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Source: *Journal of Ecology*, Vol. 17, No. 2 (Aug., 1929), pp. 282-314
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/2256044
Accessed: 31/03/2011 21:07

A QUANTITATIVE STUDY OF THE FAUNA OF SOME TYPES OF STREAM-BED

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The faunistic ecology of streams has hitherto received very scanty attention in these islands. Carpenter (**6**) has examined qualitatively the streams in a Welsh area. Gardiner (**13**) in a preliminary note gave some quantitative results obtained by the use of various pieces of apparatus, and Butcher and Pentelow (**5**) have made a quantitative study of the effects of polluting effluents on the fauna of the river Lark, a stream very different in character from those dealt with in the present paper.

The qualitative study of rapid stream populations has been prosecuted to a very considerable extent especially by German workers. Steinmann (**31**) has given a very important account of the organisms of Alpine streams and Thienemann (**32**) has similarly dealt with those of the Sauerlandes (Westphalia). The work of Carpenter (*loc. cit.*) has shown that the rapid upland streams of Wales resemble in most respects those examined by the two workers named. Hubault (**15**) has an important account of the rapid streams of eastern France with many biological data.

It is not our intention, in this paper, to present a faunistic list. Very soon we became aware that the bulk of the population was made up of a few types of organisms which varied somewhat with the environment. Also there was a very considerable variation in numbers which might be explained only by reference to the conditions. We have attempted to analyse some of the conditions and to determine their effects upon the organisms as indicated by the density of the population. One of the results has been of considerable satisfaction in that we have obtained a good idea of the structure of the fauna as a whole. Many of the organisms which have been considered as the almost entire source of food of fish, such as *Limnaea peregra*, *Gammarus pulex* and *Ephemera* spp., have been found to contribute, in many places, either no part or very little part of the total fauna. Further, the very important rôle of the Microphyta, the Ephemeroptera and the Chironomidae has been emphasised anew.

We desire here to express our indebtedness to the Leeds Literary and Philosophical Society who have made grants in aid of this research.

THE NATURE OF THE STREAM-BED.

The streams with which we are chiefly concerned are found in the West Riding of Yorkshire, the most important being the rivers Aire, Nidd and Wharfe. Owing to the methods of examination it has been necessary to limit ourselves to those portions, the extent of which is considerable, which can be approached, in fine weather, by wading, and of a depth no greater than arm's length. Such portions of the stream are usually stony and offer difficulties in the matter of sampling which we feel to have satisfactorily overcome. They are streams in which Trout and Grayling are fished. The waters are derived mainly from the hills of the Pennine Chain which consist of Mountain Limestone and Millstone Grit and carry extensive patches of peat on the higher ground. The oxygen concentration is high, generally round about saturation point.

The presence of peaty water is noticed especially during heavy rains. In spite of this contribution of softer water the general reaction of the rivers is slightly alkaline. A comparison of the fauna of the upper Aire which does not receive peaty water with that of the Wharfe, which drains extensive areas of peat, shows that the animal life, so far as we have examined it, is apparently unaffected by the periodic heavy downpourings of water from peat. As a matter of fact there is a very considerable amount of limestone present in the various stream-beds, which is derived from glacial "drift," and this will tend to correct any undue acidity due to the influx of acid waters.

The portions of the three rivers to which reference is made resemble, in some respects, Thienemann's "Äschenbach" with many of the characters of his "Forellenbach." Most of the bed is stony except in those places where dams have been constructed, but, in passing downstream and corresponding with a general decrease in the tractive power of the stream, is seen an increasing amount of finer deposit which may form banks of pebbles of various sizes and beds of coarse sand. The deposition of silt (0·05–0·01 mm.) is slight and may be quite disregarded for the present purpose. Fine sand (0·25–0·05 mm.) occurs mainly in strips of sediment along the banks. The general character of the deposit changes in passing down as there is an increase in the amount of fine sand and a decrease in the gravel (1–3 mm.). The upper portion of the stream is swifter and has a bed consisting of large stones of up to 200–300 kilog. in weight and carrying considerable growth of moss. Also there may be patches of rock-forming rapids and falls which also carry moss. The rest of the bed is more or less stable, some parts being apparently in a state of motion every time a spate arises, other portions, owing to greater stability, showing a considerable diatomaceous growth on the upper surface of the stones. In the former case the stones, of 5–15 cm. diameter, are rounded and polished with no plant growth visible to the naked eye. There is usually practically no fine detritus (below, say, 0·5 mm.) between them, and such as is present consists of pebbles of diameter 0·8–2·5 cm. Quite extensive areas of scores of metres in length may consist of this material. They are usually in midstream with shallow water, but are also found forming the convex bank of a bend. In the former case occasional large mossy boulders may form the most stable objects, while in the latter case there are usually no outstanding stones. These portions of the stream have swift current and are subject to rapid rises in water-level.

A more stable bed consists of the same kind of rounded boulders bedded in a matrix of fine material down to 0·5 mm. and offering a practically unmovable substratum. The upper part of the stones carries a considerable amount of unicellular and small filamentous algae. The latter are in small amount. Here again the water is quite shallow, it being little more than 0·5 metre deep. Such a bed may be found lying laterally to the more heavily washed substratum which was described above. The deposition of fine sand here is very slight, and about the only evidence of its presence is seen in the walls of the tubes made by larvae of Orthocladiariae which occur in abundance on the upper surface of the stones.

The above-described beds are liable to heavy washing by floods which come with suddenness, tearing off patches of moss and stirring up the bed in many places. Life is difficult for the fauna which may be present.

Where the water is deeper and more uniform in its flow the stony bottom contains a matrix made up of a large amount of small pebbles. Much of this material passes through the 3 mm. sieve, but most is held by the 0·5 mm. mesh. There is less evidence of the action of strong current on the bottom; the substratum is probably stirred only under exceptionally heavy floods. This type of bed may extend for several miles with very little change in character and with only an occasional slight increase in depth. There is no desiccation of parts of the bed such as takes place in regions similar to those which have been described above. A considerable growth of *Cladophora* spp. is present, and this assists in the holding up of fine and coarse sand (1–0·25 mm.). Stony beds of this kind afford a firm hold for *Potamogeton perfoliatus* which, although relatively insignificant in the portions which we have studied, may form very important patches for the purpose of food production for fish.

Moss is found in various places along the stream. It has been already stated that large developments of it occur on heavy stones and rock surfaces higher up. Farther down may be found extensive growths on weir aprons, stone bridges and their foundations. These situations allow of the growth of an extensive fauna which is of great importance as a source of food.

The foregoing account of the stream-bed indicates a general succession of conditions in passing down a stream, but, as a matter of fact, recurrence of a given type of bed may take place with a particular change in the slope. For instance, each weir allows usually of the development of moss on its face, while below will be found a bed of rounded, relatively unstable stones with occasionally large, projecting, mossy rocks and farther away a more stable bed of stones bearing *Cladophora*. The river Wharfe shows very well this recurrence of conditions.

THE CLASSIFICATION OF THE VARIATIONS IN THE STREAM-BED.

In the examination of the analyses of samples taken it was seen that they fell into certain fairly well-defined groups according to the occurrence of certain animal organisms. These groups agreed strikingly closely with the subdivision of the bed into the following types:

1. Loose rounded stones of more than 5 cm. diameter, forming an unstable substratum, carrying no vegetation visible to the naked eye and having a current of about 4 metres per second: a slight matrix of rounded pebbles of diameter down to 5 mm. is usually present.

2. Stones of similar size to the above set in a matrix containing material down to 9·5 mm. diameter, carrying a visible growth of diatomaceous vegetation and presenting a stable substratum.

3. Beds of mixed, small, rounded, clean stones varying from 2·5 cm. to 0·5 mm. in diameter, with a preponderance of the coarser grades with no visible vegetation. There is evidence that these beds are unstable since the component parts move very easily when disturbed.

4. Rounded or flattened stones of various sizes from 30 cm. to 2·5 cm. carrying a growth of *Cladophora* and set in a matrix of material containing much between 0·5 mm. and 0·3 mm. in diameter. Such a bed is stable.

5. Large stones or other surfaces carrying a growth of moss, such as *Eurhynchium rusciforme*, *Hypnum palustre*, *Cinclidotus fontinaloides*, *Fontinalis antipyretica*, which although fairly dense allows of the fairly easy passage of water between the stems, thus preventing the accumulation of much detritus. This type of substratum may form quite a significant portion of a stream, especially in the higher regions.

6. Thick carpets of moss, such as those named above, forming a dense growth which prevents the easy passage of water between the stems and allows of the accumulation of fine detritus. This kind of bed offers an exceptionally fine medium for the development of a fauna.

7. *Potamogeton perfoliatus* forming a more or less dense growth on a bed of type 4. It will be seen that the peculiarities of this type may be set down to the presence of this plant.

By far the greater part of the deposit in these seven types consists of material having a diameter of 0·3 mm. and over.

So far as the description of the current is concerned it has been considered unsuitable to state the rate of flow as it is very variable during a short space of time and also in adjacent places. The simple device described by Dodds and Hisaw (**9**) for the measurement of current is useful for obtaining a general idea of the speed, but there is a considerable oscillation of the water-level in the tube and this reduces materially the lower values. The Pitôt tube as used by Clemens (**7**) is unsuitable for extensive field work where weight and volume of apparatus must be considered. We have preferred to describe the current by its effects as expressed in the nature of the deposit. This appears much more satisfactory and leads to a much closer examination of the sediments and their organisms.

Methods of Collection.

Owing to the variability of the substratum certain difficulties in sampling had to be overcome in order that samples could be taken as having a quantitative value. We have found three implements of great use in making quantitative collections.

1. *The sagnet.* Devised by Needham (see **24**, p. 333) for collecting animals swept from stones by disturbance. This has been used with great profit on large irregular stones of convenient weight, since, when it is rapidly passed under a lifted block, it collects not only the organisms but also the detritus, and so gives an opportunity to discover some of the conditions beneath. Any organisms which still cling to the stone are brushed off into the net and the whole sample can be then transferred to a suitable vessel for examination and preservation, or the larger detritus is picked out and only the small material retained. If an approximate estimate of the area of such a stone be made it is possible to obtain an idea of the density of the fauna in the immediate similar vicinity, and for this reason it is preferable to use stones of similar size for rapid comparison. The sagnet is made of stout material of suitable mesh attached to an ovoid frame of galvanised iron wire. We have used a frame of 24·5 cm. × 20 cm. and a net about 20 cm. deep with 0·5 mm. mesh.

2. *The shovel-net.* We used this successfully for determining the *Ephemera* population in sand (**25**) and have found it extremely useful in sampling stones up to 7·5 cm. diameter. Its disadvantage is that an error creeps in with the sampling of larger stones, but as disturbed organisms are almost all washed into the bag behind there is little loss to be considered. With a little practice this shovel is very efficacious. The area most suitable to take was found to be 4 sq. decimetres, a larger area being too unwieldy, especially in a strong current. Sampling was done to a depth of about 8 cm.

