THE DISTRIBUTION OF BENTHIC INVERTEBRATES ON SUBSTRATA IN FAST-FLOWING STREAMS

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INTRODUCTION

The highland and moorland reaches of rivers and streams can usually be divided into riffles, with shallow fast-flowing water, and pools, with deeper slow-flowing water. The invertebrate communities living in such distinct habitats are very different and the biological reasons for this have received considerable attention. Only a limited amount of work, however, has been carried out on the spatial distributions of populations of invertebrates and their relationships to environmental factors within these, or any other relatively more homogeneous stream habitat. Scott (1958) and Ambühl (1959) have related the distributions of several species to current speeds, and Egglishaw (1964) showed that, even in what was apparently a fairly uniform stretch of riffle, the quantities of several benthic species at different sites varied greatly and were correlated with the distribution of disintegrating plant detritus. Several studies of the effects of certain factors on the distribution of selected species in experimental conditions have, however, been carried out (see Macan 1963).

The sampling difficulties imposed by the non-random distribution of most animals apply to stream riffles in the same way as they do to other habitats. The present paper sets out to explore the spatial distributions of benthic organisms (of length greater than 0·5 mm) and their relationships to certain environmental factors in riffles, as riffles usually make up by far the larger proportion of the areas of fast-flowing streams. Within riffles the greatest weight of invertebrates is found among and under stones, and so most of the observations were made on that habitat. Other habitats in riffles in which invertebrates are found, and on which observations were made, include the algal coverings on the upper surface of stones and clumps of moss.

METHODS

To examine the distribution of benthic organisms among and under stones (i.e. excluding those in algae and moss) in a riffle stretch, forty-seven samples were taken randomly in the Shelligan Burn, Perthshire (Nat. Grid Ref. 37/947293). In the stretch sampled the physical characteristics of current speed, water depth and structure of the substratum changed quickly over short distances. From another stream, the River Almond, fifty samples were taken systematically from a riffle (Nat. Grid Ref. 37/903298) where the changes in physical characteristics were more gradual. It was hoped that by comparing samples taken along some physical gradients in this latter stream the effects of certain environmental factors could be separated more easily than would be possible from the samples from the Shelligan Burn.

Each sample comprised the bottom fauna and plant material collected with a net (height 24 cm, width 24 cm, length 60 cm, 24 meshes/cm, mesh size 200 μ), used in a Surber-type manner (see Welch 1948), from a delineated area (0·093 m^2) of substratum, the sampling site. Animals living on the upper surface of the stones were not included in the sample, except for some which may have been washed off into the net as the larger stones were lifted from the water. The riffle in the Shelligan Burn included small areas which, because of their slow current speed or because their depth was greater than the height of the net being used, were not suitable for sampling and were therefore excluded from the area randomly sampled. These areas totalled less than 10% of the whole riffle. From the River Almond five rows of ten samples 75 cm apart were taken systematically across the width of the stream, except that a central column of about 2 m width was not sampled because it was too deep. At each sampling site on both streams the longest length of the largest stone and the depth of water were measured. The samples were taken in spring so as to obtain insect larvae at their largest and before the adults emerged.

The plant material in each sample was separated into four categories (1) woody pieces of stem and bark, (2) pieces of moss, (3) large particles of non-woody allochthonous material, chiefly deciduous leaves, over 0·05 g dry weight each, and (4) fine particulate matter, chiefly allochthonous but small pieces of moss and algae were sometimes present. Categories (3) and (4) together comprise the 'plant detritus'.

All weight measurements given are those of the material after 24 h at 100° C.

Details of the stretches of the two streams examined and the sampling sites are given in Table 1. Further details of the streams are given in Egglishaw (1967) and Egglishaw & Mackay (1967). The straight-line distance between the two stretches is 4·5 km.

