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SERIES A SCIENTIAE RERUM NATURALIUM No. 87

BIOLOGICA No. 6

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AND COMMUNITY STRUC-
TURE OF THE MACRO-
ZOOBENTHOS ON STONES

IN THE JÄVÄJÄNKOSKI RAPIDS ON THE RIVER LESTIJOKI, FINLAND

KALEVI KUUSELA

*Department of Zoology
University of Oulu*



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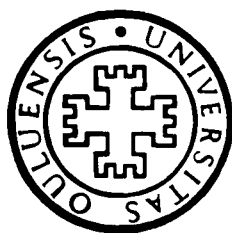
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Department of Zoology, University of Oulu, Oulu, Finland

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Abstract

In June 1965 a total of 35 cobble-sized stones were lifted from the Jäväjankoski rapids, an environment with surface flow rates of 50–125 cm/s in the oligotrophic and polyhumic river Lestijoki. These yielded a material of 7269 macroinvertebrates. The principal habitats recognized were the 'riverbed', representing the natural rapids bed with a good moss cover and a firm structure, and the 'weir', somewhat artificial and unstable with little vegetation. The main ecological gradients observed were the surface current and point flow and the size, algal and moss cover of the stones.

Many of the 102 taxa treated here as species were ones commonly recognized as rheophilous or rheobiontic. Observations were made on the optimum surface current velocity ranges for the various species and their micro-habitat preferences (exposed or protected face, moss, algal or bare surface), also in relation to current velocity. Adaptation to the current and the distribution and supply of food were all implicated in this distribution. The species were divided by feeding habits into diatomivores, bryophytivores, detritivores, carnivores and generalists with a non-animal diet. The total community was dominated numerically by the passive diatomi-detritivores, the blackflies, while detritus was also the principal food component of the active feeders.

Species not previously reported from Finland were: *Sperchonopsis verrucosa* (Protz), *Sperchon chupeifer* Piers., *Torrenticola amplexa* (Koen.) and *Hygrobatas calliger* Piers. (Acari: Hydrachnellae), and *Rheotanytarsus photophilus* G., *Zavrelia nigrifula* G., *Eukiefferiella alpestris* G., *E. tshernovskii* Pankr., *E. quadridentata* Tshern. and *Psectrocladius simulans* Joh. (Diptera: Chironomidae).

The stone communities were composed of a mean of approx. 24 species (range 10–43), and 208 individuals (18–1873); the variances indicated contagious dispersion. Most species were represented by one or two individuals at a time, and low-incidence species were the most numerous within the total fauna.

The number of species encountered increased in proportion to the logarithm of the number of stones examined. This would enable the mean number of species in preliminary surveys to be used to predict the number obtainable from given habitats. A minimum of 13 stones or 4 Surber samples from a cobble bed would seem reasonable given a predefined degree of precision of 0.1, for this would reveal approx. 82 % of the species and 95 % of the species diversity (H').

The diversity (H') of the stone communities varied in the range 1.43–3.27, and the evenness value (J') in the range 0.40–0.99. Due to the mass occurrence of blackflies on a few of the stones in the weir, H' failed to correlate with the number of species. Comparisons showed H' for the total community and its mean for the stones to agree well with values obtained in the literature. This similarity in species diversity values, and also the linear pattern of species enrichment, may both be interpreted as signs of a universal conformity in the functional structuring of stone communities.

Significant explanatory variables for the variance in community structure in simple linear regression were stone size (in dm^2), surface current (cm/s) and point flow (l/s). The dependences were either linear in character, positively (H' against dm^2 , ind. – l/s) or negatively (evenness – cm/s and l/s), or asymptotic (spp. and ind. – dm^2 , spp. – l/s), or of the optimum range type (spp. and H' – cm/s, H' – l/s, ind. – cm/s). Multiple regression analysis showed point flow to be essentially implicated in the sets of variables explaining the variance in community parameters.

Similarities (Sørensen's K, Czekanowski's PS) were noted between the stone communities especially within the riverbed and weir habitats, the outstanding consistency factors being the closed moss stands in the former and the laminar flow over the latter. The species associations observed (Dice's coincidence index) may be attributed both to these dominant features and also to the parallel ecological requirements of the species, largely in respect of food items and mode of feeding. The hypergeometric probability distribution method proved satisfactory for evaluating the significance of the similarity and association measures. The general organization of the communities follows in many respects the 'biocoenotic principles' of Thienemann and Franz.

Key words: micro-habitat preferences, food, species diversity, sampling efficiency, community similarities, species associations

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I also wish to remember here with my deepest gratitude my late uncle, Mr. Väinö Kangastalo, and his family, on whose farm I spent so many summer holidays as a boy, exploring the rapids of Jäväjänkoski to my heart's content. Without my realizing this at the time, it was this experience which enabled me to seize upon the thesis topic suggested to me by my colleague Dr. Tapani Valtonen, to whom I extend my sincerest thanks. I would also like to thank Mr. Malcolm Hicks, M.A., for translating the manuscript into English.

Finally, my thanks are due to my wife Tuula and my sons Ville and Jussi, who have helped me to persevere in this work at every stage.

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CONTENTS

ABSTRACT	3
ACKNOWLEDGEMENTS	5
1. INTRODUCTION	9
2. ENVIRONMENT	10
2.1. General geography and hydrology of the river basin	10
2.2. Sampling site	12
2.3. Local hydrological observations	12
2.3.1. Methods	12
2.3.2. Water level and flow	14
2.3.3. Temperature	14
2.3.4. Water composition	15
2.4. Habitats	17
2.4.1. Terminology	17
2.4.2. General descriptions	17
2.4.3. Current	20
2.4.4. Size and attitude of stones	20
2.4.5. Vegetation	22
3. MATERIAL AND METHODS	24
3.1. Lifting of the stones, recovery of the animals and identification	24
3.2. Statistical procedures	25
3.3. Sources of error	25
4. FAUNISTIC RESULTS AND AUTECOLOGICAL NOTES	26
4.1. Introduction	26
4.2. General composition of the communities	26
4.3. Occurrence and ecology of the taxa	27
4.3.1. Tricladida	27
4.3.2. Bryozoa	27
4.3.3. Pelecypoda	28
4.3.4. Oligochaeta	28
4.3.5. Hirudinea	28
4.3.6. Acari: Hydrachnellae	29
4.3.7. Isopoda	29
4.3.8. Ephemeroptera	29
4.3.9. Plecoptera	32
4.3.10. Trichoptera	34
4.3.11. Diptera	40
4.3.11.1. Chironomidae	41
4.3.11.2. Simuliidae	46
4.3.12. Coleoptera	50
4.4. Ecological summary	50
5. FOOD AND TROPHIC RELATIONS	53
5.1. Introduction	53
5.2. Material and methods	53
5.3. Results and discussion	54

5.3.1. Results of food analyses	54
5.3.2. Synopsis of the literature	56
5.3.3. Trophic relations	59
5.3.4. Ecological background	60
6. COMMUNITY STRUCTURE	62
6.1. Introduction	62
6.2. Numbers, occurrence and dominance relations	63
6.3. Enrichment of species	66
6.3.1. Introduction	66
6.3.2. Methods	67
6.3.3. Results	68
6.3.4. Comparisons	68
6.4. Species diversity	71
6.4.1. Introduction	71
6.4.2. Methods	72
6.4.3. Results	73
6.4.3.1. Stone communities	73
6.4.3.2. Habitat level	75
6.4.4. Discussion	76
6.5. Linear species enrichment patterns and equal diversity indices – a remark on the universal structural similarity of animal communities on stones in flowing water environments	78
6.6. Determination of an adequate number of samples	79
7. COMMUNITY STRUCTURE IN RELATION TO ENVIRONMENTAL FACTORS	82
7.1. Introduction	82
7.2. Methods	82
7.3. Results	83
7.3.1. Simple linear regressions	83
7.3.2. Multiple regressions	88
7.4. Discussion	90
7.4.1. Particle size	90
7.4.2. Surface current velocity and point flow	92
7.4.3. Vegetation	94
8. COMMUNITY SIMILARITIES AND SPECIES ASSOCIATIONS	96
8.1. Statement of the problem	96
8.2. Community similarities	96
8.2.1. Introduction and methods	96
8.2.2. Results	98
8.3. Species associations	99
8.3.1. Introduction and methods	99
8.3.2. Results	100
8.4. Discussion	105
8.4.1. Ecological background	105
8.4.2. Methodological appraisal	106
9. CONCLUSIONS	107
REFERENCES	110
APPENDIX	124

1. INTRODUCTION

Even a cursory inspection of the numerous studies available on lotic benthos (for references, see for example GEIJSKES 1935, MACAN 1963, 1974, CUMMINS 1966, HYNES 1970, WHITTON 1975, HELLAWELL 1978) will reveal a great deal of conformity in the faunal lists supplied, and frequently also a marked similarity in the descriptions of the ecological demands of the species, which, expressed as specific ecological valencies, are in a general way documented in *Limnofauna Europaea* (ILLIES 1967, 1978), for instance. Relatively good information is accessible on the manner in which the principal environmental factors operate, and on the trophic organization prevailing in flowing water. The strong current, however, renders descriptive work difficult, and it is this that may have directed research into rheobenthos emphatically towards the study of small streams. From the taxonomical point of view, it is characteristic of the great majority of investigations that the identification of the macrofauna to species has not been extended to cover by any means all of the higher-level taxa, and in many cases even determination to genus has proved impossible. Admittedly species identification has become substantially easier and more comprehensive thanks to many ingenious keys and revisions, but at the same time, with the rise of theoretically based ecology, the standards of identification have become more demanding, in such matters as the indication of community structure or of changes in this by means of diversity indices, or similarity between communities by means of similarity indices. Even so, compromises still have to be made by ecologists, as the identification of a certain group would require a high degree of specialization (e.g. Oligochaeta or Hydrachnellae) and the larval taxonomy is imperfectly known (e.g. Trichoptera, Simuliidae and particularly Chironomidae).

The work reported here is aimed at determining the macroinvertebrates living on individual stones within a section of the eurhealic rapids of a river in the early summer period, the factors affecting their distribution and the mode of operation of such factors. The relevant feeding habits and trophic relations are also determined, an additional analyses are carried out on the structure of the stone communities in terms of number of species, number of individuals and species diversity, and an estimate of the optimum size of sample sufficient to describe such communities is obtained on the basis of these measures. A further purpose of the work is to ascertain the dependence of these community parameters on environmental factors such as stone size, plant cover and current rate. Finally an evaluation is attempted of the similarities appearing between the animal communities on the stones and of the species co-occurrence relations.

2. ENVIRONMENT

2.1. General geography and hydrology of the river basin

The extent of the Lestijoki watercourse is depicted in Fig. 1. The river has a relatively narrow channel, 20–40 m in width, is generally shallow, and possesses 25 stretches of rapids. The bedrock is composed of acidic quartz diorite, granodiorite and crystalline schists. The basin, which is some 1335 km² in area (SIREN 1955), has a surficial covering of till. There are a few eskers in the upper reaches, but lower down the shores are generally composed of silt, and some clay deposits are also encountered in the middle reaches (AARIO 1960).

It is characteristic of the climate of Ostrobothnia for the gradual increase in absolute altitude inland to be matched by corresponding changes in mean temperatures and precipitation, as is to be seen in some data in Table 1.

Mires account for over 60 % of the land area of the Lestijoki basin, and approximately two-thirds of these are acid pine bogs. Only 6.3 % of the total area of the basin is occupied by lakes. In common with many watercourses possessing few lakes, Lestijoki experiences a sudden pronounced period of flooding every spring (see p. 14).

The forests in the area are predominantly poor pine forest (*Vaccinium*-type), but the river banks support a rich shrub and deciduous tree vegetation (*Alnus*, *Salix*, *Betula*). Typical shore and water plants include *Nuphar luteum*, *Sparganium* spp., *Scirpus silvaticus*, *Caltha palustris*, *Agrostis* sp. and *Filipendula ulmaria*.

Table 1. Details on the climate of the Lestijoki basin in the period 1921–1950 (from the cartogrammes in the Atlas of Finland, AARIO 1960).

	Coastal area	Kannus	Lestijärvi
Mean annual temperature	3°C	3°C	2°C
Mean temperature in July	16	16	16
Mean temperature in February	–7	–8	–9
Mean annual temperature range	23	25	26
Average mean of yearly maxima	27–28	27–28	27–28
Average mean of yearly minima	–23	–27	–29
Annual precipitation	500 mm	550 mm	600 mm
Precipitation in May	30–40	30–40	30–40
Date of lasting snow cover	5.XII	30.XI	25.XI
Break-up of lake ice	25.IV	2.V	9.V

RIVER BASIN OF LESTIJOKI

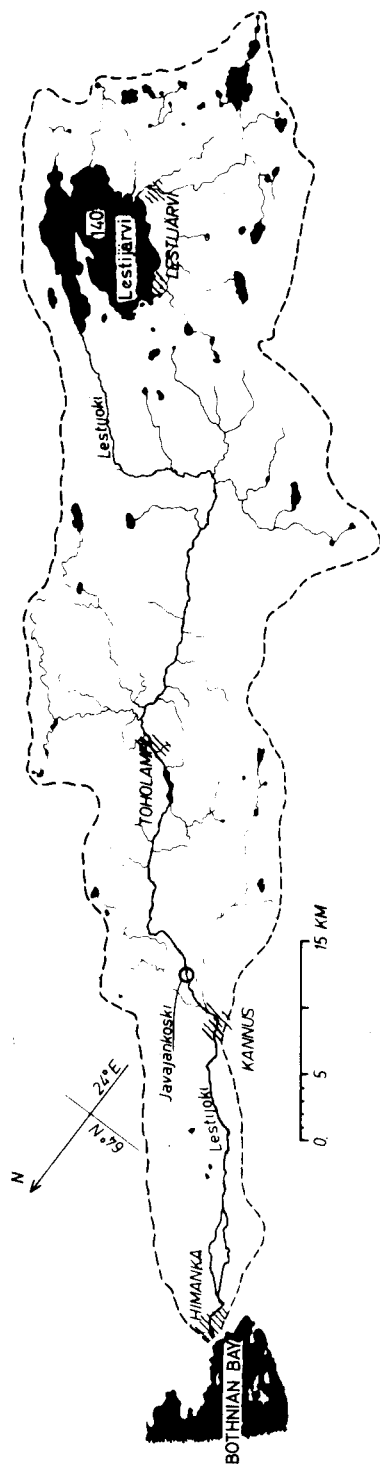


Fig. 1. Map of the Lestijoki river basin.

The population of the area, approx. 13,600 in 1970, is employed principally in agriculture and forestry (ANON. 1972). The farmland is concentrated in the area adjacent to the river. The watercourse has always been affected by random effluent loading, and it was only in 1968 that the first leaching trench was constructed into Lestijärvi with a capacity of approx. 12 m^3 of waste water per day.

2.2. Sampling site

The site for the research reported here is the upper part of the rapids of Jäväjänkoski, in the village of Heiniemi, parish of Kannus, Central Ostrobothnia (Figs 1 and 7). The rapids are around a kilometre in length and have a gradient of approx. 3 ‰.

The river bed in the upper part of the rapids was restructured in 1962, and a small basin was isolated from the rest of the rapids by a lowish stone rampart. Upstream the river is mainly relatively deep and still with a rocky bottom and silty banks for a distance of about 3 km up to the hydroelectric power station. The regulation of the flow of the river by the power station has its own characteristic effect on water levels in the rapids on the lower river, as will be seen below (p. 14).

2.3. Local hydrological observations

2.3.1. Methods

The official Hydrological Board water-level gauge (51 Lestijoki/Kannus 3, $F = 1200 \text{ km}^2$) is situated on the lower reaches of the river, five kilometres away from Jäväjänkoski ($F = 1060 \text{ km}^2$; SIREN 1955). The general course of annual flow (Fig. 2), however, may be identical at these two localities.

An artificial scale was constructed for measuring the daily fluctuations in water levels (Fig. 3), these measurements being carried out in the summer of 1971 using a tracer float of the author's own design. The zero level is the same as in 1965.

The current was calculated separately for the surface (v_s) and bottom water (v_b) as the mean of five readings in each case. The values for the individual stones examined (see section 2.4.3.) were obtained using a current meter (OTT 'X', diameter 50 mm, minimum flow 7 cm/s) at a time when the water level was at the zero mark, the exact location of the stone being indicated by a float set in position at the time of lifting. In the places where the current meter gave no reading, a value of 5 cm/s was assumed for the surface current and 1 cm/s for the bottom. The general surface current conditions of the whole area (Fig. 7) were surveyed in summer 1971 using a current meter OTT 'Arkansas V', diameter 100 mm.

The flow rate over each stone was calculated as follows:

$$q = v \cdot d \cdot 0.1 \quad (\text{l/s}),$$

where v = the mean of the current velocities v_s and v_b , d = depth (in metres) and 0.1 = constant (in metres). This indicates approximately that volume of water which flows over a stone of width one decimetre in one second, and will be referred to later as the 'point flow'. The means of the values of both v and q for the individual stones are used here to denote the flow conditions in each habitat.

The characterization of current rates adopted here is chiefly that of BERG (1948), except that the base values used are those for surface velocity:

very slight	— < 10 cm/s,
slight	— 10–24 cm/s,
moderate (medium)	— 25–49 cm/s,
swift (strong, rapid)	— 50–99 cm/s,
very swift (strong, rapid)	— ≥ 100 cm/s.

A current may also be classified by type into near laminar, or 'streaming', and turbulent, or 'rippling'.

Water and air temperatures (Fig. 4) were measured in 1965 using Lambrecht's remote thermograph. Data of LAAKSONEN (1969) are also included for comparison purposes for the upper and lower reaches of the river and for other years and seasons of the year.

The water quality data (Table 2) are based on the summary published by LAAKSONEN (1969) of series of such analyses taken from the road bridges at Toholampi and Himanka.

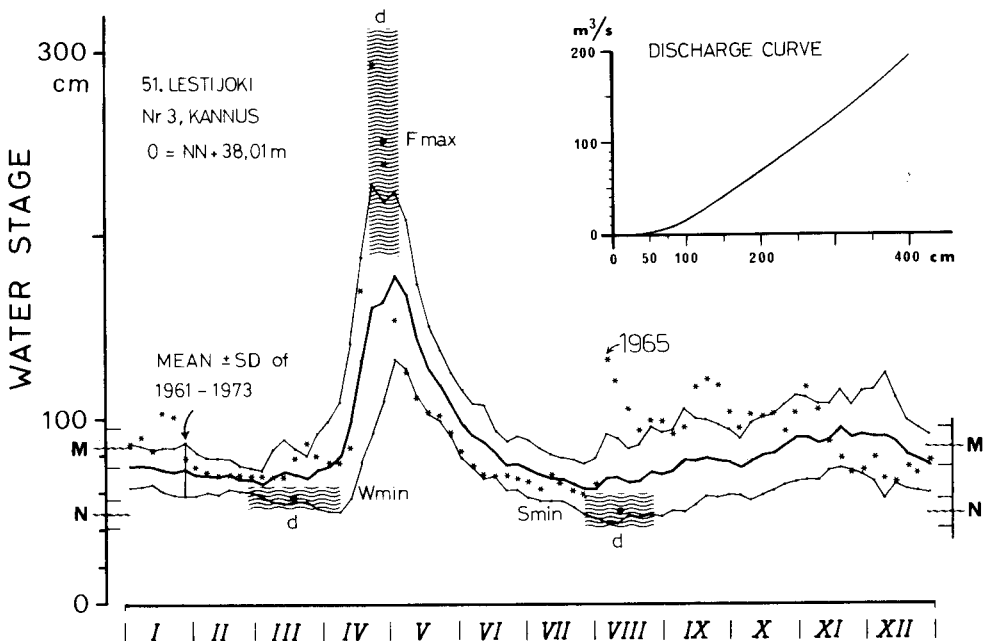


Fig. 2. Annual variation in water level at the Kannus water gauge, approx. 5 km downstream of Jäväjänkoski, indicating mean water levels \pm SD for five-day periods, mean dates (d) and values for the annual winter minimum (Wmin), flood maximum (Fmax) and summer minimum (Smin), and means \pm SD for the annual midwater stage (M) and low-water stage (N).

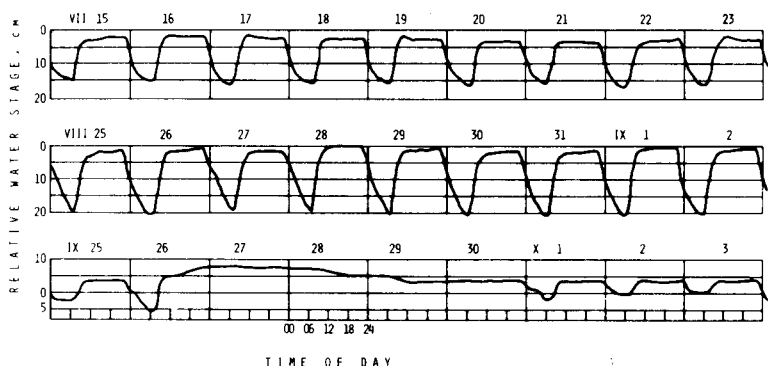


Fig. 3. Diel variation in water level at the head of Jäväjänkoski at certain periods during the summer of 1971. The arbitrary zero corresponds to approx. 75 cm on the Kannus gauge.

2.3.2. Water level and flow

The extremes of annual hydrographic variation (Fig. 2) are the early spring situation, the spring floods and the late summer period. The peak flood time is marked by a discharge of almost 50 times the mean low-water flow rates of $2.0 \text{ m}^3/\text{s}$ for early spring and $2.1 \text{ m}^3/\text{s}$ for the summer. The lowest daily values ranged between 0.9 – $2.1 \text{ m}^3/\text{s}$.

The water level at the time of study was below the long-term mean, but it remained more or less constant, at +5 cm on the artificial scale, throughout the period with the exception of a sudden rise of about 20 cm on June 8th, when the hydro-electric power station exhausted its reservoir. Closure of the sluices in the early hours of the morning then caused a slow decline in levels to a figure of approx. -12 cm, but the figure had returned above zero by midday. The daily fluctuation in water level in accordance with electricity production extended downwards to the -5 cm level at most during the period in question (cf. 1971 data in Fig. 3).

2.3.3. Temperature

Water temperatures had risen to 9°C by the beginning of the study period (Fig. 4). The early June weather then raised the mean water temperature up to the range 16 – 18°C fluctuating in general accordance with the air temperature.

During the sampling period daily maximum water temperatures varied within the range 12.5 – 19.5°C . The water reaches its daily maximum temperature in the afternoon and falls to its minimum temperature in the early morning (Fig. 5). This implies a time-lag of 1–4 hours in relation to the corresponding maximum and minimum air temperatures (see ECKEL and REUTER 1950, PLESKOT 1953, MACAN 1958b).

Since water temperatures tend to follow closely the trends in air temperatures, these latter may be employed to obtain an estimate of fluctuations in water temperature. According to the data published by the Finnish Meteorological Office for 1965, temperatures in May of that year at Lestijoki fell some 2°C below the mean May value for the normal period 1931–1960, i.e. 7.1°C , June temperatures remained around the

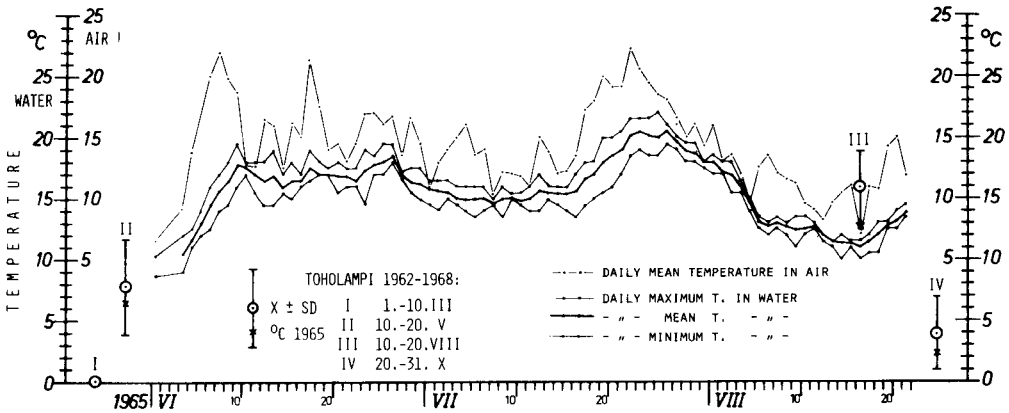


Fig. 4. Air and water temperatures at Jäväjänkoski in summer 1965 and mean water temperatures and standard deviations at the Toholampi road bridge over the years 1962-68, after LAAKSONEN (1969). Observe the difference between the two temperature scales.

normal value of 12.8°C , while in July they were again some $2-2.5^{\circ}\text{C}$ below the mean of 16.3°C . This would suggest that water temperatures at Jäväjänkoski during the period when this work was carried out would have been close to normal, even though the rise from May onwards may have been slightly steeper than usual.

2.3.4. Water composition

The water of Lestijoki is dark in colour and has a high humus content. It is relatively clear during dry weather around midsummer and also in winter, but material is easily eroded into the water from the silty banks at times of flooding or heavy rain.

The calculations presented by LAAKSONEN (1969) show regular variations in water composition according to location and time, so that values for solid matter, conductivity,

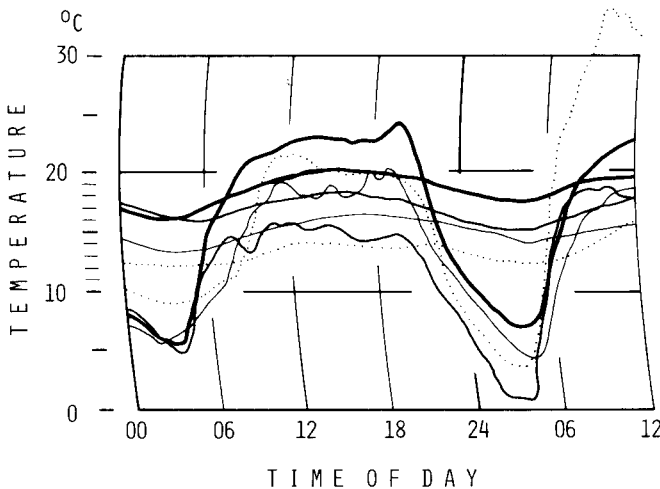


Fig. 5. Sample curves for daily variations in air (sharp curves) and water temperatures (gentle curves) on four days during the summer of 1965: dotted line - 6th June, medium line - 12th June, thin line - 6th July, heavy line - 21st July.

Table 2. Mean water quality (and SD) in Lestijoki and neighbouring watercourses in 1962–68 (after LAAKSONEN 1969).

		Lestijoki		Neighbouring watercourses	
		mean	± SD	mean	± SD
Discharge	m ³ /s	12.71	13.09	25.26	39.98
Temperature	°C	6.675	6.160	7.042	6.078
O ₂ -saturation	%	90.60	7.249	86.82	9.916
Turbidity	abs. units	12200	11200	14500	11500
Suspended solids	mg/l	15.98	19.68	20.60	21.80
Evaporation residue	mg/l	75.77	32.84	100.10	39.69
Ignition residue	mg/l	34.90	20.40	51.67	29.81
Conductivity	μS	43.49	15.46	67.31	56.64
Alkalinity	mval/l	0.1606	0.079	0.1823	0.1093
Total hardness	°dH	0.8210	0.2294	1.4020	0.9743
pH	pH	6.418	0.5716	6.344	0.5916
Colour	mgPt/l	149.40	70.00	180.00	86.71
KMnO ₄ consumption	mgKMnO ₄ /l	75.45	28.42	82.03	29.09
BOD ₅	mgO ₂ /l	2.296	1.568	2.322	1.347
Total nitrogen	mgN/l	1.027	1.280	0.9607	0.8159
Total phosphorus	mgP/l	0.0609	0.0526	0.0626	0.0507
Total sulphur	mgS/l	2.019	0.9744	5.245	4.9350
Sodium	mgNa/l	3.199	1.617	4.041	1.713
Potassium	mgK/l	1.130	0.5889	1.603	0.6673
Calcium	mgCa/l	3.077	0.9116	6.011	4.199
Magnesium	mgMg/l	1.271	0.3735	1.868	0.7604
Chloride	mgCl/l	8.385	4.425	8.447	5.244
Iron	mgFe/l	1.155	0.4826	1.684	1.029
Manganese	mgMn/l	0.0297	0.0567	1.1292	0.1389

total hardness, colour, KMnO₄ consumption, total N, total S, potassium, sodium, calcium, magnesium, chlorides and iron, for example, are systematically higher at Himanka than at Toholampi, while the seasonal variations in such measures as turbidity, solid matter, KMnO₄ consumption, BOD₅ and to some extent the trace elements are comparable with those in flow rate.

In comparison with the mean figures for the adjacent rivers (Table 2), it may be noted that the water of Lestijoki is distinctly poor in the trace elements S, Na, K, Ca, Mg, Fe and Mn and also in its solid matter content, although it remains on a par with the other rivers in its biological oxygen consumption. The water is very soft, acid, rich in humus, dark in colour and fairly rich in nutrients, although low in its mineral content. In the limnosaprobity system (SLADECEK 1973) the mean BOD₅ would correspond to a state of oligosaprobity, although for the majority of the year the river would be xenosaprobic.

In general terms Lestijoki could be regarded as a slightly polluted oligotrophic, polyhumic watercourse, as is characteristic generally of river systems in areas with a granite bedrock, till soils and a high incidence of mires (JÄRNEFELT 1958, EGGLISHAW and MORGAN 1965).

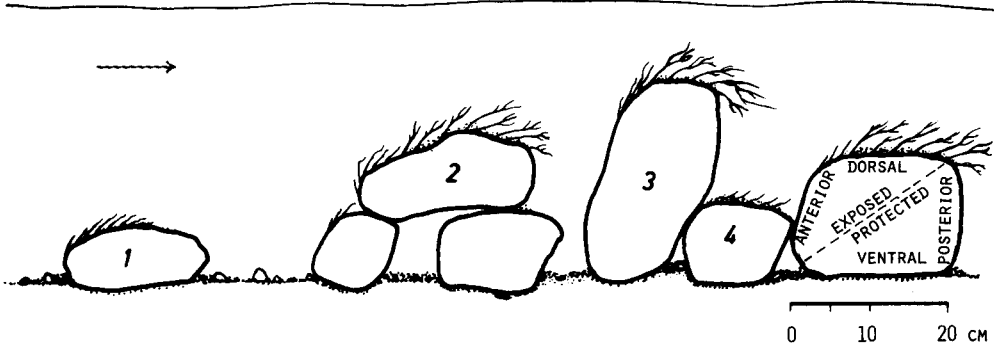


Fig. 6. Schematic representation of the attitudes of the stones on the river bed, types 1 ... 4, see text, the micro-habitats recognized and the positioning of algal and moss growths. Lines indicate algae, branched lines mosses and dots detritus and alluvium.

2.4. Habitats

2.4.1. Terminology

The term 'habitat', the site in which a given individual, population or community lives, may vary in its ecological implications in terms of both size and rank (see DICE 1952, SMITH 1966, KREBS 1972). The following concepts will be employed, here in a hierarchical sequence. The rapids as a whole constitute a 'biotope', and any part of this in which the physical environment possesses its own set of characteristics, e.g. of bottom structure, current conditions, sedimentation, etc., represents a habitat proper, in the sense in which the word is used in the title to this section. Every stone, a distinct habitat in itself, but of lower rank, is considered a basic ecological unit, but for the sake of clarity the term habitat will be avoided in this connection. Finally, any given part of a stone can constitute a micro-habitat. All levels except the micro-habitat are regarded as 'bearing' a set of inhabitants grouped into a community.

The principle adopted for determining the location of the animals on the stones is that which distinguishes basically an exposed and a protected aspect (see GEIJSKES 1935). The exposed aspect accounts for the forward and upper surfaces and also those areas on the sides which are believed to be reached directly by the current, while the protected aspect includes the remainder of the side surfaces plus the back and lower surface (see Fig. 6).

Depths (Table 3) are measured from the top of the stone to the surface of the water.

All those animals which came loose from their places of attachment during the lifting process and fell into the net or bowl, so that their micro-habitat cannot be stated with certainty, are labelled as 'displaced'.

2.4.2. General descriptions

The upper edge of the weir impounding the small basin upstream constitutes the



Fig. 7. Schematic drawing of the general structure of the upper part of Jäväjänkoski as surveyed in 1965 and current conditions as measured in 1971. The habitats studied are marked with letters (chapter 2.4.2.).

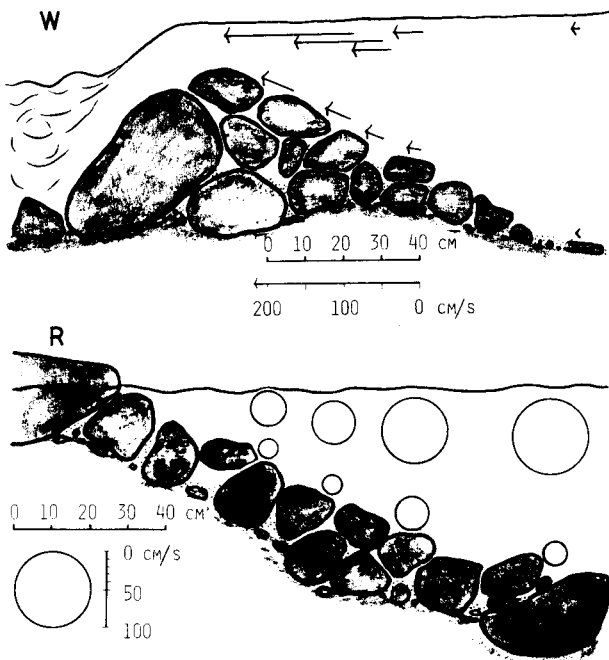


Fig. 8. Sketch of the structure and measured current conditions of the weir habitat (W), longitudinal section, and the riverbed (R), in cross-section.

weir habitat (Figs. 7 and 8). Here a mixture of gravel and stones, the latter still somewhat loosely wedged one against the other, unselected and with a mean diameter of approx. 25 cm, forms an exposed slope. Its even current increases towards the top of the weir over a very short distance, while at the same time the bottom assumes a progressively rougher profile, the gravel and smaller stones being washed out by the stronger current. This weir is a dynamic habitat, which is reshaped to some extent by every period of flooding and every occasion on which the ice breaks up.

The *riverbed* habitat (R) is located at the side of the main channel downstream the weir, a point at which the water tends to adopt a swirling motion. The channel itself is much more static in structure than the weir, and its bottom is composed of sorted stones, wedged together and of more even size (mean diameter 15–35 cm), having reached an equilibrium of erosion and deposition.

The remaining habitats are all ones with few stones on the river bed, this being chiefly composed of gravel.

The *edge* habitat (E) consists of a shallow river-bank terrace some 10–20 cm in depth with a slow current, the bottom being of coarse gravel with a few stones embedded in it. A thin film of mud could be observed. The *backflow* habitat (B) is situated in an alcove, depth 25–40 cm, below the weir. As a result of the slow, swirling current at this point, the originally stony bottom has been covered with a thick alluvial deposit, mainly of silt. The *deadwater* habitat (D) is located downstream of some large boulders in the water below the weir (Fig. 8) with such an aspect that of all the water flowing over the weir only a swirling current developing at this point comes into contact with the two stones lying at a depth of 25–40 cm on the river bed, which is here composed of small pebbles and gravel. Finally a habitat was selected from a *channel* (C) running between an area of stones left dry during the summer low-water period and the bank of the river. The even gravel bed of this channel possesses just a few largish stones (diameter 25 cm) which project outwards to be washed by the rapid streaming current.

Detritus was to be found at all these sites, both attached to the plants and also loosely deposited on the more sheltered stones and in the crevices between them. On the other hand the current on the weir in particular appeared to be sufficiently strong to prevent any deposition. Sediments had accumulated both in the backflow inlet and at the base of the weir, on the shore and on the stones lining the main channel. A small number of larger plant remains such as blades of grass, leaves and pieces of twig had fallen onto the bank, into the deep water upstream of the weir and the backflow inlet, and into the channel.

The present research thus involves both natural and somewhat artificial environments. The riverbed, channel and backflow inlet can scarcely have been affected at all by the restructuring of the river bottom, but the weir, the deadwater and the edge must still be in the process of recovering their equilibrium after this event. These newer habitats will have suffered disturbances in the form of the random re-positioning of the stones, upside down, for example, in which case the loss of the mosses from the upper surfaces would serve to reduce the area to which detritus or certain animals could become attached.

2.4.3. Current

The current in the deep water upstream of the site in question becomes somewhat swifter than the normal sluggish flow associated with such stretches of river some 200 m earlier, and with its transverse rocks and narrow channels, the outlet from this deep section assumes a quite distinct gradient. Thus the general current may accelerate to 50–125 cm/s at the heads and streams of the rapids (Fig. 7). The weir, channel and riverbed habitats are located in such areas, although it should be noted that the current at the weir has declined since 1965 with the partial collapse of the structure.