3. *The moss-sampler.* This simple piece of apparatus was described by us (**25**) as being used for sampling fine deposits. It has been applied to the accurate sampling of moss and similar vegetation and takes the whole of the material. Here the square open end of the box is placed on a patch of material having a level substratum, a knife is run round the sides to cut the vegetation and the sliding, flanged cutter is passed beneath so as to cut off the plants from the ground. The upper lid, being tightly fitted, prevents the escape of any of the contents when the whole is inverted. The material is emptied into

a suitable vessel for preservation. We have used a box of dimensions 7·5 cm. × 7·5 cm. In spite of its small size the sample is representative of the immediate neighbourhood and the numbers of organisms contained are not too great. Mottram (**23**) has used a piece of apparatus of similar design but on a much larger scale for the examination of stony beds.

THE ANALYSIS OF SAMPLES.

In the case of the moss-sampler there is practically no loss of material during sampling, but the other two nets lose material through the meshes. In order to give the samples a common basis the moss material was passed through a set of sieves the smallest mesh of which was 0·5 mm., the same as the sag- and shovel-nets.

The loss so determined was found to lie with the Entomostraca, certain Acarina, very young larvae of Chironomidae and, during the warm weather of 1925 and 1926, the newly separated buds of *Nais* sp. The Entomostraca from our area were practically insignificant and for our purpose had no value. The loss in Acarina lay with one species, about the time when most eggs were hatching and occasionally represented two-thirds of its total number. The loss in Chironomidae and *Nais* was most noticeable in summer with a low river and warm weather, and sometimes equalled or even exceeded the number retained. Besides the above-mentioned removal or organisms there was an almost complete absence of Rotifera and Protozoa. It was not our intention to deal with these groups, so that their loss does not concern us here.

It was seen that the error due to the escape of young organisms bore some relation to the numbers retained but varied from about 10 per cent. to about 66 per cent. of the total for the species. Since there was undoubtedly a similar passage of organisms through the meshes of the sagnet and the shovel-net it was decided to deal only with the part which was retained by a 0·5 mm. mesh, and so to place on a common basis the three kinds of samples.

The material was then specifically analysed and the different organisms counted. The counts obtained from samples taken by the shovel-net and the moss-sampler are expressed as numbers per square decimetre and also in terms of percentage composition; those taken from the sagnet samples are expressed as percentage composition only. In all cases the total is that retained by the 0·5 mm. mesh.

Owing to the difficulty of identifying many immature organisms such as the larvae and pupae of Chironomidae and certain other Diptera, and the smaller Oligochaeta, we have had to be satisfied with the determination of the genus or the sub-family. We are very much indebted to Dr Goetghebuer, of Ghent, for the determination of the Chironomidae, and to Mr C. D. Soar, F.R.M.S., for the identification of the Acarina.

THE PERCENTAGE COMPOSITION OF THE FAUNA.

Table I. *Average percentage composition of chief types of fauna from environments*.*

	Loose stones	Stones cemented to bottom	Small stones with lentil and pea gravel	Clado-phora on stones	Loose moss on stones	Thick moss	Potamo-geton on stones
Ephemeroptera							
Baetis	14·62	5·23	1·90	1·60	4·60	1·76	1·50
Rhithrogena	12·04	—	7·70	0·20	0·11	+	—
Ecdyurus	6·70	4·07	0·60	0·20	0·30	+	—
Ephemerella	0·8	8·56	—	9·40	11·36	4·82	4·50
Caenis	0·48	—	1·90	1·05	1·57	0·42	—
Plecoptera							
Leuctra	1·9	1·66	—	0·30	+	+	—
Chloroperla	1·28	0·17	0·60	+	0·27	0·32	0·20
Amphinemura	1·41	0·17	—	+	0·47	0·17	—
Perla	0·10	—	—	—	0·13	—	—
Isopteryx	0·41	—	—	—	—	—	—
Trichoptera							
Polycentropus	1·2	2·96	—	1·15	+	0·30	1·50
Hydropsyche	0·78	—	—	0·80	0·20	4·50	1·60
Glossosoma	2·98	3·73	3·20	+	—	—	—
Agapetus	20·1	20·96	18·20	2·00	0·21	—	—
Rhyacophila	0·74	0·13	—	1·30	0·40	0·25	+
Psychomyia	0·46	3·48	0·60	3·20	—	+	—
Hydroptila	—	0·26	—	5·40	1·74	0·19	—
Ithytrichia	—	0·13	—	0·13	—	0·46	—
Crunoecia	1·05	1·00	1·30	0·16	2·32	0·10	—
Coleoptera							
Helminthinae	3·10	7·76	34·0	8·10	6·16	4·20	—
Diptera							
Chironomidae	17·0	11·43	5·20	39·80	54·0	40·90	42·00
Simulium	3·03	—	—	0·10	1·30	1·54	1·30
Mollusca							
Limnaea	—	3·76	0·60	1·60	0·34	3·00	17·30
Ancylus	—	11·06	2·60	3·20	0·97	—	0·40
Oligochaeta							
Naididae	0·80	1·5	7·70	12·20	3·57	33·00	—
Arachnida							
Acarina	1·92	1·56	0·60	4·30	3·30	3·00	11·0
Crustacea							
Gammarus	1·3	—	0·60	+	1·23	1·02	4·5
Total = 100	94·20	89·58	87·30	96·19	94·55	99·95	85·80

* Eighty samples. + = less than 0·1 per cent.

1. *Among loose stones.* The average percentage composition shows the chief organisms to be *Agapetus*, *Baetis*, *Rhithrogena*, *Ecdyurus* and Chironomidae, these together making about 70 per cent. of the total. They are very widely distributed and show certain variations in proportion which can be correlated to a considerable extent with the nature of the environment. Especially is this seen with *Rhithrogena* and the Chironomidae. In rapid water, where the stones are of rather large size, water-worn and with indications of movement due to increased flow of water, the proportion of *Rhithrogena* will rise to as

much as 34·5 per cent. and that of Chironomidae will fall to 0·7 per cent. In other places where there is not so much evidence of violence and of movement of the stones *Rhithrogena* may fall to 1·7 per cent. while the Chironomidae may go up to 25 per cent. There is a similar but less emphatic variation in the proportions of the other organisms. On the whole it can be said that they decrease as the proportion of *Rhithrogena* increases, probably because they cannot so well withstand the heavy rush of water which is responsible for the very coarse deposit.

Table II. *Average percentage composition of fauna of main types of environment*.*

	Small stones with lentil and pea gravel	Loose stones	Stones cemented to bottom	Cladophora on stones	Loose moss on stones	Thick† moss	Potamogeton on stones
Ephemeroptera	*13·5*	*33·2*	*20·45*	*13·00*	*13·42*	8·03	6·06
Plecoptera	0·6	5·14	2·50	0·60	1·54	0·65	0·20
Trichoptera	*34·4*	*31·12*	*39·95*	*15·50*	3·10	8·00	4·73
Diptera	5·2	*20·81*	5·05	*40·00*	*65·34*	*42·00*	*44·03*
Coleoptera	33·8	3·05	10·30	5·00	6·66	4·38	2·10
Insecta	*87·5*	*93·35*	*78·25*	*74·10*	*90·06*	*63·06*	*57·12*
Gasteropoda	3·2	1·77	14·90	7·50	0·44	4·07	17·13
Hirudinea	—	—	0·75	0·10	—	1·30	3·13
Naididae	7·7	0·82	1·70	12·50	4·58	26·40	—
Tubificidae	—	0·10	—	—	—	—	14·66
Gammarus	—	1·37	—	‡	0·80	1·35	4·23
Acarina	0·6	2·00	2·35	4·50	2·82	3·25	1·03
Other Arthropoda	—	0·20	1·30	0·75	0·94	0·13	Hydra 3·50

* Thirty samples. † Eight samples. ‡ Less than 0·1 per cent.

Agapetus is strikingly variable in a way that can be correlated with the speed of the current. Two places about 3 metres apart were sampled. The surface speed of one was 2·3 metres per second while the depth was 7·5 cm., and the proportion of *Agapetus* was 35 per cent. The other had a surface speed of 3·6 metres per second with a depth of about 10 cm. The proportion of *Agapetus* here was 25 per cent. The animals were present only on the less polished stones which evidently resisted the overturning force of the water.

Psychomyia also shows the same relation to current as *Agapetus* does. In the two cases cited above it was absent from the more rapid water and made 3·2 per cent. of the total in the slower current. The genus *Nais* is practically absent from this type of stream-bed.

It may be said that the more important organisms in this region are those genera which have been named. The less important are *Leuctra* spp., Helminthinae, *Chloroperla grammatica, Amphinemura cinerea, Polycentropus flavomaculatus, Rhyacophila dorsalis,* but they must be considered on account of their regular occurrence.

Psychomyia pusilla, although mentioned above, is not to be considered as a typical inhabitant of the loose stones. When present it usually occurs on the edge where there is perhaps only an occasional disturbance due to flooding, although its hold may be regarded as somewhat precarious.

2. *Among cemented stones.* This region is generally characterised by a rather swift current of from 2·3 to 2·6 metres per second, and a sufficient depth of water to ensure a comparatively uniform flow near the bed during floods. The stability of the substratum permits an increase in the proportion of Chironomidae which build cases on the surface of the stones, constructing them of small sand grains which are deposited in small quantity during the slackening of the flow. This is especially seen when stones are large, near the bank and having many indentations on the surface, which provide shelter for many organisms with similar needs. *Ancylus* is found here in striking numbers. There is an increase in genera which dwell on the upper surface of stones. These are *Agapetus*, *Glossosoma*, *Psychomyia*, *Crunoecia*, *Ancylus*, *Limnaea.* The proportion of *Polycentropus* rises markedly. This animal constructs a net between and beneath solid objects and requires stability.

The change in the proportions of the various genera is due to the increase in the occurrence of *Ancylus*, *Ephemerella*, Chironomidae and *Agapetus. Halesus auricollis* may be considered here as it forms, in some suitable places, a by no means inconsiderable portion of the fauna, although its distribution is irregular. On large stones of from 2·5 kilog. upwards, near the bank and showing absence of the effects of flooding, it may form about 20 per cent. of the total. So abundant is it at times that the substratum appears grey with its cases made of sand grains. In the river Skirfare it has been found in great quantity sheltering in narrow and shallow cracks in the rocky bed and in slight hollows in the lee side of large stones where there is probably never more than a slight backwash from the main stream. In the river Wharfe and its tributary, the Skirfare, this species must be considered as the most important Limnophilid larva serving as fish food. Trout have been examined, the stomachs of which were charged with these larvae and their cases.

3. *Among mixed small stones.* The constitution of the fauna of the only quantitative sample taken from this type of deposit is striking in its high proportion of the larvae and adults of Helminthinae. As will be seen later the density of the population indicates the poverty of the stream-bed, probably because the amount of detritus passing through the 0·5 mm. sieve is insignificant and is indicative of the steady force of the stream which is able to carry its fine suspension to quieter regions even when there is no flooding. The genera present are practically the same as those found among the cemented stones. It is of interest to note that the nymphs of *Ephemera danica* occurred to the extent of 1·3 per cent. This organism has been shown (**25**) to live in greatest numbers where there are permanent deposits of a sandy nature having a preponderance of grains of from 1 mm. to 0·05 mm. in diameter.