Table 1. *Details of the two streams and the Surber sampling sites*

	Shelligan	Almond
Width (m)	4	12
Altitude (m)	185	204
Surface geology	Sandstone	Quartzite
Surroundings	Agricultural land; cattle pasture	Heather moor
Sampling sites		
Size of largest stone (cm), mean and s.d.	$17{\cdot}0 \pm 4{\cdot}55$	$12{\cdot}2 \pm 3{\cdot}48$
Depth of water (cm), mean and s.d.	$13{\cdot}7 \pm 3{\cdot}81$	$14{\cdot}7 \pm 4{\cdot}88$
Fine particles of plant detritus (g) mean per sample	0·504	0·580
Large particles (>0·05 g) of plant detritus, total numbers	65	1

The frequency distributions of the amounts of plant detritus in the samples from the Shelligan Burn are shown in Fig. 1. This figure also includes histograms of the amounts of plant detritus taken from the Shelligan Burn on a previous occasion, and also from another stream (Allt dos Mhuicarain, Ross-shire, Nat. Grid Ref. 28/210606) when larger numbers of samples were taken.

The longer right-hand tail on the figure for Allt dos Mhuicarain is probably due to the plant detritus in this stream being chiefly coarse grasses which entangle and are more easily retained at a site. The difference in the number of large particles, which were chiefly deciduous leaves or pieces of them, found in the Shelligan Burn and the River Almond (Table 1) reflects the differences in the surrounding vegetation of the two streams.

Regressions were calculated by the method of least squares for dry weight of fine particulate matter on the length of the longest stone at the sampling sites and a 't' test of the significance of the regression coefficients calculated. In the Shelligan Burn the fine particulate matter at a site increased by 0·023 g ($t = 7{\cdot}68$, $P < 0{\cdot}001$) and in the River

Almond it increased by 0·051 g ($t = 3{\cdot}88$, $P<0{\cdot}001$) for each increase of 1 cm in stone length. These regression values are presumably dependent on the flow conditions in the stream before the samples were taken. There was no discernible relationship between the depth of water in which samples were taken and the amount of plant detritus present.