A highly significant correlation ($r = 0.77$, $df = 75$) was obtained between the surface and bottom current in the rapids, as is often the case in natural waterways (NIELSEN 1950, SCOTT 1958). The unevenness of the river bed nevertheless leads to a situation in which the individual local values do not necessarily reveal this dependency, e.g. in the main channel. Such irregularities in flow are naturally typical of rapids.

The mode of flow at the weir habitat is streaming with a moderate to very strong current, 39–163 cm/s (Table 3, Fig. 8), while in the channel it is turbulent with ripples and a moderate to strong current, 46–61 cm/s, as also in the riverbed, 39–83 cm/s, both values very typical of rapids (Fig. 4). The deadwater site has a whirl with slight to moderate current 15–34 cm/s, characteristic of water passing over a weir (Fig. 8), and at the edge the current is very slight to slight ≤ 18 cm/s, as at the sides of channels in general. The mode of flow at the backflow site is just as the name would suggest, and the current is very slight to moderate, ≤ 29 cm/s. The median of the surface velocities observed, 49 cm/s, lies on the borderline between moderate and strong, but the mode class is clearly 'strong current'.

The habitats may be grouped according to their mean current and point flow as follows:

edge, $v = 11$ cm/s, $q = 2.5$ l/s,
backflow, $v = 11$ cm/s, $q = 4$ l/s, and
deadwater, $v = 13$ cm/s, $q = 3.5$ l/s, 'slow';
channel, $v = 43$ cm/s, $q = 7.5$ l/s, and
riverbed, $v = 39$ cm/s, $q = 9.5$ l/s, 'rapids like';
weir, $v = 63$ cm/s, $q = 19.5$ l/s, 'outflow-type'.

2.4.4. Size and attitude of stones

The size of each stone was measured in the form of an axial projection (see SCHRÄDER 1932, ALBRECHT 1953, MÜLLER 1953) by reference to the dimensions length x breadth x height (to the nearest cm) of the stone in its actual attitude, where length implies its measurement in the direction of flow of the river. The 'axis area' in dm² (Table 3) was then calculated from the dimensions length x breadth. This value will frequently reflect the area of water covering it in a more realistic manner than Schröder's "grösster Projektion".

Notes were made at the time of any occurrence of detritus or sedimentary material, the position of the stone in question in relation to others and its attitude (Fig. 6).

Table 3. *Ecological data of stones from different habitats (E ... W; the number of stones sampled in parentheses).*

	Stone no.	Axis area (dm ²)	Moss cover	Algal cover	Depth (cm)	Current speed: surface (cm/s) bottom (cm/s)		Point flow (l/s)
E	1.	1.1	0	2	20	5	1	0.5
	2.	3.1	2	0	10	12	1	0.5
	3.	2.1	1	1	25	18	15	4
	(4) 4.	2.1	0	2	25	18	16	4
B	32.	0.7	0	2	15	5	1	0.5
	(2) 33.	2.5	0	2	40	29	10	8
D	34.	2.1	0	2	25	15	1	2
	(2) 35.	3.7	2	0	30	34	1	5
C	5.	2.1	2	0	10	46	27	4
	6.	1.9	2	2	20	61	29	9
	(3) 7.	3.7	0	0	20	61	33	9.5
R	8.	1.8	1	1	20	39	14	5.5
	9.	2.2	1	0	35	41	22	11
	10.	3.1	3	0	15	43	26	5
	11.	5.8	1	2	25	46	18	8
	12.	2.3	1	1	25	46	30	9.5
	13.	2.1	0	0	25	49	17	8
	14.	2.1	1	1	25	52	27	10
	15.	1.4	2	0	25	56	15	9
	16.	3.1	2	0	15	56	21	6
	17.	1.5	1	1	25	61	37	12
	18.	2.5	1	1	25	70	18	11
	(12) 19.	4.3	1	1	30	83	39	18.5
W	20.	3.7	0	2	40	22	19	8
	21.	3.1	1	2	30	46	33	12
	22.	3.8	0	2	30	49	25	11
	23.	4.3	0	1	40	61	30	18
	24.	1.5	0	1	45	61	41	23
	25.	2.1	1	1	35	71	52	22
	26.	4.3	1	2	40	79	46	25
	27.	2.6	0	0	40	95	29	25
	28.	2.6	0	1	40	95	49	29
	29.	2.3	0	1	20	110	35	14.5
	30.	1.9	0	1	20	130	110	24
	(12) 31.	1.9	1	0	20	163	46	21

The mean dimensions (\pm SD) of the stones studied were 16.3 (\pm 3.5) x 15.9 (\pm 4.7) x 9.5 (\pm 3.8) cm, the smallest being 12 x 6 x 6 cm and the largest 18 x 24 x 24 cm. The axis area varied in the range 0.7–5.8 dm², with a mean (\pm SD) of 2.6 (\pm 1.1) dm². They may be thus classified best as 'large stones' and 'small boulders' (MACAN 1962), or 'cobbles' and 'boulders' (CUMMINS 1962). The general character of the river bed is one of boulders.

The stones were found in four main attitudes (Fig. 6): 1) lying freely on the gravel bed, i.e. with the full force of the current brought to bear on the stone, 2) lying freely on other stones, 3) lying between other stones and only partially exposed to the current, and 4) entirely protected by other stones. Attitude 1 was most typical at the edge, back-flow and channel sites, types 2 and 3 on the riverbed and weir and type 4 at the dead-water site (Appendix).

Deposits of detritus and sediment were observed both on the plant cover and on the sheltered sides of the stones in general, in cracks, on the undersides, or in places where the flow was slow or non-directional, even on the upper surfaces of the stones, e.g. in the backflow and deadwater areas.

2.4.5. Vegetation

The cover of mosses and algae on the stones was analyzed, and their abundance was estimated according to the following rough scale (Table 3):

- 0 scarcely distinguishable growth (the stone practically bare),
- 1 clearly discernable growth, but limited in extent,
- 2 abundant growth, which may still be restricted to one area of the stone, and
- 3 remarkably dense growth, normally capping the entire upstream face of the stone.

The approximate dry weight limits of the mosses per dm² were determined after one month under aerated conditions at room temperature giving values of < 1 g, 1–2.4 g, 2.5–4.9 g and ≥ 5 g respectively for the above classes. No corresponding quantitative classification was attempted for the algae.

The most commonly occurring moss species was *Hygrohypnum ochraceum*, in the midst of which a certain amount of *Fontinalis dalecarlica* could also be identified, a species which is found in greater abundance at certain points elsewhere in the rapids. Well-defined algal growths were to be found on those stones which possessed little or no moss cover, comprising chiefly the epilithic red algae of the genus *Batrachospermum* and a number of branching, ribbon-like green algae, among which it was possible to identify *Draparnaldia glomerata* and various members of the *Cladophorales* and *Zygnemales* groups, i.e. *Cladophora*, *Mougeotia*, *Zygnema* and *Microspora*. Epilithic and epiphytic examples of *Tabellaria* algae were also encountered in considerable quantities, and of Pennales diatom frustules to a limited extent, e.g. *Navicula* spp.

The riverbed habitat, being physiographically a more balanced environment, possessed an abundant, well-rooted vegetation, with a sandy deposit up to a couple of centimetres in depth to be found around the roots of the mosses. The mosses were growing mainly on the upper surfaces of the stones, and in many instances precisely on the practically current-free rear portion of this surface (AMBÜHL 1959), in such a way that where the stones happened to be of approximately the same height the moss growths on the individual stones gave the appearance of forming a continuous moss carpet on the river bottom. The mosses on the lower surfaces of the stones comprising the weir turned

out to have withered and died with time, and similarly mosses did not seem to thrive in sluggish water or in a deadwater situation in which sedimentation was occurring, i.e. at the backflow and deadwater sites. According to BUTCHER (1933), mosses do indeed become the dominant plant growth in rapidly flowing water (> 50 cm/s).

Examples of the manner of growth of the algae are to be found for the stones of the weir, where scarcely any new mosses had been able to gain root. On many of these stones the algae grew most densely on the forward part of the upper surface and on the exposed surface (Fig. 6; see AMBÜHL 1959). Algal growths encompassing the entire upper surface were found on some stones in the backflow and dead water habitats and in the deeper parts of the weir.

3. MATERIAL AND METHODS

3.1. Lifting of the stones, recovery of the animals and identification

A number of tests carried out at various sets of rapids served to demonstrate that the manual lifting method of Alm and Schröder (see SCHRÖDER 1932), in which the stones are lifted by hand under the water into a Macan shovel sampler (MACAN 1958a), cannot be used successfully in all circumstances. The method proved successful, however, under the following conditions:

- when the stone would fit into the net frame of the shovel (dimensions 22.5 x 22.5 cm), so that the displaced individuals fell into the net. This meant that stones with a maximum diameter of around 30 cm or more had to be rejected.
- when the stone was located in sufficiently shallow water, as in the main channel in particular. The strength of the current made working impossible by a depth of about 40 cm. On the other hand, the sudden drop in the water level meant that it was necessary to check that there was at least about 12 cm of water above the stone.

A total of 7269 animals were collected from 35 stones in the rapids and from the plants growing on them immediately after lifting during the period 7th–24th June 1965. The macrozoobenthos was taken to include all animals detectable by the naked eye regardless of their stage of development, i.e. including larvae, nymphs, pupae, fresh cases and cocoons and hatching imagos. Upon subsequent measurement this boundary proved to lie at approx. 1 mm. These samples, representing the exposed and protected aspects and the displaced individuals for each stone, were preserved in ethanol. In view of the difficulty experienced in separating the individuals, each Bryozoa colony was treated as one unit. Detailed statistics for the whole material are provided in the Appendix.

An attempt was made to determine the animals to species either by name or by means of an OTU (SNEATH and SOKAL 1973) filled out by reference to the nearest recognizable taxon (e.g. *Pentaneurini* sp. A, B or C, *Eusimulium* sp., etc.). Some spp. units nevertheless had to be distinguished in view of the difficulties encountered in identification. Where these probably represented the pupae of already identified species or were composed of individuals which had lost their distinguishing characteristics, they were omitted from the calculations of the numbers of species per stone, habitat or total community (see Appendix). The categories *Athripsodes*, sensu lato, spp. and Simuliidae spp., on the other hand, presumably include altogether two or three distinct species each, and thus the

indicated numbers of species in some stone communities or combinations of these are artificially low, which will naturally also have repercussions for the species diversity and evenness values (see below, p. 72).

The source for the identification and nomenclature is given in conjunction with the results for each group.

3.2. Statistical procedures

Conventional chi-square tests (two-way and multi-way contingency tables), correlation and linear regression analyses and t-tests are employed. The other methods used are described at the relevant points in the text. Levels of significance and probability are denoted in words as recommended by ELLIOTT (1971): significant, highly significant, very highly significant. Significance is expressed at the probability in the form ($p \leq$) when it is not stated otherwise.

3.3. Sources of error

A sudden change in water level occurred on the second day of the work, as a consequence of which only the stones lifted after this, with the exception of channel stone no. 5, are fully intercomparable with respect to the depth requirement.

It may be assumed that the majority of the displaced specimens fell into the net during the lifting of the stones, and that the numbers escaping should be in similar proportions to those captured. The main species which may be considered unreliable as far as their sampling is concerned are the rapid swimmers, e.g. the *Baetis* nymphs, the more clumsy crawling species, e.g. some of the Limnephilidae, and the more weakly lithophile creatures, e.g. the *Pisidium* mussels, examples of which could often be seen on the underlying gravel bed.

The collecting of the animals from the stones often took such a time to complete that some had changed their micro-habitat in the interim. These together with the creatures obtained upon rinsing the stone added to the number of displaced specimens to such an extent that at their most numerous these could account for about two-thirds of the total fauna of the stone, e.g. in the cases of stones 6 and 7 in the channel. The proportions of displaced specimens vary between the habitats within the range 7–40 %, the overall proportion of 14.5 % lying within the limits 4–20 % noted by BADCOCK (1949) in his work in the River Dee. Large proportions of displaced individuals will naturally be a source of statistical uncertainty when examining the micro-habitat preference of any species. Drifting is by nature a property of flowing water animals, and unfortunately cannot be avoided during sampling.

Detection of the smallest creatures was obviously dependent on the illumination, and this may cause some error, although not of any great magnitude, in the collection of midges, stoneflies, mayflies and watermites. Their growth as the research proceeded presumably led to an improvement in their discovery rate. Nymphs of *E. ignita* measured 1.2 mm in length on 12th June, for example, whereas by 24th June they were about 3 mm.

4. FAUNISTIC RESULTS AND AUTECOLOGICAL NOTES

4.1. Introduction

The purpose of this section is firstly to provide a general impression of the composition of the faunal communities in the habitats studied at the level of their 'principal taxa', and then to review the fauna in the order given in the Appendix, noting first the authorities for the identification of each taxon and then describing certain species of operational importance here. An attempt is made to include only the most essential results, i.e. those concerning the incidence of each group and its species (on a scale: rare, frequent, common, very common; see Fig. 14, p. 63), their abundance on the stones in relation to environmental factors and their distribution by micro-habitat. When noting the principal diet of each species no separate reference are given to the section of this work which discusses this aspect in greater detail. In view of the comments made above, references to the literature for comparative purposes will be restricted to essential instances, especially in the case of the better known species. Species records not previously reported from Finland will be indicated appropriately.

4.2. General composition of the communities

The 7269 individuals comprising the macrofauna of the stones studied consisted of 96.7 % insects, their proportion becoming progressively greater with increasing current (Fig. 9). This latter trend was largely a consequence of the greater abundance of Diptera

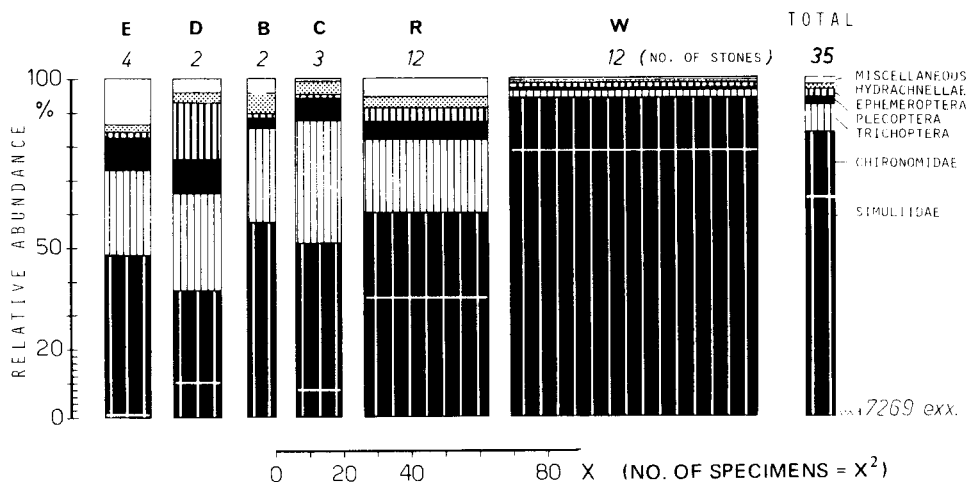


Fig. 9. General composition of the communities in the various habitats (E ... W) and in total.

under such conditions. The 'non-insect' part of the fauna appeared to thrive best on moss or alga-covered stones in the edge or backwater habitats, where the characteristic fauna included the Chironomidae and Trichoptera, and they were still well represented in the moss-covered channel and especially on the riverbed, which represents the most typical habitat in the rapids, but achieved very low proportions on the weir, where the Simuliidae were found in vast numbers. No particular group was dominant in the dead water habitat, although the Ephemeroptera were more prominent there than elsewhere, probably as a consequence of individuals drifting from the weir.

The general composition of the fauna possesses certain features in common with communities inhabiting dredged rapids (MÜLLER 1953, CARLSSON 1962) and outlets of lakes (ILLIES 1956, ULFSTRAND 1968), largely by virtue of the dominant position of the blackflies. The proportions of non-insects in the benthos of flowing water habitats generally fluctuate widely (KOWNACKA 1971, HYNES 1970), and figures below one tenth are very common. Similarly, the dominant taxon within this group, which may be Oligochaeta, Mollusca, Amphipoda or water mites, as in the present case, is dependent upon the time of sampling, the area and the characteristics of its habitats.

4.3. Occurrence and ecology of the taxa

4.3.1. *Tricladida* (identification according to REYNOLDSON 1967)

1. *Dendrocoelum lacteum* (O.F. MÜLLER), 30 exx.

This species was rare, but when found, on stones with some vegetation cover in a slight to strong current, occurred in reasonable numbers, 3–14 ind.

The species is well known from a wide variety of biotopes and micro-habitats, e.g. the River Susaa (BERG 1948). It does not tolerate strong currents, being recorded specifically in a slight current by DORIER and VAILLANT (1954), AMBÜHL (1959) and ZIMMERMANN (1961). The higher rates of flow recorded here do not necessarily invalidate this opinion, as it seems to be the micro-current that is the deciding factor. According to REYNOLDSON and YOUNG (1966) the distribution of the species is related to hardness of the water and the incidence of the water slater, an important prey animal.

4.3.2. *Bryozoa* (MARCUS 1940)

2. *Pahudicella articulata* Ehrenberg, 9 colonies

3. *Phumatella repens* L., 10 colonies

Both these species were frequent, being encountered in loosely structured colonies most typically on bare patches on stones otherwise carrying a vegetation cover. *Phumatella* most often occurred on the protected face of the stone. The Bryozoa were found in very slight to strong currents, and were concentrated mainly in the riverbed habitat.

P. articulata has been found in both lenitic and lotic biotopes, usually on the under-sides of stones, or amongst stands of *Fontinalis* in more rapidly flowing water (BORG 1941), while *P. repens* mainly inhabits quietly flowing rivers (BORG 1941, BERG 1948) and is also one of the typical passive feeders to be found at the outlets of lenitic waters (KNÖPP 1952).

4.3.3. *Pelecypoda*

4. *Pisidium* sp., 9 exx.

These bivalves were rare amongst the fauna of the stones themselves, being typically non-lithophilous creatures (see p. 00), but were later found frequently within tufts of moss mixed with sand.

In his work on the bivalve fauna of Mustionjoki, KEYNÄS (1967) observes the majority of these species to tolerate strong currents by seeking shelter. As the current increased, individuals could be seen to move away from the upper surfaces of the stones and towards the spaces between them.

4.3.4. *Oligochaeta* (BRINKHURST 1963)

5. *Stylaria lacustris* (L.), 2 exx.

6. *Pelosclex ferox* (Eisen), 8 exx.

These species were rare in their occurrence and few in number, but were found under varying current conditions up to swift.

S. lacustris is a cosmopolitan species, generally preferring fresh water (BRINKHURST 1967). In the River Susaa (BOISEN-BENNIKE and BERG 1948) it was found in abundance in quietly flowing waters amongst the submerged vegetation (see also WESTLAKE *et al.* 1972). According to SÄRKKÄ (1978), *P. ferox* is a eurytopic species which is dominant within its order in profundal biotopes of oligotrophic lakes with a high oxygen saturation. This seems to be the ecological link with its occurrence here in a rapids environment.

4.3.5. *Hirudinea* (MANN 1954)

7. *Helobdella stagnalis* L., 2 adults

8. *Erpobdella octoculata* L., 20 adults, 12 cocoons

These leaches constituted a common group, occurring in all habitats except the dead water and channel. *E. octoculata* was found with almost complete regularity (9 times out of 10) on bare protected faces of stones in a very slight to strong current.

These two species are recorded in flowing water, with a preference for soft water and stony stream beds, and with *E. octoculata* dominant (MANN 1955, DAHM 1964, KALBE 1966). The present result from Lestijoki supports the existence of such an ecological dependency.

4.3.6. *Acari: Hydrachnellae* (VIETS 1936, VIETS and VIETS 1960, nomenclature: VIETS 1967)

9. *Sperchonopsis verrucosa* (Protz), 7 exx. (not previously reported)
10. *Sperchon clupei* Piers., 15 exx. (not previously reported)
11. *Lebertia* sp. (gr. *insignis* Neum.; VIETS 1960), 19 exx.
12. *Torrenticola amplexa* (Koen.), 23 exx. (not previously reported)
13. *Hygrobates fluviatilis* (Ström.), 18 exx.
14. *Hygrobates calliger* Piers., 27 exx. (not previously reported)
15. *Hygrobates* sp., 1 ex.
16. *Hydrachnellae* sp., 1 ex.

These water mites were to be found in all habitats from practically the slowest up to the most rapid currents. Their incidence, 70 % of stones, would correspond to the designation 'very common', and the five most abundant species were all frequent. One outstanding feature is that the majority of the occurrences involved only one or two specimens per stone, while two of the stones, Nos. 17 and 25, featured as many as five of these species each. No micro-habitat or vegetation preferences could be detected.

In terms of the classifications provided by KEIDING (1948) and VIETS (1967), all the species identified here with the exception of the true *L. insignis* are representatives of the rheophilic water mites. In Keiding's opinion, the rather limited material from the River Susaa indicates that "current velocity plays no great part in the distribution of mites in a river course". The wide-scale occurrence of these species at Jäväjänkoski in relation to current speed is similarly a clear sign of their eurytopic nature, as also is their geographical distribution (see VIETS 1967).

4.3.7. *Isopoda* (BIRSTEIN 1951)

17. *Asellus aquaticus* L., 27 exx.

The waterslatter is frequent in occurrence, although restricted to slight to strong currents, tending to evade the direct impact of the current. It is known to inhabit vegetation and plant detritus deposits in the littoral zones of standing waters in particular, but is highly eurybiotic in respect of its water property demands (BIRSTEIN 1951, REYNOLDSON and YOUNG 1966). HYNES (1960) mentions that local accumulations of detritus may lead to the rise of dense occurrences of waterslatter even in rivers, and the present finds of this species in the deeper part of the weir and the deadwater area may be attributable to this cause.

4.3.8. *Ephemeroptera* (MACAN 1961, BENGTTSSON 1930, ULMER 1943)

- 18.-22. (Table 4)

All five species were encountered in the riverbed habitat, with the edge, backflow and channel habitats of relatively minor significance. In its incidence figures, this order was

Table 4. *Ephemeroptera* species identified, their incidence, and number of individuals, proportions of total fauna (approx. %) and density (approx. mean no. of ind./stone) in the various habitats and the total material.

Species	Habitats						Total	Incidence
	E	B	D	C	R	W		
18. <i>Heptagenia sulphurea</i> (Müll.)	2	—	6	1	16	13	38	19/35
19. <i>Baetis rhodani</i> (Pict.)	—	—	2	—	16	19	37	12
20. <i>Baetis vernus</i> Curt.	—	—	9	—	17	34	60	12
21. <i>Ephemerella ignita</i> Poda	—	1	16	—	3	12	32	11
22. <i>Ephemerella mucronata</i> Bgtss.	1	—	—	1	4	—	6	5
Totally	3	1	33	2	56	78	173	26/35
%	2	1	17	1	4	1	2	
Density	1	1	17	1	5	7	5	

clearly rated as very common, achieving a prevalence of 100 % on the weir, although among the individual species only *H. sulphurea* was common, the others being less frequent ($\leq 12/35$). Certain significant micro-habitat preferences emerged (Table 5).

18. *H. sulphurea* favoured stones with a greater or lesser vegetation cover, beneath which there was a certain amount of deadwater space, or on which some proportion of bare protected surface was to be found (position types 2 and 3). The nymphs tended to attach themselves firmly onto the stones, as indicated by the low proportion of detached specimens. These findings from Jäväjänkoski recall the description provided by SCHOENEMUND (1930). Other preferential habitats reported are bare stones and gravel in locations with a high current velocity in general (MACAN 1940, MADSEN 1968) and the outflow channels of lakes (ULFSTRAND 1968, SÖDERGREN *et al.* 1976), and also stony lake shores (NIELSEN 1950, HARRIS 1952), on which the waves of the lake presumably keep the stones free of mud, one ecological requirement of the species (MACAN 1940) which is fulfilled in streams by the current. The flattened shape of the larvae may be interpreted as an adaptation to living under and between stones (NIELSEN 1950, cf. HYNES 1970), a notion which finds support from the present

Table 5. *Distribution of Ephemeroptera by micro-habitat and significance of micro-habitat preference (chi-square tests).*

Species	Micro-habitats		Displaced nymphs
	Exposed	Protected	
<i>H. sulphurea</i>	4	26***	8
<i>B. rhodani</i>	11	4	22
<i>B. vernus</i>	39***	5	16
<i>E. ignita</i>	17***	1	14
<i>E. mucronata</i>	3	2	1

material. MADSEN (1968), however, who 'usually' found his larvae on the upper surfaces of stones, although well cemented in the substrate, concludes that their shape must be a device enabling them to live "an exposed life".

19 & 20. *B. rhodani* and *B. vernus*. Both these species showed a striking and consisted rheophile trend, being entirely absent from the more quietly flowing habitats and only increasing in incidence and density of population at sites where the current was stronger. Thus the most typical description of the environment of the *Baetis* larvae would be a shallow, stony place with a strong current, the stones having little or no vegetation cover, but an accumulation of detritus being present in the deadwater areas and on any plants to be found. The preference shown here for the weir habitat is presumably also due to the availability of suitable food items. The exposed faces of the stones proved the favourite micro-habitat. The large numbers of detached specimens recovered indicate a low affinity for the substrate.

Baetis is one of the most frequently mentioned genera in faunal lists from the widest possible variety of flowing water habitats (see references and discussion in GEIJSKES 1935, JONES 1949, MACAN 1957, ULFSTRAND 1968, SOWA 1975). The present observations confirm the impression given in the literature. These species certainly actively chose sites on the top ridges of the stones, where they are exposed to the current (HARKER 1953) and therefore highly susceptible to drifting, being together with *E. ignita* some of the most common drift species of all (MÜLLER 1966, ELLIOTT 1967; note their accumulation in the deadwater habitat here). The environmental description of their habitat characteristically bears a current designation of 'schnell', 'fast', 'rapid', etc., and also some mention of a stony bed with no sedimentation. The ecological segregation of the two species is based not on an examination of their micro-habitats, but rather, in MACAN's opinion (1957), on the profile of the river, *B. rhodani* occurring in streams and the upper reaches of rivers and *B. vernus* in the weedy lower reaches. Since the body lengths of the nymphs recovered from Jäväjänkoski were in the ranges 6.0–9.5 mm for *B. rhodani* and 2.0–6.5 mm for *B. vernus*, it seems that some segregation also occurs in terms of a slight difference in the timing of growth and emergence.

21. *E. ignita* occurred frequently and exhibited rheophile features, although admittedly less markedly than the *Baetis* species above, in its presence on stones even in strongly flowing currents. Its location in the slower part of the weir, in the deadwater and among the vegetation on stones may be regarded as a protective tendency, but nevertheless the preferred micro-habitat proved to be the exposed face of the stone, especially where this carried an algal growth. The presence of vegetation and accompanying detritus was reflected in the diet of the larvae.

E. ignita emerges in the literature as a eurytopic species capable of living in any type of flowing water from upland streams to lowland rivers (see DITTMAR 1955, MACAN 1957), and even on stony lake shores (TIENSUU 1939, MAITLAND 1965). The natural environments for these climbing ("kletternde") larvae (ILLIES 1968) are seen to include stony bottoms with varying types of vegetation and slow to strong current velocities (see PERCIVAL and WHITEHEAD 1929, MACAN 1957, HÄGGMAN 1960, MAITLAND 1965, LEVANDIER and DUMAS 1971, FRIBERG *et al.* 1977). The amount of *Cladophora* algae present is one of the criteria pointed out as explaining differences between habitats in the numbers of this species observed (BADCOCK 1954b, HYNES 1961, MAITLAND 1965).

Table 6. *Plecoptera* species identified. For explanation, see Table 4.

Species	Habitats						Total	Incidence
	E	B	D	C	R	W		
23. <i>Amphinemura borealis</i> Mort.	16	—	9	11	61	2	99	18/35
24. <i>Taeniopteryx nebulosa</i> (L.)	—	—	6	—	1	16	23	7
25. <i>Leuctra digitata</i> Kmp.	—	2	5	—	6	11	24	13
26. <i>Isoperla obscura</i> Zett.	1	—	—	2	2	—	5	5
27. <i>Plecoptera</i> sp.	—	—	—	—	—	2	2	1
Totally	17	2	20	13	70	31	153	27/35
%	8	3	10	7	5	1	2	
Density	4	1	10	4	6	3	4	

22. *E. mucronata* was a rare species with a euryhealic pattern of occurrence, usually being found as single examples, always on moss-covered stones.

The material of ULFSTRAND (1967) shows this species to have a significant preference for stones with a thin coating of mud, but his observation that the species would also thrive in large numbers in other biotopes in localities beyond that represented by his material would seem to hold good in the light of the results from Jäväjänkoski.

4.3.9. *Plecoptera* (BRINCK 1949, 1952)

23.–27. (Table 6)

The Plecoptera, like the Ephemeroptera, were very common in occurrence, but were not present in any great numbers, nor were they represented by very many species. These nymphs inhabited almost all the stones in the channel, riverbed and weir habitats, but the mean density within each habitat ranged from 1 to 10 ind. per stone, showing an apparent dependence upon the extent of the moss cover.

23. *A. borealis* was the dominant species numerically and also the most frequent in its incidence, being rated as common. It is clearly an inhabitant of moss-covered stones (see Appendix). Its density (ind./stone) declined with increasing current velocity, but not to a significant extent ($p \cong 0.20$). Almost exactly a half of the specimens of known

Table 7. *Micro-habitat distribution of A. borealis* nymphs by current velocity (chi-square heterogeneity).

Micro-habitats	Current rate			Chi-square
	slow	moderate	strong	
Exposed	15	20	8	19.50 ***
Protected	1	18	23	

location were taken from the exposed faces of the stones and half from the protected faces. An examination of location in relation to current velocity (Table 7) leads to the conclusion that as the current becomes stronger the larvae begin to avoid the exposed faces of the stones, even in spite of the shelter offered by the moss cover, and a strong current is already sufficient to force them onto the protected face entirely.

The obvious reason for the distribution of this species lies in the presence of fine detritus (see p. 19), which is also its chief source of nutrition. ULFSTRAND (1967) notes a very high preference for a substrate made up of stones covered by detritus in this species, and EGGLISHAW (1964) observes that the presence of detritus as a food source is an equally important determining factor in the environmental choice of *A. sulci-collis* as the protection offered by the stones. In the opinion of Egglishaw, the nature of the bottom as such and its moss cover (absent from his site) is largely dependent upon current velocity as far as its capacity to retain detritus is concerned (see ASPLUND and KARLSTRÖM 1975). In this case both the current and the structural properties of the bottom constitute, through the detritus, crucial indirect factors in determining the environment of *Amphinemura* populations.

24. *T. nebulosa* proved to inhabit the protected faces of stones and to be concentrated in the weir site with its strong and very strong currents, although it was also to be found among the mosses in the dead water habitat (cf. the mayflies). This winter stonefly constitutes a striking feature of Jäväjänkoski (KUUSELA 1976), and is found in large numbers crawling among the tufts of moss in autumn and winter. These observations serve to extend the known habitat range of the species, as it is reported to inhabit rooted vegetation in (sluggish) rivers in Britain, for instance (HYNES 1941), and both stony sites with a fast flow and also mud and detritus river beds with a slow flow in Sweden (BRINCK 1949, ULFSTRAND 1968).

25. *L. digitata* very nearly reached an incidence rate of 'common', but was not numerous on any occasion. The distribution of the individuals among the exposed and protected faces and the detached specimens, 6–9–9, is indicative of a preference for the protected face and a weak lithophile status. The occurrence of this species in relatively deep water with a moderate to strong current and its absence from the exposed stones of the edge and channel habitats (position type 1), for example, would suggest that it lives amongst accumulations of detritus beneath and between the stones. The living habits of this species, described by BRINCK (1949) as a eucoenic species in northern streams, are very poorly understood, but the present observations from Jäväjänkoski and the food analyses carried out by Brinck on a few specimens suggest that it does not differ substantially from the other *Leuctra* species in this respect. These are reported to thrive in a mixture of stones and gravel and to burrow down into this substrate, feeding on plant and moss tissues and detritus (HYNES 1941).

26. *I. obscura* was a rare predator species encountered on five moss-covered stones in currents varying from slow to strong. It is described as a naturally occurring species of northern rivers which also thrives in a number of other watercourses (BRINCK 1949). ULFSTRAND *et al.* (1971) explain the concentration of larvae among accumulations of detritus observable in their material as being due to the affinity shown by these larvae for their prey animals.

27. Plecoptera sp. probably in fact contains *Leuctra* sp. other than *digitata*, but the young nymphs of this genus are difficult to identify (BRINCK 1949).

Table 8. *Trichoptera* species identified, their incidence and distribution by micro-habitat and life stage (exp. — exposed, pro. — protected, dis. — displaced; l — larvae, p — pupae, pr — pupal remnants and empty cases).

Species	Micro-habitats			Total	Life stage			Incidence
	exp	pro	dis.		l	p	pr	
28. <i>Agraylea multipunctata</i> Curt.	4	9	3	16	16	—	—	12/35
29. <i>Ithytrichia lamellaris</i> Eat.	4	33	2	39	36	3	—	16
30. <i>Oxyethira frici</i> Klap.	—	11	—	11	1	9	1	8
31. <i>Hydroptila tineoides</i> Dalm.	21	32	8	61	22	5	34	18
32. <i>Rhyacophila nubila</i> Zett.	42	29	14	85	75	10	—	24
33. <i>Agapetus ochripes</i> Curt.	—	4	—	4	—	4	—	2
34. <i>Wormaldia subnigra</i> McL.	—	1	—	1	1	—	—	1
35. <i>Polycentropus flavomaculatus</i> Pict.	—	6	1	7	7	—	—	5
36. <i>Psychomyia pusilla</i> Fbr.	—	2	1	3	3	—	—	2
37. <i>Hydropsyche pellucidula</i> (Curt.)	1	17	4	22	18	4	—	9
38. <i>Cheumatopsyche lepida</i> (Pict.)	—	12	5	17	16	1	—	4
39. <i>Ceraclea annulicornis</i> (Steph.)	—	2	1	3	2	1	—	2
40. <i>Athripsodes cinereus</i> Curt.	1	1	—	2	2	—	—	2
41. <i>Ceraclea excisa</i> (Mort.)	2	11	2	15	12	1	2	8
42. <i>Athripsodes</i> , sensu lato, spp.	12	27	6	45	20	2	23	15
43. <i>Micrasema</i> sp.	6	4	3	13	8	—	5	5
44. <i>Micrasema setiferum</i> Pict.	38	24	7	69	3	26	40	12
45. <i>Lepidostoma hirtum</i> Fbr.	51	65	39	155	143	—	12	26
46. <i>Limnephilinae</i> sp.	—	18	—	18	3	15	—	3
47. <i>Stenophylacini</i> sp.	—	2	—	2	2	—	—	2
48. <i>Potamophylax latipennis</i> (Curt.)	—	3	—	3	3	—	—	2
49. <i>Trichoptera</i> sp.	4	2	2	8	8	—	—	5
Totally	186	315	98	599				34/35

4.3.10. *Trichoptera* (LEPNEVA 1964, 1966, HICKIN 1967)

28.—49. (Table 8)

The caddisflies constituted a very common group (34/35), being the most numerous of all the insects after the Diptera. They accounted for between a fifth and a good third of the total number of specimens in every habitat except the weir, where they reached only 2 %. The more mossy habitats, the channel, riverbed and deadwater, maintained about 2.5 times the density of these individuals, calculated per stone, compared with the other habitats, and approximately the same ratio also prevailed between these two habitat groups, in which the combined axis area of the stones was similar, in terms of the density of individuals per dm², i.e. 9.1 vs. 3.9. This is a good indication of the attractiveness of a moss substrate for these species. The best represented families were the Hydroptilidae and Lepidostomatidae, with the Leptoceridae being present in all the habitats (Table 9), while the Rhyacophilidae were also very common. All the other families showed much more restricted occurrence. Considerable differences could be seen between the habitats

Table 9. *Percentage distribution of Trichoptera families and their total numbers, proportion of total fauna (%) and density (approx. mean no. of ind./stone) in the various habitats and the total material.*

Family	Habitats						Total
	E	B	D	C	R	W	
Hydroptilidae	11 %	11 %	14 %	10 %	29 %	18 %	21.2 %
Rhyacophilidae	—	26	21	6	12	24	14.2
Hydropsychidae	—	—	2	4	3	23	6.5
Leptoceridae	13	37	29	27	2	8	10.8
Brachycentridae	9	—	16	20	19	1	13.7
Lepidostomatidae	44	16	13	27	28	22	25.9
others	22	11	5	34	8	4	7.7
Totally	45	19	56	70	290	119	599
%	25.3	27.9	28.6	36.4	21.7	2.2	8.24
Density	11	10	28	23	24	10	17

in the proportions of the various families within the Trichoptera fauna, and only some of these preferences appeared to be attributable to any general environmental or biological factors. The main associations which could be posited were those of the Brachycentridae with a moss substrate, the Hydroptilidae with mosses and algae, and the Hydropsychidae with a rapid outflow-type current (and indirectly also the Rhyacophilidae with the weir). Such general features offered no explanation for the distribution of the other families, however.