4. *Among stones bearing Cladophora.* The analyses of samples taken from places carrying a growth of *Cladophora* and similar filamentous algae show certain features which are worthy of notice. Perhaps the most striking are

the proportions of Chironomidae and Naididae which together constitute more than half the average total. *Ancylus* is relatively common, and *Limnaea peregra* is found up to 9 per cent. Further points are the very great reduction in *Rhithrogena, Ecdyurus, Agapetus* and *Glossosoma.* Each of these is associated with a swift stream and consequently more or less clean stones. The growth of *Cladophora* is usually found with a deposit of about 1·5 mm., and this does not appear to suit the organisms named above. *Heptagenia sulphurea* is present to about 0·4 per cent. The presence of the fine deposit is indicative of relatively quiet conditions near the substratum and the increase in the proportion of *Psychomyia pusilla* to 3·2 per cent., as against 0·4 per cent. in the swifter regions, may be attributed to the greater stability of this habitat.

The striking increase of *Hydroptila* spp. from 0·25 per cent. among bare stones to 5·0 per cent. in this region is also to be noted. These organisms are usually found in clusters, sometimes of a few individuals and sometimes of hundreds. They may form approximately 16 per cent. of the total. They are to be regarded as regular inhabitants of this kind of habitat, and their association in clusters suggests that they find their subsistence close to the position in which they were hatched. Klapálek (**16**) has briefly described the habitat of *H. MacLachlani* and states that the larvae "auf der Oberfläche der Steine oder zwischen den Algen leben." We have taken the adults of *H. femoralis* and *H. forcipata* in great abundance and probably the large numbers of larvae which we have collected are to be referred to these species. Certainly the pupae of *H. forcipata* have been identified. The proportion of *Hydroptila* is variable according to the form of the surface of the stone on which the larvae are found. If there are slight depressions or angles which afford shelter they are present on the upper part pressing into the angles so formed. More regularly, however, they are found beneath stones and apparently free from the subjacent deposit, but in the shelter of a more or less narrow space between the stone and the substratum.

Caenis here provides a higher proportion than in the regions previously examined. The only species so far taken in adult form from the streams considered is *C. rivulorum.* The nymph is not suited to a clinging life and is an indifferent swimmer. It appears to find here the quiet conditions for which its form seems adapted.

The Acarina show an increase which is probably due to the slowing down of the current. They are to be found running over the surface of the silty deposit as well as living beneath the stones. In the regions previously referred to they form only an insignificant portion.

5. *Among loose moss.* This type of vegetation also harbours a high proportion of Chironomidae which may form as much as 77 per cent. of the total. They usually belong to the *Orthocladius* group of the family and attach their gelatinous cases to the leaves and stalks of the moss. In spite of the decided current of water which passes through the loose growth the Chironomid larvae

are able to retain a hold by means of their cases. The Naididae do not show any increase over the proportions noticed in the previously described cases as there is practically no fine detritus among the bases of the plants in which they may burrow, and as the worms have no efficient organs of attachment, they are obviously unable to retain a sufficiently firm hold to enable any striking increase in proportion.

Among the Ephemeroptera, *Baetis* and *Ephemerella* are the most noticeable organisms, while the flat-bodied forms are poorly represented. In fact the latter are not often met with in moss and have occurred in one sample of this type to the extent of 1·6 per cent. for *Ecdyurus* and 0·8 per cent. for *Rhithrogena.* We do not consider them as essential organisms in the moss fauna.

Crunoecia irrorata attains its highest proportion in this environment which serves as a centre from which the organisms appear to migrate. Although we have not found it to make more than 11·5 per cent. of the total it sometimes gives the impression of enormous numbers, as scores of square metres may be seen to be literally covered with them when the water is low. This is especially the case where there are large slabs of rock carrying a rather thin growth of moss and a shallow layer of water which has a sufficiently low velocity to allow them to wander about.

Hydroptila spp. are regularly found among loose moss where there is a slight accumulation of fine sand among the roots. Although the average percentage is lower than that for the *Cladophora*-bearing region the genus is nevertheless fairly consistent in its occurrence, it varying from 2·0 per cent. to 3·0 per cent. of the total.

There is a noticeable diminution in the figures for Mollusca. *Limnaea peregra* is practically absent, and *Ancylus fluviatilis* may be considered as not belonging to this type of bottom since its average proportion is only 1·01 per cent. in the samples taken and its occurrence very irregular.

Gammarus pulex shows a distinct increase over the previously examined regions and is a regularly occurring organism among moss, it constituting as much as 3·0 per cent. of the total.

Perla (*P. cephalotes* and *P. carlukiana*) has been found in this environment more frequently than elsewhere, especially in its earlier instars. There is reason to regard the loose mossy growth on stones as a nursery for a considerable portion of the *Perla* fauna since only the younger stages were found. In many places, however, where *Perla* is abundant, there is a very marked moss flora, and although the proportion here is the same as among loose stones (0·1 per cent.) the actual numbers, as will be seen later, are much greater.

6. *Among thick moss.* The dense carpet of moss is characterised by the very great development of Naididae (*Nais* sp.) and Chironomidae. These are seen to comprise approximately 75 per cent. of the total and the Naididae present by far their highest proportion. They vary in amount from about 30 per cent. to 90 per cent., but occasional samples which are not easy to

classify may present much lower percentages. One such sample contained only 6·8 per cent., and at the same time very young *Agapetus fuscipes* made up 0·8 per cent. The occurrence of *Agapetus* in this sample may be partly explained by the fact that it was taken on the upstream side of a large bed of moss growing on the concrete floor of a bridge foundation. The growth was less dense than that a few feet below, and the water was being collected by the bastions so as to pass under the arch at an increased velocity. A certain amount of coarse sand was present, and the general indications were that the strongly flowing current was able to prevent a dense plant growth, thus inhibiting the increase in Naididae and leaving a sufficiently bare substratum for the anchoring of the Caddis cases. Immediately below, where the water was passing from the arch with a slightly slackened speed, the proportions were very different. *Agapetus* was absent and the Naididae formed 28·7 per cent. of the total. The mossy carpet was thick and matted, offering excellent shelter for such feeble organisms.

Ephemerella, *Hydropsyche* and *Helmis*, although making up only about 14 per cent., will be seen to contribute a very significant part of the fauna.

Limnaea peregra is not usually met with in this kind of environment and owes its mention in the table to a single sample which contained 24·3 per cent. of small specimens. Properly speaking this sample should not have been included in the present class since it was taken from a stone covered above with moss and set in a bed of deposit of material chiefly varying from 3 mm. to 1 mm. diameter. *Limnaea peregra*, *Paludestrina jenkinsi*, *Pisidium* sp., *Planorbis* sp., *Glossosiphonia complanata*, *Helobdella stagnalis*, *Herpobdella atomaria* and *Dendrocoelum lacteum* were present in the sample and are a group of organisms not considered by us to be characteristic of this class. This sample emphasises the statement by Dahl (**8**) that environments are not isolated regions with definite limits but overlap one with the other, and the borderland has a mixed fauna derived from both regions.

The genera *Ecdyurus* and *Rhithrogena* have been taken, the former in two—the latter in only one sample of this class. They were present in each sample to the extent of approximately 0·3 per cent. for each genus. These odd occurrences add emphasis to the otherwise complete absence from thick moss of the flat Ephemerid nymphs.

Ithytrichia lamellaris occurred in 50 per cent. of the collections and contributed as much as 3·1 per cent. of the sample. This is a typical moss species and has been taken by us only once from cemented stones (0·4 per cent.) and once from *Cladophora* (0·8 per cent.).

Gammarus pulex occurs here in the same proportion as it does in loose mossy growths.

It is clear that the great increase in Naididae has resulted in an overshadowing of the other genera which also show increasing proportions. Their rapid reproduction in sheltered conditions enables them easily to outstrip in number the other organisms, and, on account of their poorly developed clinging organs, they are more readily affected by variations in the density of the plant growth through which the current can act upon them.

7. *Among Potamogeton growing on stones.* This type of vegetation presents few differences in faunistic composition and proportions from those of moss and *Cladophora* and of cemented stones. Variation is mainly seen in the large development of *Limnaea peregra* which averages 17 per cent. and *Physa fontinalis* (up to 4·5 per cent.) among the Mollusca, of *Gammarus* which contributes 4·5 per cent. and of Acarina with 11 per cent. Along with the Mollusca are found the leeches, *Glossosiphonia complanata, Herpobdella atomaria* and *Helobdella stagnalis*. *Glossosiphonia* presents as much as 4·5 per cent. while *Helobdella* is lowest, the highest proportion being 0·3 per cent.

Another interesting difference is seen in the replacement of Naididae by Tubificidae which averaged 10·5 per cent. and varied from 21·6 per cent. to 9·4 per cent.

The Density of the Population.

1. *Among loose stones, cemented stones and mixed small stones.* It will be convenient to consider these three groups together since they each show approximately the same total number and carry, within certain limits, the same types. The total numbers are very small as compared with those to be noted later. The demarkation of any one region of the three is difficult since they usually contribute to form adjacent parts of the same stream-bed and merge into each other. The numbers of organisms vary very much, apparently owing to slight differences in the quantity of fine detritus deposited and in the stability of the large stones. Two samples (see Table IV) taken from small mixed stones had totals of 12·50 per sq. decim. and 31·25 per sq. decim. respectively. The difference was due mainly to the increase in Chironomidae which were able to live in a thin layer of fine detritus on the upper surface of the pebbles. Any slight increase in the force of the current would have been sufficient to wash away the deposit and probably also the cases of the larvae, in which event the totals would have been about the same.

A similar comparison can be made between two samples of large stones of 2·5–7·5 cm. diameter (see Table V), one in a current of 3·6 metres per second and carrying a population of 7·7 per sq. decim., the other in a current of 2·3 metres per second with a density of 85·3 per sq. decim. Apart from the fact that there is a slight increase in the second case owing to the introduction of other genera, the rise in number is seen to lie with the Chironomidae and *Agapetus*, both of which require a stable substratum for proper development. The stones in the stronger current exhibited evidence of movement in that they appeared smooth and well rounded and had a scanty matrix which consisted chiefly of particles above 2 cm. in diameter. The stones in the weaker current carried a thin cap of diatomaceous and other fine algal growth and were embedded in a matrix of material down to 1 mm. diameter.

It is to be observed that in both tables the slackening of the current coincides with an increase in the number of genera. It would appear that the chief controlling factor in the density of the populations above referred to was the rate of flow.

