagans* McD. and after 1 to 4 days in *Gammarus limnaeus* Smith. He showed conclusively that the circadian rhythm of colonization was closely similar to that of drift. In one case, recolonization of *Baetis* reached a much higher level than the original density. Waters suggested that this was due to delayed recolonization by *Gammarus* which allowed *Baetis* to occupy space otherwise occupied by *Gammarus* – a conclusion that needs confirming. It may be suspected that the change in environmental factors occurring in the trays when the original colonization was removed might have a considerable influence on the composition and density of the recolonization. Furthermore, Waters found that drift rate had an influence on the rate of recolonization of denuded areas.

It is difficult to compare Waters' results with those described in § 9.6. Waters started with a given initial density, to which subsequent events were related. Moreover, all his data are in terms of weights rather than individuals. In addition he paid no attention to the binary nature of the colonization, viz. the coaction between immigration and emigration. Therefore, I find it impossible to compare in detail his findings with mine; but our results do not seem to be mutually contradictory.

Irrespective of which model or – more precisely – what combination of the two models is most fitting to the prevailing conditions, there is no doubt that the drifting distances of a considerable proportion of the individuals were great. This is clear from a comparison of the total drift quantity past the sampling point and the population densities in the river parts upstream of this point. There seems to be much evidence favouring the view held by Müller (1954 a, b, c, 1956, 1966), Roos (1957), Carlsson (1962, 1967), Levanidova and Levanidov (1965), Waters (1965), Bailey (1966), and others, that drift is an integral part of the population ecology of many lotic species and communities. In fact, drift is likely to have many selective advantages. Populations may colonize areas which have become accessible owing to rises of water level, reoccupy sites which had temporarily become untenable, for example, by decreased flow, and avoid desiccation at sinking water level (Müller 1953, 1962 b, Kljutschareva 1963, Waters 1964). In addition, drift is a means of population dispersal (cf. Bovbjerg 1964). It seems to be a highly effective way of exploiting the resources available to start with a high population density in the upstream parts of a stream and gradually to reduce the pressure arising from increasing biomass by means of drift. It should be kept in mind that, from the standpoint of natural selection, the mechanism has to be advantageous for the individuals participating. Müller (1966) and Dimond (1967) refer to the fundamental function of drift as a means of reducing population pressure, and Elliott (1967 a, b) suggests that contacts between individuals often release drift behaviour; my own aquarium observations support this. Circumstantial evidence supporting the hypothesis of density dependent drift initiation is that the uppermost parts of a restricted river stretch have so far never been found to become devoid of individuals, not even of the most extensively drifting species.

Drift, then, can be regarded as an adaptive feature possessed by many lotic species which by this means benefit from the special properties of their environment.

In the lenitic biotopes there is no corresponding dispersal facility and yet considerable movements have been demonstrated, e.g. by Moon (1940), Weerekoon (1956), Berthelmes (1963) and Swanson (1967). Such movements are sometimes unaided, that is, the animals move actively from one area to another, but in other cases they make use of the relatively slow currents in lakes for their movements. This illustrates the general occurrence of population movements in almost any kind of freshwater environment.

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Резюме

1. Введение.

1.1. Настоящие исследования предприняты с целью составления фаунистического и экологического описания рек Лапландии, большинство из которых используется для строительства гидроэлектростанций.

1.2. Были изучены участки рек с сильным течением и комплексы животных, обитающие в местах с каменистым дном. Особый интерес представляет анализ Фауны Ephemeroptera, Plecoptera Trichoptera и Diptera Simuliidae.

1.3. Полевые исследования проводились в течение шести лет, общая продолжительность полевых работ около 10 месяцев.

1.4. Основные публикации, касающиеся изучения текучих вод Лапландии: Brinck & Wingstrand (1949), Brinck (1949), Müller (1953 и более поздние работы), Carlsson (1962).

1.5. Идентификация беспозвоночных проводилась в основном по определителям *Limnofauna Europaea* (ред. Illies, 1967) с небольшими изменениями: вид, прежде определявшийся как *Baetis bioculatus* L., идентифицирован здесь как *B. fuscatus* и обединен с *B. scambus* Etn.

1.6. Определяются и обсуждаются понятия »биотоп«, »комплекс«, »местообитание«.

2. Характеристика среды обитания.