Hydroptilidae 28.—31. (Table 10)

The Hydroptilidae constituted the most frequently occurring of the caddisfly families, comprising the common species *H. tineoides* and *I. lamellaris* and the frequent *O. frici* and *A. multipunctata*. The first of these was the only one to be found in every habitat,

Table 10. *Species of Hydroptilidae identified, their incidence, and numbers of individuals and density (approx. mean no. of ind./stone) in the various habitats and the total material.*

Species	Habitats						Total	Incidence
	E	B	D	C	R	W		
28. <i>A. multipunctata</i>	—	1	1	—	4	10	16	12/35
29. <i>I. lamellaris</i>	—	—	2	2	28	7	39	16
30. <i>O. frici</i>	—	—	—	1	10	—	11	8
31. <i>H. tineoides</i>	5	1	5	3	43	5	61	18
Totally	5	2	8	6	85	33	127	27/35
Density	1	1	4	2	7	2	4	

while the first three showed a preference for the riverbed and the last-mentioned for the weir. The stones of the natural rapids bed having a dense vegetation cover (marked with 2 in Table 3) provided the most favourable environment, with almost four out of five of the individuals originating from such places. This may be looked on as a manifestation of a tendency to avoid a direct current, as is also supported by the fact that the majority of individuals of every species were to be found on the protected faces of the stones. This group nevertheless covered the whole range of surface velocities, *Hydroptila* and *Agraylea* being observed to tolerate the strongest current, while *Oxyethira* was more restricted, being confined to moderate and strong currents almost exclusively in the riverbed.

A typical feature of faunal lists presented in literature is the scarcity of the Hydropsychidae species and the small proportion of the total fauna accounted for by this family (see PERCIVAL and WHITEHEAD 1929, NIELSEN 1948a, BADCOCK 1954a,b, LILLEHAMMER 1965, ZACWILICHOWSKA 1969), and it is perhaps for this reason that little effort has been made to characterize these species in terms of environment. *Agraylea*, *Hydroptila* and *Oxyethira* larvae are said to live typically among the stones and vegetation on surf shores of standing water (see SILFVENIUS 1904, BERG 1938, NIELSEN 1948b, LEPNEVA 1964), and only *I. lamellaris* demonstrates true rheophile tendencies by preferring stony sites in flowing water with a substrate of mosses and submerged plants (see also HARROD 1964), although FROST (1942) admittedly also found large numbers of *Oxyethira* at such a site. The results from Jäväjänkoski, however, testify to a clear preference for a rapids environment on the part of all these species, so that it seems that BOTOSANEANU (1967) is right in attributing the following ecological valencies to the species, all of which carry a hint of a rheophile character: *I. lamellaris* and *O. frici* – rhithron and potamon, *A. multipunctata* – limnion and potamon, and *H. tineoides* – an extremely wide range.

According to NIELSEN (1948b), the species of this group are adapted to moving amongst the filaments of algae and the stems of mosses, and it is these along with their periphytic algae which constitute the food source for these species. The preference for locations on the undersides of stones noted at Jäväjänkoski is probably brought about as a result of the current and may be peculiar to a rapids environment, but it may also be in part the consequence of the inclusion of some pupae in the populations. As Nielsen observes, the pupae of the other species excluding *Hydroptila* generally anchor themselves with strands of secretion to some firm surface, the underside of a stone or the stems of submerged plants, whereas *Hydroptila* can pupate on the upper surfaces of stones, as was evident from the present material.

Rhyacophilidae

32. *R. nubila* was a very common species, occurring in a eurytopic manner on the muddy surfaces of the stones in the backflow area and the moss-covered ones of the dead-water, both with a moderate current velocity, and at the same time on the practically bare stones of the weir, with the most rapid current of all. These finds seem to point to a highly rheophile behaviour, though certainly one in which mosses are of importance in offering shelter and/or populations of prey animals, since the riverbed possessed

more larvae than the weir, two-thirds of the larvae were obtained from moss-covered stones, and every stone on which the species was found had at least 33 % Diptera in its total number of individuals. The distribution of individuals between the protected and exposed faces of the stones, 24 and 39 respectively, does not in itself carry any statistical significance. A certain progressive preference nevertheless emerges in that the majority of the larvae on any given stone shifts gradually towards the protected face as one moves upwards through the current velocity scale from less than 50 cm/s to 50–75 cm/s and to more than 75 cm/s, with 2 out of 7 stones showing such a majority in the first case, and then 4 out of 8 and 4 out of 6. This is at least suggestive of a confirmation for the principle that the moss-free upper surfaces of stones constitute unfavourable habitats for this species in strongly flowing water (SCOTT 1958). It was not possible on the basis of the present material, however, to ascertain whether this shift towards the protected face was simply the normal avoidance of a strong current, or whether it was a mode of preparation for pupation, as the population did include 10 pupae, and this according to Scott does involve the seeking of a sheltered site.

The *Rhyacophila* species are in general among the best-known insects favouring flowing water habitats. The environmental characterizations provided for *R. nubila* usually contain, alongside some mention of the moss cover, a variety of expressions referring to a strong current, e.g. "in rapids from which spray rises" (VAINIO 1938), of "fast current" (LILLEHAMMER 1965, ULFSTRAND 1967). ULFSTRAND (1968) also observed the species in large numbers in outlet-type habitats. Depending on the measurement technique used, the descriptions correspond numerically to values of approx. 50–100 cm/s. The maximum speeds against which *Rhyacophila* species will ascend are of the order of around 125 cm/s (DORIER and VAILLANT 1954, DITTMAR 1955), but the larvae may of course live successfully in habitats with a greater current velocity by seeking appropriate shelter, as seen here on the weir.

33. *Agapetus ochripes* Curt. (Glossomatidae)
34. *Wormaldia subnigra* McL. (Philopotamidae)
35. *Polycentropus flavomaculatus* Pict. (Polycentropidae)
36. *Psychomyia pusilla* Fbr. (Psychomyidae)

These species belonging to a number of different families were all rare in their occurrence, Jävajänkoski apparently representing an atypical environment for all of them.

Pupae of *A. ochripes* were found on the under-surface of two stones on the river-bed. The species has a wide distribution, but is very seldom to be seen in faunal lists. BOTOSANEANU (1967) considers it an inhabitant of streams and mountain rivers which is krenophilous in character (ZACWILICHOWSKA 1970).

W. subnigra was found on the weir. It is known as a hygropetric and microphagous net-spinning species which thrives in rhithron habitats (BOTOSANEANU 1967, EDINGTON 1968, LEPNEVA 1964).

Larvae of *P. flavomaculatus* appeared in 4 habitats. In spite of being a species which traps its food in a web, it can survive just as well on stony lake shores as it can in outlet and rapids habitats (NIELSEN 1948a, MÜLLER 1954, ILLIES 1956, ULFSTRAND 1968). It is indeed regarded as ubiquitous (BOTOSANEANU 1967, ZACWILICHOWSKA 1969).

P. pusilla, which was encountered in the channel and riverbed, is found in very many types of aquatic habitat (BOTOSANEANU 1967, ZACWILICHOWSKA 1970), feeding on microflora which it traps by means of a sand channel (DECAMPS 1967, KAWECKA 1977).

Hydropsychidae

37. *Hydropsyche pellucidula* (Curt.)

38. *Cheumatopsyche lepida* (Pict.)

Individuals of this family were found in moderate and strong currents, with their highest incidence in moss-covered habitats, although 2/3 of them were found accumulated on stone 26 in the weir. Both species clearly preferred the protected faces of stones (Table 8).

Hydropsyche is one of the most exhaustively investigated of the caddisfly genera typical of flowing water environments (SATTLER 1958, SCHRÖDER 1976). The construction of webs by the larvae in summer is clearly a form of adaptation to the need to obtain their omnivorous diet from drift, and this constitutes a natural reason for a certain rheobiotic character, their preference range being largely moderate to strong currents in outlet and rapids habitats (see FROST 1942, MÜLLER 1954, ILLIES 1956, SCOTT 1958, AMBÜHL 1959, EDINGTON 1968, HADDOCK 1977, BAGGE and SALMELA 1978). *H. pellucidula* and *C. lepida* are reported to possess a broad ecological range in the rivers of the Carpathians, inhabiting almost the whole length of the river and occurring characteristically on stone and stone-gravel substrates (SZCZESNY 1975, ZACWILICHOWSKA 1969, 1970). It would thus seem that these species do not require the presence of mosses in their environment to the same extent as do the other Hydropsychidae species (see FROST 1942, EDINGTON 1965, 1968).

Leptoceridae (nomenclature: MORSE and WALLACE 1974)

39. *Ceraclea annulicornis* (Steph.)

40. *Athripsodes cinereus* Curt.

41. *C. excisa* (Mort.)

42. *Athripsodes*, sensu lato, spp.

The group was common in its occurrence and was found in every one of the habitats. Although being obviously concentrated in the more quietly flowing habitats, the slow or moderate currents of the edge, backwater and deadwater, it was still to be found in strong currents in the channel and more slowly flowing part of the weir. Accumulations of detritus and sediment are also seen to be environmental components which serve to regulate the distribution of these species to some extent. A very highly significant preference ($\chi^2 = 12.07$) was shown for the protected faces of stones.

Typical environments, varying slightly from one species to another, are, according to observations in the Soviet Union (LEPNEVA 1964), the firm stony and/or sandy bottoms

and littoral zones of lakes and rivers. The records available from elsewhere, although admittedly few in number, also fit in with this categorization (VAINIO 1938, NIELSEN 1948a, HÄGGMAN 1960), especially with the addition of brackish water environments (SILFVENIUS 1905, KANGAS 1969). BOTOSANEANU (1967), on the other hand, indicates only *C. excisa* as a rhithron inhabitant and the others as preferring the limnion or potamon. This tendency towards lenitic waters is in itself a sign of low rheophile properties, and this is supported by the preference for protected micro-habitats, a form of behaviour evidently also influenced by pupation (see SILFVENIUS 1905).

Brachycentridae

43. *Micrasema* sp.

44. *Micrasema setiferum* Pict.

The older habitats, even including those parts with a strong current, offered the most suitable environment for this frequently encountered group which had already entered a stage of intensive pupation (55 % empty pupae). The material points to a preference for the exposed faces of stones and a moss substrate.

M. setiferum and a number of other species of this genus are described as above all inhabitants of streams and small rivers (rhithron), preferring moss-covered stones (SILFVENIUS 1905, DITTMAR 1955, CHAPMAN and DEMORY 1963, VERNEAUX 1972, DECAMPS and LAFONT 1974). The present observations support this ecological picture, even in respect of current velocity, 20–70 cm/s (VERNEAUX 1972).

Lepidostomatidae

45. *Lepidostoma hirtum* Fabr.

This was the most common and most prolific caddisfly species of all at Jäväjänkoski, being found in all the habitats and over a broad range of current velocities, although the powerful laminar flow on the weir, and possibly also the lack of vegetation, appeared to prevent the formation of colonies in the area with a strong current. Elsewhere the tendency to avoid strong currents was manifested in the form of a preference for the protected faces of the stones, so that on 14 stones out of 23 all or the majority of the larvae were found on this surface, while a significant trend in microdistribution in this direction ($p < 0.01$) was noted with increasing current velocity, in the same manner as in the case of *A. borealis* (Table 7, p. 33; cf. *Ecclisopteryx* in SCOTT 1958). The preference of this species for moss-covered stones is clearly visible even from the mean densities of individuals per stone for the various habitats, as these conform very closely to the extent of the moss cover at each: backwater 1.5, weir 2.2, deadwater 3.5, edge 5.0, channel 6.3, riverbed 6.7. Similar conclusions may also be reached by comparing the densities in different vegetation types (Table 11).

Table 11. Mean density of *Lepidostoma hirtum* specimens per stone on stones with different vegetational cover.

Vegetation	Range	Total n	No. of stones	Mean density
Mosses dominant	3–15	60	7	8.6
Mosses and algae	2–15	61	9	6.8
Algae dominant	1–10	32	8	4
Bare stone		2	2	1

References in the literature point to *L. hirtum* as a highly ubiquitous creature in its choice of biotope, as it is reported in standing water on surf shores (LEPNEVA 1964), in brackish water (SILFVENIUS 1905) and particularly in various types of flowing water habitat up to a strong current velocity (LILLEHAMMER 1965), and is also said to frequent submerged plants in this latter biotope (FROST 1942, FRIBERG *et al.* 1977).

Limnephilidae

- 46. *Limnephilinae* Kol. sp.
- 47. *Stenophylacini* Schmid sp.
- 48. *Potamophylax latipennis* (Curt.)

Limnephilid caddis worms were occasionally observed in slow or moderate currents, always attached to the underside of stones, so that it is even possible that part of the population was left behind in the gravel of the stream bed (p. 25). *P. latipennis*, the only species successfully identified, represents the most rheophile genus within the tribe and subfamily (LEPNEVA 1964). This species tolerates a wide range of biotopes, hard bottoms of stones or gravel in the surf zone and slow to strong currents in flowing water, generally sheltering underneath the stones, where plant detritus particles, the main food item of the larvae, tend to settle (see NIELSEN 1942, SCOTT 1958, BAGGE 1968, BAGGE and SALMELA 1978).

49. Trichoptera sp.

This residual taxon accounts for a number of smallish campodeiform larvae, all similar in appearance, found mostly in the riverbed habitat.

4.3.11. *Diptera*

Practically a half of the species recorded at Jäväjänkoski fall within the order Diptera,

Table 12. Occurrence of Chironomidae and Simuliidae in the various habitats and the total material (N – number of individuals, % – proportion of total fauna, Density – approx. mean no. of ind./stone, Spp. – number of species; see p. 24).

		E	B	D	C	R	W	Total
N (%)	Chironomidae	84 (47)	39 (57)	53 (27)	83 (43)	337 (25)	828 (15.6)	1424 (19.6)
	Simuliidae	1 (1)	–	20 (10)	15 (8)	465 (35)	4163 (78.5)	4664 (64.2)
Density	Chironomidae	21	20	27	28	28	69	41
	Simuliidae	1	–	10	5	39	347	133
Spp.	Chironomidae	15	11	15	11	21	23	31
	Simuliidae	1	–	4	4	11	19	19

these being divided among the families Chironomidae and Simuliidae (Table 12). This groups is by far the dominant one in the total fauna, being represented on every stone and in such numbers that it became the largest single group in every habitat. The weir habitat stands out in this respect, having an overwhelming proportion of Diptera. This uneven distribution was largely a consequence of the irregular occurrence of the Simuliidae, as the Chironomidae showed a strikingly uniform pattern of occurrence throughout, with the exception of the weir. The richest Diptera fauna was provided by the weir and riverbed habitats, but if the remaining habitats are combined, in which case the number of stones studied becomes more comparable with the numbers in the weir and riverbed, these too show a similar diversity.

This is taxonomically a difficult group, and it has been necessary to include some unnamed species.

4.3.11.1 Chironomidae (THIENEMANN 1944, HENNIG 1950, FITTKAU 1962, PANKRATOVA 1970, BRYCE and HOBART 1972, HIRVENOJA 1973)

50.–84. (Table 13)

The distribution of the species by subfamily was 4, 4, 1 and 22, a pattern which coincides statistically ($p > 99.9\%$) with that observed by THIENEMANN (1954) in lower mountain streams, those of the 'Mittelgebirge', in terms of χ^2 (heterogeneity). At the same time it deviates from the faunae of the lowland flowing water habitats described by LINDEGAARD-PETERSEN (1972) by virtue of its very large number of Orthocladiinae species. THIENEMANN (1954) had already pointed out that the species composition tends to alter gradually downstream in the river, and this emerges very neatly from the comparative tables of LINDEGAARD-PETERSEN (1972). The internal distribution of the Chironomidae species at Jäväjänkoski, resembling as it does that recorded in rhithron areas, thus serves to indicate that the rapids may function even in their potamon area as a habitat which retains faunal features of the upper reaches of a river, in which stenothermal conditions with an abundance of oxygen are typical.

Table 13. Species of Chironomidae identified, their incidence, and numbers of individuals in the various habitats and the total material, and distribution by micro-habitat (exp. — exposed, pro. — protected, dis. — displaced).

Species	Habitats						Micro-habitats			Total	Incidence
	E	B	D	C	R	W	exp.	pro.	dis.		
50. <i>Ablabesmyia monilis</i> (L.)	1							1		1	1/35
51. <i>Pentaneurini</i> sp. A	3	2	6	1	9	6	17	6	4	27	14
52. <i>Pentaneurini</i> sp. B			4		1	1	4	2		6	3
53. <i>Pentaneurini</i> sp. C			1			1			2	2	2
Tanyodinae, <i>Pentaneurini</i> (total)	4	2	11	1	10	8	21	9	6	36	
54. <i>Eutanytarsus</i> sp.	1						1			1	1
55. <i>Rheotanytarsus</i> sp.			2		2		4			4	2
56. <i>Rheotanytarsus photophilus</i> G.		7	13	4	55	230	109	152	48	309	27
57. <i>Zavrelia nigrifula</i> G.	1						1			1	1
Chironiminae, <i>Tanytarsini</i> (total)	2	7	15	4	57	230	115	152	48	315	
58. <i>Parachironomus</i> sp.	1				1		2			2	2
Chironominae, <i>Chironomini</i> (total)	1				1		2			2	
59. <i>Eukiefferiella alpestris</i> G.		12	1			259	217	46	9	272	11
60. <i>Eukiefferiella tshernovskii</i> Pankr.	1		1	7	12	23	28	9	7	44	12
61. <i>Eukiefferiella quadridentata</i> Tshern.				2	6	10	10	3	5	18	9
62. <i>Eukiefferiella</i> sp.		9			2	115	83	18	25	126	10
63. <i>Eukiefferiella</i> sp. pupae				2				1	1	2	
64. <i>Synorthocladus semivirens</i> (Kieff.)						3	2	1		3	3
65. ' <i>Orthocladus</i> ' sp. A	13		10	17	33	21	46	32	16	94	25
66. ' <i>Orthocladus</i> ' sp. B	3	1	6	5	38	61	58	24	32	114	23
67. ' <i>Orthocladus</i> ' sp. C		1	1		1	5	5		3	8	6
68. ' <i>Orthocladus</i> ' sp. D						2			2	2	1
69. ' <i>Orthocladus</i> ' sp. E			1		2		2	1		3	2
70. ' <i>Orthocladus</i> ' sp. pupa						1	1			1	
71. <i>Cricotopus triannulatus</i> (Macqu.)	7			12	21	16	24	13	19	56	18
72. <i>Cricotopus albiforceps</i> (Kieff.)	1				2		1	1	1	3	2
73. <i>Cricotopus bicinctus</i> (Mg.)	34	1	2	24	65	21	49	20	78	147	27
74. <i>Cricotopus trifascia</i> Edw.					4	3			7	7	6
75. <i>Cricotopus</i> sp. A	8			7	8	2	9	6	10	25	11
76. <i>Cricotopus</i> sp. B	1			1	24	10	24	9	3	36	13
77. <i>Cricotopus</i> spp. pupae					2	2	3		1	4	
78. <i>Psectrocladius simulans</i> Joh.	5	1				1	3	1	3	7	5
79. <i>Rheocricotopus effusus</i> (Walk.)			3	3	18	2	18	7	1	26	10
80. <i>Parametrioctenus stylatus</i> (Kieff.)						1	1			1	1
81. <i>Corynoneura scutellata</i> Winn.		1						1		1	1
82. <i>Thienemanniella</i> Kieff. sp.	2	2	1		20	20	33	6	6	45	17
Orthocladinae (total)	75	28	26	78	260	578	617	199	299	1045	
83. Chironomidae sp.		2	1		1	12	15	1		16	4
84. Chironomidae spp. pupae					8		7	2	1	10	
Totally	84	39	53	83	337	828	777	363	284	1424	35/35

Amongst the 31 species present, *R. photophilus*, '*Orthocladus*' sp. A and sp. B and *C. bicinctus* were all very common, *C. triannulatus* and *Thienemanniella* sp. were common, and the remainder were either frequent or rare, these latter designations thus being characteristic of the group as a whole. The highest numbers of individuals were recorded in the case of *R. photophilus*, *E. alpestris* and *C. bicinctus*. A preference for the exposed surfaces of the stones, calculated in terms of the total numbers of individuals, was a feature common to almost all species, and may thus serve as a broad general characterization for the preference of the group as a whole.

The following species have not previously been reported from Finland (according to the manuscript 'Checklist of Diptera of Finland'; Bernhard Lindeberg, pers. comm.): *Rheotanytarsus photophilus* (sensu LEHMANN 1970), *Zavrelia nigrifula* (sensu BRYCE and HOBART 1972), *Eukiefferiella alpestris*, *E. quadridentata*, *E. tshernovskii* and *Psectrocladius simulans* (sensu PANKRATOVA 1970).

50.–53. Pentaneurini

The species not named here were relatively similar to those described by BRYCE (1960) under the genus *Pentaneura* (later attributed by FITTKAU *et al.* 1967 to the genera *Thienemannimyia* and *Trissopelopia*). These freely moving larvae were generally to be found on the exposed surfaces of stones, and were common to all the habitats, although with a slight concentration in the deadwater. Sp. A (?*Th. northumbrica* (Edw.)) was the most frequent and most abundant of the species, while *A. monilis* is a very well-known species which lives amongst plants (BAGGE 1968) and is not especially rheophile (see FITTKAU *et al.* 1967). The Tanypodinae, of the pentaneurinian type, have adapted morphologically to a way of life involving predation upon small invertebrates (HENNIG 1950) in various habitats including the lotic ones noted by FITTKAU *et al.* (1967) as the principal environments for precisely those general mentioned above, *Thienemannimyia* and *Trissopelopia* (see also ZACWILICHOWSKA 1969, 1970).

54.–57. Tanytarsini

This group is composed almost entirely of individuals of *R. photophilus*, which occurs in moderate to very strong currents with a concentration in the weir habitat. A preference for the exposed surfaces of the stones was noted in certain individual cases, suggesting that the majority trend in favour of the protected surface within the total population of this species may well not be an indication of avoidance of the current, but rather a sign of the need for a fairly vigorous flow arising from the passive mode of feeding of this larva, typical of the whole genus, employing a web secreted between the horns of the case (WALSHE 1950, 1951; THIENEMANN 1954). Thus the location of the larvae on the stones would be governed by the micro-distribution of the current, and suitable conditions could offer themselves in quite unexpected places, on bare surfaces of stones and also amongst various forms of vegetation in swiftly flowing water, their preferred biotopes (LEHMANN 1970, VERNEAUX and VERGON 1974).

Z. nigrifula is known as a species inhabiting standing water (FITTKAU *et al.* 1967).

58. Chironomini

Parachironomus sp. was encountered on the protected faces of stones in the riverbed and edge habitats. The species of this genus are known from potamon and standing waters for the most part (FITTKAU *et al.* 1967).

59.–83. Orthoclaadiinae

59.–63. the genus *Eukiefferiella* (identification sensu Pankratova 1970)

The various species are all frequent in their incidence, but *E. alpestris* and *E.* sp. (Fig. 10) stand out by virtue of their dominance in absolute numbers and their concentration in the weir habitat. The fact that these species thrive in moderate to strong currents and prefer the exposed face of the stone, regardless of the quantity of type of vegetation present, would suggest a rheophile nature. The preference for an

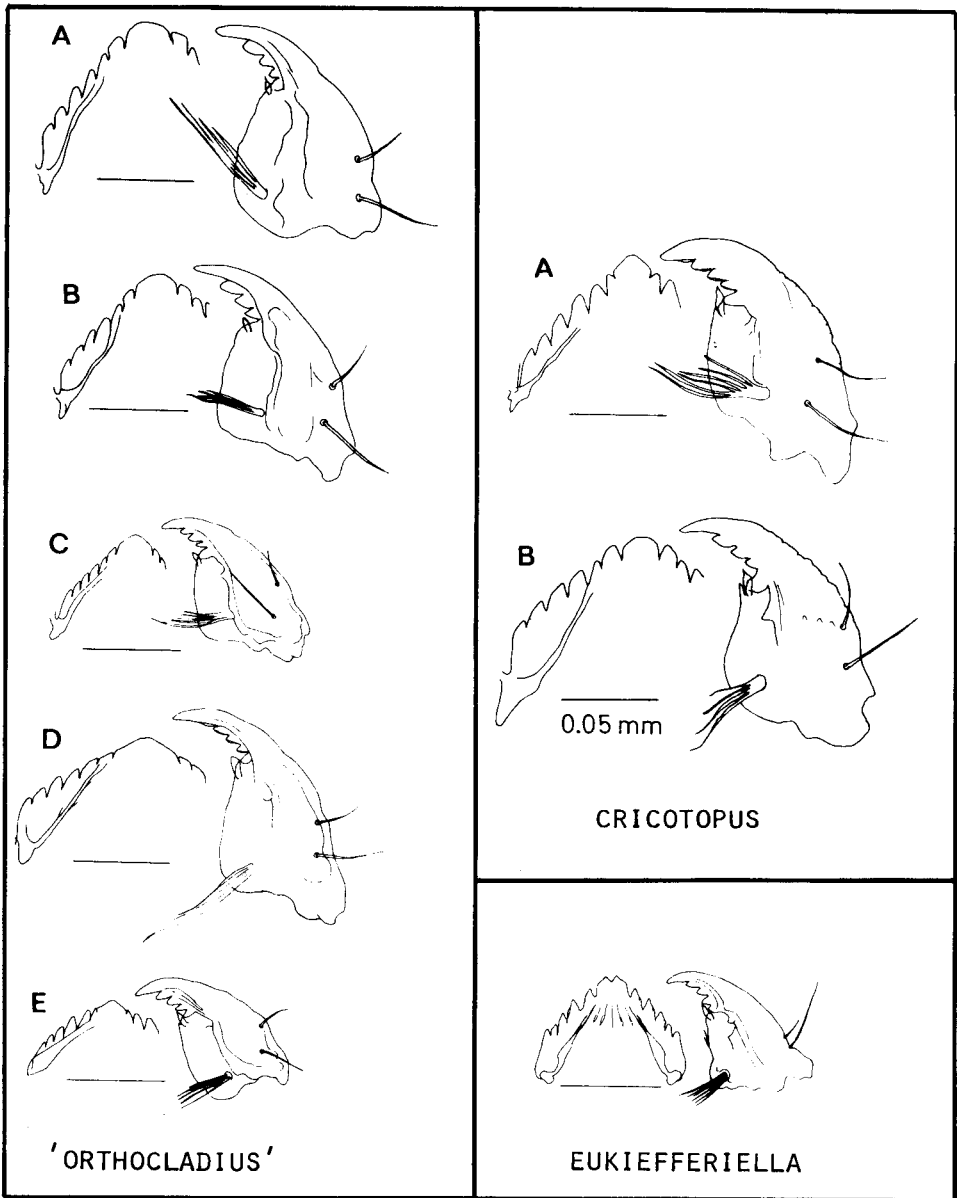


Fig. 10. Features of the hypochilum and mandible used in distinguishing the unnamed Orthoclaadiinae species.

exposed position is also reflected in the few ecological notes available on these species (PANKRATOVA 1970, KOWNACKI 1971, KOWNACKI and KOWNACKA 1973). *E. alpestris* is reported in mountain streams and the surf shores of large northern lakes, *E. tshernovskii* in rivers and the littoral zones of lakes and *E. quadridentata* on stones in mountain rivers. Many representatives of this genus have been found in submerged

mosses in rivers and springs (HUMPHRIES and FROST 1937). The specimens encountered at Jäväjänkoski provide a valuable addition to the existing information on the ecological valency and distribution of these species.

64. *Synorthocladius semivirens*

Three specimens were found on an alga-covered stone in the strong current section of the weir. The species has a wide distribution, and is euryoecic, appearing in the littoral zones of lakes (THIENEMANN 1944) and the potamon (BERG 1948, LEHMANN 1971), and even in crenon waters (VERNEAUX and VERGON 1974).

67.–70. '*Orthocladius*'

In spite of clear distinguishing characteristics in the hypochilum and mandible (Fig. 10), it was impossible to identify this group to species. The most numerous species, A and B, were often obtained from vegetation, and showed herbi-detritivore feeding habits. The numbers appearing in the various habitats testify to a wide current tolerance, species B emerging as somewhat more rheophile than species A.

71.–77. the genus *Cricotopus*

Four species could be identified by reference to HIRVENOJA (1973), typical samples of adults from the head of the rapids at Jäväjänkoski being taken for personal identification by Hirvenoja himself. Two species remained at the operational level (Fig. 10).

These species preferred the edge, channel and riverbed habitats, where they accounted for 61 %, 53 % and 38 % of the total Chironomidae individuals respectively, compared with 3–6 % elsewhere. Their pattern of occurrence was characterized by a broad current tolerance, and their environmental requirements by a preference for genuine rapids conditions, including moss-covered stones, with a food supply in the form of epiphytic and epilithic diatoms for *C. bicinctus* and mainly detritus for *C. triannulatus*. A preference was shown for the exposed faces of the stones. The large number of detached specimens suggests that *C. bicinctus* is quick to react to interference by breaking loose from the stone or diatom flush upon which it is located.

The species named by reference to the surveys by HIRVENOJA (1973, 1975) possess a certain euryoecic property in that they can thrive not only in lakes and flowing water, but also in brackish water, although it is only *C. bicinctus* which has been described as 'truly a creature of stream environments' (GEIJSKES 1935). The observations from Jäväjänkoski indicate that the other species may similarly tolerate strong currents, with *C. triannulatus* coming closest to *C. bicinctus* in this respect. The latter is also described by NIETZKE (1937) as "Wanderformen zwischen Pflanzen und Steine", which may be precisely the reason for the high propensity for detachment.

78. *Psectrocladius simulans*

PANKRATOVA (1970) classifies this species as an inhabitant of surf shores and the vegetation in quietly flowing rivers. This weak rheophile character is also reflected in its appearance here principally in the edge habitat.

79. *Rheocricotopus effusus*

This species was frequent, occurring largely in habitats with a good moss cover. According to LEHMANN (1969), it enjoys a rheophile and oxybiontic existence in tubes of mud on plants and stones in rhithron waters.

80. *Parametriocnemus stylatus*81. *Corynoneura scutellata*

These occurred as single specimens. The first is reported from streams in the Tatra mountains (KOWNACKA and KOWNACKI 1967) and mossy springs in Denmark (LINDEGAARD *et al.* 1975), and the second in all types of inland waters (FITTKAU *et al.* 1967), including sites where it appears among vegetation subject to wave action (PANKRATOVA 1970).

82. *Thienemanniella* sp.

Larvae were found on practically a half of the stones, with slightly more occurrences in the riverbed and weir habitats than in the others. A distinct majority of the specimens came from the exposed face of the stone. Many species of this genus inhabit clumps of moss in various types of flowing water environment (THIENEMANN 1944). This taxon was characteristic among plants in a slight to very slight current (BERG 1948).

83. Chironomidae sp. — larvae, small, with an Orthocladian contour.

84. Chironomidae sp. — pupae, probably belonging to species mentioned above.

4.3.11.2. *Simuliidae* (RUBTSOV 1959–64, USSOVA 1961)

85.–103. (Table 14)

The total blackfly material, comprising 4664 individuals, was distributed by stage of development as follows: larvae 26.74 %, pupae 22.81 %, fresh remnants of pupae 50.36 % and adults 0.99 %. Many of the species represented here were just going through

Table 14. List of species of Simuliidae, their incidence, and the number of specimens obtained in the different habitats and micro-habitats and totally. 'Ecology' refers to the biotope preferences as stated by ZWICK (1978).

	E	D	C	R	W	Micro-habitats		Total	Incidence	'Ecology'*
85. <i>Metacnephia trigonia</i> (Ldstr.)	-	-	-	1	166	148	17	2	167	9/35
86. <i>Eusimulium</i> sp. ex gr. <i>vernum</i> (Macqu.)	1	-	-	-	2	1	2	-	3	3b
87. (? <i>meigeni</i> Rz. & Carls.)	-	-	-	2	2	1	2	1	4	3a,b,f
88. <i>aureum</i> (Fries)	-	1	1	20	34	10	20	26	56	3-4
89. sp.	-	-	-	6	8	7	7	-	14	2-3a,b
90. <i>Schönbaueria pusilla</i> (Fries)	-	-	-	1	4	4	1	-	5	-
91. <i>Parabyssodon transiens</i> (Rz.)	-	13	1	39	329	218	71	93	382	4a,b
92. <i>Simulium rostratum</i> (Ldstr.)	-	-	-	-	1	1	-	-	1	4a,b
93. <i>tuberosum</i> (Ldstr.)	-	-	-	-	17	12	2	3	17	3b, 4c
94. <i>argyreatum</i> Mg.	-	-	-	-	5	3	2	-	5	3a,d,4a
95. <i>truncatum</i> (Ldstr.)	-	-	-	-	3	-	3	-	3	3a,b,14
96. <i>venustum</i> sensu Rubtsov 1959-64	-	-	-	-	41	17	17	7	41	3b,14
97. <i>verecundum</i> sensu Rz.	-	-	-	19	107	81	22	23	126	(3,4a,b)**
98. sp. ex gr. <i>venustum</i> Say	-	-	-	25	224	201	40	8	249	3a,b,14
99. <i>moritans</i> Edw.	-	-	-	5	16	18	3	-	21	-
100. <i>austeni</i> Edw.	-	-	-	-	3	2	1	-	3	3,4a
101. <i>reptans</i> (L.)	-	4	1	275	2922	2441	468	293	3202	3a,4a
102. sp.	-	2	-	2	50	48	6	-	54	3a,b,4
103. <i>Simuliidae</i> spp. indet.	-	-	12	70	229	201	50	60	311	-
	1	20	15	465	4163	3414	734	516	4664	28/35

* 2 Quellen und Quellabflüsse; 3 Bäche und kleine Flüsse, Rhithral;

4 Flüsse und grosse Ströme, Potamal; 14 Seeausflüsse, Wehre, Mönche;

a Strömung mässig, laminar; Makrophyten üppig; Grund sandig-keisig bis schlammig;

b Strömung stark, turbulent; Makrophyten spärlich; Grund steinig;

c reissende Hochgebirgsbäche in Felsbetten ohne Makrophyten;

d moorig;

f temporär.

** RUBTSOV (1959-64).

their metamorphosis phase at the time when the samples were collected, and it is for this reason that the pupal remnants were also included within the totals for the stone communities. In the case of *S. reptans*, for instance, the proportion of specimens other than larvae or pupae increased day by day during the sampling period from a couple of percent at the outset practically to 100 %, while the proportion of pupae fell from around 80 % to one or two percent. Similarly, *M. trigonia* was found in pupal form at the beginning, but later only empty pupae or cocoons occurred, while *P. transiens* began to pupate from the middle of June onwards.

A total of 19 Simuliidae taxa were distinguished, one of these being the indeterminates, Simuliidae spp. (see p. 24), which included many young larvae, all of similar appearance, which could not be identified from the keys employed.

S. reptans was by far the dominant species, accounting for over 2/3 of the specimens obtained and being very common in its incidence. Other major species which were successfully identified were *P. transiens*, *M. trigonia*, *S. verecundum* and *S. sp. ex gr. venustum*, each of which accounted for no more than 2.70 %, and *E. aureum*, which although much less significant numerically, was the only other species besides *S. reptans* to achieve an incidence level of 'common'. All the other named species were typically rare and limited in numbers. Every one of the species was concentrated in the weir habitat, and only *E. sp. ex gr. venum*, *E. aureum*, *P. transiens*, *S. reptans* and the indeterminates were to be found at all beyond the weir and riverbed, and then only in small numbers. The Simuliidae appeared to avoid areas with a current velocity below moderate, and the largest populations were observed in the strong current area of the riverbed and the strong – very strong area of the weir, with the latter habitat having an overwhelming advantage in terms of density. No interspecies ecological specialization was seen as far as location was concerned.

The larvae and pupae of the blackflies show a high degree of ecological adaptation in their feeding and respiration, taking full advantage of the current for these purposes, and it is well-known, of course, that these functions require an appropriate combination of environmental factors, in which current velocity, mode of flow, substrate and sedimentation play the leading parts (see WU 1939, ZAHAR 1951, CARLSSON 1962, 1967, USSOVA 1961, MAITLAND and PENNEY 1967).

The blackflies have always been observed to be highly rheobiontic in their current velocity requirements, the optimum range being reported almost without exception to be from strong to very strong. The creatures are known, for instance, to remain firmly attached to their substrate at velocities of up to 280 cm/s (DITTMAR 1955). This capacity for attachment thus also serves in a natural way to determine the upper limit of their current tolerance, while the lower limit is that required for the food items to be transported within reach of their cephalic fans, for their gills and respiratory filaments to be washed continuously with fresh, oxygenated water, and for their excreta, together with any descending alluvial matter, to be removed from their immediate surroundings. The relation between current velocity and food particles appears to be the decisive factor in this sense, as the amount of food drifting within reach per unit time is directly dependent upon the current, so that a given area of substrate can maintain larger numbers of these animals in rapidly flowing water than in a relative quietly flowing area. Situations of laminar flow such as are found at the outflows of lakes or the heads of rapids guarantee a more or less even, continuous supply of nutrients, and the same holds good of the

front upper surfaces of stones, a micro-habitat which is highly suitable for these larvae by virtue of its corresponding rapid laminar flow. The other surfaces, with their slower current velocity and swirling mode of flow, present difficulties connected with food supply, the most essential of which is precisely the lack of direction in the approach of food items. The firmness of the substrate, for its part, is a feature which may contribute to the attachment of the larvae, although differences have admittedly been noted between the various species in this respect, and the leaves of submerged plants such as *Sparganium* which trail in the current may be particularly densely populated on occasions.