2. *Among stones bearing Cladophora.* The density of the population here indicates a decided reduction in the severity of the conditions. *Rhithrogena*, which is peculiarly adapted to strongly flowing water, is practically absent, and *Agapetus* and *Glossosoma* are also very poorly represented. There is a

Table III. *Average number per square decimetre of different types of environment.*

	Loose stones	Stones cemented to bottom	Small stones with lentil and pea gravel	Cladophora on stones	Loose moss	Thick moss	Potamogeton on stones
Ephemeroptera							
Baetis	3·9	0·22	0·75	0·50	23·03	25·03	10·60
Rhithrogena	3·87	—	3·00	—	0·04	0·57	10·60
Ecdyurus	0·75	2·00	0·25	0·75	0·08	0·57	8·00
Ephemerella	2·8	4·60	—	45·00	198·00	38·82	5·30
Caenis	0·12	—	0·75	0·37	15·33	0·57	—
Plecoptera							
Leuctra	0·54	1·00	—	0·50	3·30	0·83	8·00
Chloroperla	0·5	0·3	0·25	+	1·52	5·71	8·00
Amphinemura	0·41	0·3	—	+	1·61	3·11	13·30
Perla	0·08	—	—	—	1·20	—	—
Isopteryx	0·12	—	—	—	—	—	2·66
Trichoptera							
Polycentropus	0·14	1·50	—	—	1·00	3·01	—
Hydropsyche	0·38	—	—	0·50	0·90	305·60	16·00
Glossosoma	1·9	1·85	1·25	—	—	—	—
Agapetus	9·6	13·60	7·00	0·25	—	2·03	—
Rhyacophila	0·23	0·12	—	0·25	0·50	12·80	13·30
Psychomyia	0·46	0·37	0·25	1·50	—	0·25	—
Hydroptila	—	0·25	—	25·17	27·13	3·10	—
Ithytrichia	—	0·12	—	—	—	10·80	—
Crunoecia	0·1	0·87	0·50	0·12	6·51	2·50	—
Coleoptera							
Helminthinae	0·63	4·22	13·00	19·30	53·14	245·31	5·30
Diptera							
Chironomidae (Orthocladiariae)	5·58	1·92	2·00	176·25	368·12	1455·00	2032·00
Simulium	0·71	—	—	—	7·12	24·00	272·00
Mollusca							
Limnaea	—	1·87	0·25	—	1·50	—	—
Ancylus	—	3·87	1·00	—	0·03	—	2·66
Oligochaeta							
Naididae	0·08	0·62	3·00	173·25	28·76	1968·00	—
Arachnida							
Acarina	0·10	1·00	0·25	0·12	31·40	204·00	32·00
Crustacea							
Gammarus	0·16	—	0·25	+	27·60	7·80	—
Average total per square decimetre	33·16	46·00	33·75	443·83	797·82	4319·41	2439·72

+ = present but less than 0·1 per square decimetre.

very marked increase in Naididae, Chironomidae, Helminthinae, Hydroptilidae and *Ephemerella*. The thick growth of this plant offers a very suitable shelter for such organisms as can scramble through it, and the fine and coarse sand which is held up offers a convenient medium in which Chironomidae may

Table IV. *Showing increase especially in* Chironomidae *with presence of fine detritus.*

Bell Busk, River Aire, 5. ii. 27. Small mixed stones

	No fine deposit		Fine deposit present	
	No. per sq. decim.	%	No. per sq. decim.	%
Rhithrogena	1·0	7·9	0·25	0·8
Ecdyurus	0·25	1·96	0·5	1·6
Baetis	3·75	29·95	2·0	6·45
Caenis	0·25	1·96	0·25	0·8
Simulium *l.*	2·0	15·7	—	—
Chironomidae *l.*	*3·0*	*23·5*	*23·0*	*73·4*
Hexatoma *l.*	—	—	1·5	4·8
Other dipterous *l.*	—	—	0·5	1·6
Helminthinae *l.*	0·25	1·96	0·25	0·8
Rhyacophila *l.*	0·5	2·9	0·75	2·4
Polycentropus *l.*	0·25	1·96	—	—
Glossosoma *l.*	0·25	1·96	—	—
Stenophylax *l.*	0·75	5·8	0·25	0·8
Hydroptila *l.*	—	—	0·75	2·4
Chloroperla	—	—	0·25	0·8
Amphinemura	—	—	0·75	2·4
Gammarus	0·25	1·96	—	—
Ancylus	—	—	0·25	0·8
Total	12·50		31·25	

l. = larvae.

Table V. *Showing increase in density of Agapetus, Glossosoma, Psychomyia and* Chironomidae *with slackened current.*

Grassington, River Wharfe. 17. iii. 27.

	Speed of current 3·6 metres/second		Speed of current 2·3 metres/second	
	No. per sq. decim.	%	No. per sq. decim.	%
Rhithrogena	0·75	8·8	1·5	1·7
Baetis	0·75	8·8	9·25	10·7
Agapetus *l.*	*2·1*	*25·0*	*31·0*	*35·5*
Glossosoma *l.*	*0·5*	*5·9*	*9·7*	*11·3*
Rhyacophila *l.*	—	—	0·25	0·3
Crunaecia *l.*	0·6	7·4	—	—
Stenophylax *l.*	—	—	0·25	0·3
Sericostoma *l.*	—	—	0·25	0·3
Micropterna *l.*	—	—	0·75	0·9
Psychomyia *l.*	—	—	*2·75*	*3·2*
Helminthinae *l.*	1·2	14·6	1·0	1·1
Chironomidae *l.*	*1·75*	*20·5*	*21·5*	*25·0*
Hexatoma *l.*	0·1	1·47	—	—
Perla	—	—	0·25	0·3
Amphinemura	—	—	1·0	1·1
Isopteryx	—	—	0·25	0·3
Nais	—	—	5·25	5·8
Acarina	—	—	0·37	4·4
Total	7·75		85·32	

l. = larvae.

build their tubes and in which the Naididae may burrow. This *Cladophora* region, with a population ten times greater than those previously considered, must be regarded as providing an enormous quantity of food material for such carnivorous organisms as live in and about it.

The closeness of the growth of this plant probably offers disadvantages to some of the organisms which are present in the purely stony environments. Slender insects, such as *Baetis* with its laterally placed gill lamellae, flat insects, like *Ecdyurus* and *Rhithrogena*, would be at a disadvantage in moving through the growth, while *Agapetus* and *Glossosoma* do not appear to favour surfaces carrying much fine detritus, probably because they need to cling firmly to a solid substratum. Their cases and the bristly armature which is found on the anterior portion of the body do not appear suitable for straining the water which, among the filaments of *Cladophora*, contains a suspension of fine material.

3. *Among loose moss on stones.* The total here is about double that of the previous case. Chironomidae and *Ephemerella* together may provide more than 500 organisms per square decimetre. The loose growth enables the animals to move freely but favours those with clinging organs. This is to be noted in connection with the Naididae which, though possessing bristles, apparently cannot retain sufficient hold to increase beyond about 30 per square decimetre, a contrast with 170 in *Cladophora*. The shelter and space render possible a very great development of several groups such as *Baetis*, Helminthinae, Acarina and *Gammarus*. The thin layer of coarse sand which is usually found forming a floor to the mossy growth permits *Caenis* to burrow with ease and safety.

Large stones carrying a growth of this nature and bearing a population of some 800 animals per square decimetre will add greatly to the sum total of edible material.

4. *Among thick moss.* The densest population occurs among the blankets of moss which grow on falls of various kinds and on large patches of rock and other objects. The close growth prevents little more than a seeping of water through it so that the Naididae, which were scarce in the loose moss, now present enormous numbers. In fact, there is an increase in nearly all the genera except those which require freedom of movement or a smooth substratum.

The greatest increase is seen in those which are not very mobile as the Naididae, Acarina, Chironomidae, Helminthinae and *Hydropsyche*. The thick growth offers a very favourable medium in which the larvae of the last-named genus may build their tubes. *Ephemerella* averages only about 40 per square decimetre as against about 200 in the loose moss.

Thienemann (**32**), in writing on the moss fauna, says that typically, in summer, there is a great abundance of young larvae which live on stones as more mature forms. He says also that Oligochaeta rarely occurs in moss.

We find, besides the large numbers of *Nais*, *Eiseniella tetraedra* which increases in number in mossy patches towards the side of the stream where there is a slackened current and slight depth of water. It is quite true that the young stages of many animals which in other places live under stones, are present in moss. So far as many species of the Trichoptera are concerned they do not appear to pupate in it but to pass down-stream at the end of larval life and to undergo pupation while attached to the underside of stones. This applies especially to *Rhyacophila*, *Hydropsyche*, *Polycentropus* and *Crunoecia*. The other organisms are always numerous, and there is no indication that the mossy regions become very much depleted by the migration of the fauna.

5. *Among Potamogeton perfoliatus.* Only one attempt was made to determine the density of the population in this type of bed. Usually the plants are semi-erect with a length of about half a metre. Sampling is a matter of uncertainty. The single sample was taken from a bed of pebbles about 8 cm. diameter, cemented and covered with a diatomaceous slime. The stems of *Potamogeton* were about 0·3 metre long and lay prostrate. The shallow water (owing to the dry summer of 1925) had enabled a great development of *Simulium* and Chironomidae. This sample presented the faunistic characters of cemented stones, loose stones and loose moss. The plants offered a suitable environment for *Simulium* and Chironomidae, and the stones supported *Rhithrogena*, *Ancylus*, Plecoptera and *Hydropsyche*. The absence of *Limnaea peregra* is interesting. This species is a fairly regular inhabitant of *Potamogeton perfoliatus*, but probably the current was too swift, owing to the shallowness, to allow of any development. Further, that part of the river, which consists of a great stretch of cemented stones without visible vegetation, very rarely carries *Limnaea peregra*.

Notes on the Biology of some Fluviatile Organisms.

In order better to understand the significance of the data presented in the tables it will be convenient to examine the relations between the various animals and their environments. In spite of the considerable amount of work done on freshwater organisms there is still a scarcity of information regarding the biology of many of the European fluviatile species. This refers especially to the immature stages of Plecoptera, Ephemeroptera, many Diptera and Trichoptera. American workers have contributed much regarding their own species. Needham and Lloyd have collected these data into a very useful work (**24**). Hora (**14**, **14** *a*) has also compiled a considerable amount of information on animal life in torrential streams and has presented some remarkable data regarding adaptations of various animals to the rapid waters of Indian mountain streams. Dodds and Hisaw (**9**) have described the biology of a number of American Plecoptera, Ephemeroptera and Trichoptera. Steinmann (**31**, **31** *a*), Thienemann (**32**), Schoenemund (**29**), Rousseau (**27**) and Lestage (**17**, **17** *a*) have contributed important works on the biology of European species, but it is necessary to know much more before an adequate idea is obtained of the economy of the stream.

The account which follows concerns only a limited number of species, since they are the most important from the present point of view, and contribute, by far, the greater part of the population.

Ephemeroptera.

Miall (**20**), Rousseau (**27**) and Lestage (**17**) have summed up the important facts already known relating to the European species of this order. There are still many species the nymphs of which are unknown. We have reared a number of the less known species which will be described in another place.

Baetis spp. Steinmann (**31**) has shown that *Baetis gemellus* and *B. alpinus* lack a well-developed middle cercus, since, he says, such a structure would be of no use in rapidly flowing water. On the other hand, the species which inhabit the Wiesenbach and the Graben can swim and have three caudal cerci provided with hairs. As a matter of fact the nymphs of this genus, which are abundant in our streams, are also provided with three fringed cerci which form a caudal fan. They can swim readily in still water, making rapid, short essays lasting four or five seconds. This swimming is only spasmodic. The insects appear soon to tire and sink to the bottom. The nymphs of *Baetis binoculatus* are swept away by a current of 1·3 metres per second, and at 0·7 metre per second they move through the water in short and quickly expended efforts. The conditions in which we have made our collections are such that swimming by *Baetis* is practically impossible. The nymph is here essentially a clinger. Eaton (**10**) says that *Baetis* and *Centroptilum* have the same habits. We have found the latter occasionally in great numbers, and each time the insects were running over the bed of practically still diverticula of streams. The bottom consisted of clean organic detritus indicating quiet conditions. We have only once found, in a mass of *Elodea*, the two living together, and neither was abundant. Our experience is that *Centroptilum luteolum* does not occur in water which flows swiftly enough to sweep away the fine organic matter.