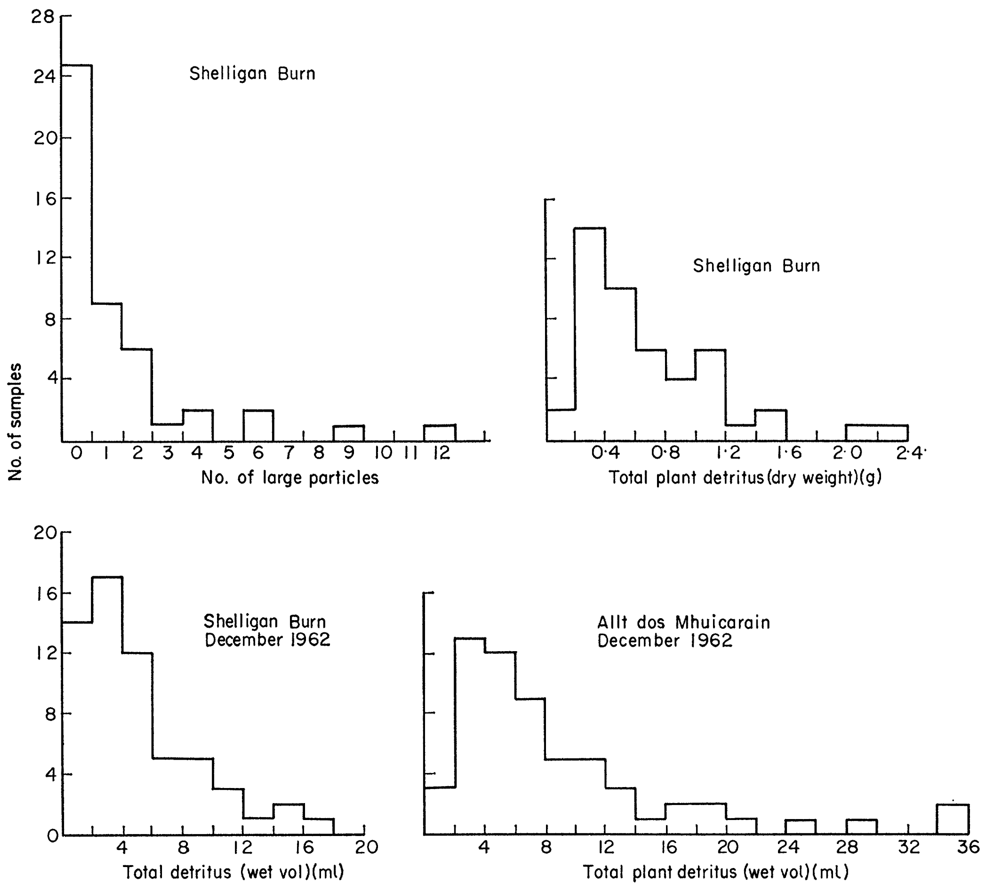

FIG. 1. Frequency distribution diagrams of the amounts of plant detritus in samples from riffles.

Samples of animals present in moss growing on large stones in riffles were collected by lifting the stones from the water and cutting the moss from about 100 cm^2 of stone surface. The depth from the upper surface of the stones to the water surface was usually 12–16 cm. Six moss samples were taken from each of four streams, the Shelligan Burn, Allt Menach (Nat. Grid Ref. 37/097595), the Fender Burn (Nat. Grid Ref. 27/895673) and Allt dos Mhuicarain between 25 February and 10 March 1964. Surber-type samples of bottom fauna with plant detritus from moss-free sites were also taken, in order to compare the composition of the two communities.

To investigate the distribution of bottom fauna on the upper surface of stones in riffles, the stones enclosed by a horizontal square frame with 30·5 cm sides were lifted into a bucket and scrubbed with a small brush to obtain the algal covering. Ten such samples were taken from the River Almond, the Shelligan Burn and the Fender Burn.

At each sampling site the lengths of the enclosed stones were measured. The algae were dried and weighed as it was expected that their amounts would be a main factor determining the quantities of bottom fauna present. The samples were taken in August at which time the larger stones have an obvious covering of green algae.

BOTTOM FAUNA AMONG STONES IN RIFFLES

Frequency distributions of the organisms

The frequency distributions of the numbers of the commonest species in the samples from the riffles in the Shelligan Burn and the River Almond were generally clearly non-random. Even the numbers in each column of five samples taken from the same distance from the banks of the River Almond, and which might have been regarded as more alike, did not follow a Poisson distribution. In most cases the variances were significantly high, and the standard deviations increased with increase in the means. A logarithmic transformation was found suitable for turning the skewed distributions into reasonably normal ones and for stabilizing the variances so that they no longer depended on the means. The means and variances on the log scale are given in Table 2. There were

Table 2. *The means and standard deviations on the logarithmic scale of the twelve commonest species and* Dinocras cephalotes *and* Caenis rivulorum *in the samples from both streams (the species are arranged in decreasing order of variance in the Shelligan Burn)*

	Shelligan			Almond		
	Mean	Variance	s.d.	Mean	Variance	s.d.
Simulium sp.	0·832	0·4061	0·637	0·411	0·1547	0·393
**Latelmis volkmari* Panzer l				0·997	0·3225	0·568
Hydroptila sp.				0·664	0·3058	0·553
Baetis rhodani (Pictet)	1·995	0·1407	0·375	0·961	0·0590	0·243
**Elmis maugei* Bedel l	0·769	0·1358	0·369			
Rhyacophila dorsalis (Curtis)	0·696	0·1201	0·347			
Esolus parallelopipedus Müller a	0·737	0·1040	0·322	0·738	0·1322	0·364
E. parallelopipedus l	1·177	0·1030	0·321	1·669	0·2165	0·465
Dinocras cephalotes (Curtis)	0·390	0·0999	0·316	0·390	0·1109	0·333
Caenis rivulorum Eaton	0·632	0·0886	0·298	0·447	0·0883	0·297
Amphinemura sulcicollis (Stephens)	1·172	0·0881	0·297	1·350	0·0688	0·262
Dicranota sp.				0·722	0·0861	0·293
Rhithrogena semicolorata (Curtis)	1·264	0·0777	0·279	1·046	0·0559	0·236
Leuctra inermis Kempny	1·883	0·0591	0·243	1·465	0·0400	0·200
Isoperla grammatica (Poda)	1·281	0·0573	0·239	0·748	0·0442	0·210
Chloroperla torrentium (Pictet)	1·231	0·0532	0·231	0·926	0·0580	0·241