The general principles set out above serve well to explain the distribution of the blackflies observed at Jäväjänkoski. The water passes over the weir in places in a highly directional, rapid laminar flow, while in the riverbed it tends to swirl about in a torrent. Thus the weir, with its abundance of sites with a firm substrate, offers an excellent opportunity for the larvae to establish themselves in locations with a constant velocity of flow. It appears from the density figures that it is the central part of the upstream face of the weir which represents the optimal site in respect of nutrient supply, for by the upper part the strength of the current seems to cause attachment problems which outweigh the advantages gained in feeding, as may be seen from the micro-habitat distribution of the community on stone 31, for example. The paucity of blackflies in the lower part of the weir and the edges of the river bed, and their absence from the backwater area, may be accounted for partly by the weak current and partly by the insufficiency of the nutrition obtainable purely in the form of drift, while interference from sediments and the oppressive effect of the algal overgrowth may also play some part in this. Such patches of algal covering only part of the exposed surface of the stone do not yet seem to have prevented dense accumulations of blackfly larvae elsewhere however (see USSOVA 1961).

The outstanding ecological role of the blackfly larvae in the flowing water communities consists of the utilization of the organic particles drifting in the water for nutritional purposes. This mode of existence, which requires a continuous flow of water, may be seen as one of the principal reasons why one habitat or micro-habitat (e.g. stone 27) may contain a variety of species with no obvious signs of specialization or competition, although some ecological specialization has admittedly been noted. The species may develop at different times, for instance, although there is still a great deal of overlapping (CARLSSON 1962), some species prefer exclusively the lake outlet habitats, while others avoid these almost entirely (see ULFSTRAND 1968), and some inhabit stony bottoms, while others are confined to the leaves and stems of plants (see USSOVA 1961). Ecological indicators for individual species are listed in many other sources as well (e.g. ZAHAR 1951, RUBTSOV 1959–64, CARLSSON 1962, DAVIES 1966, ZWICK 1974), and RUBTSOV (1967) provides a summary of the types of flowing water preferred by the various species, information which has been filled out by ZWICK (1978) with descriptions of the mode of flow and nature of the substrate. These are the data which form the source for the ecological categorization provided here in Table 14. We are, of course, dealing here with generalizations from large numbers of observations, and the result is sufficiently comprehensive and flexible that the present material does not reveal any essentially new features of the ecological requirements of these species. The most frequent habitat descriptions corresponding to species found here involve a moderate laminar current and an abundance of macrophytes in the rhithron, but the

vegetation described would seem inappropriate. Such a vegetation is to be found at the head of the rapids, however, implying the presence of potamon-type habitats with an abundance of plants in the immediate vicinity upstream, some 40–150 m away. Since the blackflies are known to be highly susceptible to migration, which may be triggered off by changes in the water current or degree of suspension (CARLSSON 1962, USSOVA 1961), as in fact occurs at Jäväjankoski, it may well be that many of the species have found their way into this material via stones which represent secondary or subsequent habitats. In the case of those species which are encountered here in large numbers and carry an outlet habitat ecological tag, the weir may indeed be the primary habitat and any others downstream of this secondary.

4.3.12. *Coleoptera* (REITTER 1908–1916)

104. *Helophorus* sp. (Hydrophilidae), 1 adult

105. *Elmis aenea* (P. MÜLLER) (Dryopidae), 13 larvae, 3 adults

The *Helophorus* species are generally to be found in the littoral of standing water (REITTER 1908–1916). With the exception of one larva, all the present specimens of *Elmis* were recovered from moss-covered stones on the riverbed. Large populations of this species are reported in streams, particularly amongst stands of *Fontinalis* (SAA-RINEN 1938, DITTMAR 1955, HÄGGMAN 1960), and beneath the stones or amongst algae near the shore of lakes (WESENBERG-LUND 1943). The current velocities reported are normally slight to moderate, and less often strong.

4.4. Ecological summary

The crucial questions posed in the majority of the faunistic and ecological reports used as sources in the above discussion were in effect: What animals are characteristic of certain habitats, what ecological properties do the animals require of their environments, and in general, what habitats lie within the ecological valency of each given species? In the majority of instances the present observations served to support the basic existing notions on the ecology of the 'trivial' species, with the greatest number of new findings emerging in the case of the Chironomidae species. The principal feature to stand out from the present results is the general eurytopic character of the taxa identified, even though various preferences were also statable. The occurrence of the species in respect of current velocity was predominantly euryrhealic, typically covering the range from slow to strong currents (see BAGGE and SALMELA 1978), but preferences could be noted in terms of the type of current, laminar outflow type *contra* turbulent rapids type. Similarly, quite clear micro-habitat preferences appeared to apply in respect of the location of the animals on the stones, both in terms of the exposed vs. protected face and of the type of surface: bare, algal, moss-covered, etc.

The benthic macroinvertebrates studied here may be classified simply on the basis of current requirements or tolerance into three groups, *rheotolerant*, true habitats in standing or quietly flowing water, *rheophile*, true flowing-water species, and *rheobiontic*,

flowing-water species for which the current, sometimes a current of considerable strength, is vital for respiration and feeding. Although the site studied is not sufficiently comprehensive to allow the tolerant species to be determined with certainty, it does enable the major part of the fauna to be recognized as rheophile. Even so, many of these latter species are also mentioned in the literature as thriving in the surf zone of standing waters, so that the borderline with the tolerant group becomes a very diffuse one. The most typical representatives of the rheobiontic species here were many of the passive feeders such as the Simuliidae, *Rheotanytarsus*, the Hydropsychidae and the Polycentropidae.

Outstanding examples of species favouring an 'exposed' environment are the black-flies, which are to a considerable extent lithophile, as also are the *Baetis* nymphs, although some of these latter were also found as algicola and bryocola. This preference for an algal or bryophyte substrate proved in itself to be a property of a much more diverse group of species, with *E. ignita* and *A. multipunctata* representing algicoly, *A. borealis*, *R. nubila* and *M. setiferum* representing bryocoly, and the majority of the Orthocladiinae a general preference for a vegetational substrate.

A preference for vegetation in the substrate may well in itself be a sign of requiring protection from the current, and in this sense it is difficult to discriminate between this and a preference for the protected face of the stone in the case of taxa such as *A. aquaticus*, the Hydroptilidae, the Hydropsychidae or *L. hirtum*, which exhibit both modes of occurrence. *A. borealis*, *R. nubila* and *L. hirtum*, for instance, are all species which move from the moss cover to the protected face of the stone with increasing current velocity, while a clear preference for a protected face habitat was demonstrated typically by *E. octoculata*, *H. sulphurea* and the Bryozoa, and also *Pisidium*, *Leuctra* and the Limnephilidae, which also possessed a slight lithophile character. In contrast, the most eurytopic group of all was the water mites, for which no obvious preferences could be demonstrated.

Illumination and temperature constitute the primary factors for the dynamics of the communities. Thus the rapid rise in temperature in early June from just under 10° to 17° led to a visible revival in the algal stands, and it may well be that the wide fluctuations in oxygen exchange in these plants (see MACAN 1963) could be the reason for the meagre fauna to be found among them at Jäväjänkoski. The timing and rhythm of metamorphosis is also largely dependent upon trends in water temperature (USSOVA 1961, CARLSSON 1962, HYNES 1970). The adults of *Taeniopteryx nebulosa* emerged as the ice was starting to break up, and the individuals of the succeeding generation had reached a size that brought them to the borderline of the macro-fauna by the end of the study period. Species to emerge at the beginning of June included *Oxytrhira* and *Micrasema*, and blackflies were seen in flight throughout the observation period. The greatest extent of growth in the larvae during the period of rising temperatures was noted in *L. hirtum*, *E. ignita* and *Baetis*. Thus the development of the community gains its rhythm from the progressive departure of adult insects and entry and growth of new populations of larvae.

The crucial background factor to the various habitat preferences is the functioning of the non-animal environment. This may be seen in a very pronounced form in a rapids situation, since the current velocity regulates first and foremost the quantity of stones

and gravel present and the nature and extent of the vegetation, and then also the amount of free organic material trapped by this and the amount of material transported in the water itself. All these factors in turn serve to determine the distribution of nutrients available to the animals in a given habitat. At the same time the various members of the faunal community are adapted to particular functions, and it is for this reason that their occurrence can be restricted by current velocity, vegetation, accumulations of detritus, etc., to the extent that an apparent preference for a protected location may in actual fact also reflect a tendency for the creatures to place themselves 'near their food bowl'.

5. FOOD AND TROPHIC RELATIONS

5.1. Introduction

A large number of analyses have been carried out on the food contents of macroinvertebrates from lotic benthos (for references, see HYNES 1970, MALICKY 1973, CUMMINS 1973, KAWECKA 1977). Since such work usually considers the food of a small number of species at a time, however, the resulting impressions of trophic relations within the communities are largely generalizations based to a greater or lesser extent on family relationships and approximations. Such a practice has seemed acceptable in a sense, because of the difficulty experienced in indentifying many of the taxa, a problem that still persists today. Similarly the dictum that local conditions produce local results put forward by MUTTKOWSKI and SMITH in 1929 has been regularly upheld as a universal truth in later work. Even though the majority of herbivores and detritivores are observed to be extensive, non-selective feeders, their distribution and abundance is largely dependent indirectly on nutritional factors, mediated by the physical environment (see EGGLESHAW 1964, ULFSTRAND 1967, CUMMINS 1975). On the other hand predator-prey relations may affect faunal associations, especially in a quantitative sense, as has been observed in lenitic waters (MACAN 1966, KAJAK *et al.* 1968, STEFFAN 1968, MACAN 1977).

The aim of this part of the work was to gain a general impression of the dietary habits of a number of macroinvertebrate species, their trophic relations, partly based on information gleaned from the literature, and the consequences of diet as ecological factors in the rapids community studied here.

5.2. Material and methods

The mid-gut contents of 175 invertebrates representing 24 species or species groups were examined. The specimens were chosen at random, except that all larvae of *E. mucronata*, *I. obscura*, *M. setiferum* and *P. stellatus* were included, and some additional examples of large nymphs of *E. ignita* were obtained for comparison purposes from an extra sample taken on 4.7.1965 not included in the main material.

The preparation procedure included the following steps: sagittal dissection of the body wall with a scalpel, extraction of the gut with forceps, removal of the gut into a drop of water on a microscope slide, slitting of the mid-gut wall, extraction of the food material by a rolling motion and cleaning of its surface of any gut tissue or peritrophic membrane, and insertion of this material under the glass cover-slip in a manner that would ensure

even dispersion. The food components were identified qualitatively under the microscope, and the relative abundance of each was estimated by eye using an application of the cover percentage method familiar to botanists.

The food components were classified as follows (see Fig. 11; for plant species, see p. 22):

diatoms	single cells and cell groups
filamentous algae	usually pieces of filament with several cells
mosses	leaf fragments and rhizoids of varying size
detritus	mostly fine-to-medium particulate organic matter (FPOM-MPOM in the system of BOLING <i>et al.</i> 1975) of complex origin, always with associated non-photosynthetic micro-organisms, especially decomposition bacteria. Pollen grains are also included here.
animal matter	amorphous tissue-like material and (commonly) fragments of cuticle, head capsules or parts of such, and setae. Pieces of dead exuviae could seldom be distinguished from live cuticles.
mineral particles	sediment grains or crystals (always present but not included in the quantitative estimates).

The scheme employed for describing abundance involved placing each component except the mineral particles on an arbitrary scale of major, habitual or occasional constituent, a practice which serves to reveal dietary preference, at least. In relative terms this represents a scale of very abundant, abundant and rare, corresponding roughly to $\geq 50\%$, 49–20% and $< 20\%$ cover on the slide.

The numbers of individuals representing the species in the community were so varied that the dominance method as defined by BROWN (1961), in which the proportion of animals in which each component is dominant is recorded, was considered statistically inappropriate for this survey. Instead the diets of the individual specimens for each species were summed to obtain the average food preference, as seen in Table 15. The resulting trophic relationships, based predominantly on these figures, are outlined in Fig. 11.

5.3. Results and discussion

5.3.1. Results of food analyses

Some preliminary remarks should be made on the individual variations observed within certain species and on the prey animals consumed by given predators before presenting a summary of the results proper. In cases of relatively invariable dietary composition reference can be made directly to Table 15.

One specimen of *H. sulphurea* had its gut full of pollen grains, and the three mature nymphs ready for emergence all had empty intestines, as did the two corresponding examples of *B. rhodani*. Considerable differences were found between the smaller and larger nymphs of *E. ignita*, the dietary composition being more obviously meaningful with increasing length of the nymph. Detritus was common in all cases, but the majority

Table 15. Relative abundance of food items of certain invertebrate species or groups (see text). Key: + main component, + habitual component, • minor component.

Taxon	n	diatoms	algae	mosses	detritus	animals
<i>Cricotopus bicinctus</i>	7	+	•	•		
<i>Cheumatopsyche lepida</i>	6	+	+	•	•	
<i>Ephemerella ignita</i> , < 3 mm	5	+	•		•	
Simuliidae	12	+	•	•	+	
<i>Rheotanytarsus photophilus</i>	8	+	•		+	•
<i>Eukiefferiella tshernovskii</i>	5	+	+		+	•
Orthocladinae	9	+	+	•	+	
<i>Lepidostoma hirtum</i>	5	+	+	•	+	
<i>Amphinemura borealis</i>	5	+	•	+	+	
<i>Potamophylax stellatus</i>	3	•	+	+	•	•
<i>Ephemerella mucronata</i>	6	•	•	+	+	•
<i>Micrasema</i> sp.	3	•		+	+	
<i>Ephemerella ignita</i> , ca. 5.3 mm	5		•	+	+	
<i>Cricotopus triannulatus</i>	8	+	+	•	+	
<i>Thienemanniella</i> sp.	6	+			+	
<i>Ephemerella ignita</i> , ca. 3.2 mm	6	•	+	•	+	
<i>Baetis rhodani</i> + <i>vernus</i>	9	•	+		+	
<i>Heptagenia sulphurea</i>	13	•	•	•	+	
Leptoceridae	11	•			+	•
<i>Micrasema setiferum</i>	3			•	+	•
<i>Asellus aquaticus</i>	6				+	
<i>Hydropsyche pellucidula</i>	7	•	•	•	+	+
Pentaneurini	7	•	•		•	+
<i>Rhyacophila nubila</i>	7	•	•		•	+
<i>Isoperla obscura</i>	5				•	+
<i>Erbobdella octoculata</i>	8					+
Totally	175					

of the other components acquired a coarser texture in the larger specimens. Some gill plates and femoral cuticles of *H. sulphurea* and respiratory filaments of simuliid pupae were recognized among the animal matter in the diet of *E. mucronata*.

Although detritus was always present in large quantities, the main proportion of the diet of *A. borealis* consisted of diatoms and/or mosses. The prey of *I. obscura* comprised small chironomid and simuliid larvae, and pieces of unidentified insects were also seen. A few cells of diatoms and algae were embedded in the animal matter.

The food of *R. nubila* was found to have included blackfly larvae, pupae and a hatched adult, chironomid larvae and an emerging *Micrasema* caddisfly. Diatoms and algae were frequently present, but in small numbers. The diet of *H. pellucidula* was found to include a variety of insects from the community, while *L. hirtum* showed no major food preference. Three larvae of *Athripsodes* spp. ready for pupation had their gut empty, while five contained pieces of blackfly cuticle and trachea and caddisfly larvae. One larva of *P. stellatus* had its gut full of mosses and detritus, and two had very large quantities of filamentous algae and small amounts of diatoms and cuticle fragments.

The guts of the Pentaneurini spp. larvae contained a great deal of animal matter interspersed with frequent cuticle fragments and setae of simuliid and chironomid larvae, and '*Orthocladius*' sp. B was also identified. In *R. photophilus* the proportion of diatoms varied from occasional to an amount corresponding to the main bulk of the diet, and cuticle fragments were observed in one case. One example of *E. tshernovskii* had detritus as the main component of the diet, one diatoms and one algae, and at other times these food classes were abundant. Two larvae of the species contained a few animal fragments. The proportion of diatoms and algae in *C. triannulatus*, in addition to the main component, detritus, varied from none at all to very abundant, and mosses were also found in two specimens, while diatoms were very abundant in every case in *C. bicinctus*, with detritus usually a minor component and algae and cuticle fragments only coming to light by chance. The group of nonselected Orthocladinae larvae presented major inter-individual differences in respect of their main diet, which could be diatoms, algae, detritus or mosses, and it was difficult to discern any standard trend. In contrast, the Simuliidae larvae had a fairly uniform diet of diatoms and detritus.

H. octoculata leeches were found to have swallowed chironomid larvae ('*Orthocladius*' sp. B, *C. triannulatus* and *C. bicinctus*), simuliid larvae of three species and a baetid larva, but the observation of a paste-like substance in three crops and the presence of detritus masses with no recognizable chitinous fragments suggests a non-insect component in the diet. The gut of the isopod *A. aquaticus* contained detritus as the only true nutritive component, although mineral particles were conspicuous, and even very abundant in some cases.

Although all types of food item except for the filamentous algae occur as the major food component in some species or other, the most characteristic of all is detritus. Arrangement of the material according to the characteristic component or the presence of several simultaneous habitual components leads to the formation of a variety of feeding types: carnivores, detritivores, herbivores (comprising diatomivores and bryophytivores) and combined herbivore-detritivores. As a broad generalization, herbi-detritivory would be the most usual category.

Euryphagy appears to be common and monophagy quite rare (cf. *A. aquaticus*, *E. octoculata*), but there are two borderline cases, carnivory with omnivorous features, in *H. pellucidula*, Pentaneurini, *R. nubila* and to a lesser extent *I. obscura*, in which the non-animal items may originate from the prey itself, and detritivory with certain herbivorous characteristics, in the large nymphs of *E. ignita*, *H. sulphurea*, *Athripsodes* and *Micrasema*, in which the plant cells may have been eaten dead as a part of the detritus which had not yet fully decomposed. On the other hand, the occasional occurrences of animal matter in the gut of herbivores or detritivores may be an indication of positive feeding on exuviae or other animal debris that may have accidentally fallen within reach.

5.3.2. Synopsis of the literature

Although the heptageniids are predominantly algal grazers (ULFSTRAND 1967, CUMMINS 1975), *H. lateralis* is mentioned by JONES (1950) as being a typical detritivore, as *H. sulphurea* also appears to be above. The diet observed in the *Baetis* nymphs corresponds in some measure to that reported for *B. rhodani* by JONES (1950), and

BROWN (1961) reaches similar conclusions, but emphasizes the significance of food supply as a source of variation in individual diets, e.g. the proportion of algae becoming greater at the time when these begin to bloom (see also KAWECKA 1977). *E. ignita* is generally described as an omnivore, having some animal material in its diet (WISSMEYER 1926, PERCIVAL and WHITEHEAD 1929, SCHOENEMUND 1930, JONES 1950), or detritivore (KAWECKA 1977), but this predatory feature was not observed in the present specimens, which admittedly included only immature nymphs. Fully grown nymphs of *E. mucronata*, for instance, appear to be true scavengers.

Detailed studies on the diet of stonefly nymphs have been carried out by HYNES (1941) and BRINCK (1949). As was observed in the case of *A. borealis*, so Nemouridae nymphs, too, take in both live plant material and also detritus. *Taeniopteryx nebulosa* is another species which shows a preference for the latter component. The *Leuctra* species are detritus and algal feeders (both filamentous and diatoms) (JONES 1950), and although the setipalpien *I. obscura* is predatory, upon chironomids, algae and detritus occupy an important place in the diet of this species, too, the proportions depending primarily on supply factors.

The Hydroptilidae, not examined here, are generally phytophagous (SILTALA 1907, NIELSEN 1948b). *Agraylea* and *Hydroptila* both bite into individual cells of filamentous algae and suck at them, while *Oxyethira* feeds on algal filaments and *Ithytrichia* on periphyton. With a few exceptions (see MALICKY 1973), the larvae of *Rhyacophila* are well-known as active predators, primarily consuming larvae of the Chironomidae and Simuliidae (SILTALA 1907, SLACK 1936, BADCOCK 1949, SCOTT 1958, CARLSSON 1962, THUT 1969, BURTON and MCRAE 1972). Arne Fjellheim (personal communication) has observed, however, that the younger larvae of *R. nubila* are herbivores, and it is not until the instars III–V that they become carnivores. *Agapetus* spp. are mentioned by ZACWILICHOWSKA (1969) as being diatomivores. *W. subnigra* is reported to have 'überwiegend nur Schlamm-partikelchen' and some fragments of phanerogames (SILTALA 1907), which in view of its feeding mechanism which involves filtering, is indicative of a herbi-detritivore diet. Polycentropiid and hydropsychiid larvae are also known to collect their food by a net mechanism. *C. lepida* is stated by Siltala to be a herbivore, feeding on algae and higher plants, and thus to be an exception among the hydropsychiids, which in general have euryphagous-carnivorous feeding habits (DITTMAR 1955, SATTLER 1958, KAWECKA 1977), and to differ from *P. flavomaculatus*, which also accepts insect larvae (JONES 1950). *Athripsodes* spp. are phytophagous to varying extents (SILTALA 1907, MALICKY 1973). Siltala also found insect fragments among the plant tissue consumed by *A. cinereus* (cf. SLACK 1936), and LEPNEVA (1966) names *A. excisus* as phytophagous, but there are no recorded observations on the diet of *A. annulicornis*. In contrast to the present result concerning *M. setiferum*, admittedly based on only three specimens, the larvae of *Micrasema* spp. are reported to consume fragments of mosses, and the young instars to feed on periphytic algae, too, as is the present case of *Micrasema* sp. (CHAPMAN and DEMORY 1963, DECAMPS and LAFONT 1974). The algae-dominated omnivorous diet of *L. hirtum* described by SILTALA (1907) is confirmed here, while the feeding habits of *P. latipennis* are seen to involve herbi-detritivore features with a preponderance of coarse items (see SCOTT 1958). This omnivorous aspect is also widely encountered in the limnephilid species in general (see SILTALA 1907, MALICKY 1973).

Major differences are found between the chironomid faunae reported in the literature, and also between these and that described here, complicating any dietary comparison and allowing generalizations to be made only at the sub-family or tribe level (see THIENEMANN 1954, STEFFAN 1968, BRYCE and HOBART 1972, KAWECKA and KOWNACKI 1974). The Pentaneurini species are predators with incidental algiphagy, and the Orthocladiinae are characterized as a group by a detritivorous and algivorous diet. The examples found here, and some reported elsewhere (LINDEGAARD-PETERSEN 1972, COFFMAN 1967, CUMMINS 1973) show some specialization, but fit well within these categories. The larvae of *Rheotanytarsus* filter their food items by selecting the particle size to some extent (WALSHE 1950, 1951), the mode of feeding being herbivorous-detritivorous (or purely detritivorous — KAWECKA 1977), including the intake of some animal debris (JONES 1950, COFFMAN 1967).

A large number of the Simuliidae are filter feeders (CHANCE 1970), but some are algal and deposit grazers (BURTON 1973) and some can probably adopt both habits (MULLA and LACEY 1976). Many analyses show, however, that both diatoms and detritus (within a certain size range — CHANCE 1970, LADLE 1972) are characteristic items in the diet independent of species (ZAHAR 1951, CARLSSON 1962, MAITLAND and PENNEY 1967).

The predominant food of *D. lacteum* in nature is mainly oligochaetes, but under experimental conditions mainly the internal juices and tissues of *A. aquaticus* (REYNOLDSON and YOUNG 1963; see also De SILVA 1976). *Plumatella* and other bryozoans are sessile and thus prefer allochthonous microfauna and microflora for their food (KNÖPP 1952, HYMAN 1959). *E. octoculata* preys on all invertebrates in the community (MANN 1962), even on its own species, although its main food may well comprise chironomid larvae (ELLIOTT 1973). According to BÖTTGER (1970), predators, parasites and scavengers can all be distinguished with certainty among the Hydrachnellae, and his survey of the literature includes reference to one species of the Sperchonidae and also *Lebertia insignis* which prey on chironomid larvae, and *Hygrobates calliger*, which also feeds on 'Kleinkrebse', although the primary food of the genus *Hygrobates* appears to be the larvae of Ephemeroptera, while the watermites of Hygrobatidae seem to be general predators.

A. aquaticus favours large diatoms and periphytic algae, but if these are unobtainable it will feed on dead macrophytes and detached leaves (WILLER 1917). Later characterizations place it in the category of a wide-range detritivore (LEVANIHOV 1949, HYNES 1960, REYNOLDSON and YOUNG 1966, PRUS 1972).

Elmis aenea accepts plant material, especially algae (WESENBERG-LUND 1943), and its larvae are heavily dependent upon algae, chiefly diatoms (CHAPMAN and DEMORY 1963).

Individual variations to be observed in the diet of certain species may be traced back to a variety of causes, although it is difficult to support these with unambiguous evidence. Some indications are to be found (BRINCK 1949, BROWN 1961), but these remain somewhat speculative for the present. Feeding, as discussed by CUMMINS (1973) and GRIFFITHS (1973), is usually defined as selective if the composition of the food differs from that of the surrounding food supply. Cummins concludes with some conviction that the term 'restricted food intake' would provide a sounder basis for the study of this phenomenon, in which case only *A. aquaticus*, *C. bicinctus* and the Simuliidae would

fall into this category, having diets which are quite regularly of similar composition.

What are the factors which determine the composition of the diet? The location of the microhabitat may naturally compel the animal to feed on those items which are available rather than the favourite items for the species, a situation which comes about when an over-supply of secondary dietary components has arisen, for instance. At the same time, the feeding mechanism, either anatomical or constructional, can restrict the diet in respect of particle size, although this can still allow a variety of items. This is to be seen in the diets of many passive feeders (collectors). Generally speaking, primary consumers tend to be non-selective generalists, since their food intake is to a considerable degree regulated not only by the local characteristics of the habitat, but also by the age of the animal itself. Opportunism is a basically safe strategy for individual development and for the survival of the species.

5.3.3. Trophic relations

The trophic relations of the rapids community are described semiquantitatively in Fig. 11. The sources of food are indicated qualitatively only, and the animals are grouped according to their food habits. The primary consumers consist of bryophyal, algal, diatomal, diatomal-detrital and detrital feeders, whose main diet is denoted by the thick lines, and herbivore-detritivores, whose dietary assortment is shown by the finer lines. The prey species of the predators are grouped by means of the brackets, and the

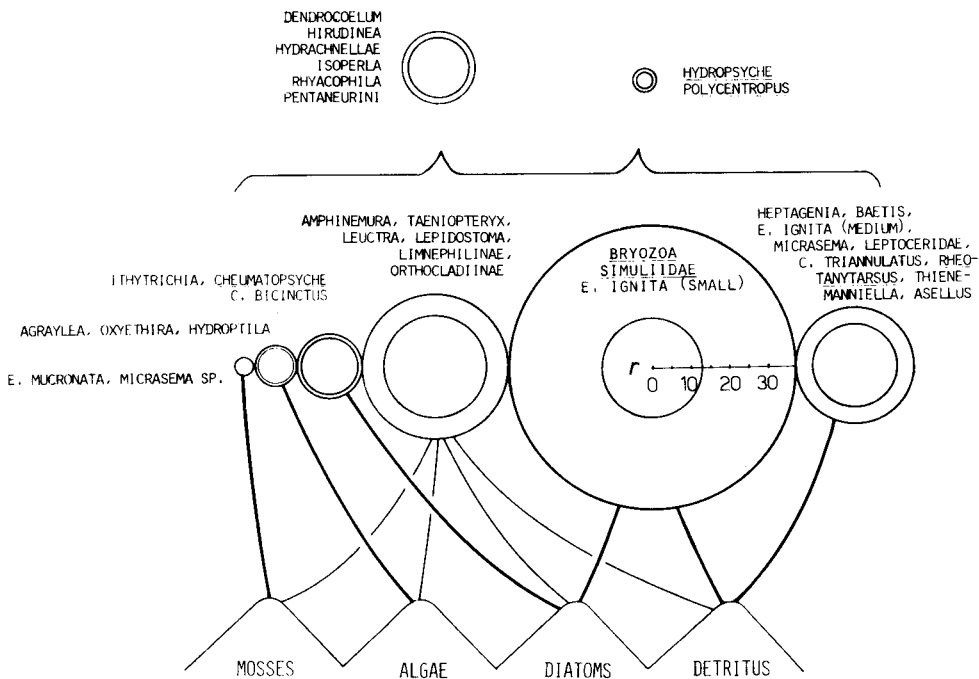


Fig. 11. Trophic relations in the rapids community. For explanations, see text.

drift collectors and filterers are underlined. The total size of each group is expressed by means of the area of the circle concerned, the inner circle referring to the size when the weir habitat is excluded.

Consumption of mosses, filamentous algae and diatoms is in the main characteristic of a limited number of species and individuals among the primary consumers, while the great abundance of the filtering Simuliidae renders the diatomal-detrital feeders the most significant group in the whole community. A large number of species are herbivore-detritivores or detritivores proper, the first group, however, containing no mayflies and the latter no stoneflies. Detritus is thus the most conspicuous single source of food, especially when it is borne in mind that all the other species gain some profit at least from detrital matter. Most predators are active feeders which additionally possess certain specific prey animals, while the passive collectors are rare, and their trophic position is to some extent intermediary between the primary and secondary consumers, as also are the scavengers which utilize animal debris, which on a nutritional basis in particular should be placed at a higher level among the primary consumers. On the other hand, it must be noted that active predators may also behave as tertiary consumers, as has been seen above.

When the weir material is omitted and the trophic relations studied in the remainder of the community, a very large majority of the creatures fall into the class of diatomal-detrital feeders, since about half of the total herbivore-detritivores and detritivores originate from this habitat, while the riverbed supports the main body of the bryophytal, algal and diatomal feeders and the predators.

The ratio between the numbers of predators and prey animals is approximately 1:48 in the weir, 1:9 elsewhere and 1:22 in the community as a whole. Thus the mechanically overturned habitat, unusual for rapids in general, seems to reduce the ratio to about one fifth of that which holds for a normal rapids habitat, where the ratio obtained may in any case be somewhat too small, as the algal overgrowth on the weir would cause the blackfly population to emigrate in favour of the riverbed.

5.3.4. Ecological background

Many reasons can be found for the distribution detailed above. The ecology of the simuliids involves certain requirements in respect of the type and rate of the current, the food supply, riverbed conditions, sedimentation and vegetation. The current is accepted as a cardinal factor, since it ensures a supply of oxygen and food and the removal of excreta and alluvials (WU 1931, ZAHAR 1951). Wu even considers this a more important factor than the food supply itself. The latter, however, is regarded by Zahar as primary, because of the food supply/flow rate relationship. Thus the dense standing crops of filtering animals to be found at the outlets of lakes are due precisely to such a rich supply of planktic food in a body of water flowing at a uniform swift rate (see MÜLLER 1954, 1956, ILLIES 1956, CARLSSON 1962, ULFSTRAND 1968). There is a great difference in the quantity and nature of the benthic fauna, for instance, between a river outlet and the rapids below it.

Such outlet features, together with the relatively bare stones, make the weir a favourable environment for the simuliids, and it is probable that the food supply on the river bed

is not as poor as the number of animals would suggest, but rather the conditions for settling and feeding are inferior because the stones are covered by mosses, the bottom is more sheltered and the current is turbulent. Simply the physical structure and age of the habitat are of great importance at Jäväjänkoski. The labelling of any factor as 'primary' is a risky procedure, however, as ecologically the effects of the factors are always operative in combination, and are dependent on local characteristics and the size rank of the habitat.

The vegetation influences the location of the animals, although the primary effect of this is difficult to distinguish from protection behaviour. Mosses and algal growths, of course, maintain populations of animals which feed on them, i.e. bryophytivores, algivores or diatomivores, and the bryophytes are also of some importance indirectly in that they tend to gather detritus (cf. the detritivores *Amphinemura* and *Micrasema*) and act as a substrate for epiphytic algae and diatoms (cf. the algivores and diatomivores, the Hydroptilidae and the Chironomidae). Similarly, the detritus which accumulates in dead water and under stones may directly influence the location of some detritivores (e.g. *Heptagenia*, *Asellus*, *Rheotanytarsus* and Orthocladinae spp.; see EGGLESHAW 1964, ULFSTRAND 1967), and also act indirectly to concentrate the predators close to their prey animals, e.g. the leeches, *Rhyacophila* and *Isoperla*, which feed on some dipterous larvae (see ULFSTRAND *et al.* 1971).

Rhyacophila regularly inhabits stones, where dipterans are clearly dominant, accounting for not less than 33 % of the community. These sluggish caddis larvae seem to attack immobile animals, pupae and adults just emerging and unable to escape in preference to eating the more rapidly moving mayfly or stonefly nymphs, although the relative abundance of these latter on the stones may be similar to that of the dipterans, e.g. on stone 35 (see THUT 1969). Since predation implies an active search for prey, it is to be assumed, as SCOTT (1958) argues in detail, that the micro-habitat position of the *Rhyacophila* larvae is largely regulated by prey distribution.

6. COMMUNITY STRUCTURE

6.1. Introduction

The material comprises 102 labelled taxa, treated here as species (see p. 24). This then permits an analysis to be made of the statistical relations prevailing within the animal communities of the stones in the rapids and certain models for the distribution of the species between the stones to be examined. The purpose here is in effect to determine these relations on the basis of the primary data listed in the Appendix, employing as statistical measures the numbers of species and individuals, occurrence and dominance figures for the species, and the species diversity of the communities at different levels. In this way it is hoped to gain an impression of the efficiency of the collection method in relation to the abundance figures obtained.

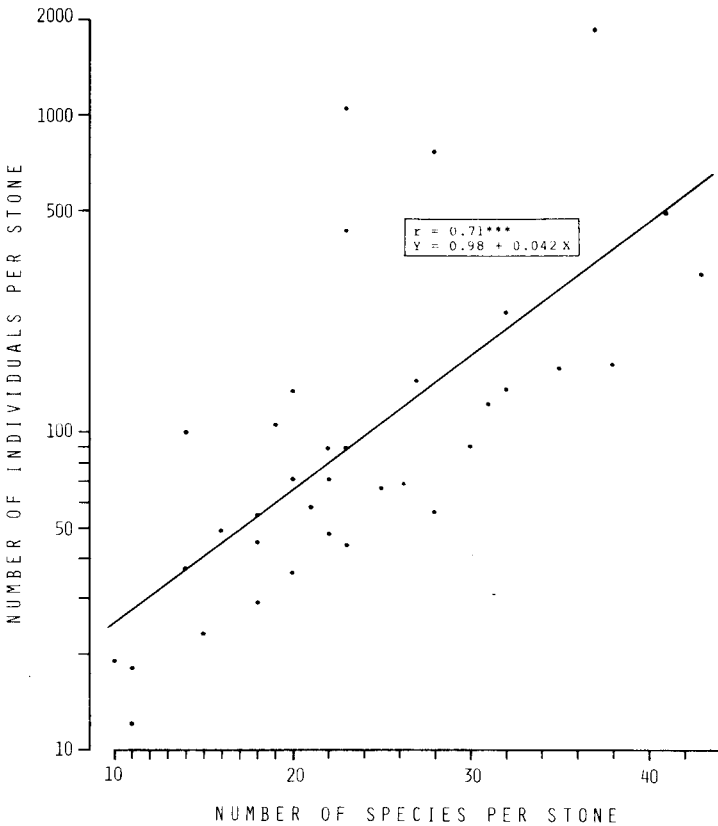


Fig. 12. Relationship between the number of individuals and number of species (see p. 24) on the stones.

6.2. Numbers, occurrence and dominance relations

The mean figure for the number of animals per stone was 207.7, but with a very considerable standard deviation of ± 363.3 . Since $\bar{x} < s^2$ (for variance, see ELLIOTT 1971), the community may be said to show a high degree of aggregation, thus representing the 'contagious distribution' model. In a similar way, the mean number of species per stone, 23.7 (SD ± 8.5), would represent contagious dispersion of the total species among the stones. A very highly significant correlation and dependence ($t = 5.80^{***}$) is observed between the numbers of individuals and numbers of species on the stones (Fig. 12).