The nymphs of *Baetis binoculatus*, *B. pumilus* and *B. rhodani* live mostly clinging to the undersides of stones where there is space for them to move. They are absent from that part of the stone which is buried, thus differing from some Plecoptera. Only where the current slackens do they come to the upper surface which they leave on the slightest alarm. Steinmann (**31**) noted that the nymphs of *Baetis* inhabited, preferably, inundated moss.

In Yorkshire the genus *Baetis* is the commonest and most widely spread of the order. Practically every stream which affords facilities for oviposition (see **25** *a*) is found to contain the nymphs. We have observed that the greatest numbers of *Baetis* are found where stones project above the water surface. Especially is this so in the shallow streams where the females can readily enter the water for oviposition by creeping down the sides of the emergent boulders.

The range of the genus is throughout the trout and grayling regions and occasionally has been taken from lowland rivers with a depth of 4 metres.

Dodds and Hisaw (**9**) have drawn attention to the success of the invasion of this genus into the stream, and point out that the most successful Mayfly is not the flattened form but the one with a rounded body.

Rhithrogena semicolorata. Dodds and Hisaw (**9**) have described the arrangement of the gill lamellae in the nymph of *Iron* sp. in which the first pair of plates are large, overlapping below the thorax, the last pair curve inward in a similar manner and the intermediate five pairs extend latero-posteriorly, each overlapping the one behind, the first pair over the second and so on, to that an elliptical sucker is formed. They show how the organism is adapted to live in a straight flow in a swift stream utilising the force of water acting on the peculiarly flattened body to press it to the substratum. *Iron longimanus* lives above, as well as beneath stones. *Rhithrogena semicolorata* is similarly organised and behaves in the same way. There does not appear to be any other apparatus taking part in the formation of the sucker than the gill lamellae and the venter. The claws are used on rough surfaces, but on a wet glass-smooth surface the sucker is very efficient. The claws are not necessarily used in aiding adhesion as an animal easily attaches itself when they are removed. During the attachment by means of the sucker the insect can slide itself along even against a strong current. The power of the sucker is very great as it will withstand a powerful jet of water from a pipette placed a couple of millimetres away. Swirling water also is unable to dislodge it. The femora are not strikingly flattened.

The animal is very well fitted for life among the loose, smooth, rounded stones. It provides up to 34 per cent. of the total in this type of bottom, and is practically absent from vegetation but may be present on the underside of stones bearing moss if there is not fine detritus about. We find it in various sizes of streams, it being abundant in brooks of 1 metre wide as well as in the rivers.

The nymph is a poor swimmer even in still water. The legs are flexed alongside the body with the femora inclined backwards and slightly outwards and the tibiae bent forwards. When carried along by the stream this insect, like many other nymphs of the order, spreads out its cerci, tilts up the posterior end and describes arcs until it comes to the bottom. Steinmann (**31**) says that this species is more a mountain form than *R. aurantiaca*. In our district it occurs down to near sea-level where conditions are suitable.

Ecdyurus venosus. Steinmann (**31**) drew attention to the flattened femora of this nymph and considered that they increased the adhesive surface. He also described (**31** *a*) in more detail the adaptations to a rapid water habitat.

We have found that this nymph with its very broad head and prothorax does not press its body closely to the substratum with a current of a little over 2 metres per second acting directly upon it but brings only the anterior edge of the head close to the ground. The projecting lateral edges of the pronotum cover the bases of the anterior femora, and all the latter slope outwards and backwards while their surfaces slope outwards and forwards. Thus quite an extensive surface is offered to the current and the animal is able to creep forwards with ease. It is unable to swim against such a current and is carried away when its hold is broken. The power of retention is not nearly so great as that of *Rhithrogena*, and this, no doubt, accounts for its low numbers in regions where *Rhithrogena* is abundant.

Ecdyurus venosus is very abundant in such places as carry a stable bottom with very little fine detritus, and bear blue-green algae or a diatomaceous growth. It is also found under mossy stones. Its shape does not allow of easy movement through thick matted vegetation, and thus accounts for its practical absence from moss.

In suitable circumstances these nymphs frequent the upper surface of stones, but usually they are found on the under surface.

Ecdyurus lateralis is often found in the same stream as *E. venosus*, but normally occurs along the edges in small bays and other places where the current is much reduced. It lacks the flat form, the broad head and pronotum of *E. venosus* and seeks shelter from a current of 1·3 metres per second. It cannot swim in a current of about 0·8 metres per second. This nymph is more usually found, in Yorkshire, in the upper part of streams towards the moors. It is quite abundant at altitudes varying from 200 ft. to 2000 ft.

Carpenter (**6**) has recorded *E. lateralis* from cascades, gorges and similar places with rapid current. We find that *E. venosus* populates such habitats while *E. lateralis* has a range restricted, at least partially by the current, to the quiet edges where the bottom is quite stable and there is considerable opportunity for obtaining shelter.

Ephemerella ignita is a characteristic nymph from the vegetation zones. It is, for practical purposes, no swimmer, but is able to clamber through *Cladophora* and moss. The greatest average number of this species has been found among loose moss, while *Cladophora* and thick moss have about the same average number but considerably less than loose moss. However, *E. ignita* nymphs have been found to the extent of 196 per square decimetre in thick moss. Among the flowering plants it is not strikingly abundant except in places where algae, such as *Oedogonium*, are present.

We have drawn attention (**25** *a*) to the details of the form of the ova and of oviposition in this species and have shown that the egg-masses are caught up by moss. The very young stages which we have taken have been obtained from moss, and the inference is that a very considerable proportion of those nymphs found in adjacent portions of the stream-bed have migrated from the mossy portions.

Caenis rivulorum. This organism does not contribute a very striking proportion of the stream fauna, but attention must be drawn to the fact that it may occur in loose moss to the extent of 72 per square decimetre. It is a feeble nymph, requiring shelter which it appears best to obtain among the stems of loose moss and *Cladophora* through which it moves easily. In July enormous swarms of adults may be seen in the evenings near bridges, especially those carrying moss.

Plecoptera.

It will be seen that the Plecoptera constitute at most only some 2·5 per cent. of the total fauna. Schoenemund (**29**) has contributed much on the biology of this order, and Lestage (**17** *a*) has described the habitat of the nymph of *Leuctra geniculata.*

The nymphs are all feeble swimmers even in still water. The larger genera, *Perla*, *Perlodes* and *Chloroperla*, cling tenaciously and are found among bare stones and stones carrying moss.

Leuctra and *Amphinemura* are, in our experience, the most abundant genera, and the commonest species are *L. hippopus*, *L. Klapáleki*, and *Amphinemura cinerea. Amphinemura* is apparently a burrower in the sand beneath stones or among vegetation, as its spiny nymph is usually found covered with fine detritus, with only its prothoracic gills free. The nymphs of *Leuctra* are usually found on the under surface of cleaner stones or burrowing among the coarser detritus down to 0·5 mm. diameter.

In spite of the fact that *Perlodes* and *Perla*, especially the latter, are found, about the time of maturity, in large quantities under suitable stones, they are relatively uncommon during the rest of the season. *Perlodes* has not been included in the tables on account of its relative scarcity.

Perla cephalotes and *P. carlukiana* are found in Yorkshire. The former extends slightly higher into the hills than does the latter, but we have found them in approximately equal numbers in the lowest places where the environment is suitable.

Perlodes mortoni extends from sea-level to the upper parts of the trout streams. It requires well-oxygenated water and little fine detritus and lives among bare stones and stones carrying moss. In the latter the number is relatively high.

The genera *Leuctra*, *Amphinemura*, *Protonemura*, *Isopteryx* and *Capnia*, are all found among stones where the bottom is stable. It is noticeable that the first two genera extend into the region where *Rhithrogena* is abundant and are usually found together. They lie well down below the large stones. As the bed increases in stability their numbers go up, especially among stones carrying moss.

Trichoptera.

Among stones carrying very little or no vegetation the larvae of Trichoptera make approximately one-third of the total. This is due to the great development of the genus *Agapetus* which does best in the absence of vegetation apart from the unicellular and small filamentous algae. *Agapetus fuscipes*, *Glossosoma vernale*, *Psychomyia pusilla*, *Tinodes waeneri* and *Tinodes* sp. (probably *T. dives*) form a very considerable proportion of the Trichoptera and of the whole fauna. They live on the sides and upper surface of the stone, the first two in cases shaped like coffee-beans, made from coarse sand and fine gravel grains held together by silken threads, the other two building tunnels varying in length up to 2 cm., consisting of fine sand grains cemented by secretion and attached to the substratum. These latter tubes are usually covered by a growth of calcareous blue-green algae which also invests a large portion of the surface of the stones. The substratum is generally stable except in extreme flooding.

Hydropsyche instabilis, although forming only a small proportion of the total moss fauna, is significant on account of its actual numbers per unit area. They vary from 70 to over 1000 per square decimetre, depending on the season. Shortly before the main period of emergence it is usual to find thick moss to contain over 200 per square decimetre.

This organism weaves its *cul-de-sac* among the stems and leaves of moss, with the opening on the upper surface and tilted slightly upstream. An examination of the table of densities will show that it is very poorly represented in the other regions described, but, where there is a stable stony bed with a steady flow and not likely to be subject to the effects of drought, *Hydropsyche* is regularly found living in the cleft between the stone and the substratum. The form of the net does not lend itself to strong colonisation of beds of aquatic flowering plants. Siltala (**30** *a*) has figured and described the eggs of *Hydropsyche* sp. He says that the females of this species swim and cement the eggs to the undersurface of bodies. Since, in the district under consideration, the largest numbers of larvae have been collected from moss submerged by swiftly running water, though in summer it be only a thin sheet, it is difficult to comprehend how small insects such as *Hydropsyche* could control their movements so as to swim down through the stream. The probability is that they creep in from the sides and make their way along the bottom. We have seen this take place in the case of *Rhyacophila dorsalis*, and females of Chironomidae have often been taken from beneath emerging stones in strong currents.

Three collections taken at the same time, in June, from beneath Harewood Bridge on the river Wharfe, show that the largest number, 283 per square decimetre, occurred in midstream at the lower side of the arch where the water was slackening in speed, 32 per square decimetre in midstream at the upper side where the water was swiftest, and 3·6 per square decimetre near the bank a few feet below the arch where the water spread out at a much reduced speed over a mossy concrete platform. A similar relation was seen in collections made in the following February and June.

Crunoecia irrorata is most abundant in moss which is not so dense as to inhibit locomotion. Although enormous numbers may be seen over considerable patches of rocks bearing a scanty growth of moss, we have not found more than 32 per square decimetre. It may be regarded as an organism characteristic of the mossy portions of the larger streams. On occasions, with a falling stream-level, great quantities are left stranded on flat rocks and in the slight depressions in which they collect as desiccation takes place. They finally die if the weather remains dry.