Abbreviations. l, larvae and a, adults used for insects with aquatic adults.
* *Elmis* (*Helmis*) *maugei* = *E. aenea* (Müller), *Latelmis volkmari* = *Limnius volkmari*.

significant differences among the variances of the observations from both the Shelligan Burn and the River Almond. The species in Table 2 are in order of decreasing variance of the observations from the Shelligan Burn. The order by variance in the River Almond was significantly correlated with the order in the Shelligan Burn, the value of the Spearman rank correlation coefficient (r_s) being 0·761 ($P<0{\cdot}01$).

Distribution of organisms across the width of stream

The distributions of several species across the width of the River Almond, except for the central 2 m which was not sampled, are shown in Fig. 2. The figure also includes the size of the largest stones, the depth of water and the weight of fine particles of plant detritus. The height of each column is the mean of five samples.

The second line of diagrams in Fig. 2 shows that there are benthic organisms (*Isoperla grammatica*, *Rhithrogena semicolorata* and *Leuctra inermis*) which are fairly evenly distributed across the width of the stream. These are followed by four species whose

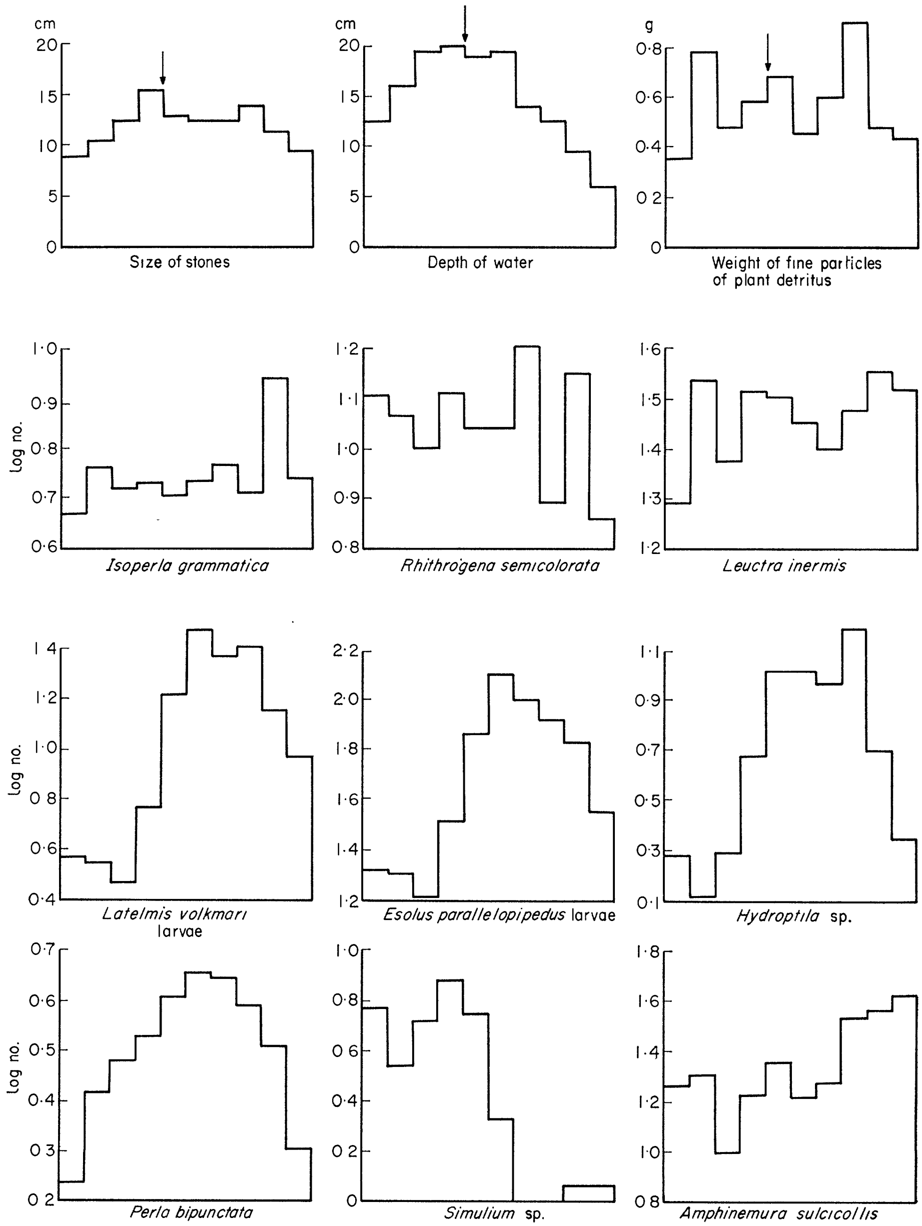

FIG. 2. The size of three environmental factors and the population density of nine species of benthic invertebrates across the width of the River Almond. The height of each column is the mean of five samples, the transformation log $(x+1)$ being used for the invertebrates. The arrows indicate the position of the 2 m gap that was not sampled.

populations are clearly more dense in the centre of the stream. Finally there are two species whose populations show opposite trends (*Simulium* sp. decreasing and *Amphinemura sulcicollis* increasing) towards one bank of the stream.