The abundance figures for the various species (in individuals per stone) lay in the range 1–1216, with a mean of 8.7. On the basis of the mean number of species in each abundance class (Fig. 13), it may be concluded that the mean fauna for one stone would consist of 9.5 species represented by one individual each, 4.5 represented by 2 ind., 2.2 by 3 ind., 1.8 by 4 ind., etc. Thus the median situation is represented by the class with 2 individuals (cf. the mean value above). This steep slope in the cumulative percentage curve suggests that abundant species, e.g. ones with more than the average number of individuals, are very few and far between, being found in only one case out of eight, while species with ≥ 20 individual occur in only one case out of 19. This distribution would follow the relationship between abundance and number of species most commonly found in communities in a natural state (see WILLIAMS 1953, 1964).

The record of the incidence of the various species (Fig. 14) points in the same direction as the above, suggesting that the fauna consists primarily of rare species, the median value falling upon the class with 5 occurrences out of 35 stones. Particular attention is attracted by the extremely rare species, those appearing on only 1 or 2 stones. A highly significant correlation ($r = 0.26$) and regression relationship ($b = 0.58$) prevails between the mean abundance of a species and its incidence.

The statistical position of each species within the community may be shown, for instance, by the 'index of dominance' (KOWNACKA 1971, KOWNACKI 1971), which

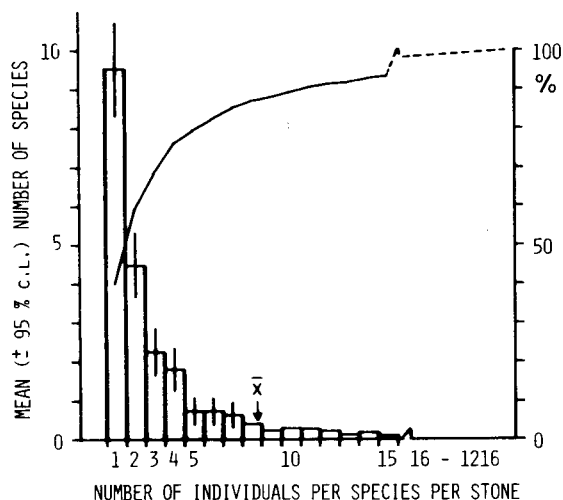


Fig. 13. Mean numbers of species (see p. 24) with given numbers of individuals per stone and cumulative percentage curve for the number of species. \bar{x} indicates the mean abundance of species per stone.

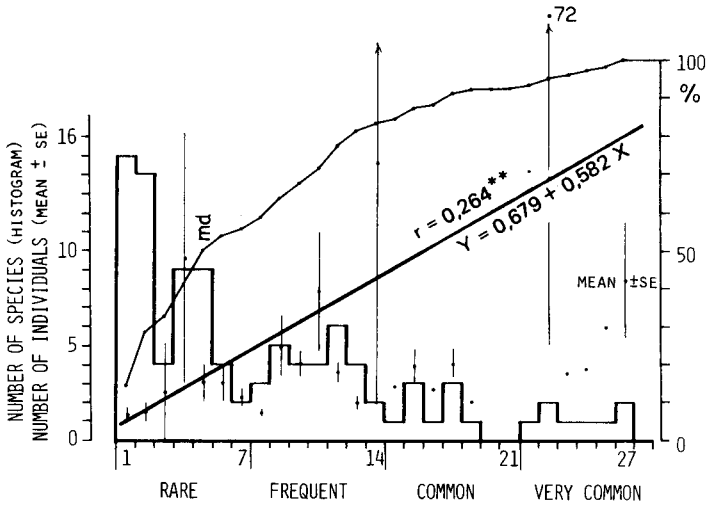


Fig. 14. Distribution of the species (see p. 24) by incidence (histogram where md points the median class, and cumulative percentage curve), mean number of individuals per occurrence (mean \pm SE), and dependence of this upon incidence (regression line).

takes account of both the number of individuals of each species and also its incidence. (It should be borne in mind here that the values obtained are valid for comparison only within the one community, since the index is dependent upon the total number of individuals in the population.) It immediately emerges (from Table 16) that the extremely abundant *Simulium reptans* achieves such a high index of dominance that no other dominant species can be listed at all for the community as a whole, although taxa such as *Athripsodes* spp., *Eukiefferiella alpestris* and *Cricotopus bicinctus* are dominant within certain habitats taken separately. In consequence, subdominant status is achieved with a relative abundance of only approx. 2 %. The majority of such species or species groups would be classed as very common, although some species with similar relative abundance figures are found which would be considered adominant A, e.g. *Rhyacophila nubila*, '*Orthocladus*' sp. A. *E. alpestris* is an example of a species which is subdominant within the total community, but whose index is based on a somewhat restricted pattern of occurrence, being confined largely to the weir (incidence 11/35). The overwhelming position of *S. reptans* is reflected in the fact that subdominant status is a rarer thing and the total species spectrum less even in its dominance pattern in the weir than in the riverbed or any of the other habitats.

Thus we find the animals identified have a rather uneven distribution amongst the stones of the rapids both in terms of species presence and in actual numbers of individuals, the overall community consisting of a large number of species represented by just a few specimens at the most, and a small number of numerically dominant species, with approximately two species in 23 accounting between them for as much as 70 % of the fauna. At the same time, the higher the incidence of a given species among the stones, the greater its abundance can also be expected to be on any one stone. It is also probable with this type of distributional model that one would be constantly encountering new species sets among the communities on the stones.

The ecological explanation for this is a complex one. One essential factor in the case of Jäväjänkoski is nevertheless the existence of a highly aggregatory species, the black-

Table 16. List of species having an index of dominance of at least 1.00 in certain communities (R, W, or oh = other habitats together) and totally. Relative abundance and incidence in the total material is also shown. Explanation of boxes: black-dominant species (index ≥ 10), crossed - subdominant (1.00-9.99), thick walled - adominant A (0.10-0.99), thin walled - adominant B (< 0.10).

	oh	R	W	Σ	%	INCIDENCE
AMPHINEMURA BOREALIS	☒	☒	□	□	1.36	18/35
ITHYTRICHIA LAMELLARIS	□	☒	□	□	0.54	16
HYDROPTILA TINEOIDES	☒	☒	□	□	0.84	18
RHYACOPHILA NUBILA	□	☒	□	□	1.17	24
ATHRIPSOIDES SPP.	☒	□	□	□	0.62	16
MICRASEMA SETIFERUM	☒	☒	□	□	0.95	12
LEPIDOSTOMA HIRTUM	☒	☒	□	☒	2.13	26
PENTANEURINI SP. A	☒	□	□	□	0.37	14
RHEOTANYTARSUS PHOTOPHILUS	☒	☒	☒	☒	4.25	27
EUKIEFFERIELLA ALPESTRIS	□	□	☒	☒	3.74	11
'ORTHOCLADIUS' SP. A	☒	☒	□	□	1.29	25
- " - SP. B	☒	☒	□	☒	1.57	23
CRICOTOPUS TRIANNULATUS	☒	□	□	□	0.77	18
- " - BICINCTUS	☒	☒	□	☒	2.02	27
- " - SP. B	□	☒	□	□	0.50	13
METACNEPHIA TRIGONIA	□	□	☒	□	2.30	9
PARABYSSODON TRANSIENS	□	☒	☒	☒	5.26	14
SIMULIUM VERECUNDUM	□	□	☒	□	1.73	9
- " - REPTANS	□	■	■	■	44.05	23
SIMULIIDAE SPP.	□	☒	☒	☒	4.28	22

flies, which has captured those habitats most suited to it, i.e. the bare rocks and rock patches, and thereby achieved an overwhelming dominance. This may well be a characteristic feature of the time of year, of course, and differ markedly from the situation at other times (see ULFSTRAND 1968), and it may be for this reason that the species which are commonly found to prey upon the blackflies still remain adominant. The community also contains a large number of 'occasional species' with low dominance and incidence figures, which may be either the residual members of a population on

the point of emergence, or else species which are rare and infrequent in this biotope, but nevertheless stable in their occurrence, or perhaps external species brought in by drift, or species whose habitat would be marginal to the rapids, e.g. the water's edge or deadwater area.

6.3. Enrichment of species

6.3.1. Introduction

Lotic biotopes have proved without exception to be rather variable mosaics in which it is difficult to find ecologically consistent habitats or evenly distributed animal communities. It is thus easy to justify such pronouncements as those to the effect that "to sample randomly, . . . , is a highly dubious procedure" (WURTZ 1960), "to assess populations in terms of numbers or biomass per unit area therefore presents formidable, perhaps insurmountable difficulties" (HYNES 1970), or "it is impossible to obtain accurate and reproducible quantitative measurements" (ROBACK 1974). One important problem in this field of research has thus been felt to be the reliability obtained for the statistical parameters describing the animal community or any species population. NEEDHAM and USINGER (1956) demonstrate that even in a fairly homogeneous stone bed considerable numbers of Surber samples are required in order to determine the number of animals per unit area (73 samples) or their weight per unit area (194 samples) in a reliable manner (according to the corrections proposed by CHUTTER, 1972, one would actually need as many as 448 samples to determine the number of individuals). Nevertheless, only 2 or 3 samples are needed to obtain "at least 1 representative of each of the *commonest genera* of bottom-dwelling insects". The calculations of GAUFIN *et al.* (1956) suggest that "3 Surber samples yield, on the average, 68 and 72 %, and 6 samples 85 and 88 % of the species observed in two series of 10 samples from riffles". HARRIS (1957) even concludes that 2 samples should suffice in routine surveys. The tests carried out by CHUTTER and NOBLE (1966) similarly enabled these authors to conclude that "3 Surber samples bring in highly satisfactory results in general river surveys including species, number and weights", for by this stage some 64–85 % (extremes of 95 % confidence) of the number of species obtained in ten samples will already have been collected. When examining the efficiency of sampling at sites comprising total areas of approx. 8.5–11 m², ULFSTRAND (1968) notes that only small increments occurred beyond a standard area of about 6 m².

The facts presented above demonstrate clearly that each statistical measure that one aims to construct for an animal community places its own distinct and often local demands on the sampling frequency. It is therefore necessary to reach some compromise between the number of samples and the reliability of the measures obtained, and to accept certain limitations on the accuracy of the statistics. In the case of the total numbers of animals present and their biomass, it seems to have become accepted practice to consider the results adequate if their standard error is equal to 20 % of the mean. In ELLIOTT's opinion (1971) this is "a reasonable error in most bottom samples". Results obtained on this principle are normally regarded as acceptable in general surveys, in

which a record of the 'most common species' may be sufficient, but the purpose of any given piece of research may impose its own restrictions, so that parameters describing community relations, such as faunal similarities, species affinities and diversities (and parameters associated with these) require extensive species-specific identifications (or the observation of taxonomic units at some other consistent level).

An attempt is made in the following to analyse the cumulative growth of the species list as the samples for the different stones are added to the material. The results are then compared with others obtained mainly by the Surber method. Finally (Chapter 6.6.) it is then possible to discuss what would be the minimum number of samples needed for adequate species detection in the study of benthic communities in flowing water.

6.3.2. Methods

The species enrichment pattern (Fig. 15) is calculated both empirically and by computation following the formula of GAUFIN *et al.* (1956), the initial data being the presence/absence statistics for the species (taxa). The empirical accumulation is calculated from the actual numbers of species found on the stones, combining these progressively to represent totals for 1, 2, 3, ... 34 and 35 stones respectively. Each of these combinations is estimated for 35 different events, and the means (and SD) of these figures are taken to represent the species accumulation.

The theoretical course of species enrichment is determined by adopting the formula of GAUFIN *et al.* (1956), the complete derivation of which is presented in the original paper, so that only a brief survey is required here. The calculations, which require knowledge of the incidence of the various species (see Fig. 14), are based on the determination of the average probability P_k that a species will be found on the k -th out of a set of $k \leq n$ stones but on no previous one, given that it has appeared on at least one out of the present set of n stones, where $n = 35$ in this instance.

When $k = 1$,

$$P_1 = \sum_{i=1}^n (i/n) (S_i/S),$$

where S_i is the number of different species appearing in i out of the n stones, and S is the total number of species observed, which here = 102.

In general form this may be expressed as:

$$P_k = \sum_{i=1}^{n-k+1} \frac{c_{n-k+1}^i \cdot (i)}{c_n^i \cdot (n-k+1)} \cdot S_i/S.$$

Since $\sum_{k=1}^n P_k = 1$, then $S \cdot P_k$ is the average number of new species contributed by the k -th of a set of stones drawn from n , and $S \cdot \sum_{k=1}^{k'} P_k$ the average number of different species observed in sets of k' stones drawn from n .

The coefficient $\frac{c_{n-k+1}^i \cdot (i)}{c_n^i \cdot (n-k+1)}$, where c with its subscripts indicates the common calculation of combinations with given conditions, is a theoretical construct, and has to be computed separately for every possible set of i and k before $S \cdot \sum_{k=1}^{k'} P_k$ can be determined.

The dependence of the number of species upon the number of samples taken was determined by simple linear regression, using the logarithmic transform of the number of samples (LINCON/program, H1640 System Application Programs 1970). The species accumulation figures were compared on the basis of their regression coefficients using the t -test.

6.3.3. Results

The empirical and theoretical species accumulation values coincide well, with only certain minor exceptions ($t = 0.875$, $p = 0.38$ NS). The number of species identified increases rapidly at first, with the first five stones contributing about 60 % of the species and the first fifteen about 85 % (Fig. 15). At the same time the probability of encountering a new species declines, so that from the 20th stone onwards it is below 0.01, while the mean number of new species identified at that stage is less than one per stone. As is to be expected, the standard deviation from the mean in the empirical curve decreases as the number of samples rises, so that the mean for the first sample is 23.7 ± 8.5 , that after the 10th 78.2 ± 4.3 , and after the 25th 96.2 ± 2.2 . The standard error of the mean falls below 1 % of the mean after the 15th stone, implying that this number of samples would suffice to reveal 86.8–90.5 % of the species at a confidence level of 95 %, a slightly more optimistic figure than that obtained in the theoretical calculations.

The regression curve for the number of species against the log of the number of samples proves to be very close to linear, and the coefficient of correlation is high ($r = 0.9976$) and the 95 % prediction belt narrow. This is also true for the 'Surber'-specific enrichment line ($r = 0.9979$).

6.3.4. Comparisons

Empirical observations by botanists (from GLEASON, 1922, onwards) suggest that within the limits of one association, there is a straight-line relation between the number of species identified and the logarithm of the number of quadrats (excluding very small areas), and correspondingly, WILLIAMS (1943) states that doubling the period of observation gives a constant increment of new species in light-trap experiments to collect Macrolepidoptera. These two ideas are confirmed by PRESTON (1948) and WILLIAMS (1964) with many examples from various biological communities ('universes') sampled with units much larger than in the present case. This nevertheless provides a fair indication that such a linear relation may well be universally valid for running water benthos, even when individual stones are taken as the sampling units. The purpose of the comparison to be made below is to determine how far this linearity may be generalized to apply to running water communities elsewhere in the world, and to what extent it may be used to predict the numbers of species to be found in different flowing water habitats.

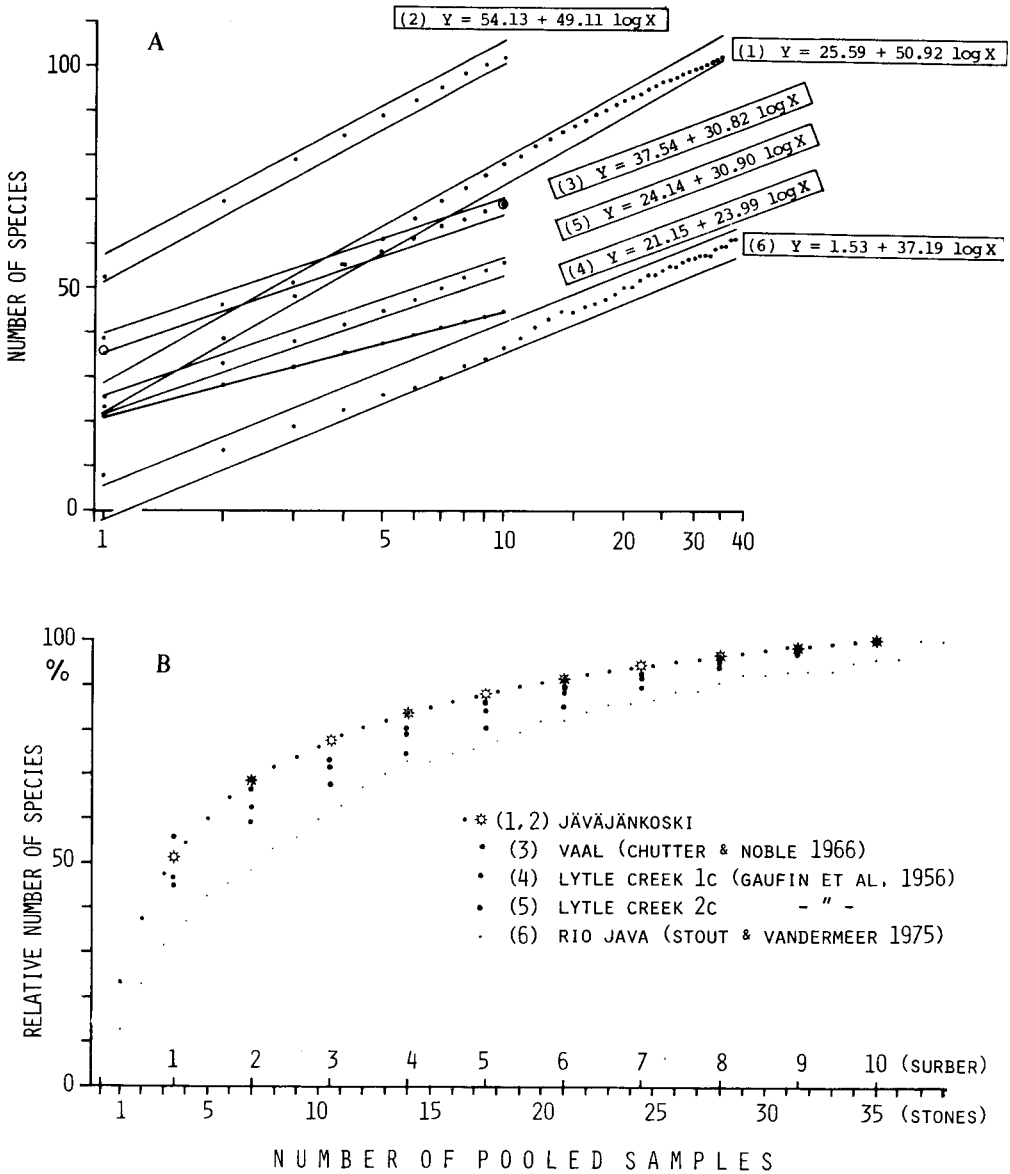


Fig. 15. Species (see p. 24) enrichment values for the stones of Jäväjänkoski (1) and transformed to correspond to Surber units (2), together with comparative values from other flowing water sites (3 ... 6), A in absolute numbers, and B in percentages (see text). The pairs of lines (slight arcs in fact) are the limits of 95 % confidence for individual values of y , the regression line itself being omitted for the sake of clarity. The small circles in A (3) are the beginning and end points of the regression line for the Ammannäs material (ULFSTRAND 1968), the abscissa of which is calibrated in m^2 . In B this line practically coincides with the Jäväjänkoski Surber transform.

STOUT and VANDERMEER (1975) present species accumulation data for an insect study based on the sampling of individual stones in the upper branches of small streams, an example of which, in adapted form, is provided in Fig. 15, while the points on the diagram presented by ULFSTRAND (1968) are employed to determine estimates for the numbers of species and to calculate semilogarithmically the combined linear dependence of the percentage of species on the log of the standard area in m^2 . Since in principle the square foot area of a Surber sampler would correspond to approx. 3.5 of the medium-sized stones (cobbles and small boulders) of mean area $2.6 m^2$ studied in Jäväjänkoski, this arithmetical dependency may also be exploited to describe the species accumulation in these rapids in terms of Surber units. This would then enable a comparison to be made with parameters developed by reference to the results of GAUFIN *et al.* (1956) and CHUTTER and NOBLE (1967).

In order to evaluate the linearity of the species accumulation function, correlations between the number of species and the log of the number of samples, and regression curve at a 95 % prediction limit, and the increments of new species determined after the Williams principle of doubling are also calculated for various sets of comparative data (Fig. 15, Table 17).

The outstanding feature distinguishing the Jäväjänkoski material from the other data studied is undoubtedly the large number of species involved. This may well be due not only to natural differences in animal communities, but also to the lower accuracy requirements set in other experiments and the intentional exclusion of certain taxa, and it is presumably as a consequence of these factors that whereas the course of the values plotted curves downwards slightly in these comparative cases, it is seen to curve upwards at Jäväjänkoski. When presented in a relative diagram this is manifested in the arrangement of the curves at different levels. Thus an asymptotic levelling is seen in the species accumulation pattern at Jäväjänkoski as the number of samples increases, whereas

Table 17. Correlation coefficients (*r*) between numbers of species and sampling units and the increments of new species (as the nearest integer) resulting from doubling the number of units: 2 ... 32 according to real data, *c* according to regression coefficients. Group I comprises stone samples, II Surber samples, and III samples on a sq. metre basis; *e* – empirical, *t* – theoretical (see Fig. 15).

Collection		<i>r</i>	Increment at each step						<i>c</i>
			1	2	4	8	16	32	
I	Present, <i>e</i>	0.997	(24)	13	19	19	15	12	15
	Present, <i>t</i>	0.997	(24)	15	17	18	15	12	15
	Rio Java	0.992	(8)	6	9	10	13	12	11
II	Present, <i>t</i>	0.998	(52)	17	15	14			15
	Vaal	0.997	(39)	7	9	10			9
	Lytle Creek, 1c	0.999	(21)	7	7	7			7
	Lytle Creek, 2c	0.997	(25)	8	9	11			9
III	Ammarnäs area	0.908	(26)	17	6	18			15

in the other data the discovery rate for new species at least persists at its original level. The very high correlations and narrow prediction belts on the regressions nevertheless indicate that all the courses of species accumulation approximate to a straight-line model. Even so, significant differences do appear between the accumulation rates themselves ($p < 0.001$ in the t-test) in all cases except between Lytle Creek 2c and Vaal when expressed in terms of real values and in all except between 1c and 2c and between Vaal and Jäväjänkoski taking the relative values. Considerable variation is found in the constant obtained on the doubling principle in certain instances, but the decrease in the increment at the end of the series acts as a further sign of the asymptotic nature of the accumulation curve in the case of Jäväjänkoski, for in the other sets of data the trend is even in favour of a progressively greater predicted increment of new species.

Since the intercept y on the species accumulation line most often falls close to the mean value for the number of species identified from the samples, it is possible on the basis of the mean number of species in the first series of samples (\bar{s}), the logarithm of the number of samples (n) and the total number of species obtained from these samples (S_n) to state that regression equation by which one may predict the number of species recoverable (S_N) with a number of samples N (where $N > n$):

$$S_N = \bar{s} + \frac{S_n - \bar{s}}{\log n} \cdot \log N,$$

in which the quotient represents the coefficient of slope.

This equation is similar in essence to that proposed by PRESTON (1948), except that in the latter case the intercept y represents the species captured in the first year (the first sample) rather than the mean of several samples. This latter would indeed be a safer starting point from a predictive point of view, at least in a material such as the present one, where the numbers of species vary quite extensively (10–43 spp./stone), for the reality of a straight line as a basis for predictions is naturally limited. It is highly probable, as the Jäväjänkoski material suggests, that the species accumulation pattern, both on a normal scale and when presented logarithmically, will really prove to be asymptotic, converging towards the potential number of species for each community (one possible starting point for the determination of which might be the total species list for flowing water communities for the province or for the country as a whole, data which are still far from being complete). It is indeed demonstrated by PRESTON (1948) and WILLIAMS (1964) that the enrichment lines for large sampling units, such as the quadrats used by botanists or any larger than this, take the form of sigmoid curves when very large numbers of samples are used, indicating a clear decrease in the discovery of new species. This general rule appears also to apply to small sampling units such as stones of 'cobble' dimensions.

6.4. Species diversity

6.4.1. Introduction

Shannon's formula (see PIELOU 1975) is used extensively as an indicator of the diversity of communities of organisms, and the resulting measure, H' , is considered a

fairly accurate device for expressing mathematically the structure of an animal community. Similarly, the species evenness measure, J' , makes it possible to compare materials of differing size in a meaningful way. Such a concept of diversity has proved appropriate for the study of spatial and temporal variations in the composition of flowing water communities both in the field and in experiments with artificial stream-beds (see, for instance, WILHM and DORRIS 1968, WILHM 1970b, GLIME and CLEMONS 1972, ULFSTRAND *et al.* 1974, ULFSTRAND 1975, SLOBODCHIKOFF and PARROTT 1977).

6.4.2. Methods

In the virtually species-level material (see p. 24) described here, both the stones and the habitats would be acceptable as ecological units, and the diversity of their faunal assemblages is capable of analysis by means of the diversity and evenness measures referred to above in such a way that it then becomes possible to examine the influence of the number of species and the numbers of individuals of each species on the index obtained. The results may then be compared in a generalized sense with data presented in the literature. Later an examination will also be made of the dependence of the diversity index upon environmental factors within the rapids (chapter 7).

The calculations are based upon the following familiar formulae:

$$\begin{aligned} \text{diversity } H' &= - \sum p_i \cdot \ln p_i, \quad \text{and} \\ \text{evenness } J' &= \frac{H'}{\ln S}, \end{aligned}$$

where p_i denotes the proportion of each particular species in the community, S is the total number of species, the species richness, and $\ln S$ is the theoretical maximum diversity (H'_{\max}).

The inclusion of two or three species in each of the categories *Athripsodes*, *sensu lato*, and *Simuliidae* spp. (see p. 24), naturally implies that the diversity values should in effect be slightly higher in certain communities than those obtained here by treating each taxon as a single species. If we assume that each taxon represents two unknown species present in equal proportions, we may calculate that the values for H' will increase by 2.5–8 % and those for evenness by 0–3.7 %. Thus the diversity values employed here (Appendix) would not express the real species diversities of the communities in every case. It is highly probable, however, that these indices do in fact come close to the true situation, as usually only one species within each taxon seems to be present on each stone. The spp. pupae left unidentified (see p. 24) were incorporated into the diversity index calculations by including them under the 'most probable' species in each instance.

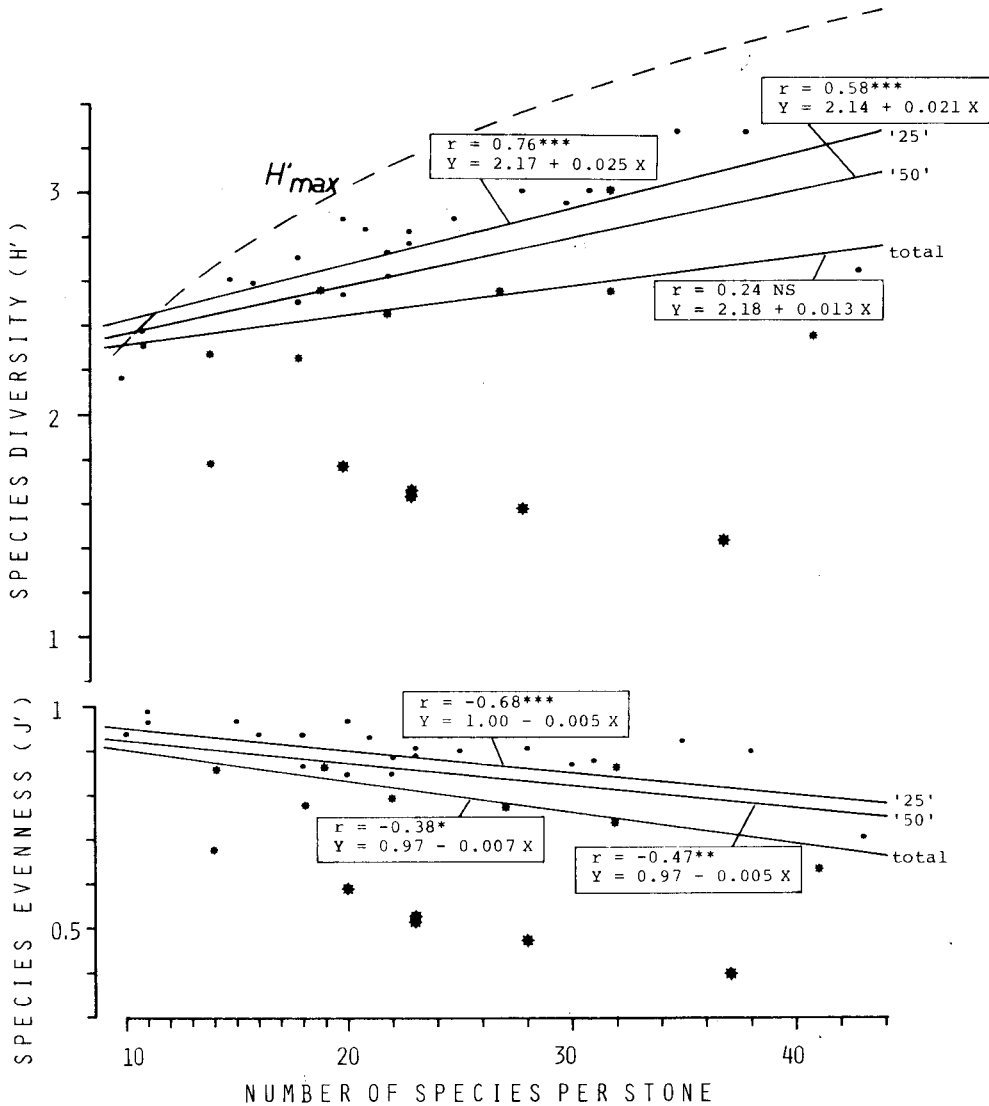


Fig. 16. Species diversity (H') and evenness (J') plotted against number of species (see p. text). The correlation coefficient and regression line are calculated for all stones (total), excluding those having species with 50 % ('50'; big stars) and 25 % ('25'; small stars) dominance respectively. The H'_{max} corresponding to each number of species is indicated.

6.4.3. Results

6.4.3.1. Stone communities

The calculations for H' and J' , expressed to three decimal places, are presented in Appendix. (B), and the figures (Figs 16 and 17) are constructed on the basis of these calculations and the numbers of species on the stones.

The diversity index varies in the range 1.43–3.27, corresponding to evenness values of 0.40 and 0.92 respectively for these extreme figures, the maximum evenness, 0.99, being achieved at a diversity of 2.37. The two extreme communities referred to here are practically the same in their numbers of species, 37 and 35, but show a marked difference in the number of individuals, 1873 and 159 respectively, with the corresponding proportions accounted for by the dominant species being 64.9 % and 8.2 %. The mean diversity index, 2.49 ± 0.47 (SD), would correspond to 12 evenly distributed species per stone. The deviation of this value from the true average, 23.7 species per stone, provides a rough indication that the distribution of individuals is uneven, as is also denoted by the evenness value of 0.81.

It should nevertheless be noted that the majority of the observations are concentrated in the area above the average figure, and that a number of values, mostly for the weir at the point of most rapid flow, are then scattered in an irregular manner over the whole range of distribution, exercising a considerable influence both on the weightings of the averages for both indices and on their interdependences. These latter communities are characterized by the fact that in each case one species accounts for at least 50 % of the total number of individuals. For this reason, the examination of the correlation and regression values (Fig. 16) includes not only r for the total material but also intermediate situations excluding stones having a species with a dominance of ≥ 50 % ('50') or a dominance of ≥ 25 % ('25') respectively.

No statistically significant correlation or regression holds between diversity and number of species for all stones, but both the correlations and the regressions become very highly significant in those intermediate situations where the dependence of H' upon species richness also emerges more clearly. The species evenness correlates with the number of species over the total material and shows a somewhat significant dependence

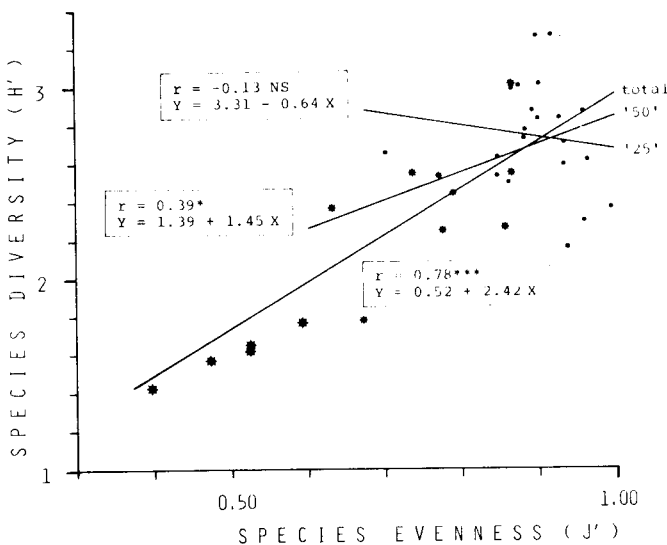


Fig. 17. Species diversity (H') in relation to species evenness (J') (see text). The correlation coefficient and regression line are calculated as in Fig. 16 (see text).

in regression analysis, but a very highly significant relation is only reached between these two factors in the situation $\geq 25\%$.

In order to estimate the influence of the diversity components, H' is plotted against evenness in Fig. 17. Here the correlation ($r = 0.78$) and regression ($t = 7.24$) are both very highly significant, even though the correlation appears to arise largely because of the influence of the divergent group of stones, towards which the curve appears to be directed, as the change in correlation coefficients would suggest ('50' = 0.39, '25' = - 0.13 NS). The same trend may also be distinguished when H' is compared directly with the numbers of individuals on the stones ($r = - 0.61^{***}$, '50' = 0.05 NS, '25' = 0.43 NS).

The conclusion may be reached that the stones of Jäväjänkoski fall into two categories as far as the diversity of their communities is concerned. The majority ($n = 30$) show a highly significant direct correlation between H' and the number of species and a very significant negative correlation between evenness and the number of species, but the communities of a smaller divergent group mainly from the weir habitat cause the diversity to fail to correlate with number of species over the total material and evenness to correlate with it less strongly, while the negative regression becomes very significant. The confusion is very well illustrated by the fact that the variation in diversity in the whole material of stones appears to depend principally upon the evenness component, whereas for the majority of the stone communities, in which no species achieves a dominance of as much as 50 %, it is the number of species which effectively determines the magnitude of the diversity index.

6.4.3.2. Habitat level

Major differences in diversity are to be seen between the habitats (Table 18). The sample size from these being rather variable, the most meaningful comparison is to be achieved on the basis of evenness. Here it should be noted that the evenness index is higher for the 'smaller' habitats than it is for the riverbed and weir, the values arranging

Table 18. Numbers of species identified (S) and individuals ($Ind.$), total species diversity (H') and evenness (J') of habitats, species diversity as the mean of stones (\bar{H}'), and proportion of the most abundant species (%) in the various habitats (E . . . W) and the total material. (Note the limitations upon S , H' , J' and \bar{H}' stated on p. 24 and 72).

	E	B	D	C	R	W	Total
S	40	23	41	37	76	79	102
$Ind.$	178	68	196	192	1334	5301	7269
H'	3.05	2.75	3.36	3.11	3.41	2.10	2.73
J'	0.83	0.88	0.90	0.86	0.79	0.48	0.59
\bar{H}'	2.33	2.43	2.76	2.77	2.73	2.20	2.49
%	19.1	17.6	8.2	12.5	20.8	55.1	44.4

themselves in practically the same order as the percentages of the dominant species in each case. The weir, in particular, stands out markedly from the other habitats on these parameters, and although it is a relatively new habitat by comparison with the rapids themselves, it possesses a greater number of species than do the rapids proper, e.g. the riverbed habitat, even though its diversity index is very much lower. This latter is an immediate consequence of the fact that, as an extreme environment in its flow conditions and the nature of the river bottom, it is a favourite site for mass occurrences of black-flies. This same reason may also be held to account for the generally low diversity and uneven occurrence of the various species in the whole area at the head of the rapids.

The mean diversity for the stone communities is lower than that for the habitat as a whole everywhere except on the weir. This arises partly from the fact that species occurring in the form of single individuals in the stone communities tend to achieve exaggerated importance, whereas these are combined and evened out when considering the habitat as a whole.

6.4.4. Discussion

The literature nowadays offers a fairly extensive body of data based on Shannon's formula for the comparison of rapids and riffle habitats in terms of the diversity of their macroinvertebrate communities (see references in Table 19). There are nevertheless certain difficulties and risks associated with the comparison of these dimensionless diversity values, mainly arising from differences in the methods used. Such problems involve, for instance, the size of the 'macrofauna' and its content (e.g. benthic insects or macroinvertebrates) and the taxonomic status of the term 'species' in view of the many difficulties encountered in identification (e.g. some families which are equated with a single species), and it is also important to be sure that the number of samples taken is sufficient for the diversity to reach an asymptotic level (see WILHM 1970a). Similarly, the season of the year in which the material is collected is of considerable significance, as lotic communities typically vary greatly with the time of year (WILHM and DORRIS 1968, MACKAY and KALFF 1969, HYNES 1970). The above facts are taken into account in the summary provided in Table 19, in which the diversity indices are expressed for comparison purposes as reference values in relation to \ln (i.e. $H' = -\sum p_i \cdot \ln p_i$). Some of the results recorded have required further calculations based on data extracted from tables and figures.