Polycentropus flavomaculatus is the only member of the Polycentropidae which is significant for the present purpose. It is widely distributed throughout the stony region and in the adult condition is found throughout the greater part of the year. The larvae are least abundant in the *Cladophora* region and among the more sterile small stones. Its numbers are nowhere striking, but its wide distribution gives it an importance in stream economy.

The larva builds a loose web beneath stones and, as in *Hydropsyche* and *Rhyacophila*, pupation takes place in a rough case of stones bound together by silk.

Rhyacophila dorsalis is very widely distributed. It is well known as occurring among stones, creeping freely on the unburied underside and among the moss covering the upper surface. As many as 46 per square decimetre have been taken from thick moss.

We have taken two species, *R. dorsalis* and *R. obliterata*. The latter must be very rare since only two of the larvae which have been examined from our collections were not *R. dorsalis*.

The Hydroptilidae are represented by the genera *Hydroptila* and *Ithytrichia*. The former is found as groups of organisms chiefly beneath stones bearing *Cladophora*. It may also occur among moss where as many as 112 per square decimetre have been taken. The only species identified in the adult condition were *H. forcipata* and *H. femoralis*.

Ithytrichia lamellaris attaches its larval case to the stalks of moss to which we have found it exclusively confined.

Coleoptera.

Our experience of Coleoptera, so far as this present work is concerned, is practically entirely confined to the sub-family Helminthinae of the family Dryopidae. These insects, especially the genus *Helmis*, have a remarkably wide range of conditions. Enormous numbers are found in the denser growths of moss, varying from 80 to 1200 per square decimetre. The small size, flattened bodies, strong claws and spiny pleura of the larvae enable them to cling to almost any surface, to utilise any shelter and to creep through almost any vegetation. They appear always to seek shelter since we have not taken any from the upper surface of bare stones. The adults have similar habits to those of the larvae, but they also clamber up among the more distal parts of plants as they have very powerful and long hooked claws. Reitter (**26**) says that the larva of *Macronychus* leaves the water in order to pupate in damp wood. We have examined many samples taken at different times of the year and, although larvae and adults of *Helmis*, *Limnius*, *Esolus*, *Latelmis* and *Riolus* have been found, there has never been a pupa present. The inference is that these genera, as in *Macronychus*, leave the flowing water and pupate at or near the margin of the stream.

Thienemann found *Helmis maugei* to rank first in abundance in running water and *Hydraena gracilis* second. The latter animal has not occurred in our collections. We found *Helmis*, *Limnius* and *Latelmis* to be abundant, while *Esolus* was less numerous and *Riolus* was rare. The larvae of *Limnius* are regularly found among bare rounded stones where *Rhithrogena* is dominant. Its cylindrical body, tapering rapidly posteriorly, its very tough exoskeleton and its very strong short legs enable it to move without risk of damage in the coarse detritus beneath the stones.

The larvae as well as the adults of Helminthinae are found all the year round. There is a greater proportion of young larvae in October and November than at other times.

Diptera.

Needham and Lloyd (**24**, pp. 225) have said, "By far the most important of the aquatic Diptera, in the economy of nature, are the Midges," and further (**24**, p. 227), "Midge larvae are among the greatest producers of animal food." We have shown that, in the vegetation, the Chironomidae make up from 40 to 54 per cent. of the total fauna. In Tables IV and V it is shown that there is a relation between the speed of the current, the nature of the detritus and the density of the Chironomid population. The very rapid portions with no fine deposit are practically devoid of these larvae. By far the greater portion of the midge larvae in our area consists of Orthocladiariae. This is especially the case among moss where they contribute up to 97 per cent. of the Chironomidae. They are also abundant on the upper surface of stones where their cases, reinforced with fine sand grains, may be seen forming more or less sinuous marks. The tubes are made of a gelatinous secretion to which adhere particles of various kinds and are attached to stones, plant stems and other substrata. *Potamogeton* stems and leaves offer a good foundation. *Tanytarsus* occurs in varying quantities, under stones and in thick sheets of moss. This larva moulds a ridged tube of secretion and detritus which lies recumbent along its whole length or is more or less erect at the oral end, depending on the state of the current in the immediate neighbourhood. Clemens (**7**) has shown in a valuable study on the ecology of the Mayfly, *Chirotenetes*, that there is a great reduction of current beneath a stone which is tilted so that the downstream end is raised. Although the water may strike the upstream end at a velocity of 3·0 to 3·5 ft. per second the speed beneath may be practically nothing. We have noticed this many times and consider it a very important factor in determining the occurrence of oviposition in such places by small insects such as Chironomidae and *Baetis*. We have found, under a partially submerged stone of approximately 20 × 20 × 20 cm., 110 egg-masses of some Orthocladiarian. The stream was a typical rapid stream frequented by the organisms characteristic of the type. Miall and Hammond (**21**) state that an egg-mass of *Chironomus dorsalis* may contain from 668 to 1102 eggs.

For the abundant development among stones of the tube-dwelling Chironomidae it is necessary for the bed to have stability. The smallest numbers are obtained in places where the stones are liable to movement. Moss presents a favourable environment, especially where it is dense, as the slow moving water, in passing through, is unable to dislodge the cases and the food material.

The abundance of Chironomidae, as with most insects, is largely dependent upon the previous weather. A sample taken in June of 1926 from thick moss gave 3200 per square decimetre. Another taken from, as nearly as possible, the same place in June 1927 contained 1470 per square decimetre. The weather in the earlier part of 1926 was quite favourable with plenty of sunshine and a low river which afforded a good opportunity for the emergence of adults and for oviposition. The weather during the earlier part of 1927 was cold until the end of May, the first few days of June were warm and sunny, and from mid-June onwards was very wet and cold. Development during this later period must have been very seriously inhibited and the emergence of adults to produce the summer brood must have been very much interfered with.

Simulium is not at all abundant in the region investigated. Although it is apparently common in the shallow streams we have rarely found more than 35 per square decimetre.

Edwards (**11**) has described the larvae and pupae of the British species. Britten (**4**) states that the female of *S. equinum* enters the water and attaches its eggs to the substratum in a soft gelatinous mass to form a single layer. The larvae are often found in swarms on a stone. The probability is that they remain largely in the neighbourhood of their birthplace. More rarely are they found singly, and in these cases it is likely that they have been carried downstream from swarms.

Apart from the Chironomidae the Diptera contribute no great portion to the total numbers of the fauna of the more rapid streams.

Mollusca.

Ancylus fluviatilis appears to require conditions similar to those of *Agapetus*. Its powerful foot and conical shell with the apex tilted posteriorly are adapted to life in strong currents. The greatest development is found on rounded stones carrying a thin growth of unicellular algae, i.e. a stable bed. The numbers decrease markedly with the appearance of moss among which detritus collects. We have found as many as 300 on and under stones of approximately $20 \times 20 \times 5$ cm. in shallow brooks. Here are usually found many larvae of *Baetis binoculatus* and *Simulium* (e.g. *S. ornatum*).

Although *Ancylus* is typically found on the upper and lateral surfaces of a stone it may be numerous beneath if there is sufficient space and if the water be shallow. The eggs of *Ancylus fluviatilis* are laid in roughly circular plano-convex capsules which are attached to stones at the flat side. The area of the capsule is about equal to that of the foot of the animal. It consists of a thin basal membrane to which is sealed the edge of the tougher transparent membrane, and the double edge is securely fastened to the substratum. The lower membrane is free except at its edges. The capsule has a grey appearance owing chiefly to the presence of usually seven yolky eggs. The form of the body is admirably adapted to existence in strong currents, and an attached capsule will resist a very powerful jet of water.

Limnaea peregra is found more in the grayling region than in the trout region. Its greatest numbers are found further down where the water runs more quietly. Owing to the large surface exposed by the shell in proportion to the foothold it is more liable to be washed away than is *Ancylus*.

In the trout region it is generally associated with *Halesus auricollis* along the bank on the large stones which are practically never uncovered during the summer. A region which is subject to rigorous heavy flooding does not possess many *Limnaea peregra*.

In the parts of the streams examined for the present purpose this species does not form any significant portion of the fauna. At times, however, as in June, the young may occur in hundreds under a stone set in a deposit of coarse and fine sand. This is due to the fact that many egg-masses may be laid together. In one case a stone of about $20 \times 20 \times 10$ cm. carried 1013 newly hatched snails besides 17 egg-masses not yet hatched. Such samples have been rare, but they serve to populate considerable areas by the subsequent migration of the organisms. A single sample of this kind may give a wrong impression of the abundance of the particular animal and indicates the need for repeated sampling both at the same and later times.

Naididae.

Thienemann (**32**) says that Oligochaeta are rarely obtained from moss. Of the larger Oligochaeta we find *Eiseniella tetraedra* as a frequent inhabitant of the lateral portions of moss beds where the current is slack and there is no more than about 3–4 cm. of water. In thick moss with a strong current it is present to the extent of about 6 per square decimetre, and similarly among stones in a stable region.

Tubificidae and similar undetermined worms are practically confined to the phanerogamic vegetation and silted regions where they may contribute as much as 46 per cent. of the total. Samples of *Ranunculus* have contained 46 per cent., of *Potamogeton* 21 per cent. and of silty beds 21 per cent.

The Naididae offer a very interesting example of distribution. They are very abundant in thick moss where as many as 12,000 per square decimetre have been found. There is much variation in the numbers. This appears to be dependent, in part, on the time of the year, on the condition of the river during the previous few weeks, and on the thickness of the moss growth. The minimum figures for thick moss are in the neighbourhood of 400 per square decimetre, but it is seen (Table III) that the average is about 2000. There appears to be a single species, *Nais elinguis*, present.

Although this animal is present in loose moss its density is much less than that in the denser growth. Not more than 100 per square decimetre have been found.

The reason for this wide difference may be sought in the fact that the particular *Nais* is of small size with relatively feeble setae. Some Chironomid larvae are little larger in size or stronger in armament but they form cases which are adherent. Moreover, the cases are usually made in relatively calm conditions, and once being anchored the larvae may persist. *Nais*, on the other hand, builds no attached case and, as water flows easily through loose moss, there is a tendency to wash out the small fragments of detritus and loose animals, especially during times of flooding. In thick moss the circumstances are different, as has been previously mentioned. There is a dense felt which allows only a slight current of water to pass through and affords a secure foothold for the short setae and feeble bodies of the worms.

The Naididae are among those Oligochaeta which reproduce asexually. This takes place in the warmer portion of the year and practically ceases during the winter. We have made several determinations of numbers at different times of the year and at different places at the same time. The following (Table VI) presents a summary of the results:

Table VI.

Harewood Bridge, River Wharfe

Date	Previous weather	Temperature	Number of Nais per sq. decim.
Series 1. Midstream, immediately below the south arch			
9. vi. 26	Very warm with low river	61° F.	8355
16. ii. 27	Wet; heavy water; surface speed approx. 7 metres per second	44° F.	1422
30. vi. 27	Very cold; low river	59° F.	464
Series 2. 1 metre from right bank in shelter of south end of bridge			
9. vi. 26	Very warm with low river	61° F.	3776
16. ii. 27	Wet; heavy water; surface speed approx. 7 metres per second	44° F.	25
30. vi. 27	Very cold; low river	59° F.	2208

The two sets of figures indicate a marked reduction in numbers during the winter and a failure to attain to the original figure for the previous year. The continuous decline in Series 1 may have been due to the very heavy washing to which the moss bed was subjected during the earlier part of 1927. Series 2 shows an expected increase in the early summer which was no doubt assisted by the shelter offered by the bridge.