2.1. Область, где проводились исследования, расположена в Шведской Лапландии (66°с.ш. и 16°в.д.). Ее основные характеристики даны на рис. 1 и 2 (2.1.1.). Высота над уровнем моря 380–550 м. Виндельельвен – восьмая по величине река Швеции (2.1.2.). Геологи включают эту область в состав Каледонской горной цепи (2.1.3.). Температура воздуха показана на рис. 3, осадки – на рис. 4, продолжительность снегового покрова – на рис. 5 (2.1.4.). Колебания температуры воды в течение года приведены на рис. 6. Измерения температуры воды проводили в районе Сорсель (рис. 1). Данные по продолжительности ледового покрова рек в разных пунктах исследований даны на рис. 7. Данные по скорости течения – на табл. 1 по сезонным изменениям скорости течения – на рис. 8 (2.1.5.). Самые высокие пункты исследования расположены в зоне субальпийских березняков у границы высокогорной бореальной таежной зоны. Макроскопическая растительность в реках очень редка (2.1.6.). Признаки загрязнения, а также другие следы деятельности человека отсутствуют (2.1.7.).

2.2. Расположение 10 основных пунктов, где проводился сбор материала, показано на рис. 2. Имеет значение удаленность пункта от озера (Рис. 9–16) (2.2.1.). Течение рек в основном быстрое, в участках loc. D и loc. P. течение более медленное (2.2.2.). Дно рек покрыто крупными камнями (Табл. 3). Количество мелких органических и неорганических частиц измерялось с помощью портативной помпы. Результаты исследований приведены в табл. 4. Содержание детрита колеблется в течение года (Рис. 17). Наибольшее количество зарегистрировано осенью после листопада (2.2.3.). Водоросли в наибольшем количестве встречаются у выхода рек из озер (Табл. 5) (2.2.4.). Содержание органического нерастворимого материала показано в табл. 6, результаты плаанктонных сборов – в табл. 7 (2.2.5.). Освобождение рек ото льда задерживается в некоторхы участках речной системы. Местные различия температуры воды регистрировались термографами (Рис. 18). Амплитуда колебания дневых температур приведена в табл. 8. Маленькие речки имеют более высокие и более ранние температурные пики, чем большие реки. Близость озер повышает осенью температуру реки (2.2.6.). Содержание кислорода довольно высокое (Табл. 9), удельная проводимость неизменно низкая (Табл. 10). Характеристика ионного состава воды приведена в табл. 11 (2.2.7.). Наиболее важные показатели, характеризующие реки в пунктах исследования, сконцентрированы в табл. 12 (2.2.8.).

3. Групповой состав и плотность попуяций отдельных видов беспозвоночных и зоогеографический анализ фауны.

3.1. Список видов составлен на основе анализа сборов бентоса.

3.2. Проверка метода исследований показала, что он достаточно эффективен для характеристики группового состава комплексов животных (Рис. 19).

3.3. Список видов, собранных во всех исследованных пунктах, приведен в табл. 13. Среди них выделены 4 группы, различающиеся по обилию и встречаемости. Группа »D« – доминантные виды, »S« – вторично доминантные, »I« – обычные, но с редкой встречаемостью и »A« – редкие виды. Данные по видовому составу этих групп и численности отдельных видов приведены в табл. 14, на основе их можно рассчитать относительное доминирование каждого вида.

3.4. Плотность популяций отдельных видов в каждом местообитании приведена в табл. 15 (3.4.1.). Это – величины того же порядка что и в большинстве других районовв Европы с умеренным климатом. Это показывает, что условия Лапландии вовсе не так суровы для этих беспозвоночных, как иногда полагают (3.4.2.). Различия между условиями обитания в стоячих и текучих водах относительно невелики в районах с холодным климатом. Поэтомму некоторые виды животных могут проникать далеко на север, в места, которые по своим физико-географическим особенностям заметно отличаются от условий обитания этих же видов в более южных районах (3.4.3.).

3.5. Распространение некоторых видов строго локализировано (3.5.1.). Комплексы беспозвоночных у истоков рек отличаются тем, что в их состав входит некоторое количество видов, характерных для озер. Кроме того, лишь некоторые Simuliidae встречаются в устьях рек вблизи озер. Другие Simuliidae избегают этих мест (3.5.2.). Установлены некоторые заметные различия в наборе видов в маленьких речках, в частности, в составе Trichoptera. Предполагается, что имеет место перемещение некоторых видов животных, вызванное конкуренцией (3.5.3.). Причины изоляции экологически сходных видов обсуждаются для всех групп животных (3.5.4.).

3.6. Комплексы животных состоят из широко распространенных Европейских видов, исходно южных элементов и сибирских северо-восточных видов. Как показано в табл. 17, среди веснянок зарегистрировано много северо-восточных элементов. Доминантные виды встречаются здесь среди обеих зоогеографических группировок.

3.7. Состав других групп беспозвоночных кратко представлен.

4. Проблема характеристики и классификации биотопов текучих вод и обитающих в них комплексов животных.

4.I. Сделаны попытки создать единую для всего земного шара классификацию биотопов текучих вод и соответствующих комплексов животных.