A quite wide range of variation in diversity is encountered between sites and between the samples taken from these, extending from figures of under 0.5 recorded for chloride and acid-polluted streams (WILHM 1970b) to the present values of over 3.0 for some communities on the stones and moss-covered bed of the rapids. With the exception of the polluted waters studied by Wilhm, however, there appears to be a clear concentration of average values and values for combined material in the area above 2.25, with even the diversities on individual stones lying in the range 2.25–3.00 in 3/4 of cases. Differences again appear in the case of the average evenness values, although with the exception of the insect communities on moss habitats, the evenness values may be said to be striking in their similarity as between combined sets of material. Since the waters studied here may be deemed practically unpolluted on the basis of the descriptions

Table 19. Comparison of the diversities ($H' = -\sum p_i \cdot \ln p_i$) of the various macroinvertebrate communities. Sources: 2 CHUTTER and NOBLE (1966), 3 WILHM (1970b), 4 ULFSTRAND *et al.* (1974), 5 RANSOM and PROPHET (1974), 6 MASON (1976), 7 WARD (1976), 8 GLIME and CLEMONS (1972), 9 SLOBODCHIKOFF and PARROTT (1977).

Type of water Geographical position	Season	Diversity H'		Evenness J'		No. of species		Background of community. Notes on identification.
		Range	mean	Range	mean	Range	Total material	
1) Present study Finland	June	1.43-3.27	2.49	0.40-0.99	0.81	10-43	102	Individual stones (35).
"	"	2.10-3.41	2.96	0.48-0.90	0.79	23-79	—, —	Habitats (2-12 stones each).
2) River South-Africa	Oct.						68	10 x Surber. Many OTUs in genus level.
3) Streams USA	May-July	1.83-3.20	2.37	0.69-0.81	0.74	11-54		Miscellaneous, mainly Surber. 9 sites from various clean water streams.
"	"	0.29-1.11	0.95					Miscellaneous, 21 sites from various polluted streams.
4) Stream Sweden	spring						57	4 x 0.25 m ² trays, exposed 32 days.
5) Creeks Kansas	June	2.23-2.60	2.40	0.66-0.84	0.74	21-34	95	2 x Surber, the means from 8 stations. 10 species excluded.
6) Stream British Columbia	April	1.95-2.50	2.25	0.55-0.75	0.63			Tray of 0.14 m ² , 20 intrariffle units. Diptera of family level.
7) River Colorado	annual						32 64 70 49	3-6 x Surber, 4 sections of a river.
8) Stream New Hampshire	April		0.83		0.39		25	Handful of mosses, 46 units. Only insects included, Chironomidae as a single OTU.
9) Stream Ontario	May-July	1.70-1.88	1.78					Area of 2 m x 2 m, hand picking, 3 months (á 2-3 samples). Only insects over 2 mm in size included.

provided of their environment, the diversity values obtained for their lotic benthos communities may be said to support the conclusion reached by WILHM (1970b) from his source material that the diversity (\log_2) usually varies between 3 and 4 (2 and 2.8 for \ln) in clean water streams and is less than 1 (0.7 for \ln) in polluted areas. Such a reduction in diversity may also be brought about by the artificial limitation of the number of species, as may be seen most clearly in works dealing only with insects.

6.5. Linear species enrichment patterns and equal diversity indices – a remark on the universal structural similarity of animal communities on stones in flowing water environments

We have already pointed to certain similarities in the structure of benthic macro-invertebrate communities in flowing water throughout the world. With their skewed species distribution, both on an incidence basis and when calculated as 'number of species vs. number of individuals', so that they follow a negative binomial distribution, the 'reversed J', it seems that one characteristic which they possess in common is the presence of many species with few individuals and low incidence and a few species with many individuals and high incidence, as also holds good in many other biotopes (see WILLIAMS 1964). The linear outcome of the species accumulation calculations may well be due entirely to these statistical relations. Since the diversity index aims at the concise mathematical expression of precisely this community structure, one may expect to obtain similar diversity values for communities which are congruent as far as species distribution is concerned.

One may now look for a reasoned background for such conformities. On similarly structured stony beds of naturally flowing streams the current can be expected to function in the same manner everywhere, creating a selection of potential habitats and niches, and the purpose and activities of the faunal community will also be the same in their basic arrangements, containing intracommunity roles belonging to a system based largely upon trophic relations. These roles are occupied by typical ranges of species at each locality, and the outcome is a set of isocoenoses, i.e. structurally and functionally comparable faunal communities (BALOGH 1958). One good example of this is the well-known set of lake outflow rapids communities, with their dominant group of passive feeders (KNÖPP 1952, ILLIES 1956, MÜLLER 1956). ILLIES (1961a,b) provides evidence for this isocoenotic principle deduced from the analysis of stream and river ecosystems throughout the world into two parts, the rhithron and potamon, each containing its own epi-, meta-, and hypo- types. In this way streams which are quite distinct one from another in terms of animal geography may maintain practically identical animal communities, even though composed of taxonomically quite distant species. This convergence is manifest not only in an anatomical parallelism, but also in a characteristic way in the community structure. The present results indicate that the isocoenotic principle also holds good for more restricted macroinvertebrate communities such as those on the beds of rapids. It is indeed probable that the benthic structure of these communities is regulated within the whole flowing water ecosystem on the same, primarily current-dictated, principles in every case.

Community, as a functional entity, is the result of the combined effects and interaction of many abiotic and biotic elements. Any stress exerted on the natural environment, e.g. in the form of pollution or regulation of river flow (WILHM 1970b, CAIRNS and DICKSON 1971, WARD 1974) will reduce the complexity of its systems, however, and this should be seen in a lowering of the diversity index. The comparisons made here do, in fact, lead us to believe that this diversity index, based as it is on information theory, should be regarded as a relevant tool not only for the concise expression of community structure, but also as a parameter for water quality criteria (WILHM and DORRIS 1968, CAIRNS and DICKSON 1971, FRIBERG *et al.* 1977). One should nevertheless beware of employing this measure as an end in itself, as a simple determination of the number of species in relation to the number of individuals may be a less tedious and equally successful way of comparing the structure of simple organic communities.

Since a species is involved in the diversity index merely in the capacity of an operational unit, any similarities emerging in the comparison of index values will be expressions of functional similarities due to the structure of the faunal communities, which is naturally quite a different thing from a real faunal similarity (p. 96). In the latter sense, of course, this index is highly limited in its applicability, and would appear best suited to the monitoring of changes occurring within a single community with time or as the result of environmental influence. Even in this case one is almost speaking still in terms of functional similarity, since it is a question of a change in the species fulfilling a given intracommunity role.

6.6. Determination of an adequate number of samples

The course of the species enrichment curve raises the eventual question of the number of samples (stones) which would be required to obtain an adequate representation of the species relations in each habitat, and how this may be related to the number required to determine reliably the numbers of individuals present. Curves for these two functions are presented in Fig. 18, employing the index of precision method (ELLIOTT 1971). An equation deemed suitable for general use would be

$$n = \frac{s^2}{D^2 \cdot \bar{x}^2},$$

where \bar{x} = the mean number of samples, s^2 = their variance and D = the index of precision, i.e. the required standard error as a proportion of the mean.

This equation suggests that the present material reflects the species with an accuracy of 6.1 % and the numbers of individuals with an accuracy of 29.5 %. The desired level of accuracy, 20 %, standard error of the mean, is achieved after only four stones as far as the species list is concerned, but would require 77 stones in the case of the individual numbers. This large discrepancy is in conformity with observations made in connection with earlier work on lotic benthos (p. 66). Since only 55 % of the species will be caught after four stones, it is obvious that the accuracy requirements should be raised considerably in this respect, as would be necessary especially for the determination of the similarity

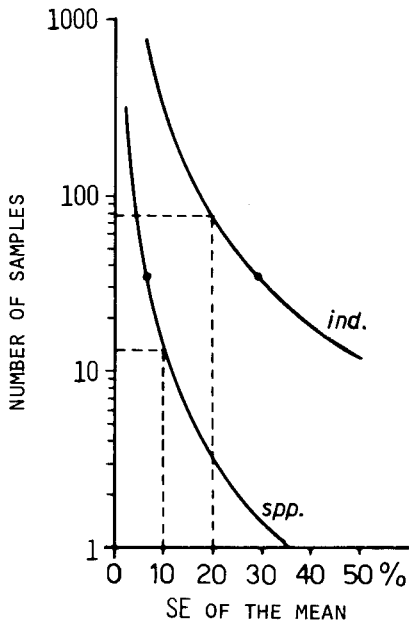


Fig. 18. Numbers of stones required for sampling species (spp.) and individuals (ind.) at different levels of precision (%), after ELLIOTT (1971). Actual precisions obtained from the total material are indicated by dots on the curves.

and diversity parameters for the communities, in which the numbers of species identified play an important role. On the other hand, whatever accuracy value is laid down, this is merely an artificial limit, and thus an attempt was made in the present instance to approach the problem via the following alternative solutions:

- I – a probability of the occurrence of new species of less than 0.01 (the value of P_k in the formula of GAUFIN *et al.* 1956), this also being a value consistent with the most common expressions of statistical significance,
- II – a standard error of the mean of 10 %,
- III – an increase in diversity of less than 1 % (see JÄRVINEN and VÄISÄNEN 1973), which will nevertheless only be adopted here in a form based on the values for H'_{\max} ($= \ln S$) derived from the species accumulation curve, and
- IV – an increase in the diversity value above the 95 % asymptotic total diversity value and a levelling in the estimated series of samples using progressive pooling (Fig. 19; see WILHM 1970a).

Obvious differences are to be seen between the results of these alternatives (Table 20). The first principle provides a very broad picture of the fauna, with a substantially higher total number of species than in the other cases, but it is the third which should be considered the optimistic solution, since the H'_{\max} from the species accumulation curve upon which it is based does not reflect the evenness component, for in this material diversity alone correlates with species richness only in those samples in which no species achieves a relative abundance of over 50 % on any one stone. Using the fourth principle the species diversity is found to level out from around the ninth sample onwards, as it reaches 95 % of its maximum value. Since this method is based on a single series of estimates, it would seem too subject to risk to be able to give a reliable impression of the increase in diversity. After all, the mean number of new species per stone continues to

Table 20. Numbers of stones to be sampled (n) as determined by the four alternative methods discussed in the text, and the percentage attained (s) out of the total number of species, percentage of total diversity reached (H') and accuracy achieved (SE of the mean in %).

Method	n	s	H'	SE
I	20	90.7 %	97.9 %	8 %
II	13	82.2	95.8	10
III	9	74.3	93.6	12
IV	9	78.4	> 95.0	

be exceeded up to the fifteenth stone (Fig. 19). The drawback with all three of these methods, however, is their complexity of execution compared with the second principle, which in turn suffers from the weakness that, unlike the others, it takes into account the total number of species recovered, and thus may be misleading if the set of samples happens to be lacking in variance. The standard deviation in the number of species nevertheless seems to be reasonably characteristic in the case of the rapids studied here.

It would thus seem that the index of precision method, subject to the constraints mentioned above, should prove an adequate means of delimiting the desired number of samples in such a manner as to ensure a sufficiently accurate representation of the fauna and its diversity in the case of a body of flowing water with a 'cobble' bed (-6 — -7 on the phi scale), especially in view of its technical simplicity. An accuracy requirement of a 10 % standard error of the mean would be suitable, but this could naturally be tightened further according to the aims and resources of the research. In this way one would very soon also reach the criterion of a 0.01 probability of new species occurring. The requirement of 13 stones established above, when translated into Surber units, would slightly exceed the three units which is the number recommended in the literature for routine and general surveys. On the other hand, four units would obviously guarantee a more complete picture of the fauna, particularly in the case of the many infrequent and less numerous species which are nevertheless typical of rapids communities.

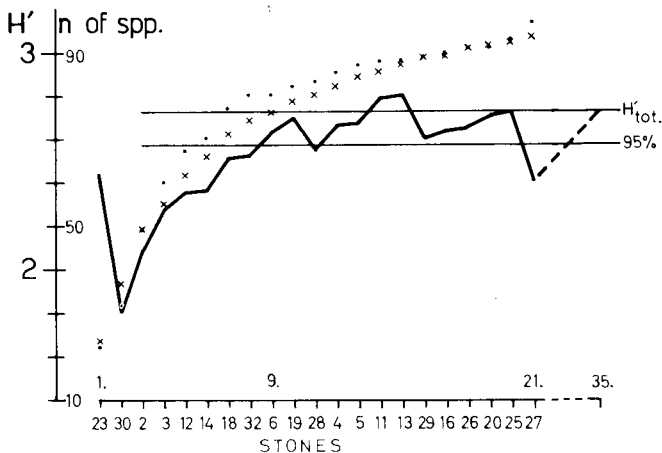


Fig. 19. Increase in species diversity (broken line) and number of species (dots) in random series of 21 stones out of the 35 combined progressively. The diversity of total material (H'_{tot}) and its 95 % level are indicated by lines and the mean species enrichment by crosses.

7. COMMUNITY STRUCTURE IN RELATION TO ENVIRONMENTAL FACTORS

7.1. Introduction

The discussion entered into above and the extensive bibliographies compiled by such scholars as HYNES (1970) provide a clear picture of the multifarious complex of ecological factors which is involved in regulating the structure and abundance of a river-bed fauna. On a local scale, these factors are dominated by the gradient of the channel and the rate of flow, based on the total discharge of the river, since it is these which determine and maintain the structure of the river bed. The outcome of this is a multi-featured physiographical mosaic inhabited by organisms each adapted to certain flow conditions, lending the overall faunal community its typical patchy distribution pattern, the populations of the various species then being distributed according to a stable system of preferences in respect of these conditions, often involving quite specific ranges. Considered in this way, it is the current which is primarily responsible for the whole structure of the community. There are nevertheless other individual ecological factors which, when examined in isolation from the above complex, can also be observed to exercise a controlling influence on the faunal community, so that differences in the distribution of the community within the one habitat, including differences at the micro-habitat level, can be shown to have causal relationships with such factors as the particle size and stability of the substratum, the probability of silt accumulation, the distribution patterns of detritus deposition and drifting food particles, other food sources including the vegetation (which is also relevant in affording shelter) and the availability of colonization space. Once one approaches the realm of the trophic resources of the water, however, one is close to discussing a biological rather than environmental factor operative in the distribution of the animal community.

The aim in the following is to determine the extent to which the community on a stone is dependent on the substratum itself and on the flow conditions prevailing above it. The relevant relationships here, bearing in mind the remarks made above on species numbers and diversity (pp. 24 and 72), are the dependence of the numbers of species and individuals (and the logarithms of these) and the indices of species diversity and evenness upon the size of the stone, i.e. its breadth, length, axis area and axis volume, the moss and algal cover, the surface current velocity and the point flow.

7.2. Methods

At the first stage the correlations are calculated from the whole material using simple linear regression analysis (Table 21). It should be noted that, as it happens, all the signi-

ificance values presented in the table also apply as they stand to the corresponding regression coefficients (as calculated by the t-test). The typical courses of these dependences (Figs. 20–22) are then estimated using the HONEYWELL (1970) 'BASIC LCRVFT/multiple curve fitting' program, or by applying simple regression analysis in a stepwise manner adding data points in pairs from the smallest to the largest environmental variable, or alternatively in the reverse order, until the probability (p) figure for the correlation coefficient (r) indicates the minimum risk (see Fig. 21A). Since the stones in the weir differ markedly from the others, not only in being practically bare of vegetation, but also in the animal communities they support, these are marked on the diagrams with a distinctive symbol. Because of these discrepancies the above analyses are also carried out in certain instances using the remaining material excluding the weir, and can then be regarded as representing a 'normal' rapids bed.

7.3. Results

7.3.1. Simple linear regressions

Among the environmental variables employed here the amounts of mosses and algae show a highly significant intercorrelation ($r = -0.44^{**}$), as also do the amount of mosses and depth ($r = -0.46^{**}$), i.e. the mosses decrease in amount with depth and are replaced by algae, the correlation of which is positive with depth, though not significant ($r = 0.26$). Also, as may be expected since one is derived from the other, the axis area and axis volume are intercorrelated, and also the length and breadth of the stone, while the point flow correlates with both depth and surface velocity.

The following trends emerge from the linear correlations (Table 21). The number of species is directly dependent upon the size of the stone, and is increased by a more pronounced moss cover and reduced by a higher proportion of algae, although not significantly in this case. It does not, however, correlate significantly with either depth or surface velocity, although the point flow, which combines these factors, does explain its variance at the significant level.

The number of animals on a stone is independent of the size of the stone, but is likely to be reduced by the presence of mosses or algae, and to be increased with a highly significant degree of certainty by any rise in the point flow.

Species diversity is directly dependent upon the size of the stone and its moss cover. A reduction in H' and J' is consequent upon increasing surface velocity or point flow.

The logarithmic transforms yield higher correlation coefficients than are obtained from the actual numbers in almost every case. Axis area emerges as the best explanatory stone-size variable, and point flow has a greater explanatory power than surface velocity for all parameters except diversity.

In respect of which of the environmental variables is this linear dependence really valid? In theory a continuous reduction in the particle size of the river bed, i.e. in the colonization space on the stones, or a continuous increase in flow rate, i.e. exerting a larger drag upon the stones in relation to that which the animals are capable of withstanding, would eventually lead to extinction of the community, and in both instances the direct influence of such trends would be reflected in a decline in its species diversity.

Table 21. Correlations of numbers of species and individuals in the stone communities (actual and logarithmic), species diversity and species evenness with certain environmental factors (correlation coefficient and its significance in simple linear regression).

Parameters	Number of species		Number of individuals		Diversity	Evenness
	actual	log	actual	log	H'	J'
Breadth of stone	0.38*	0.39*	0.06	0.01	0.36*	0.10
Length of stone	0.30	0.38*	-0.05	0.08	0.19	-0.10
Axis area of stone	0.44**	0.47**	-0.02	0.17	0.39*	0.05
Axis volume of stone	0.36*	0.37*	0.09	0.07	0.39*	0.11
Moss cover	0.29	0.31	-0.21	0.10	0.40*	0.16
Algal cover	-0.22	-0.25	-0.22	-0.34*	0.05	0.22
Water depth	0.29	0.24	0.20	0.03	-0.05	-0.25
Surface velocity	0.29	0.33 ¹⁾	0.52**	0.66***	-0.45**	-0.68***
Point flow	0.40*	0.45**	0.56***	0.68***	-0.41*	-0.69***

1) 0.55***, if stone 31 is omitted

In the case of the logarithmic transform of the number of species and the stone size variables, a curvilinear dependence relationship can be shown to be more appropriate, as this hyperbolic function yields a very highly significant correlation coefficient (Fig. 20A). This would imply that any increase in the axis area of the stone would raise the number of species very sharply at first, but this would very soon slow down. By this latter stage the regression would seem to be non-significant once again, as one might presume from the nature of the regression line (incl. stones $\geq 1.4 \text{ dm}^2$). The hyperbolic function also proves the most suitable for explaining the dependence of the number of individuals upon axis area (Fig. 20B), the correlation being very highly significant once the weir communities are excluded. Species diversity, on the other hand, appears to bear a straight-line relationship with axis area, especially with the weir material again left aside.

Thus the following simple relationship could be stated for the 'normal rapids bed situation'. The larger the stone, the greater the number of species and individuals to be expected on it and the greater the variety to be found in the community, the increase in both species and individuals per unit surface area of stone nevertheless declining steeply at larger surface areas, and becoming statistically independent after an area of approx. 2 dm^2 at the latest. The increase in species diversity nevertheless remains constant.

The dependence of the number of species upon surface velocity proves fundamentally non-linear (Fig. 21A), a direct linear correlation ($p < 0.001$) obtaining up to a velocity of 83 cm/s , but a negative one ($p < 0.01$) holding good from 71 cm/s onwards. Such a dependence relationship would probably best be reflected in a parabolic function, for such a curve, that of a second-degree polynomial, would seem on inspection to be the most appropriate. This would make the number of species directly dependent upon surface velocity within the range 'very slight' to 'swift', negatively so in the area between 'swift' and 'very swift', and more or less independent at velocities of 'moderate' and 'swift'.

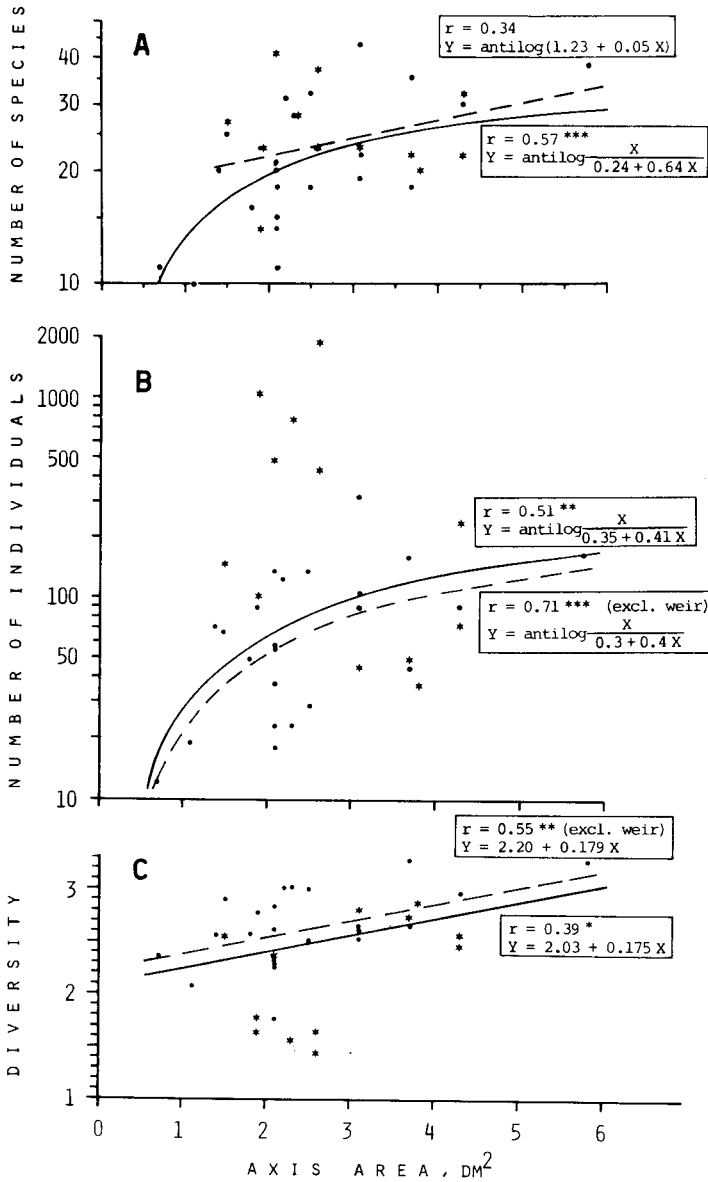


Fig. 20. Numbers of species (A) and individuals (B), and species diversity H' (C) (see p. 72) in the stone communities in relation to the axis-area of the stones. Dashed lines: (A) regression including stones. $> 1.4 \text{ dm}^2$, (B) and (C) excluding the stones in the weir (margined with stars).

The surface velocity serves to explain the number of individuals on the stone just very slightly better when expressed as a power function (Fig. 21B), and this curve would certainly seem a more sensible form for the dependence relationship as far as 'very swift' surface velocities were concerned. The material nevertheless only provides weak evidence of this decline to be expected in the numbers of individuals at very high surface velocities.

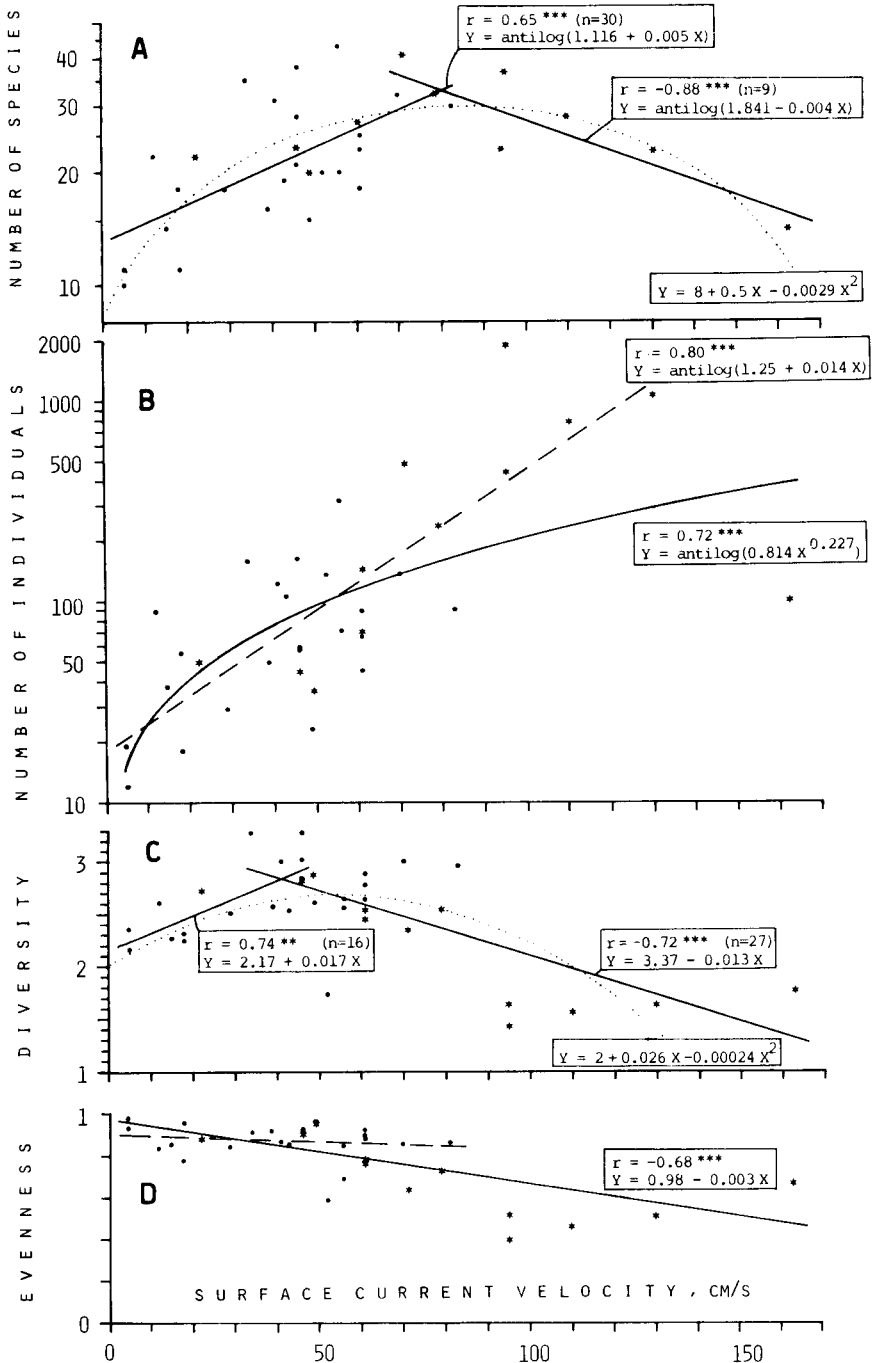


Fig. 21. Numbers of species (A) and individuals (B), species diversity H' (C) and evenness J' (D) (see p. 72) of the stone communities in relation to the surface current velocity above the stones. Dotted curves: (A and C) eye-fitted second degree polynomial functions; dashed lines: (B) stone 31 omitted, (D) non-significant dependence in the material excluding the weir. Stars are the values from weir.

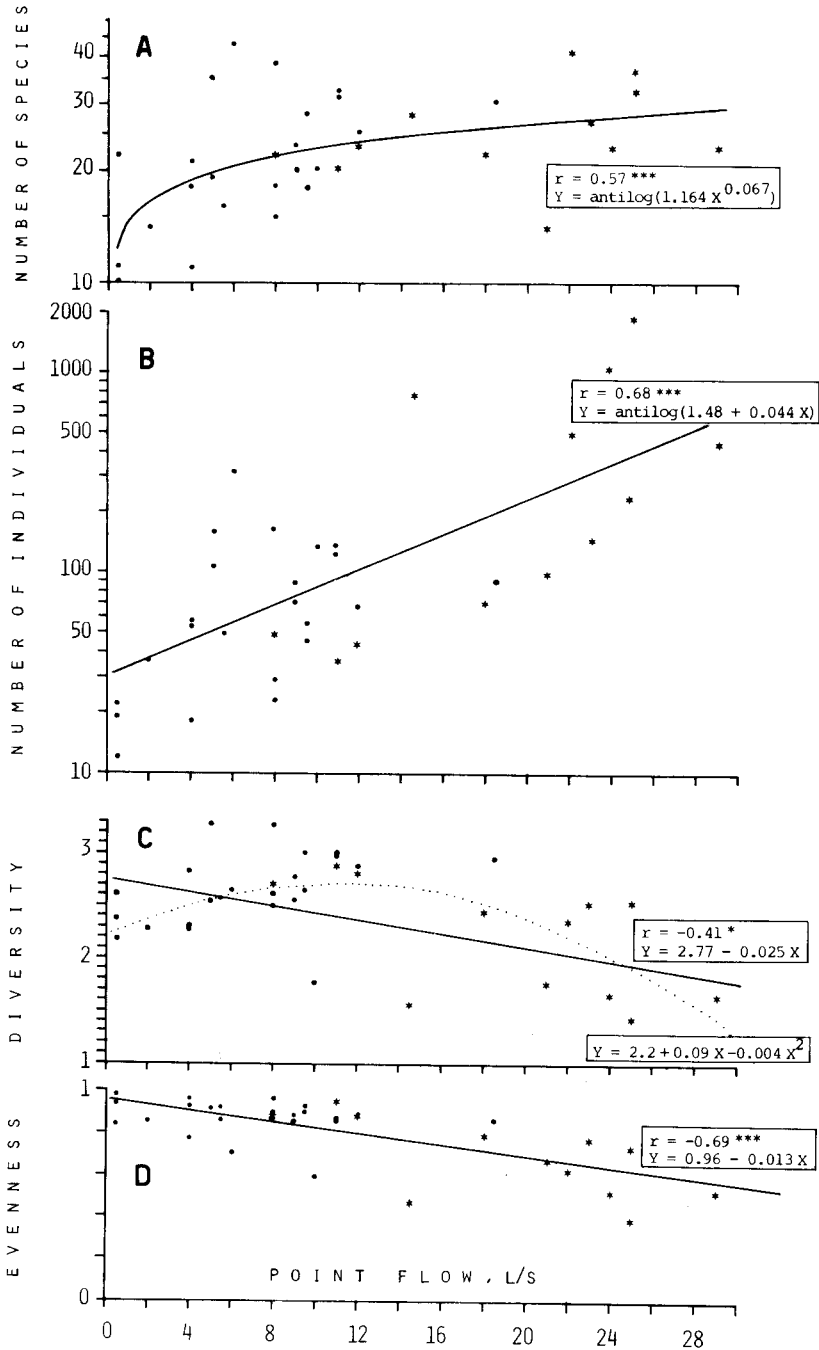


Fig. 22. Relationship between community parameters (as seen in Fig. 21) and point flow. Dotted line in (C) is an eye-fitted second degree polynomial function.

Up as far as a moderate surface velocity the faunal communities increase in diversity (Fig. 21C), while an independent situation and higher index values can be seen to be concentrated in the area from 'moderate' to 'swift', but as one moves towards the 'very swift' end of the scale an extremely abrupt decline in diversity sets in, chiefly as a consequence of certain of the weir communities, in which one species may gain a dominance of more than 50 %. A similar step-wise decline is also to be seen in the evenness values (Fig. 21D), although the linear correlation with surface velocity is still maintained at the very highly significant level. It should be noted, however, that evenness is not dependent upon surface velocity to any significant extent in the 'normal rapids bed' cases.

In summarizing the effects of surface velocity, therefore, it may be said to restrict first the species diversity of the stone communities (from the 'moderately swift' category onwards), then the number of species (from 'swift' onwards) and finally, only very late indeed, the number of individuals (in 'very swift' currents).

Point flow correlates very strongly with surface velocity ($r = 0.80^{***}$), but nevertheless shows some differences from it in the manner in which it explains the quantitative aspects of the stone communities. Thus, for instance, the number of species soon becomes constant, and thus independent of the amount of water flowing past, rather than declining as it does at high surface velocities (Fig. 22A). The dependence of the number of individuals (Fig. 22B) and the evenness of the species distribution (Fig. 22D) on the point flow is in each case linear, but in the case of species diversity (Fig. 22C) a parabolic curve would seem more appropriate, as was found with surface velocity.

A comparison of surface velocity and point flow as explanatory variables shows the latter to possess slightly higher degrees of significance in its correlations with the number of species and individuals and with species evenness, while the weir communities show a less deviant scatter, e.g. in diversity and evenness. This may well be due primarily to the stabilizing effect of depth, for the drag exerted by the current weakens with depth (so that the boundary layer becomes thicker, for instance; see AMBÜHL 1959), and points with different surface velocity readings may prove similar in their point flow values.

7.3.2. *Multiple regressions*

The coefficient of determination, equal to the square of the correlation coefficient, is generally used to measure the proportion of the variation of y determined by x and to depict how well the line describing the regression explain the dependence between the variables. In this way the variation in number of species and number of individuals, expressed logarithmically, is found to be 22 % dependent on axis area and 47 % dependent on point-flow in linear regression (Table 22) and 33 % dependent on axis area and point-flow and 52 % dependent on point-flow alone in curvilinear regression (Figs. 20–22). The question now arises of whether any combination of environmental variables can be identified which explains the total variations in the various community parameters for the stones better than will any one variable alone.

For this purpose the HONEYWELL (1970) computer program 'BSTEP/stepwise multiple regression' was used, which determines which of a set of linear regression equations produced by the stepwise addition and deletion of variables fits the data best.

The final equation contains only significant variables ($p \geq 0.05$, $F = 4.14$), and an analysis of variance then indicates what proportion of the total variance of y is explained by this linear regression. The environmental variables employed in the calculations here are axis area and point flow, which proved the best explanatory variables in the simple regression analysis above, and also moss cover. No others are used, as all the remaining ecological factors available are found to correlate with these three, although calculations were performed for comparative purposes using surface current velocity instead of point flow.

The following results emerge from these tests (Table 22):

- The actual numbers of individuals on the stones and their species evenness are dependent only on the point flow, while the majority of the variance of these parameters appears to be due to other factors not studied here.
- The variation in the numbers of species is quite clearly influenced by all three variables, axis area, point flow and moss cover, the proportion of the variance explained by axis area alone being doubled upon inclusion of the other two.
- The moss cover variable does not contribute very much to the explanatory power of the regression equation for the log of the number of individuals when applied in addition to point flow, but these two variables together do succeed in explaining the majority of the variance.
- Only species diversity is explained better by a combination of variables containing surface current rather than point flow.

The general conclusion can be reached from these results that point flow plays a very important part in governing the nature of the animal communities on the stones, while the size of the stone is of importance in determining the number of species present and their diversity, and the moss cover influences both the number of species and the

Table 22. Multiple regression of the community parameters on the environmental variables axis area (A), moss cover (B) and point flow (C), and the coefficient of determination for each combination (I) and the corresponding combination with point flow replaced by surface current velocity (II). The order of the variables in the equations is that of their entry into the analysis. The significance of each combination of variables as an explanation of the linear regression is indicated.

Best-fit linear equation		Coefficient of determination (%) and significance	
		I	II
No. of species	= $7.75 + 2.27 A + 0.50 C + 3.98 B$	44.9***	19.6**
Log no. of species	= $1.02 + 0.05 A + 0.01 C + 0.08 B$	53.6***	40.3**
No. of individuals	= $-82.01 + 25.74 C$	31.0***	27.4**
Log no. of individuals	= $1.27 + 0.05 C + 0.02 B$	56.0***	45.3***
Diversity, H'	= $2.28 - 0.03 C + 0.20 A$	37.3***	49.0***
Evenness, J'	= $0.96 - 0.01 C$	47.6***	45.7***

number of individuals, in both cases mainly when these are expressed logarithmically. It is also seen that even the multivariable combinations scarcely explain more than half of the total variance in any instance, suggesting that in addition to chance, there must be other environmental or biological factors governing the species assemblages and incidence of these animals on individual stones, or else that the regression in the case of these combinations of variables is not a linear one, as the multivariable analysis forces one to assume (in spite of the fact that such a regression equation does account for a very highly significant proportion of the total variation), but rather that the relationship may be best described as a curvilinear one, as in the case of certain individual variables above. Probable additional relevant factors not evaluated here would include the distribution of detritus and the general structure of the bed of the rapids beneath the stones, especially in terms of its looseness and adherence qualities, variables which would be difficult to index numerically.