The figures obtained for density of *Nais* in *Cladophora* indicate that this plant forms a more suitable habitat than loose moss and the purely stony regions. They may be interpreted in the same way as those already dealt with.

Among stones without visible vegetation these worms form only a negligible portion of the fauna.

Their absence from phanerogamic vegetation is to be noticed. In the sand which is held up by *Ranunculus* and *Elodea,* Tubificidae and similar worms take the place of *Nais*. Naididae are also practically absent from about the stones on or among which *Potamogeton perfoliatus* grows.

Gammarus pulex.

This species is generally not abundant in the larger streams of this district. Although in brooks we have taken as many as 130 from beneath a stone of about 20×20 cm. the numbers in similar places in the larger streams are usually negligible. Only in one sample have we found a large number. This was in loose moss which had 130 per square decimetre. Otherwise the maximum total was 32 per unit area.

It thrives best in thick moss from which fairly consistently the higher figures have been obtained. The highest proportion obtained was 10 per cent. from *Potamogeton perfoliatus.*

Gammarus pulex is a relatively constant inhabitant of phanerogamic vegetation.

Although it is a powerful swimmer in still and slowly flowing water *Gammarus* very quickly seeks shelter from a current which is sufficiently strong to transport fine sand. This was especially well appreciated in the case of a small stream with a steady, swift flow except along pebbly stretches of the bank. The bottom was of fairly uniform stones varying from 2·5 cm. to 5 cm. In the swift portion *Rhithrogena* was dominant with few *Gammarus* in the crevices. At the side the stones carried a thin covering of fine detritus and *Gammarus* was seen swimming in this portion. There was a well-marked line between the two currents which also marked the limit of the organism's freedom.

Acarina.

The Acarina which have been found in the various regions are largely characterised by the almost complete absence of swimming structures. Many of them, as *Hygrobates, Pseudosperchon, Atractides,* are provided with spines and bristles and have strong claws. On the whole it may be said that the mites flourish best where there is a stable bottom with plenty of shelter. There does not appear to be any definite correlation between the character of the Acarine fauna and the environment. The common species are found throughout the stream, the only striking difference between one part and another being seen in the numbers per unit area.

The following species have been commonly taken in the various types of environment:

Hygrobates longipalpis
H. naicus
H. nigromaculatus
Lebertia porosa
Pseudosperchon verrucosus
Sperchon tenuabilis
Atractides anomalus
Aturus scaber
Megapus spinipes

The Food Relations of some of the Aquatic Invertebrates.

Needham and Lloyd (**24**) have emphasised the importance of Chironomidae and Ephemeroptera as herbivores. Bengtsson (**3**) has examined the nymphal gut contents of European species of Ephemeroptera and finds them to be almost entirely diatomaceous. Morgan (**22**) says that the nymphs of Ephemeroptera are voracious herbivores and come next to the aquatic Diptera as plant eaters. They will consume any suitable material which is present. Siltala (**30**) has made an extensive study of the food of European trichopterous larvae and has collected information from the literature relating to the matter. Lloyd (**18**) has determined the food of a large number of American trichopterous larvae. They resemble the European larvae in their requirements. Mertens (**19**) states that while the nymphs of the large Plecoptera are carnivorous, those of *Chloroperla* are omnivorous and those of the smaller Plecoptera are phytophagous. He does not state anything further regarding the smaller forms.

We have examined the gut contents of a variety of organisms from a number of localities. The results show that the carnivorous species do not form more than approximately 10 per cent. of the total fauna of a given type of substratum. The following list indicates the proportion of carnivorous animals (excluding Vetebrata) for the different habitats dealt with in this paper:

Carnivores among

1.	Loose stones	6 %
2.	Cemented stones	3 %
3.	Small loose stones	1 %
4.	*Cladophora* on stones	3 %
5.	Loose moss	2 %
6.	Thick moss	5 %
7.	*Potamogeton*, etc.	11 %

(Leeches among *Potamogeton* form 5 per cent. of the total population.)

The statement which follows shows that those animals which form the greater portion of the fauna derive their nutriment chiefly from the Algae, especially the Diatoms and Desmids. The number of species existing on other material is small.

Ephemeroptera	
Baetis binoculatus B. rhodani B. pumilus Ecdyurus venosus Rhithrogena semicolorata Heptagenia sulphurea *Caenis rivulorum	*Diatoms, desmids*, filamentous algae
Ephemerella ignita	*Moss*, filamentous algae, unicellular algae
Plecoptera	
Perla cephalotes P. carlukiana Perlodes mortoni	Rhithrogena, Baetis, Ecdyurus, Chironomidae (chiefly Orthocladiariae)
Perla cephalotes of 5 mm. length	Small Chironomidae, moss, larval Copepoda, unicellular algae
Chloroperla grammatica	Tanypus and Orthocladiarian larvae, Baetis, desmids, filamentous algae. They may feed exclusively on algae
Leuctra hippopus L. Klapáleki	*Unicellular and filamentous algae*, moss fragments
Trichoptera	
Stenophylax stellatus	*Phanerogamic matter*, mixed plant detritus, fragments of chitin (probably detrital)*
Halesus auricollis	*Diatoms*, filamentous algae*
Rhyacophila dorsalis	*Chironomid larvae*, Hydroptila, filamentous algae
Agapetus fuscipes	*Diatoms* and other unicellular algae
Glossosoma vernale	*Diatoms, desmids*, filamentous algae, gelatinous algal masses
Hydropsyche instabilis	*Chironomid larvae* (chiefly Orthocladiariae), Nais, fragments of moss, Ephemerella
Polycentropus flavomaculatus	*Chironomid larvae*, Helmis larvae, Nais
Plectrocnemia conspersa	Baetis, Chironomid larvae
Crunoecia irrorata	*Moss*
Psychomyia pusilla	*Diatoms*, desmids and other unicellular algae, moss fragments
Tinodes waeneri	*Diatoms*, other unicellular algae, moss fragments
Hydroptila sp.	*Diatoms* and other unicellular algae
Diptera	
Chironomidae, viz. Orthocladiariae Tanypinae Tanytarsus	Diatoms and other unicellular algae, filamentous algae
Simulium reptans	Moss, diatoms and other unicellular algae, filamentous algae, brown organic debris
Hexatoma sp.	*Diatoms, desmids*, filamentous algae, moss fragments*
Crustacea	
Gammarus pulex	Chironomidae, detritus
Oligochaeta	
Nais sp.	*Diatoms*, other unicellular algae, organic detritus
Hirudinea	
Herpobdella atomaria	Tubificidae, Chironomidae
Helobdella stagnalis	Physa, Limnaea
Glossosiphonia complanata	Physa, Limnaea, Sphaerium, Pisidium
Mollusca	
Limnaea peregra Ancylus fluviatilis	*Filamentous* and unicellular algae and other plant matter
Hydrozoa	
Hydra sp.	Chironomidae

Italicised names of food material indicate preponderating portion of gut contents.

* A considerable quantity of sand usually found in the gut.

It is to be noticed again that some of the animals, e.g. *Chloroperla*, *Rhyacophila*, are facultatively herbivorous in the later larval life and may be found feeding entirely upon vegetation. Also *Ephemerella* has occasionally been taken with animal matter in its gut. This, however, is not by any means an important part of its diet and may be regarded as accidental.

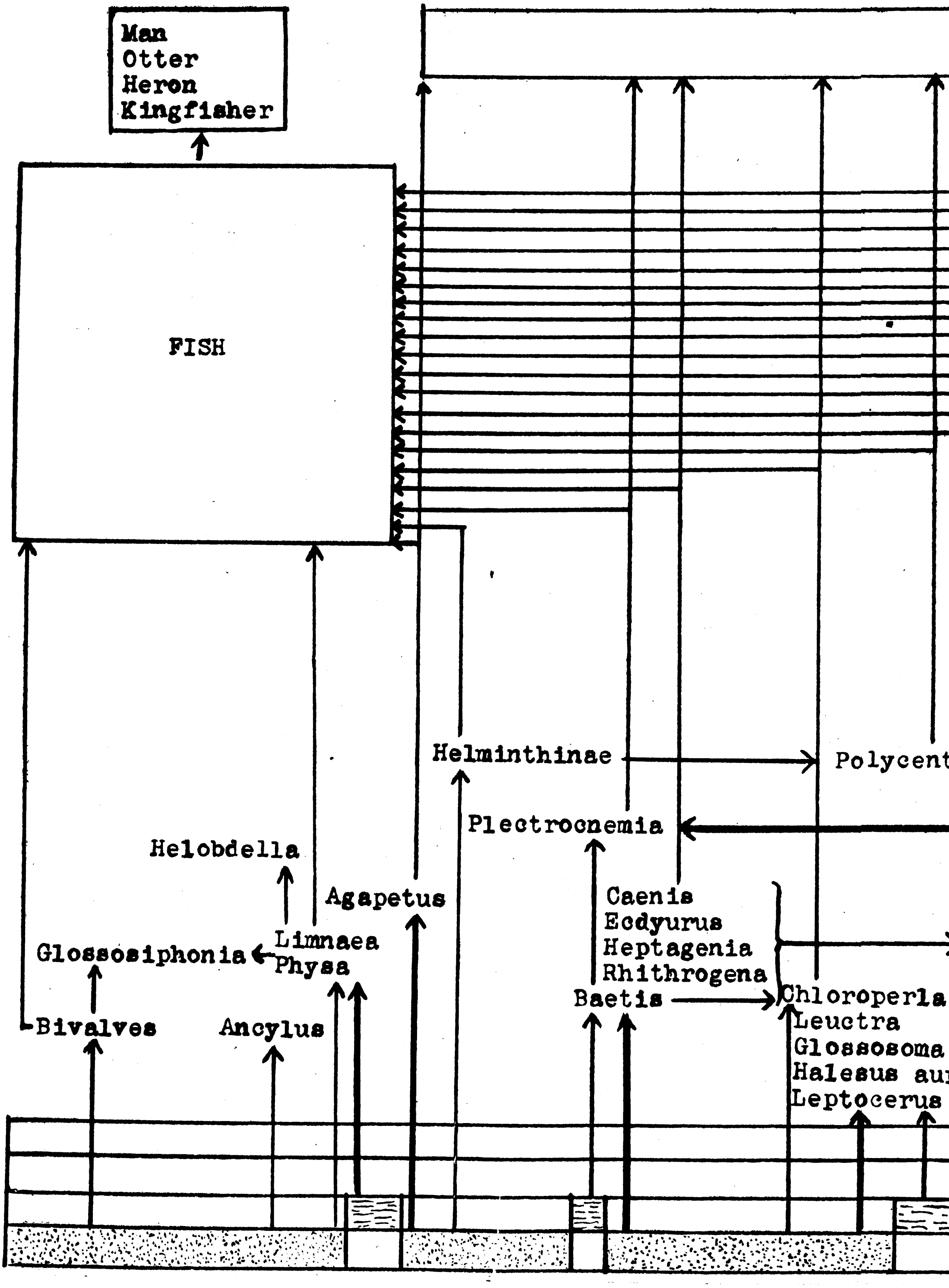
Only two genera, *Ephemerella* and *Crunoecia*, make any considerable use of moss as an article of diet. When found in situations which do not carry moss their guts contain algae, but in these places the organisms are few in number: the bulk of them derive their food material from the moss. The occurrence of moss in the gut of *Hydropsyche instabilis* may be due to the fact that *Ephemerella ignita* has been eaten. The specimens examined had been taken from moss which also contained *Ephemerella*. The very young stages of the carnivores mentioned feed on vegetable matter, especially upon the Algae.