4.2. Для классификации биотопов использованы характеристики отдельных факторов среды. Наиболее важным из них является характеристика донного субстрата. Установлены взаимосвязи между отдельными факторами среды. Очевидно, можно использовать разделение биотопов на типы »*rhithron*« и »*potamon*«.

4.3. Попытки классификации биотопов и соответствующих зоокомплексов по признаку присутствия определенных видов животных признаны неудачными. Этот способ классификации может применяться лишь в пределах небольших, строго ограниченных географических районов.

5. Характеристика численности бентосных форм беспозвоночных.

5.1. Кратко описаны предварительн ые исследования.

5.2. Описана техника сборов. Камни поднимали со дна, а беспозвоночных, которые соскальзывали с поверхности камня, ловили сетью. Величину поверхности камня определяли умножением длины на ширину.

5.3. Из всех методов сбора материала с каменистого дна лишь один оказался применимым для данного грубого субстрата. Животных мельче 2–3 мм часто невозможно было учесть.

5.4. Собранных животных промывали дестиллированной водой, высушивали, пока на их поверхности не оставалось капель воды, и взвешивали.

5.5. Мозаичность распределения беспозвоночных на дне затрудняет учет их численности. Численность животных в пробах, взятых в одном участке, может разниться почти вдвое. Поэтому при подсчетах численности ошибка обычно довольно большая.

5.6. В целом исследована поверхность 13378 камней, составляющая в целом площадь около 250 м^2 (Табл. 18).

5.7. Данные по численности бентосных форм представлены в табл. 19–28. Об'яснения к таблицам даны в тексте в разделах 5.7.1.–5.7.10.

5.8. Особенно высока численность беспозвоночных у истоков рек в короткий летний период (Рис. 30–31). После вылета Simuliidae численность представителей этой группы в истоках рек резко снижается (Рис. 32). Отношение между численностью беспозвоночных в истоках рек и в других участках русла в период массового размножения Simuliidae различается более чем в 20 раз.

5.9. В 1964 г. численность беспозвоночных была в целом выше, чем в другие годы. Это касается всех групп (Табл. 30–32).

5.10. Общая численность беспозвоночных в исследованных реках Лапландии несколько ниже, чем в подобных реках более низких широт.

6. Плотность популяций беспозвоночных в некоторых местообитаниях.

6.1. Ошибка при учете животных в сборах обычно выше при подсчете количества особей, нежели при определении их биомассы на единицу площади.

6.2. Плотность популяций беспозвоночных в некоторых местообитаниях показана в табл. 33.

6.3. Общее количество личинок и куколок Simuliidae одновременно встречающихся в озерах у истоков рек (loc. A) достигает примерно 35 млн.

7. Колебания численности, перемещения популяций, продукция и продуктивность.

7.1. Исследовались факторы, вызывающие частые радикальные изменения численности беспозвоночных, которые были зарегистрированы во время исследований.

7.2. Определяются различия между терминами продукция и продуктивность.

7.3. В некоторых случаях причиной изменения численности могут быть миграции животных из более глубоких в более мелкие участки рек, либо передвижения вдоль русла реки. Установлено, что данные по численности Ephemeroptera, Plecoptera и Trichoptera обычно не соответствуют [оценке продукции этих групп.

7.4. Подобные перемещения, но в меньших размерах, наблюдались у Simuliidae, обитающих у истоков рек. Однако, определения продукции в этих участках производились очень неточно. В настоящей работе результаты определения продукции очень занижены (7.4.1.). В участке loc. A в июне-июле 1963 г. продуктивность *Schönbaueria annulitarsis* около 0,65 г/м²/день. В июне-июле 1964 г. общая продуктивность ком плекса Simuliidae в том же участке составляла 3 г/м²/день (7.4.2.). В участке loc. E продуктивность ниже (7.4.3.). Продуктивность комплекса Simuliidae в участке loc. A в 1964 г. была примерно 1,6 кг/день, что соответствовало биомассе около 65 кг. Количество нерастворимого органического вещества, поступающего в реку из озера, около 4320 кг/день, т.е., примерно в 2700 раз больше, чем увеличение веса комплекса Simuliidae в течение суток (7.4.4.).

8. Отношение дрифта и популяций бентоса.

8.1. Дрифт – передвижение бентосных организмов по течению реки.

8.2. Сборы дрифта проводились с помощью планктонных сеток на середине реки и у дна вблизи берега. Сборы проводились в течение 24 час. Всего исследовано 6 серий.

8.3. Циркадный ритм выражен гораздо лучше осенью, нежели летом (Рис. 33). Циркадный ритм выражен также и у экзувиев, но менее четко, чем у живых организмов.

8.4. Установлены определенные различия между дрифтом в верхних и нижних слоях воды (Табл. 35–36). Экзувии распределяются случайно в массе воды, иногда их несколько больше в придонных слоях.