7.4. Discussion

7.4.1. Particle size

The argument for taking the individual stone as the unit for the location of a definable animal community was based on the fact that a stone in itself constitutes a natural, finite habitat, and at the same time a basic unit in the structure of the bed of the rapids. Thus the community inhabiting a given point in the stream may be said to consist quite simply of those individuals and species occupying that position at the point in time concerned, and is in no sense a mean value, as would be the case if the unit were taken to be an area of the stream bed of greater or lesser extent, e.g. a Surber sample. It is for this reason that the samples used here retain a considerable particle-specific variation, which would be smoothed out if larger areas were used (with an accompanying loss of information). The advantages of operating with individual stones rather than a mean or median stream-bed particle size, for instance, may also be seen in the fact that they constitute a much more clearly defined and easily measurable environmental variable.

With the exception of the work of CHUTTER (1968), who observes that the surface area of the stone is a relatively insignificant factor in determining the density of individuals, the dependence of the numbers of species and individuals in stone communities upon the size of the stone itself has remained unresolved. Hence comparisons will be made below largely with descriptions based on varying sampling areas. In such cases the characteristics of the river bed are generally estimated simply by eye or in terms of the general structure expressed in the familiar concepts of mean or median particle size (INMAN 1952) or the Wentworth particle size scale (see CUMMINS and LAUFF 1969).

The sediment composition and stability of a river bed reflect the flow relations prevailing at that level (MOON 1939, PLESKOT 1962), so that with some generalization, and taking into account the soil type involved in each case, it can be concluded that the faster the flow, the coarser and cleaner (i.e. possessing less fine sediment) the bed will be, whereupon it will increase in physical complexity. The better this situation

persists in a stable state, the greater the variety and complexity of the vegetation which will establish itself there, and the better the selection of food items available to the animal communities both in an immediate sense and indirectly through the detritus accumulating on the plants and between and beneath the stones. Thus, as the habitat becomes more varied, so the fauna should also become more varied, as has also been shown in the case of island bird communities (MacARTHUR and MacARTHUR 1961) and marine decapods (ABELE 1974), for example. Correspondingly, structurally homogenous stream beds, such as those composed largely of sand, have been observed to possess a poorer macrofauna than more heterogeneous beds of gravel and stones (SPRUELS 1947, MACKAY and KALFF 1969) or stones with accompanying vegetation (PERCIVAL and WHITEHEAD 1929, HYNES 1961, MINCKLEY 1963), and a richer fauna can be expected even when the sediment is well stabilized (MACKAY and KALFF 1969, HYNES 1970, DeMARCH 1976). Such a bed may also be efficient in retaining allochthonous detritus, which has been found to be important as a regulator of the micro-distribution of the benthic fauna, largely in its capacity as a source of nutrition (EGGLISHAW 1964, ULFSTRAND 1967; see also REICE 1974, RABENI and MINSHALL 1977).

The abundance of the fauna and/or the occurrence of individual species have been found to correlate with the size class of the stones in the stream bed as such, with an increase in total abundance through the size classification 'gravel – small rubble – medium rubble – large rubble' (WENE and WICKLIFF 1940), where these rubble classes correspond to axis areas of approx. 1, 1.7 and more than 1.7 dm² respectively. Similar trends, also possible within a single order (e.g. caddisworms – PENNAK and Van GERPEN 1949), are pointed out by MACKAY and KALFF (1969) in a progression from sand through gravel to stones, and also RABENI and MINSHALL (1977) in four classes of riffle sediment of less than 70 mm in diameter, although not in similar pool sediments. It should be noted, however, that this latter work attributed the primary responsibility for the micro-distribution to the detritus element, although establishing the substratum particle size at the same time as the principal factor in the distribution of this detritus.

CHUTTER (1968), using as his measure the 'number of individuals per 1000 cm²', observed that "any macroinvertebrate species density often showed a significant correlation with stone surface area", while the total fauna only once showed a correlation with surface area, and then a negative one. In the work of FRIBERG *et al.* (1977), the number of individuals in the communities ($\log N_{\text{tot}}$) showed a negative correlation with median particle size within the range 0.6–105 mm, but only in autumn, while the number of species (S_{tot}) and the species diversity (H') both correlated positively with this parameter. S_{tot} has similarly been shown to be related to mean particle size in stony bottom habitats of less than boulder class (DeMARCH 1976). On the other hand, it is claimed by ALLEN (1959) that "neither the total surface area available to the animals nor the size of the largest stones shows any correlation with the abundance of the fauna", which serves as a good indication that this dependency relationship is to a great extent conditional upon the criteria used for measuring particle size.

The role of stone size appears to be a significant one not only as a factor governing choice of habitat in individual species, but also as probably the sole determinant of the richness of the community as a whole, whether this is expressed as the number of

individuals or species or as species diversity. In this respect, it is characteristic for this richness, both in the Jäväjänkoski results and in those reported in certain of the references in the literature, to increase not in a linear manner, but rather asymptotically, as the stream bed becomes coarser or the stones larger. This trend is very clear in the reference data if one plots the results of RABENI and MINSHALL (1977) or FRIBERG *et al.* (1977). Even in the latter case the plot of S_{tot} against median particle size shows a much better fit with a hyperbolic curve than with a straight line, the correlation coefficients being 0.96*** and 0.84** respectively for the autumn samples and 0.80* and 0.49 NS for the spring samples. Results seem to vary greatly as to which size class makes up this evening-out phase. Using the particle size categories of CUMMINS (1962), the deceleration in faunal richness appears from the gravel (RABENI and MINSHALL 1977) or pebble stage onwards (FRIBERG *et al.* 1977), or perhaps only within the cobble class (WENE and WICKLIFF 1940), as is the case with the present results. An examination of the whole size scale from sediment to boulder would really be necessary in order to establish the overall nature of this dependency relationship.

As far as the determination of the richness of the faunal communities is concerned, the use of stones, with the actual size as the relevant parameter, or larger sections of the stream bed, with the parameter a unit based on the particle size distribution, may thus be seen to provide us with similar information. How, then, does the individual stone or particle function in respect of the nature of the animal community? The explanation would appear to lie simply in the fact that the larger the stone that is involved, the more stable it will be in its position and the more extensive the space it offers for colonization. Alongside this effect, the current in the stream, the point flow, which was frequently found in combination with stone size in the multiple regression results, serves to increase the diversity of this space by creating variable series of current velocities on the surfaces of the stones (see 'dynamische Drucke' of KRESSER 1953). The most obvious of these variations is the dichotomy 'exposed side/protected side' (TRIVELLATO and DECAMPS 1968). At the same time, the more extensive and structurally uneven the surfaces over which the water flows, the broader the consequent flow type regime even within the scope of a single surface.

7.4.2. Surface current velocity and point flow

It has already been noted in the discussion on the autecology of macroinvertebrates that many rheophilic species live in their greatest abundance at a certain current speed and become progressively scarcer in areas slower and faster than this, as has been described by a number of other investigators (see ZAHAR 1951, SCOTT 1958, AMBÜHL 1959, MORETTI and GIANNOTTI 1962). In the same way, CHUTTER (1969) observed that flow rate was of importance in regulating the local incidence of certain species, but was of the opinion that it did not exercise any obvious effect upon the inter-site variation in species density. The present results, however, suggest that a significant positive correlation exists in this case between the numbers of individuals on the stones and the current rate, even though the 'optimum range' model alluded to above does not hold good for these figures, but only for the numbers of species present and the

index of species diversity. Similarly, the experimental tests of ZIMMERMANN (1961) showed an increase in the number of species and an evening-out in their distribution from the slowest rate of flow, 5 cm/s, to the fastest, 80 cm/s, but gave no figures for values beyond this speed. KAMLER (1967), on the other hand, found the optimum range model appropriate to the Ephemeroptera and Plecoptera faunae both separately and together, with the maximum figures occurring in the area 20–60 cm/s, i.e. at slightly slower rates of flow than the peaks observed at Jäväjänkoski. Surprisingly, the mean current variable, in the range 10–32 cm/s, failed to explain the variance in any of the community parameters in the work of FRIBERG *et al.* (1977).

Rheophilic and rheobiontic animals, like the corresponding plants, are adapted to make greater or less use of the current, particularly in their mode of respiration and feeding (see NIELSEN 1950, AMBÜHL 1959, HYNES 1970), and it is these inherent needs which govern the distribution of the species among the stones, to a large extent precisely with reference to this habitat requirement. The evaluation of the influence of particle size above was based entirely on the assumption of constant flow conditions. As the flow rate increases, however, a whole set of hydrodynamic and hydrobiological consequences ensue, including a weakening of the boundary layer (AMBÜHL 1959), an increase in the drag exerted by the current, a broadening of the flow type regime, etc., but also the area representing a given flow rate both decreases in size and shifts in position, at the same time as the amounts of oxygen, nutrients and other food items passing that point within a given unit of time similarly increase (see RUTTNER 1926, ZAHAR 1951, AMBÜHL 1959). Even though a more discriminating species may not always give way to a more resilient one under such conditions, at least the number of examples of the former will decrease as its colonization space is reduced in size. Such population changes in species terms are clearly detectable here in that the passive feeders, largely the blackflies, become dominant both in terms of the number of individuals and of the species composition of the community in the areas of more rapid current.

If the point flow is used as an environmental variable instead of the surface current, the differences observed in the distribution of the macroinvertebrate communities are relatively small, but it is significant that the resulting increase in the number of species becomes independent of this factor at a fairly early stage. Since the amount of food available is linked in an essential manner with the rate of flow, it is precisely the number of individuals which increases in such a case (see ZAHAR 1951, MÜLLER 1956, ILLIES 1956). The simultaneous reduction in species diversity and the maintenance of the number of species at the same level, are in turn indications that that part of the fauna which benefits from the increased flow, namely the blackflies, achieves an extension in its own species range which compensates for the decline occurring in the number of other species.

The water speed of a river as an environmental factor is quantified almost inevitably in terms of current, and it has very often been emphasized that whether this is measured at the surface, as near as possible to the bottom, or at any other depth, it will not indicate directly the boundary layer conditions to which bottom animals are immediately susceptible (see JAAG and AMBÜHL 1963, MACAN 1963, HYNES 1970). This is undoubtedly also the case with the point flow, which has been relatively little used for this purpose, presumably because it is slightly more cumbersome to measure. Its use may nevertheless be justified on the following grounds: it quite obviously gives a direct

impression of the amount of food material available to the animals, it takes account of water depth, and its inclusion in the multi-variable combination provides a more satisfactory explanation of the variance in the community parameters, with the only exception of species diversity, H' , than does that of any other measure of current.

7.4.3. Vegetation

River beds containing mosses, rooted plants and filamentous algae are more abundantly inhabited by invertebrates than are stony beds, and their animal communities differ from each other in their dominance structure. This classic observation by PERCIVAL and WHITEHEAD (1929) has gained support from later work, including that of KAMLER (1964), KOWNACKA (1971) and KOWNACKI (1971) (see also HYNES 1970). Little research has been carried out on moss-covered river beds, however, with the exception of species determinations (see THORUP 1966, KOWNACKA 1971, GLIME and CLEMONS 1972, LINDEGAARD *et al.* 1975), and information relevant to the dependence of the community parameters used here upon the vegetation cover of the habitat is even more rarely to be found, in works such as those of FRIBERG *et al.* (1977) and KAUPPINEN (1978) primarily. Even in these cases, in fact, the material used differs very markedly from that studied here, for while these results are based on a restricted area of Jäväjänkoski, the first of the above papers refers to a series of Surber samples from a number of streams and the second to similar samples from various sets of rapids on the river Kiiminginjoki. Thus both the distances between the sites and also the resulting faunistic variations would presumably account for the differences in the results compared with the present work. There may also be some significance in the fact that the dominant moss at Jäväjänkoski is the relatively low-growing *Hygrohypnum*, whereas elsewhere it is *Fontinalis*, and in the fact that the negative correlation between the mosses and filamentous algae may be interpreted as implying competition between these for colonization space, which was resolved in favour of the algae at least on the weir, which having recently been disturbed, was still in a labile state, whereas the mosses had certainly held their own on the riverbed with its climax-phase vegetation.

The influence of the moss cover upon the community parameters at Jäväjänkoski is depicted in correlations which are similar in direction to those reported by FRIBERG *et al.* (1977), whereas the thirty samples from Kiiminginjoki taken in June 1976 show a significant direct correspondence ($p < 0.05-0.001$) between the frequencies of the majority of taxa and the total fauna on the one hand and the moss cover on the other (KAUPPINEN 1978). The negative correlation between the number of species in the stone communities and the amount of algae present which was noted here, however, is at odds with the findings of FRIBERG *et al.*, so that all told this comparison is by no means a clear-cut matter, and the explanations put forward below perforce take on the nature of indirect conclusions and speculations.

The tendency for an increase in the moss cover to add greater diversity to the animal communities must quite obviously be a reflection of the increase in habitat diversity. This is first and foremost a consequence of the greater size of the moss polster and the actual surface area occupied by mosses, providing improved opportunities for colo-

nization both on top of the polster and in its interior recesses. Secondly, moss clumps of increasing size possess the capacity to collect and retain progressively larger amounts of detritus, algal matter and animal debris (see GLIME and CLEMONS 1972, JOHNSON 1976), at least up to a certain rate of flow (ASPLUND and KARLSTRÖM 1975). Thus a recovery in trophic conditions can be expected right from the level of bacteria and protozoa, precisely the situation which one might expect to be exploited by those chironomids (HUMPRIES and FROST 1937, FROST 1942, THIENEMANN 1954a, KOWNACKI 1971) and young Perlidae (KAMLER 1964), which establish themselves in considerable numbers on the mossy surfaces of stones. The same ecological explanation can also be adduced for the large populations of Chironomidae on algae (NEEL 1968, KOWNACKA 1971, KOWNACKI 1971), which are then characterized by a small variety of species (KOWNACKI 1971). The correlation calculations for Jäväjänkoski also point to such a relationship. Such a micro-habitat preference would allow room for the interpretation that there is indeed a positive correlation between the number of individuals and the phytomass, as deduced by both FRIBERG *et al.* (1977) and KAUPPINEN (1978).

In the case of Jäväjänkoski, this increase in habitat diversity as a consequence of the moss cover would seem above all to add new species to the communities and even out the proportions of individuals of the various species, so that the species diversity value H' also increases. The recovery in the numbers of individuals is nevertheless not of the order that would cause the statistical value of the vast masses of blackflies occurring on the bare stones and/or those with little moss to be exceeded. A similar sharp rise in the total population figures was caused by *Gammarus pulex* in the material of FRIBERG *et al.* (1977), but no such phenomenon is reported at all in Kiiminginjoki.

In conclusion it must be admitted that only indicative trends emerge from the present results. The influence of the plants present appears to be very largely dictated by environmental factors of both spatial and temporal import, although some of the differences noted may well have arisen as a consequence of inconsistencies in parameter distribution or contamination in the plant cover. It has nevertheless been seen that even a very rough classification of the phytomass present would seem to enable dependency relationships to be discerned.

8. COMMUNITY SIMILARITIES AND SPECIES ASSOCIATIONS

8.1. Statement of the problem

Although the animal communities on the stones proved heterogeneous in the numbers of species and individuals recorded and in their general diversity, certain consistent groups could be identified and certain dependency relationships set up. The present statistical analysis is naturally insensitive to the real biological situation as far as the true species are concerned, and consequently the question arises as to the extent to which the communities are similar in kind, as judged from the species proper, and to what extent the species tend to form associations, i.e. what are the affinity relations between them.

8.2. Community similarities

8.2.1. *Introduction and methods*

Many mathematical formulae of greater or lesser complexity have been proposed for measuring the degree of faunal resemblance between communities, either based on the simple presence/absence of species or on quantitative data (see GOODALL 1973).

SØRENSEN's quotient of similarity, or 'community coefficient' (1948), expressed in a simple alternative form by LOOMAN and CAMPBELL (1960) as $K = \frac{2C}{A+B} \cdot 100 (\%)$,

is based on the presence and co-occurrence of species in pairs of samples, the symbols standing for: A = total number of species in first sample, B = total number in second sample, and C = species common to both. The merit of the calculation lies in its simplicity, which has led to its widespread use, first for purely botanical comparisons, but later also for the comparison of benthic animal communities in flowing water (BAGGE 1968, GLIME and CLEMONS 1972).

Conclusions on the degree of similarity between communities reached entirely on the basis of Sørensen's K values may be misleading in cases where arbitrary percentages are used as the limiting values, for as LOOMAN and CAMPBELL state (1960), 'minimum quotients of 30, 50 or 70 % set for similarity may have the same significances', as will also be seen in the present work. MOSIMANN (1968) demonstrated the suitability of the hypergeometric probability distribution for determining accurate probability values and significances for the degree of similarity observable in animal communities. This is the procedure used by GLIME and CLEMONS (1972) for comparing the communities of natural and artificial moss beds in a stream.

The quotient of similarity gives equal weight to all the species present independent of their abundance. In order to include the quantitative aspect, it is necessary to use CZEKANOWSKI's coefficient of 'percentage similarity' (1909). A simplified form of this formula (see GOODALL 1973) would be:

$$PS = \frac{2 \sum \text{Min}}{A + B} \cdot 100 (\%),$$

where A = total number of individuals in one sample, B = total number in the second sample, and $\sum \text{Min}$ = the sum of the lesser numbers of each species for the two samples. This index has been used frequently for measuring biotic similarity in marine bed animal communities (see LAPPALAINEN *et al.* 1977).

The method adopted for evaluating the faunal similarity of the stone communities in the present instance involves a combination of Sørensen's K coefficient and Czekanowski's PS in the forms set out above. The statistical significance of Sørensen's quotient is then tested by an application of the hypergeometric probability distribution method in which the degree of co-occurrence is obtained by multiplying together the number of possible ways each event could occur and dividing this by the total possible events. A reduced form of this equation would be the following (for the theory and its argumentation, see MOSIMANN 1968):

$$P(x) = \frac{\binom{m}{x} \binom{N-m}{n-x}}{\binom{N}{n}},$$

in which N = total number of species (here 102; see p 24),

n = number in first (richer) sample,

m = number in second sample. and

x = number common to both samples.

This probability reveals the risk of the pair of animal communities in question being different. The results obtained from these indices may be compared visually in the form of dendrograms (Fig. 24) compiled by the nearest-neighbour clustering strategy (see SNEATH and SOKAL 1973).

The aim in the present case is to obtain some idea of the kinds of similarity to be encountered between the animal communities on the various stones and of whether any closely comparable communities are to be found, and if so to what extent and for what reasons. At the same time an attempt is made to evaluate the suitability of these methods for the determination of similarity.

8.2.2. Results

The similarities between the animal communities on the stones varied from 0 % to over 70 % with both indices (Fig. 23). There were only three cases in which Czekanowski's coefficient was larger than the corresponding value for Sørensen's quotient, all involving stones with little moss of them and communities dominated heavily by the simuliids (50.3–76.9 %). Significant faunal similarities are to be found from an index of 31.8 % upwards on Sørensen's scale, although some non-significant cases were still recorded up to 43.5 %. A comparable overlapping may also be found in the other risk levels (Fig. 23). Such irregularities are naturally mathematical in origin and indicative of weakness inherent in the indices themselves.

A 'nearest neighbour' clustering of the communities according to Sørensen's quotient enables groupings to be obtained (Fig. 24) in which every community has a statistically significant similarity with at least one other. Stones numbers 18 ... 17 are seen to form one major group with considerable internal homogeneity, Group A, containing a distinguishable sub-group Aa, while stones 26 ... 14 comprise a moderate affinity group B, with three sub-groups, 26 ... 35, Sub-group Ba, 30 ... 28, Sub-group Bb, and 22 ... 34, Sub-group Bc, standing out to a greater or lesser extent. Finally stones 1 ... 4 represent a group of lesser homogeneity, Group C.

This general grouping is considerably altered if the communities are reorganized according to Czekanowski's coefficient within the limits allowed by the clustering procedure,

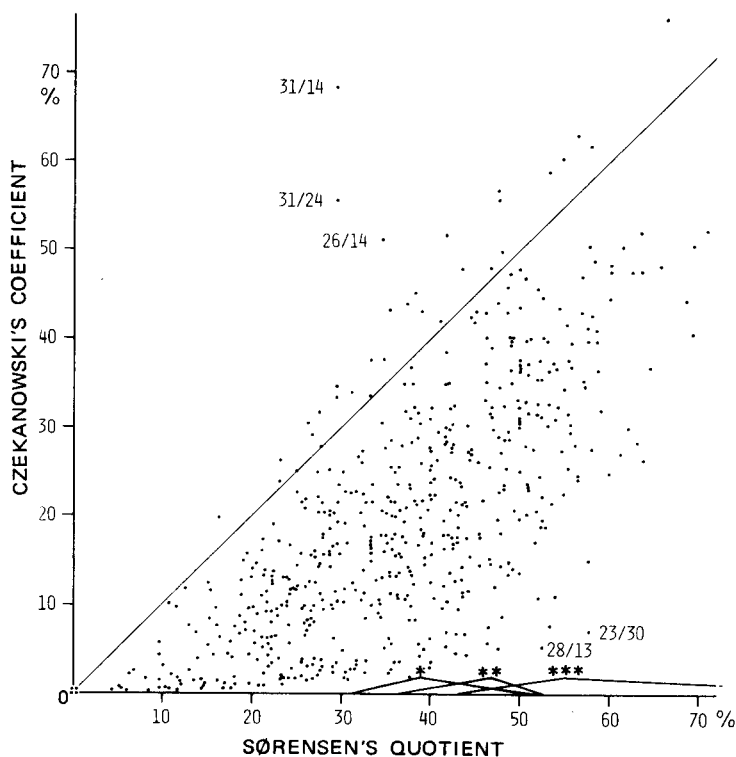


Fig. 23. Correlation of values for Czekanowski's coefficient with those for Sørensen's quotient. The extreme and median values for each significance level of Sørensen's quotient are indicated on the abscissa. The diagonal line indicates equality between the two measures. Certain pairs of communities are labelled with their stone numbers.

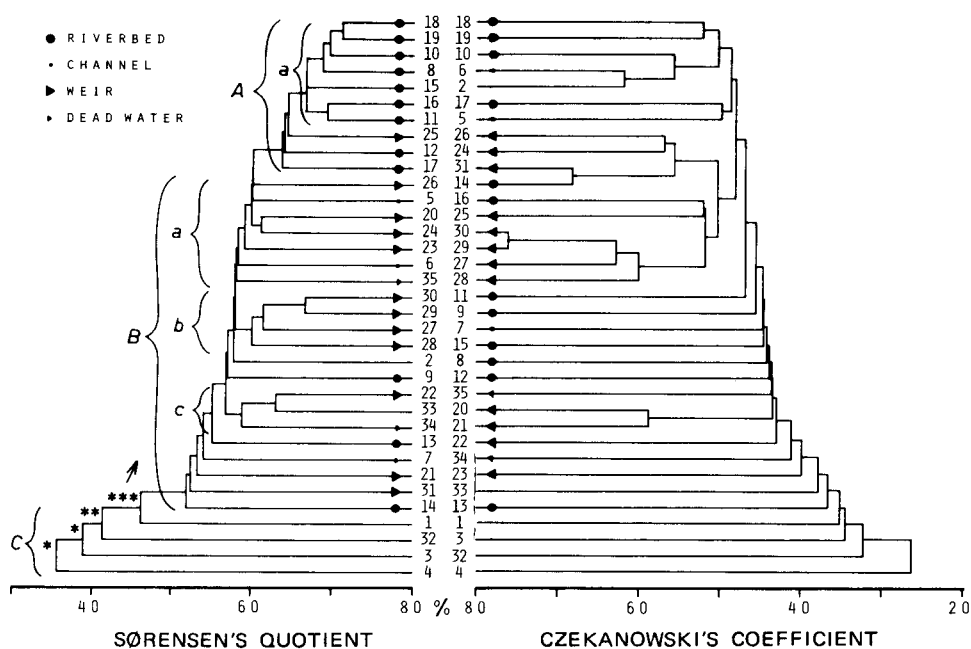


Fig. 24. Dendrograms showing the percentage similarities between the animal communities on the stones (numbered in the centre of the diagram) expressed in terms of a presence/absence analysis by Sørensen's quotient and in quantitative terms by Czekanowski's coefficient. For explanation of the groupings, see text.

but aiming at an arrangement corresponding as closely as possible to that given by Sørensen's quotient. Only Group C, Sub-groups Bb and Bc and part of Sub-group Aa continue to give anything like the same picture of the similarity relations between their component communities with this quantitative measure as they did on the basis of the simple presence/absence data.

8.3. Species associations

8.3.1. Introduction and methods

The animal communities on the stones were found to resemble each other to a greater or lesser extent, if only for the theoretical reason that the frequency distribution of the species would presuppose that certain ones would appear together with a certain degree of probability. This 'positive coincidence' of species is to be expected on the basis of the trophic organization of the communities and also the abiotic requirements of the individual species. Similarities in feeding habits, e.g. among the blackfly species, or the predator – prey relationship, in spite of the fact that most predators have considerable preference alternatives in their diet, constitute justifiable natural reasons for coexistence, which in such a case would be a matter of true association. Similarly abiotic and non-animal factors in the environment such as the discharge rate in the river or vegetation

patterns, especially where such factors are connected with diet or choice of micro-habitat, may lead to positive coincidence. In the light of these considerations, it is clear that not every calculation of the degree of association will necessarily incorporate the true biological interrelations operative between the species.

The concepts of 'species association' and 'similarity between samples' are in effect two different ways of looking at the same thing. One available measure of association is the 'coincidence index' proposed by DICE (1945), $CI = 2a/(2a + b + c)$, which, when formulated to apply to presence/absence data, is observed to be analogous to Sørensen's index (see GOODALL 1973). This equation may be applied to the measurement of species association on an occurrence basis in the transform

$$CI = \frac{2C}{A + B} \cdot 100 (\%),$$

in which A = number of samples containing species a, B = number containing species b, and C = number containing both species. The hypergeometric probability distribution principle may be used to calculate its level of significance, the resulting probability value p indicating in this case the risk of the coincidence of any two species being a matter of chance.

In the presentation below all the species are compared one with another, and the results are arranged on plexus diagrams (Figs 25 and 26), which in principle include all those species with a statistically highly significant coincidence index, or an index $\geq 75\%$ (even with $p > 0.05$). In certain cases, however, even levels of significance of $0.01 \leq p \leq 0.02$ are included in order to verify the positions of some species or groups of species, but many of the coincidences carrying significances in the range $0.02 \leq p \leq 0.05$ have been omitted from the diagram in order to preserve a sufficiently distinct plexus construction. These restrictions yield an association pattern for 43 species, representing 73.5 % of the individuals in the total material.

8.3.2. Results

The highest degrees of coincidence are shown by the triplet *R. nubila* – (89.3 %) – *S. reptans* – (88.0 %) – *R. photophilus* – (82.4 %) – *R. nubila* (Fig. 25). The coincidences reach statistical significance ($p < 0.02$) by the level of 44.4 % (*C. lepida* – *P. transiens* – *S. pusilla*), but not in every case, as in seen from the non-significant coincidence of 80 % between the species *C. bicinctus* – *Orthocladus* sp. B. – *R. photophilus*. The thick plexus lines on the diagram are seen to occur between species with high incidences, an indication of the dependence of the degree of coincidence upon the frequency of the given pair of species. The significances do not yield such a result, however, and neither does the degree of coincidence correlate with the degree of significance.

The plexus construction serves to reveal a variety of complex and unidirectional assemblages. On the grounds of degree of coincidence, species groups II and III are seen to be rather separated from the main association, group I, but once the degree

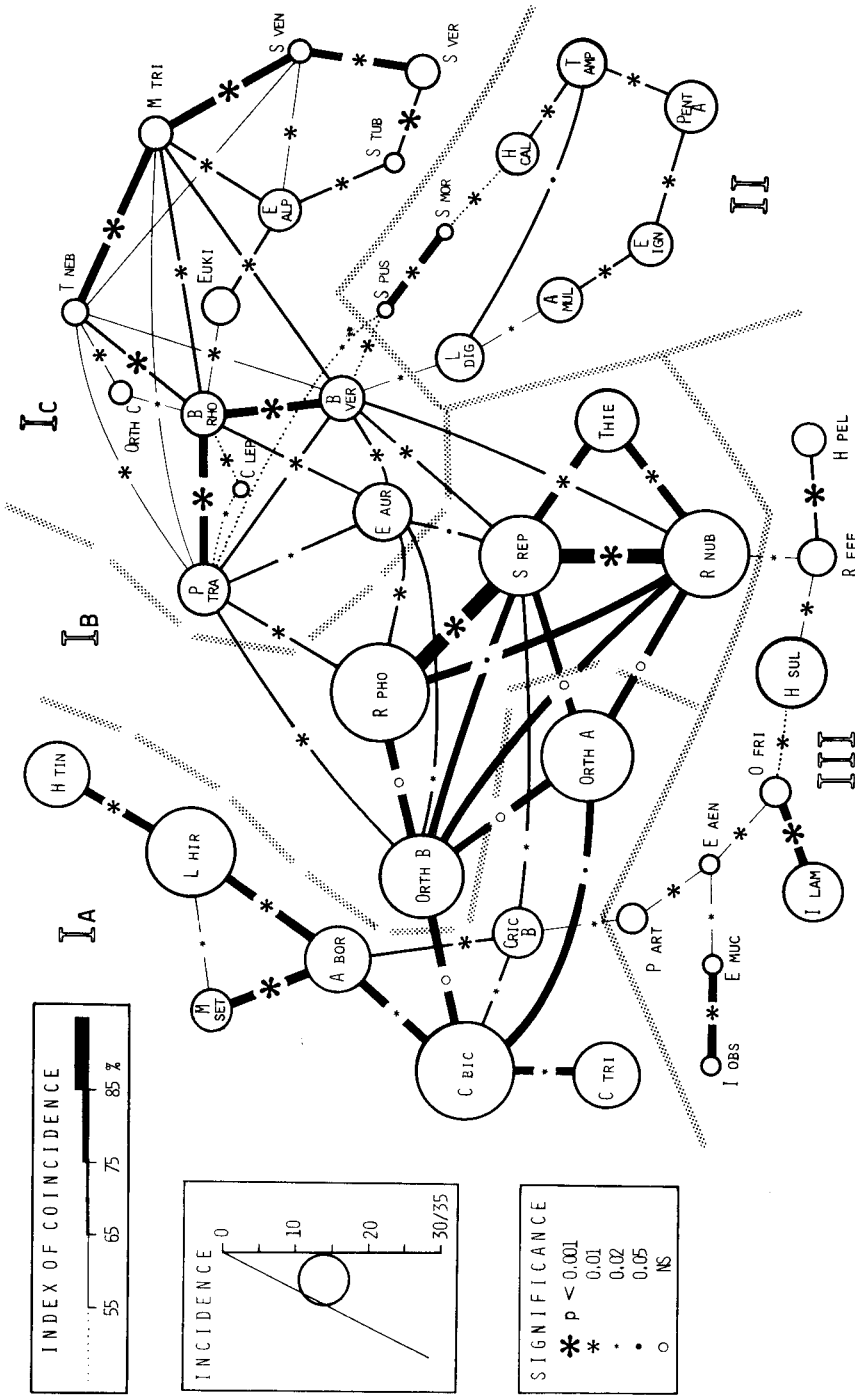


Fig. 25. Interspecific associations on stones according to the degree of coincidence (DICE 1945) and significance (hypergeometric probability distribution), see text. Symbols: circle with abbreviation - species (see Table 23) and its incidence, lines - index of coincidence, asterisks - significance, dashed bands - boundaries of associations I-III.

of significance is taken into account, the delimitation of groups becomes more complicated in places. It nevertheless seems appropriate to divide group I into subgroups A, B and C, largely because of the very highly significant coincidences operating within each, as is also true within II and III (even though these internal cohesions do occur mainly between 'consecutive' species).

When setting out to interpret the species associations, one may well ask such questions as what common ecological features are possessed by coincident species, whether the associations comply unambiguously with the ecological factors or with habitat, for example, and what part is played by their biological relationships. To facilitate this examination, each species is tabled (Table 23) and marked according to that habitat in which most of its occurrences are recorded, and according to its most common micro-habitat.

The following observations arise from these comparisons:

- Almost without exception those species forming associations are concentrated both numerically and in their range of occurrence in the riverbed and weir habitats.
- As far as their principal occurrences are concerned, the species in Groups IA and III are concentrated in the riverbed, those in Groups IC and II on the weir and those in Group IB occur on the riverbed and/or the weir.
- Only those species in Group III are characterized by occurrence on the protected sides of the stones.

In this sense, Group IB represents a transitional form within I, the ecological distinction being based on the flow rate and vegetation requirements of the species, Group IA favouring moss-covered stones and IB and IC stones covered to a greater or lesser extent by algae, but the IB species being more markedly rheophile. This rheophilic characteristic is also a mark of some of the other groups, although Group II is also phytophile and Group III both phytophile and hypolithalic. These internal characteristics of associations, may be illustrated best by an examination of certain pairs or groups of species with particularly high degrees of coincidence.

IA. *A. borealis*, *M. setiferum* and *L. hirtum*, inhabit moss-covered stones and have characteristic herbivore-detritivore feeding habits.

IB. *R. photophilus* and *S. reptans* favour sites with a high flow rate, partly on account of their passive feeding habits, and form an association in spite of having somewhat opposed micro-habitats. *R. nubila*, on the other hand, is a predator, feeding on the dense blackfly populations, for instance, and enters this association on purely biological grounds. (It is interesting to note that its association with *R. photophilus* is practically without significance, as no predator-prey relationship obtains between them). Being a worm of small dimensions, *Thienemanniella* appears to have adapted well to a rapid current, feeding on the epilithic microflora and detritus affixed to the cocoons of blackflies.

IC. The common feature for the blackfly and *Baetis* species is a requirement and preference for a strong current and the exposed faces of stones together with passive feeding habits. *T. nebulosa*, which lives among mosses as a fully-grown larva, would seem out of place in this association. The young larvae encountered here may well have been carried onto the weir from the basin above, where the accumulation of detritus may serve both as a hatching site for the eggs and also as a source of food.

II. *S. pusilla* and *S. morsitans* stand out from the rest of the blackflies because of their phytophile character (USSOVA 1961). It is impossible to specify any common

Table 23. Species of the associations noted in Fig. 25, with notes on the habitats (W = weir, R = riverbed, o = other habitats) in which each species had its most frequent incidence (I) and most abundant occurrence (O), and preferred micro-habitats (? = no preference observed).

			I	O	Micro-habitats	
					exposed	protected
IA	H tin	Hydroptila tineoides	R	R		+
	L hir	Lepidostoma hirtum	R	R	+	
	M set	Micrasema setiferum	R	R		?
	A bor	Amphinemura borealis	R	R	+	
	Cric B	Cricotopus sp. B	R	R	+	
	C bic	Cricotopus bicinctus	R	R	+	
	C tri	Cricotopus triannulatus	R	R	+	
	Orth A	Orthocladus sp. A	R	R	+	
IB	R pho	Rheotanytarsus photophilus	W	W		+
	S rep	Simulium reptans	RW	W	+	
	R nub	Rhyacophila nubila	RW	R	+	
	Thie	Thienemanniella	RW	RW	+	
	Orth B	Orthocladus sp. B	RW	W	+	
IC	E aur	Eusimulium aureum	W	W		?
	B ver	Baetis vernus	W	W	+	
	B rho	Baetis rhodani	W	W	+	
	C lep	Cheumatopsyche lepida	W	W		+
	P tra	Parabyssodon transiens	W	W	+	
	T neb	Taeniopteryx nebulosa	W	W		+
	Orth C	Orthocladus sp. C	W	W	+	
	M tri	Metacnephia trigonia	W	W	+	
	S ven	Simulium venustum	W	W	+	
	S ver	Simulium verecundum	W	W	+	
	S tub	Simulium tuberosum	W	W	+	
	E alp	Eukiefferiella alpestris	W	W	+	
	Euki	Eukiefferiella sp.	W	W	+	
II	S pus	Schönbaueria pusilla	W	W	+	
	S mor	Simulium morsitans	RW	W	+	
	H call	Hygrobatas calliger	RW	R	+	
	T amp	Torrenticola amplexa	W	W		?
	Pent A	Pentaneurini sp. A	o	o	+	
	E ign	Ephemerella ignita	W	W	+	
	A mul	Agraylea multipunctata	W	W		+
	L dig	Leuctra digitata	W	W		?
III	H pel	Hydropsyche pellucidula	R	W		+
	R eff	Rheocricotopus effusus	R	R	+	
	H sul	Heptagenia sulphurea	R	R		+
	I lam	Ithytrichia lamellaris	R	R		+
	O fri	Oxyethira frici	R	R		+
	E aen	Elmis aenea	R	R	?	
	P art	Paludicella articulata	WR	W	?	
	E muc	Ephemerella mucronata	R	R	?	
	I obs	Isoperla obscura	o	o	?	

ecological feature for this chain-like association sequence, any more than one can for group III. This latter includes *H. pellucidula* and *R. effusus* from the riverbed, which nevertheless have different micro-habitats. In contrast *I. lamellaris* and *O. frici* appear to occur on roughly the same stones, and their ecological differences do not emerge from the present material. Most of these hydroptilids were at the pupal stage, so that

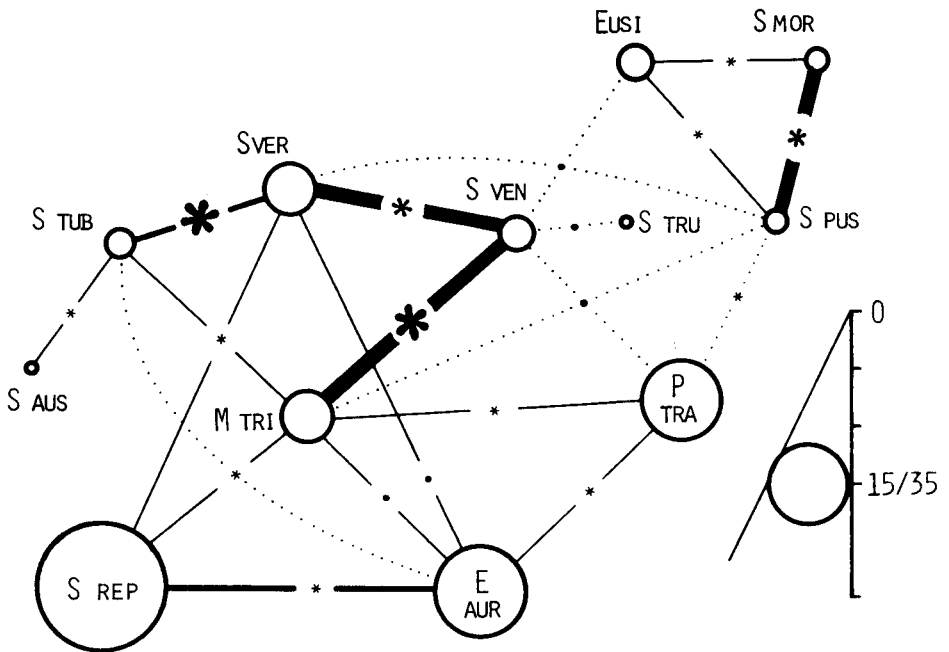


Fig. 26. Interspecific associations of blackflies on stones. Explanation as in Fig. 25.

this preference for the undersides of stones, where *H. sulphurea* also lives, may simply reflect a desire for protection during pupation. No particular ecological requirements can be attributed to *I. obscura* and *E. mucronata*.