The food chains (Table VII) express very plainly the relations of the organisms to each other and to the fundamental foods. It is clear that the conditions favouring the growth of unicellular and filamentous algae, i.e. stable substratum, will also aid in the development of a considerable insect fauna.

It may be noted here that there is a quite definite association between the leech, *Glossosiphonia complanata*, and *Limnaea peregra*, *Physa fontinalis* and the bivalves, especially *Pisidium* sp. It shows well when the analyses of samples from phanerogams are tabulated. *Herpobdella atomaria* is much more closely associated with Tubificidae and Chironomidae and may occur in numbers in the absence of Mollusca. We have not found this leech to contain any recognisable molluscan fragments. It may exist upon other organisms; from a chalk stream a number were taken which had been feeding entirely on Cladocera.

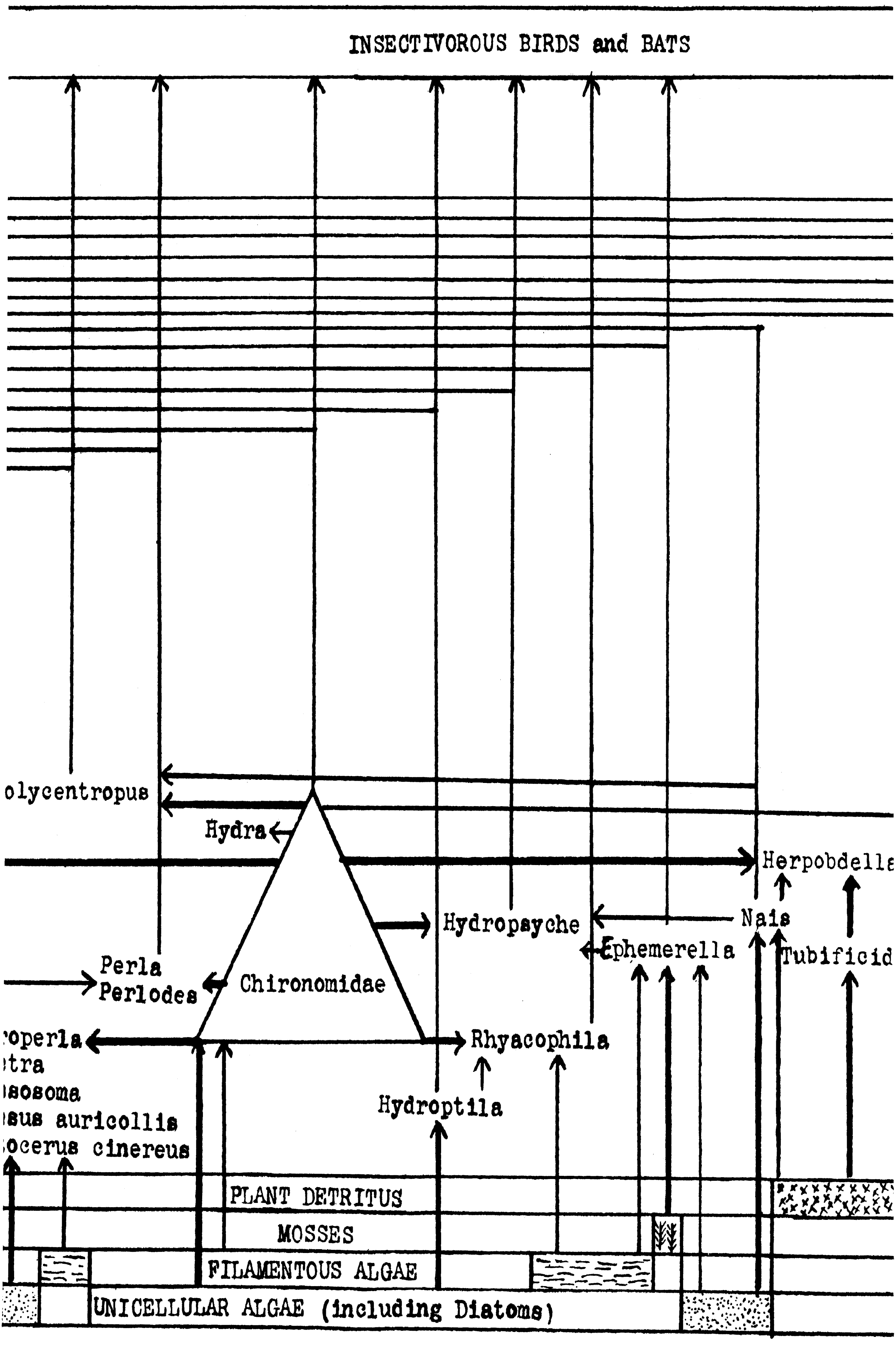
Elton (**12**, pp. 63–8) uses the term "niche' to signify the place of an organism "in its biotic environment, its relations to food and enemies." In the present case certain of the organisms fill the very important niche of converting vegetable matter into animal food. These are, especially, Chironomidae, *Agapetus*, *Ephemerella*, Naididae. They are the "cattle" which graze on the extensive algal pastures. The first, third and fourth then serve to nourish a considerable variety of other invertebrates which finally fall to the needs of the carnivorous vertebrates of the neighbourhood.

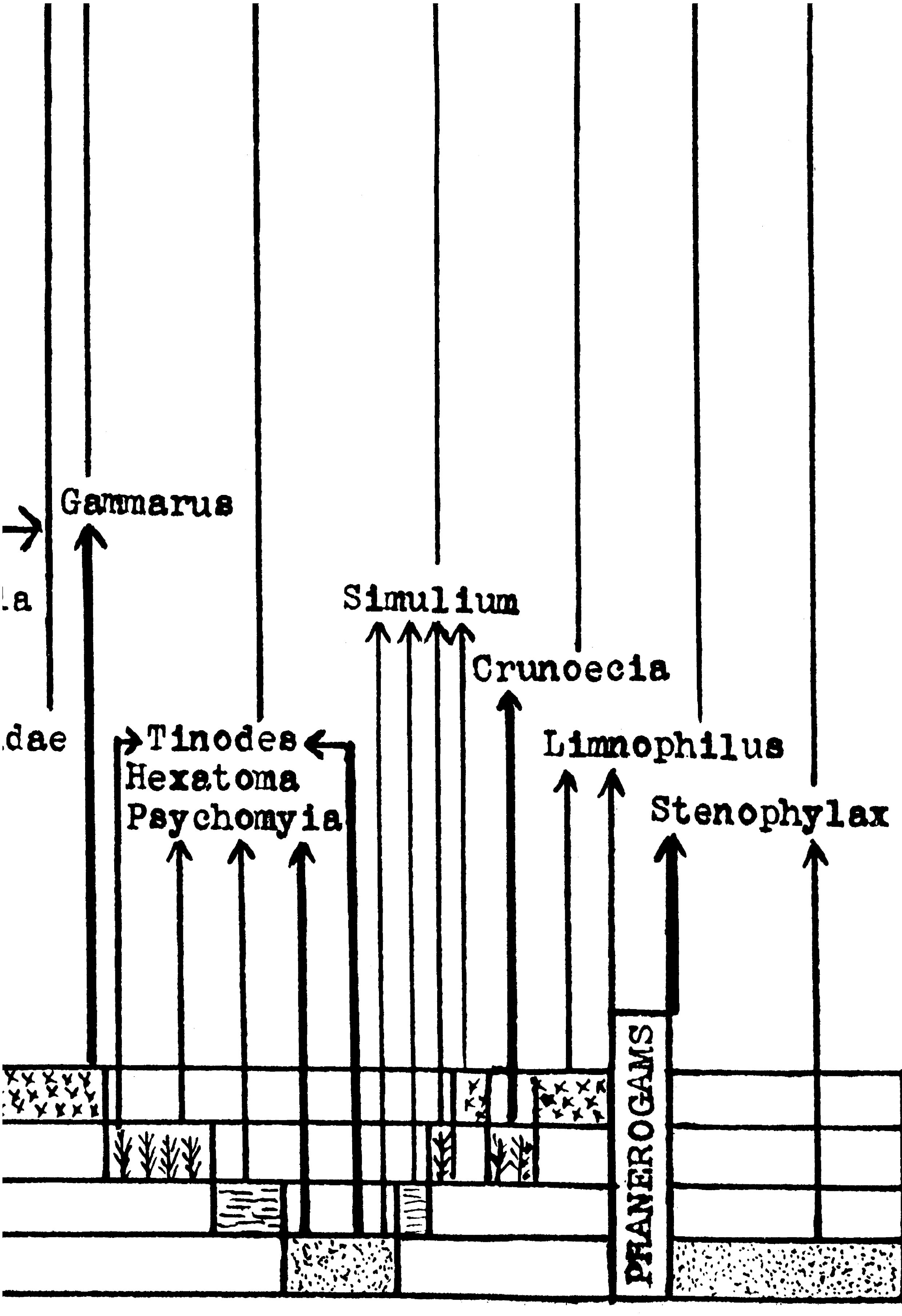
An examination of the table of gut contents shows that, in the first six types of habitat, the proportion of organisms feeding mainly upon algae is from 75 to 90 per cent. of the total, and that among *Potamogeton* it is about 67 per cent.



Man
Otter
Heron
Kingfisher
FISH
Helminthinae
Polycent
Plectrocnemia
Helobdella
Agapetus
Caenis
Ecdyurus
Heptagenia
Rhithrogena
Limnaea
Physa
Glossosiphonia
Baetis
Chloroperla
Leuctra
Glossosoma
Halesus au
Leptocerus
Bivalves
Ancylus

Table VII. *Diagram showing the general food relations.*





Gammarus
.a
dae
Tinodes
Hexatoma
Psychomyia
Simulium
Crunoecia
Limnophilus
Stenophylax
PHANEROGAMS

AN ESTIMATION OF THE VALUE OF THE QUANTITATIVE DETERMINATION OF FLUVIATILE BIONOMICS.

It may be argued that the value of the results presented is materially reduced owing to errors which arise during and owing to the manner of taking samples. While it is agreed that a certain amount of loss does take place it is so slight as to be negligible. In fact the figures obtained may be regarded, for practical purposes, as presenting an approximately correct statement of numbers.

The method of attack has afforded a very useful means of studying the fluviatile conditions. It has shown strikingly the variations in species and numbers which can be correlated with changes in the physical character of the stream and has allowed those variations to be numerically presented. It has enabled the discovery of the important organisms in the economy of the stream and has presented facts which bear upon the problem of maintaining or increasing the population for the purpose of feeding fish.

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