Association of the fauna with environmental factors

The association of the commonest species of bottom fauna with the amount of fine plant detritus, the size of the largest stone and the water depth at sites were analysed by the method of multiple regression (Mather 1951) and the results are given in Table 3 (Shelligan Burn) and Table 4 (River Almond). Only separable species with a mean density per sample of at least 2·9 were included in the analysis, larvae and adults of the same species being considered separately. This gave fourteen groups for the Shelligan Burn and thirteen for the River Almond with nine common to both streams.

Table 3. *The estimated partial regressions of the numbers of certain benthic organisms occurring among stones in a riffle in the Shelligan Burn on the amount of detritus, the size of the largest stone and the depth of water at the sampling sites*

	Mean	Animals/ detritus b_1	Animals/ stones b_2	Animals/ depths b_3
PLECOPTERA				
Leuctra inermis	87·1	107·58***	9·65	−9·84
Isoperla grammatica	20·8	26·35***	−3·27	0·04
Chloroperla torrentium	18·3	4·93	1·42	−4·26
Amphinemura sulcicollis	17·3	25·82***	−0·43	−3·13
EPHEMEROPTERA				
Baetis rhodani	130·0	230·44***	−5·97	−11·29
Rhithrogena semicolorata	20·7	16·63**	−1·93	−0·91
Caenis rivulorum	4·3	4·45**	0·79	−0·33
TRICHOPTERA				
Rhyacophila dorsalis	5·4	7·42***	1·06*	0·18
COLEOPTERA				
Esolus parallelopipedus l	18·5	−3·09	3·07	−2·99
E. parallelopipedus a	6·2	9·84**	0·93	−0·71
Elmis maugei l	7·6	20·96***	−0·22	−0·26
DIPTERA				
Simulium sp.	16·6	30·67***	0·49	4·73**
Clinocera sp.	8·9	8·04***	0·45	−1·28
PLATYHELMINTHES				
Crenobia alpina (Dana)	3·4	6·44**	1·58**	−0·73

* P = 0·05–0·02; ** P = 0·02–0·001; *** P <0·001.