The blackfly species constitute a consistent and ecologically fairly homogeneous group, and it is only by analysing their mutual association relations (Fig. 26) that it is possible to distinguish differences in affinity between them. *S. pusilla* and *S. morsitans* then stand out at once in the manner described above, while the remainder fall to some extent into two groups, the more frequent species, *S. reptans*, *E. aureum* and *P. transiens*, and the less frequent, *M. trigonia*, *S. truncatum*, *S. verecundum* and *S. tuberosum*. The first of these is a weak association, representing a transition between Groups IB and IC, but the latter is more substantial, and belongs to the nucleus of association IC.

The following summary can now be given of the general ecological labels which may be applied to the species associations distinguishable on the stones of the rapids (Table 23):

Group IA represents a phytophile and rheophile association typical of the moss-covered, eurhealic bed of the rapids.

Group IB is an epilithic, highly rheophile association occurring in the disturbed parts of the bed of the rapids.

Group IC represents the lithic and rheobiotic association appertaining to the same habitat.

Group II accounts for the phytophile aspect of the same habitat, being a rheophile association thriving mainly amongst the algae.

Group III constitutes a hypolithic rheophile association typical of the eurhealic bed of the rapids.

8.4. Discussion

8.4.1. Ecological background

All the stones placed in the similarity group A above had a good covering of mosses. With the exception of No. 25 from the weir, all these were from the riverbed. The first stones in Group B, Nos. 26 and 5, were similarly moss-covered. This kind of stone featured a wide range of surface flow rates, even though the predominant rate was at least moderate. Sub-group Bb, on the other hand, consists of moss-free weir stones from an area of strong to very strong current, factors which apparently led to optimal conditions for the development of an outstandingly large population of blackflies.

The similarity tests showed that even stones located some distance away from each other could possess animal communities which resembled each other to a significant extent. Such a statistical similarity does not necessarily imply particularly great correspondences in ecological details in individual cases, however, although it is true that the highest percentage similarities are to be found in cases where these habitat factors, especially concerning the moss cover, are consistent. Since the measurement of similarity on the basis of the quantities of specimens of the various species disrupts the general similarity model derived from the presence data to a considerable degree, the moss-covered stones probably represent a climax situation for the rapids habitat in general and its fauna is detectable in a relatively similar form on any stone whatsoever. At the same time these stones would seem to serve as a centre of dissemination in which some species or group of species may gain a foothold as a direct consequence of some change in the substrate structure, develop into a strong, viable population and eventually cause pairs of communities which are similar in their species composition to differentiate (e.g. in the case of stones Nos. 28/13, 23/30, etc., see Fig. 24). (Such changes have been observed to take place at Jäväjänkoski in the form of the removal of the moss cap from a stone as a result of the daily variation in water level, the cap having frozen to the underside of the ice cover, or the overturning of stones by the pressure of ice slabs even on a relatively tightly compressed river bed during the spring flood season.)

Just as the grouping of the stone communities by reference to their mutual similarity immediately assumed features connected with their spatial distribution, so the species associations correspondingly serve to demonstrate that the various habitats in the bed of the rapids maintain their own typical species assortments, which in turn form these definable associations. Even so, it is possible for the fauna of one habitat to comprise a number of such groups, differing in their affinity properties. The heterogeneity which is typical of the structure of flowing water habitats may thus also be attributed to the manner in which the animals themselves are organized into communities. In this respect the most rational factors to emerge as distinguishing features between associations are the amount and type of vegetation, manner and rate of flow in the river, and biological requirements such as feeding habits.

8.4.2. *Methodological appraisal*

When evaluating the implications of the two principal concepts involving the measurement of similarity, i.e. the degree of coincidence and degree of significance, attention should be drawn first of all to the fact that the first of these does not take into account the total number of observations ($= N$) from which data are derived, nor the number of samples from which each species is absent. The test of significance, on the other hand, employing the hypergeometrical probability distribution, does concern itself with these facts in calculating 1) the number of ways in which each species may occur on N stones, 2) the number of ways in which a species of lower frequency may occur on stones in common with others, and 3) the number of ways the stones not inhabited in common may be arranged. Since this method takes as its basic assumption that every stone is available for habitation by the various species, the occurrence of given species on the same stones would imply not only mutual association relationships, but also some degree of selection of its faunal surroundings in respect of each stone, whenever some clustering of species is found on it which deviates from the expected random distribution (cf. faunal similarities). In view of the comprehensiveness of its starting point, the significance test alone may be regarded as a sufficient measure of association (as also of faunal similarity) when determined simply on the basis of species occurrence. This judgement is supported by the fact that it is possible to find results with the same index of coincidence deriving from different starting points (see MOSIMANN 1968), the distinctions between which can be ascertained in their simplest form only as the risk of a random distribution based on results indexed by the hypergeometrical probability method. For example, in the situations (1) A 21, B 9, C 9 and (2) A 19, B 11, C 9, in which the numerator of the index of coincidence, $2C$, and the denominator, $A + B$, remain the same even though A and B are different, the degree of coincidence is in each case 60 %, but the probability of the pure chance, with $N = 35$, is $p_1 = 0.004$ and $p_2 = 0.030$ respectively.

9. CONCLUSIONS

One of the main results to emerge from this investigation concerns the manner in which environmental factors function to affect both the attitudes of the species in the rapids and their community structure. This may be seen, for instance, in the following observations:

- both individual species and species groups tend to occur in the manner of an optimum range model in relation to current velocity,
- the choice of location within the habitat or the stone was based in the last resort upon the interaction of current, substrate and food, although within limits determined to a great extent by the degree of adaptation of each species,
- the low proportion of predator species may be attributed to the fact that the section of the rapids with little vegetation and a near-laminar flow proved inordinately propitious for the blackfly larvae, collectors of diatoms and detritus,
- the community parameters at the level of the individual stone were closely dependent upon the size of stone and rates of current and flow, and the flow rate was invariably involved in the explanation of dependences by multiple regression analysis.

It is worth noting that the simple dependences mentioned above were curvilinear in character, i.e. the biotic variation was either realized in the form of parabolic and hyperbolic curves or followed a linear rise and fall pattern typical of the optimum range model. Such a curvilinear relationship is in a sense the natural and expected form for a flowing water environment, as both an insufficient and a corresponding excessive rate of flow, for instance, will be demonstrably restrictive for the animal communities on the basis of velocity requirements and attachment capacities alone. The existence of such a relationship has generally failed to be noticed, however, perhaps partly because simple linear regression as such may yield statistically significant values, and partly because the range of the environmental parameters is often too narrow, a situation which is difficult to avoid in experimental studies.

It may also be noted that in almost every case a better explanation of the variations in the numbers of species or individuals was obtained using a logarithmic rather than a natural scale, which supports the notions of the non-arithmeticity of abundance variations in nature, as exemplified in the case of other biotopes by WILLIAMS (1964). According to this rule, which appears to be general for all natural organic communities, there will be very few species with a high abundance, but a large number with a low abundance, as is seen to be the case in this fairly restricted rapids habitat. The corollary of this is, of course, that the faunal records will consist largely of species with a very low incidence rate.

The mosaic pattern of distribution so familiar in flowing-water benthos is well in

evidence here both in the case of the species recognized and in that of the individual specimens, the tendencies for aggregation serving as an indication that the stones of the rapids bed differ in their status as potential habitats. This is fundamentally due to the small-scale topography of the bed and the flow patterns determined by it, which are also crucial for the habitat distribution of those eggs or nymphs which reach their habitat by passive means, through oviposition or drift (see HYNES 1970). In spite of the random distribution arising in this respect, a certain regularity can be detected in the location of the species making up the stone communities, as emerges in the linear increase in species enrichment in relation to the logarithm of the number of samples. Recalculation of a number of other sets of results provides evidence of the general applicability of this relationship and suggests that it may be possible to use it for predicting the number of species present at a site and estimating the optimum number of samples to be taken on the basis of a preliminary test. The similarity in the magnitude of both the diversity index and evenness value within the faunal communities of stream beds in different areas again argues in favour of some general ecological regularity in the structure of communities, the background for which is formed by the potential range for specific habitat or niche selection.

Significant similarities were noted in the species contained in the various communities, this being principally the case within single habitats. It is particularly striking, though, that such correspondences may manifest themselves even in the case of stones situated some distance away from each other, both spatially and ecologically. This emphasizes the importance of micro-habitat factors such as moss cover or absence of vegetation, in combination with the mode of flow. In this way the bed of the rapids, in all its structural heterogeneity, appears to recreate certain conditions at various points, in true mosaic fashion, and thus to maintain broadly identical faunal communities at these sites. One guarantee of this may well be the fact that the majority of the species are euryphagic in their feeding habits, i.e. generalists, so that it would be rare to find locations which would be utterly undesirable for them in this respect. It is this community similarity, of course, which lays the foundation for the species affinities noted here, in which respect the ecological system is certainly a reality, as the part played by chance proved statistically insignificant in the vast majority of cases. Among the circumstances leading to such affinities, one may distinguish behavioural aspects such as vegetation preferences, the need for a protected location, both alone and in combination with the former feature, the need for a laminar mode of flow, and most fundamental of all, the various habits associated with feeding.

The use of the hypergeometric probability distribution proved successful for testing the statistical significance of both the extent of similarity and the degree of affinity, and it is quite applicable as it stands for expressing the degree of association between species without the use of index values, as it achieves a level of statistical significance in itself, i.e. it expresses the degree of risk that a given affinity may be purely the product of chance. It may also be employed as the basis for species ordination.

The above suggests that the individual stone can indeed be regarded as the basic unit for describing the ecology of a rapids bed and would even seem to function in a relatively independent manner in this respect, inasmuch as the variations in quantity and diversity between the animal communities are largely to be explained precisely in terms of the

stones and the properties of their immediate physical environments. It is statistically self-evident, on the other hand, that this dependency relationship will also incorporate partial communities which deviate one from another in their relation to the mean structure, or 'normal instance' for the biotope. This latter is represented best by the riverbed habitat, while the weir was typically deviant, and both naturally possessed their own characteristic structural features.

Finally we should make a cursory examination of the extent to which the animal communities at the various levels observe the 'biocoenotic principles' in their organization. The first two of these principles were originally formulated by THIENEMANN (1954b) and the third by FRANZ (1952/53), and various aspects of them have been submitted to intensive theoretical deliberations and measured against a wide range of observations over the intervening years (see CODY and DIAMOND 1975, ANGER 1975), but as HYNES (1970) puts it, they are "repeatedly rediscovered and put forward as new ideas".

1. 'Je variabler die Lebensbedingungen einer Lebensstätte, um so grösser die Artenzahl der zugehörigen Lebensgemeinschaft.'

This pronouncement serves well to express the relationship between the number of species and the axis area of the stone, if one regards it as axiomatic that an increase in axis area will lead to greater habitat diversity.

2. 'Je mehr sich die Lebensbedingungen eines Biotops vom Normalen und die für meisten Organismen Optimalen entfernen, um so artenärmer wird die Biozönose, um so charakteristischer wird sie, in um so grösserem Individuenreichtum treten die einzelnen Arten auf.'

The first condition here is fulfilled by the weir in relation to the riverbed, and also by the interrelation between some of the stones. The faunal community in the weir habitat certainly becomes less diverse, that is, it becomes characterized by the group of passive feeders, which appear in great abundance, but the decline in the number of species does not occur here, as the impoverishment of the other groups is compensated for by an increase in species within the dominant one.

3. 'Je kontinuierlicher sich die Milieubedingungen an einem Standort entwickelt haben, je länger er gleichartige Umweltbedingungen aufgewiesen hat, um so artenreicher ist seine Lebensgemeinschaft, um so ausgeglichener und um so stabiler ist sie.'

The riverbed represents the bed of the rapids at a balanced phase, with the 'richness in species' manifested only in its high species diversity. No direct conclusion can be reached concerning the greater stability of its faunal community, as the evaluation of this would require a time perspective, but its higher mean value for the diversity of the constituent communities, and the smaller deviations from this, in comparison with the weir may be regarded as a hint at the buffering capacity of this section of the rapids.

This comparison serves to demonstrate that in many ways the 'biozönotische Grundprinzipien' do make their presence felt even in the case of the stones of these rapids, a relatively restricted biotope, although full applicability would seem to require adjustments in the case of the concepts of species richness, species diversity and stability, subjects which are discussed critically by ORIANS (1975), for instance.

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Appendix. Detailed analysis of the invertebrate material by species and stones, A (pages 1–6), and community data for the stones, B (p. 7). Number of individuals in A are stated separately for the exposed face/protected face/detached specimens, and data on the date of sampling, occurrence of sediments on the stone and attitude of the stone on the river bed are also provided. Occurrences not included in the numbers of species for the stones are underlined. See text for the species authorities and other explanations. Interpretation of part A: p. 1 and 2, species 1–49 and 50–105 on the habitats edge, backflow, deadwater and channel, p. 3 and 4 same on the riverbed and p. 5 and 6 on the weir.

APPENDIX, A. 1(7)

	1	2	3	4	32	33	34	35	5	6	7
1. Dendrocoelum lacteum			-/3/-								
2. Paludicella articulata									-/+/-		
3. Plumatella repens	+/-/-		-/+/-								
4. Pisidium sp.											
5. Stylaria lacustris		2/-/-									
6. Peloscolex ferox	1/-/-									-/1/-	
7. Helobdella stagnalis			-/2/-								
8. Erpobdella octoculata	1/-/-		-/6/-		-/1/-	-/1/-					
9. Sperchonopsis verrucosa											
10. Sperchon clupei										-/1/-	
11. Lebertia sp. (gr. insignis)		-/-/1		1/-/-			3/1/-	-/-/1			-/2/1
12. Torrenticola amplexa				-/-/		2/-/-				-/3/-	
13. Hygrobatas fluviatilis			-/1/-			1/-/-					
14. Hygrobatas calliger						1/-/-					
15. Hygrobatas sp.											
16. Hydrachnellae sp.											
17. Asellus aquaticus		2/1/-	-/1/-				1/1/2	3/-/1			
18. Heptagenia sulphurea		-/2/-						1/5/-		-/1/-	
19. Baetis rhodani								1/1/-			
20. Baetis vernus								8/-/1			
21. Ephemerella ignita						-/-/1	9/-/2	5/-/-			
22. Ephemerella mucronata		1/-/-								-/1/-	
23. Amphinemura borealis	2/-/-	13/1/-						7/2/-	-/6/-	-/3/-	-/1/-
24. Taeniopteryx nebulosa								4/2/-			
25. Leuctra digitata						-/2/-		3/2/-			
26. Isoperla obscura		-/1/-							-/1/-	-/1/-	
27. Plecoptera sp.											
28. Agraylea multipunctata						-/1/-		1/-/-			
29. Ithytrichia lamellaris							2/-/-		-/2/-		
30. Oxyethira frici									-/1/-		
31. Hydroptila tineoides		-/1/-				-/-/1	-/1/-	3/1/-		-/2/2	
32. Rhyacophila nubila						4/1/-		12/-/-		-/3/1	
33. Aqapetus ochripes											
34. Wormaldia subnigra											
35. Polycentropus flavomaculatus			-/1/-							-/-/1	
36. Psychomyia pusilla											-/1/-
37. Hydropsyche pellucidula									-/1/-	-/1/1	
38. Cheumatopsyche lepida								-/1/-			
39. Ceraclea annulicornis											-/2/-
40. Athripsodes cinereus							1/-/-				
41. Ceraclea excisa							1/-/-		-/3/-	-/-/2	-/2/-
42. Athripsodes, sensu lato, spp.	3/-/-	-/2/-	-/1/-		-/1/-	-/6/-	-/3/1	7/1/2	-/4/-	-/-/3	-/3/-
43. Micrasema sp.								5/-/-	-/3/-		
44. Micrasema setiferum	1/-/-	-/3/-						4/-/-	-/8/-	-/-/3	
45. Lepidodroma hirtum	3/-/-	11/3/-	-/2/-		-/2/-	-/1/-	-/2/2	-/3/-	-/3/1	2/7/5	-/-/1
46. Limnephilinae sp.			-/8/-					-/3/-			
47. Stenophylacini sp.					-/1/-	-/1/-					
48. Potamophylax latipennis		-/1/-							-/2/-		
49. Trichoptera sp.						-/1/-					

A. 2(7)

	1	2	3	4	32	33	34	35	5	6	7
50. Ablabesmyia monilis			-/1/-								
51. Pentaneurini sp. A				3/-/-	-/1/-	-/-/1	1/-/-	4/1/-		-/1/-	
52. -" sp. B								3/1/-			
53. -" sp. C							-/-/1				
54. Eutanytarsus sp.				1/-/-							
55. Rheotanytarsus sp.								2/-/-			
56. -" photophilus						7/-/-	1/-/-	4/7/1	-/2/-		-/-/2
57. Zavrelia nigritula		1/-/-									
58. Parachironomus sp.		-/1/-									
59. Eukiefferiella alpestris					-/-/1	9/2/-	1/-/-				
60. -" tshernovskii		1/-/-							-/1/-	-/2/1	-/-/3
61. -" quadridentata											-/-/2
62. -" sp.						7/2/-		1/-/-			
63. -" sp. pupa											
64. Synorthocladius semivirens											
65. 'Orthocladius' sp. A		7/2/2	-/1/-	1/-/-				10/-/-	-/4/-	-/1/6	1/2/3
66. -" sp. B		1/-/2			-/-/1			6/-/-	-/2/-		-/-/3
67. -" sp. C					-/-/1			1/-/-			
68. -" sp. D											
69. -" sp. E							-/1/-				
70. -" sp. pupa											
71. Cricotopus triannulatus		2/1/-	-/-/3	1/-/-					-/3/-	-/-/4	-/1/4
72. -" albiforceps	1/-/-										
73. -" bicinctus	1/-/-	3/2/6	-/1/19	2/-/-	-/-/1			2/-/-	-/2/-	-/5/11	-/1/5
74. -" trifascia			-/1/-								
75. -" sp. A		5/-/1		1/-/-						-/1/5	-/-/1
76. -" sp. B		1/-/-							-/1/-		
77. -" sp. pupae											
78. Psectrocladius simulans		2/-/1	-/-/1	1/-/-	-/-/1					-/2/1	
79. Rheocricotopus effusus								3/-/-			
80. Parametrioctenus stylatus											
81. Corynoneura scutellata					-/-/1						
82. Thienemanniella sp.				2/-/-		2/-/-		1/-/-			
83. Chironomidae sp.						2/-/-		1/-/-			
84. Chironomidae spp. pupae		2/-/-									
85. Metacnephia tridonia											
86. Eusimulium sp. ex gr. vernum			-/1/-								
87. -" (2. meigeni)											
88. -" aureum								1/-/-			-/-/1
89. -" sp.											
90. Schönbaueria pusilla											
91. Parabyssodon transiens								10/3/-			-/-/1
92. Simulium rostratum											
93. -" tuberosum											
94. -" argyreatum											
95. -" truncatum											
96. -" venustum											
97. -" verrucosum											
98. -" sp. ex gr. venustum											
99. -" morsitans											
100. -" austoni											
101. -" reptans								4/-/-	-/1/-		
102. -" sp.								2/-/-			
103. Simuliidae spp. indet.									-/6/-	-/1/3	1/1/-
104. Helophorus sp.				1/-/-							
105. Elmis aenea											

	18/1/-	-/32/23			-/6/6	20/9/8	-/57/1		2/16/27		
TOTAL.	54/24/14			14/1/-	35/17/4		119/34/6		2/37/50		
DATE	7.	7.	7.	7.	18.	18.	24.	18.	10.	9.	9.
SEDIMENTS	-	+	+	+	+	+	-	+	-	-	-
ATTITUDE	1	2	1	1	1	1	4	4	2	1	1

A. 3(7)

	8	9	10	11	12	13	14	15	16	17	18	19
1.		3/-/11						-/-/9				
2.		+/-/-		-/+/-								
3.				-/+/-			-/+/-	-/+/-	+/-/-		-/+/-	-/+/-
4.				-/1/-								
5.												
6.							-/1/-					
7.												
8.	-/3/-		-/2/-	-/4/-				-/1/-	-/1/-	-/2/-		-/1/-
9.		1/-/-	-/1/-						1/-/-	1/-/-		
10.					1/-/-					1/-/-		
11.				-/1/1					-/1/-	-/1/-		
12.		1/-/-							2/1/-	1/1/-	-/-/2	
13.			1/-/-	-/1/-		-/-/1			1/-/-	1/-/-	-/-/3	-/1/-
14.		1/1/-		1/1/-					4/-/1		-/-/6	-/1/1
15.												
16.												
17.		4/1/-			1/-/-							-/2/1
18.		-/-/1		-/1/-	-/-/1	2/-/-	-/2/-		1/2/1	-/1/-	-/2/-	-/2/-
19.				2/-/-	-/-/2				4/-/8			
20.				-/1/-					6/-/8		-/-/2	
21.				1/-/-	-/-/1				-/-/1			
22.		1/-/-			1/-/1				-/1/-			
23.	-/4/-	2/-/-	1/-/3	10/2/2	-/4/4			-/1/1	1/8/1	6/2/2	-/7/7	1/1/-
24.									-/-/1			
25.	-/-/1	1/-/-		-/2/-		-/-/1					-/-/1	
26.					1/-/-				-/-/1			
27.												
28.	-/1/-	-/-/1		-/2/-								
29.		1/-/-	-/5/-	-/9/1	-/1/-		-/2/1		1/-/-	-/1/-	-/2/-	-/4/-
30.		-/1/-		-/4/-	-/1/-		-/1/-		-/1/-	-/1/-		-/1/-
31.	-/5/-	12/-/1	1/4/2	-/4/-	-/1/-	-/2/-	-/1/1	-/2/-	-/1/1		-/3/-	-/2/-
32.		3/1/-	-/2/-	4/3/1	3/2, 1		-/2/-	-/-/1	2/1/-	2/1/-	-/2/-	-/2/-
33.							-/2/-			-/2/-		
34.												
35.				-/2/-						-/1/-		
36.				-/1/-								
37.					-/1/-		-/1/-	-/1/-	-/2/-		-/1/-	-/1/-
38.					-/1/-							
39.												-/-/1
40.							-/1/-					
41.		1/-/-										
42.				2/-/-								-/2/-
43.		1/-/2									-/-/1	
44.	-/3/-	6/-/-	22/2/2						4/-/1	-/4/-	1/3/1	-/1/-
45.	1/4/1	10/-/2	5/5/5		-/-/2	-/-/1	-/6/-	4, 3/-	2/-/2	2/5/-	-/2/3	1/8/6
46.	-/7/-											
47.												
48.												
49.		1/-/-		3/-/-	-/1/-		-/-/1					

A. 4(7)

	8	9	10	11	12	13	14	15	16	17	18	19
50.												
51.				3/1/-	-/-/1				2/-/-		-/2/-	
52.										-/1/-		
53.												
54.												
55.		2/-/-										
56.	-/1/-		2/-/-	3/8/1	-/4/-	1/-/-	-/2/-	35/2/-	1/9/-		1/4/-	4/5/-
57.												
58.				-/1/-								
59.												
60.				3/-/2			1/-/-		-/1/-	4/1/-		
61.				1/-/-		-/-/2			-/1/-	-/1/-	-/1/-	
62.										2/-/-		
63.					-/1/-				-/-/1			
64.												
65.		1/4/-	3/2/-	1/2/1		1/-/-	-/1/-	2/-/-	2/2/3	-/2/-	2/1/2	1/-/-
66.			1/1/2	1/5/5	1/-/1	-/1/-		4/-/-	3/1/4	-/2/-	1/1/2	1/-/1
67.									-/-/1			
68.												
69.								2/-/-				
70.												
71.	3/-/1	2/4/2	1/1/-					1/-/-		1/1/-	1/1/-	1/-/1
72.		-/1/1										
73.	-/1/2	3/2/2	3/-/6	1/2/5	1/-/-	1/-/1		13/-/-	2/1/4	3/1/-	1/-/6	1/1/2
74.		-/-/1							-/-/2		-/-/1	
75.	-/-/1		1/1/1	-/1/1			1/-/-			1/-/-		
76.	-/2/-	2/1/-	1/3/-	-/1/-				1/-/-	-/-/2		6/-/-	3/1/1
77.								<u>1/-/-</u>				<u>1/-/-</u>
78.												
79.				7/2/-	1/-/-			2/-/-	2/1/-		1/1/-	1/-/-
80.												
81.												
82.		9/1/-	-/-/1		1/-/-	3/-/-			3/-/-		-/1/-	-/1/-
83.		-/1/-										
84.	<u>1/1/-</u>		<u>1/1/-</u>						<u>1/-/-</u>		<u>2/-/1</u>	
85.									1/-/-			
86.												
87.								1/-/-	-/1/-			
88.				-/3/4	-/-/2		1/-/1		2/-/5			2/-/-
89.	-/1/-					-/1/-					1/3/-	
90.											1/-/-	
91.				-/-/2	1/-/-			7/1/-	13/4/5	3/-/3		
92.												
93.												
94.												
95.												
96.												
97.						1/-/-			15/-/1			2/-/-
98.							17/-/2		6/-/-			
99.											4/-/-	1/-/-
100.												
101.	-/1/-	1/-/1	1/1/-	11/3/2	2/-/1	2/1/-	43/-/29	1/-/-	79/30/18		22/1/11	7/5/2
102.						-/1/-						1/-/-
103.	2/2/-		1/1/1	5/3/-	1/6/-		1/-/12	1/-/-	-/4/6	11/-/-	-/3/3	-/3/-
104.												
105.				1/4/-	-/-/1				-/-/2			

TOTAL	7/36/6	75/18/30	47/32/26	60/74/29	15/23/18	11/7/5	64/23/47	48/12/11	162/75/80	34/31/-	46/42/48	28/46/16
DATE	9.	12.	9.	11.	12.	12.	9.	10.	12.	10.	9.	10.
SEDIMENTS	-	-	-	-	-	-	-	-	-	-	-	-
ATTITUDE	3	2	2	3	2	2	2	2	3	4	3	4

A. 5(7)

	20	21	22	23	24	25	26	27	28	29	30	31
1.							-/4/-					
2.	+/-/-	+/-/-				-/2/-	+/-/-					
3.		+/-/-										
4.			-/1/-				-/6/-					
5.												
6.					2/-/-							
7.												
8.		-/1/-	-/1/-				-/3/-	1/-/-	-/2/-			
9.						-/-/1						-/1/-
10.	-/-/1	1/-/1		-/1/-	1/1/1	1/-/-			1/-/-	-/3/-		
11.	1/-/-		2/-/-		-/-/2							
12.	-/1/-		1/-/-		-/1/-	-/-/2		-/1/-	2/1/-			
13.	2/-/1	1/-/-	1/-/-			1/-/1			-/-/1			
14.			1/-/-		-/1/3	-/1/-		2/-/-		-/1/-		
15.								-/-/1				
16.									-/1/-			
17.			-/1/1		-/-/1		-/3/-					
18.	-/2/1	-/-/1	-/3/1	-/-/1	-/-/1		-/2/1					-/1/-
19.		-/-/2			2/-/1	-/-/3	-/-/1	2/1/1		-/-/2	-/-/1	-/2/1
20.	-/-/1				3/-/-	9/2/-	1/-/-	6/-/2	-/-/1	-/2/-	6/-/1	
21.	-/-/3	-/-/3	2/-/-	-/1/1		-/-/1		-/-/1				
22.												
23.					-/-/1	-/-/1						
24.					-/3/1			-/-/4		-/3/-	1/1/-	-/3/-
25.	-/-/1		1/-/-		-/-/1	-/-/3	1/2/-		-/1/1			
26.												
27.												
28.	-/-/1		1/-/-	-/1/-		2/1/-		2/-/-	-/1/-	-/2/-		-/-/1
29.	-/2/-	-/1/-	-/2/-	-/1/-					-/1/-			
30.												
31.		-/1/-	2/2/-									
32.	1/-/-			-/1/-	3/2/-	1/-/-	-/1/1	6/-/1	-/1/-	1/-/-	-/-/7	-/2/-
33.												
34.						-/1/-						
35.			-/2/-									
36.												
37.							1/8/3					
38.		-/1/-					-/9/5					
39.												
40.												
41.			1/2/-			-/-/2	-/1/-					
42.	-/1/-	-/1/-	-/1/-		-/1/-							
43.			-/1/-									
44.												
45.	4/3/3	5/3/1	1/1/-		-/1/-	-/-/4						
46.												
47.												
48.												
49.									-/1/1			

A. 6(7)

	20	21	22	23	24	25	26	27	28	29	30	31
50.												
51.	-/-/1		2/-/-		1/-/-	1/-/1						
52.						-/-/1	1/-/-					
53.												
54.												
55.												
56.	1/4/2	4/-/2	1/1/-	-/4/1	12/8/-	23/23/1	7/13/1	10/ 13/23	16/10/1	-/8/4	4/2/7	-/24/-
57.												
58.												
59.				-/2/1	-/2/1	1/1/1	6/-/-	76/14/5	13/5/-	12/15/-	99/5/-	
60.					2/-/-	14/2/1		3/-/-		-/1/-		
61.						6/-/1	2/-/-			1/-/-		
62.		1/-/-		-/6/17	6/2/1	46/8/3	12/-/-	1/-/4		8/-/-		
63.												
64.				-/1/-		1/-/-	1/-/-					
65.	1/-/1	-/1/-		-/-/1	2/1/-	6/1/-	2/-/-		1/-/-		2/-/2	
66.	-/-/1	-/-/1		-/-/1		21/4/-	4/-/1		1/1/-	3/3/2	10/2/5	-/1/-
67.						3/-/-	1/-/-	-/-/1				
68.		-/-/2										
69.												
70.		1/-/-										
71.						3/1/-		3/-/-	1/-/-	1/-/-	3/-/4	
72.												
73.		-/1/-		-/-/1		6/-/5	2/-/-	3/-/1	1/-/-		-/-/1	
74.		-/-/1						-/-/2				
75.				-/1/-				-/1/-				
76.					5/-/-	2/-/-	3/-/-					
77.		1/-/-									-/-/1	
78.						-/1/-						
79.				-/1/-			1/-/-					
80.		1/-/-										
81.												
82.	2/-/2			-/1/1	2/1/1	2/-/-	2/-/-	2/1/1			2/-/-	
83.					1/-/-	11/-/-						
84.												
85.				-/5/-		1/-/-	3/-/-	99/6/-	10/-/-	14/4/-	20/2/1	-/-/1
86.								1/-/-	-/1/-			
87.						-/1/-					-/-/1	
88.	-/1/-	-/-/2		-/2/-	4/-/-	-/2/-	-/3/-		-/5/3	-/4/4	-/-/4	
89.						-/1/-		6/-/-		-/1/-		
90.								2/-/-		-/1/-	1/-/-	
91.		1/-/-					4/-/-	90/17/48	29/-/3	18/40/11	42/-/15	-/6/5
92.								1/-/-				
93.				-/1/-	-/1/-				4/-/-	4/-/-	4/-/3	
94.								2/1/-			1/1/-	
95.								-/1/-				-/2/-
96.						1/-/-	6/-/-	-/2/1	-/-/1	10/15/-		-/-/4
97.				-/4/-	5/-/-			2/1/-	18/-/1	12/15/4	26/2/17	
98.								151/-/-			27/40/6	
99.								1/-/-		12/3/-		
100.								1/1/-		1/-/-	1/-/-	
101.	-/-/1			-/10/1	38/1/-	172/2/1	85/-/-	1046/102/68	245/1/6	197/254/40	485/38/86	-/17/26
102.								1/5/-	44/-/-			
103.	-/1/-			-/-/2	24/-/-	64/2/-	23/1/-	4/-/16		15/14/2	46/-/12	-/2/1
104.												
105.						1/-/-						

	13/15/20		16/18/2		108/23/14		168/57/13		386/29/19		780/93/174	
TOTAL	18/10/16		-/43/28		402/58/34		1526/167/180		309/392/70		-/61/39	
DATE	16.	16.	18.	18.	18.	24.	16.	14.	15.	16.	14.	15.
SEDIMENTS	+	+	-	+	-	-	-	-	-	-	-	-
ATTITUDE	3	3	3	1	2	2	3	2	2	2	2	2

APPENDIX, B. 7(7)

Stone no.	Numbers of spp. ind.		Species diversity	Species evenness
1.	10	19	2.160	0.938
2.	22	89	2.617	0.847
3.	18	55	2.250	0.778
4.	11	18	2.303	0.961
5.	21	58	2.826	0.928
6.	23	89	2.773	0.885
7.	18	45	2.701	0.934
8.	16	49	2.591	0.934
9.	31	123	3.005	0.875
10.	19	105	2.551	0.866
11.	38	163	3.265	0.897
12.	28	56	3.011	0.904
13.	15	23	2.608	0.963
14.	20	134	1.767	0.590
15.	20	71	2.537	0.847
16.	43	317	2.646	0.703
17.	25	67	2.880	0.895
18.	32	136	3.001	0.866
19.	30	90	2.950	0.867
20.	22	48	2.728	0.883
21.	23	44	2.825	0.900
22.	20	36	2.876	0.960
23.	22	71	2.446	0.791
24.	27	145	2.548	0.773
25.	41	494	2.350	0.633
26.	32	238	2.551	0.736
27.	37	1873	1.427	0.395
28.	23	434	1.645	0.525
29.	28	771	1.578	0.474
30.	23	1047	1.636	0.522
31.	14	100	1.779	0.674
32.	11	12	2.369	0.988
33.	18	29	2.499	0.864
34.	14	37	2.261	0.857
35.	35	159	3.269	0.919

ERRATA AND ADDENDA

page	for	read
3	blacflies	blackflies
10	luteum	lutea
19	dewnstream	downstream
22	depotists	deposits
25	proporitions	proportions
28	p. 00	p. 25
34	berween	between
35/Table 10, figures in line 31:		5 1 5 4 41 5
— „ —	— „ —	5 2 8 7 83 22
36, 51	Oxyethhira	Oxyethhira
41	This groups	This group
	Chrinomidae	Chironomidae
42/Table 13,	Orthocladiinae (total) displaced	299 229
53, 55	P. stellatus	P. latipennis
58	LEVANIIDOV	LEVANIDOV
60	collectros	collectors
62/Fig. 12	$y = 0.98 + 0.042x$	$\log y = 0.98 + 0.042x$
76	environemnt	environment
86	decond	second
97	comunities	communities
99	quantiative	quantitative
109	demosntrate	demonstrate
114	add: HÄGGMAN, A. (1960) Evertebratafauna i Glomsån i Esbo socken. — Notulae Entomol. 40: 122–131.	
115/Kawecka and Kownacki . . .	Chrionomidae	Chironomidae
116	LINDEGAARD, C. and C. PETERSEN	LINDEGAARD-PETERSEN, C.
Appendix/	species 6., stone 1	2/—/—
	species 31.,	3/1/—
	Lepidodtoma	Lepidostoma

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