8.5. Исследованы пробы воды определенного обема с »донным« и »свободным« дрифтом (Табл. 37) (8.5.1.). На этой основе вычислено количество беспозвоночных, участвующих в дрифте в течение суток (Табл. 38–39) (8.5.2.).

8.6. Имеется определенная зависимость между обилием воды и численностью животных в дрифте (Рис. 34).

8.7. Большое значение имеет вопрос о том, все ли стадии развития беспозвоночных участвуют в дрифте с одинаковой частотой (8.7.1.). В большинстве случаев установлена корреляция в распределении животных в дрифте и на дне реки. Обсуждаются некоторые исключения (8.7.2.).

8.8. Отношение между количеством особей в дрифте и количеством животных на дне в каждый данный момент составляет около 0,01%.

8.9. Высчитано соотношение между общей численностью бентосных беспозвоночных (рис. 2), и их численностью в дрифте (Табл. 42). Установлено, что через пункт сбора беспозвоночных, расположенный около устья реки, в течение суток проходит около 1% от общей численности бентоса. Большая часть животных уносится в озеро и вероятно погибает.

8.10. На рис. 35 показана скорость гибели беспозвоночных. Однако, эти потери восполняются за счет того, что жизненный цикл у многих форм очень короткий. Даны характеристики некоторых участков, дающих пополнение дрифту.

9. Заселение имплантируемых субстратов.

9.1. Проведены полевые исследования по определению скорости дрифта и преферендума некоторых видов в отношении местообитаний.

9.2. На дно рек опускали подносы, покрытые тонкой тканью с внутренней стороны и с различными субстратами, помещенными на них.

9.3. Циркадный ритм заселения субстратов животными оказался сходным с ритмом дрифта (Табл. 43).

9.4. Скорость заселения зависит от обилия воды (Табл. 44, Рис. 36). Наиболлее интенсивное заселение субстратов наблюдается вскоре после половодья, когда вода начинает спадать.

9.5. Субстраты, имплантируемые в местах с разной скорострю течения, заселялись различными по составу комплексами организмов (Табл. 45) (9.5.1.). Глубина оказывает отрицательное влияние (Табл. 46) (9.5.2.). Размеры частиц субстрата имеют большое значение для большинства видов (Табл. 47) (9.5.3.). Сравнивалась интенсивность заселения поверхности камней, взятых со дна реки и покрытых водорослями, и камней, взятых со скал, без растительности. В первом случае обнаружено большее количество животных, среди которых преобладали виды, известные как потребители водорослей (Табл. 48) (9.5.4.).

9.6. Процессы заселения исследовались в течение длительного времени в 4 сериях опытов (Табл. 49) (Рис. 37). После первоначального заселения устанавливается баланс при котором одинаково интенсивно протекают как иммиграция, так и эмиграция беспозвоночных. Окончательные результаты позволяют предполагать, что в течение суток с субстрата исчезает около 25% популяции (Рис. 38).

9.7. Состав комплексов беспозвоночных в имплантируемых субстратах обычно отличается от того, что наблюдается на естественном донном субстрате (Табл. 50).

9.8. Помещение подноса с субстратом в участки с очень медленным течением (почти стоячая вода) сопроваждается активной эмиграцией некоторых видов животных (Табл. 51).

10. Некоторые взаимосвязи между микрораспределением животных, их пищевым преферендумом и жизненным циклом.

Виды, питающиеся преимущественно микроскопическими водорослями, обитают на голых камнях, где они омываются водой. Потребители детрита обитают в более укрытых местах. Первая категория беспозвоночных находит наиболее обильную пищу летом, и в этот период зарегистрирована наиболее высокая численность представителей данной группы (почти все Ephemeroptera). Запасы пищи для потребителей детрита более постоянны. Однако, количество детрита зимой несколько выше, и численность животных, питающихся детритом, тоже возрастает зимой (большинство Plecoptera). Установлено, что *Apatania wallengreni*, развивающаяся зимой, предпочитает детрит голым камням, а *A. stigmatella* развивающаяся летом, наоборот, предпочитает селиться на голых камнях. Пищевой преферендумм может существенно влиять на продолжительность и сезонные особенности жизненного цикла животных, хотя другие факторы среды также имеют большое значение.

11. Протяженность и значение дрифта.

Наблюдается частичное перемещение популяций вглубь. Это однако должно компенсироваться миграциями животных на поверхность воды, что обычно наблюдается у взрослых насекомых. Установлено, что у ряда видов дрифт оказывает существенное влияние на численность популяции, у некоторых видов влияние дрифта на численность незначительно. Некоторые моменты процесса дрифта, в частности, начало движения и оседание животных на дно, нужно рассматривать как активные стадии, в то время как сама транспортировка животных – пассивная стадия дрифта.