The units are: 1 g dry weight of detritus, 5 cm stone length, 5 cm water depth.

It is clear that of the three environmental factors examined the amount of plant detritus is the factor with which most benthic organisms were associated. The numbers of twelve groups in the Shelligan Burn and six in the River Almond increased with increase in the detritus. Using trays containing plant detritus set into the bed of the Shelligan Burn, Egglishaw (1964) showed that for *Leuctra inermis*, *Amphinemura sulcicollis*, *Isoperla grammatica* and *Baetis rhodani* the plant detritus was a causal factor in determining their distribution. Tables 3 and 4 show that, with one exception, these species were significantly associated with the plant detritus at sites, but not with the size of the stones or the water depth. The anomalous result for *Isoperla grammatica* in the River Almond may be due to the low density of the population when the samples were taken. In the Shelligan Burn five other species, *Rhithrogena semicolorata*, *Caenis rivulorum*, *Esolus parallelopipedus* adults, *Elmis maugei* larvae and *Clinocera* sp., increased significantly with increase in plant detritus but showed no significant association with stone size or water depth.

The numbers of two species in the Shelligan Burn and five in the River Almond increased with increase in the size of the largest stone at the sampling sites. Four of these species increased with increase in the amount of plant detritus also.

Only *Simulium* sp. in the Shelligan Burn and *Simulium* sp. and *Rhithrogena semicolorata* in the River Almond increased in numbers significantly with increase in the depth of water. It was presumably the related increase in current speed in the deeper water of the riffles that determined the population density of the *Simulium* sp. The latter are filter-feeders and are known to occur most densely at sites where the current is fast (Ambühl 1959; Maitland & Penney 1967), presumably because most food passes such sites. *Rhithrogena semicolorata* is known to migrate into deeper water prior to emergence (Harker 1953) and this behaviour may account for its association with water depth in the River Almond. The samples from the River Almond were taken nearer to the emergence time of this species than were those from the Shelligan Burn.

Table 4. *The estimated partial regressions of the numbers of certain benthic organisms occurring among stones in a riffle in the River Almond on the amount of detritus, the size of the largest stone and the depth of water at the sampling sites*

	Mean	Animals/ detritus b_1	Animals/ stones b_2	Animals/ depths b_3
PLECOPTERA				
Leuctra inermis	30·5	24·02***	2·42	0·83
Isoperla grammatica	5·2	−0·72	0·49	−0·69
Chloroperla torrentium	8·7	−3·55	−0·77	2·76
Amphinemura sulcicollis	24·6	21·74*	1·10	−7·47
Perla bipunctata	2·9	2·64**	1·28**	0·35
EPHEMEROPTERA				
Baetis rhodani	9·4	3·91*	0·47	2·60
Rhithrogena semicolorata	11·4	−3·81	−0·55	2·09**
TRICHOPTERA				
Hydroptila sp.	8·0	8·08**	11·01***	0·43
COLEOPTERA				
Esolus parallelopipedus l	70·1	18·36	28·69*	−6·50
E. parallelopipedus a	6·8	−1·21	5·18**	−0·18
Latelmis volkmari l	16·3	2·71	10·95***	0·18
DIPTERA				
Simulium sp.	2·9	−1·52	0·59	1·97***
Dicranota sp.	5·4	4·13**	0·08	−1·24**

* P = 0·05–0·02; ** P = 0·02–0·001; *** P <0·001.

The units used are given in Table 3.

Of the twenty-nine significant associations between the different species and the three environmental factors measured only one was negative. In the River Almond the numbers of *Dicranota* sp. decreased with increase in the water depth. It is probably the faster-flowing water in the deeper parts of the riffle which makes the environment unsuitable for these large, cylindrical larvae which are devoid of means of attachment.

Chloroperla torrentium is the only species that is not significantly associated with any of the factors measured in both streams. This species has been shown to be sometimes randomly distributed in riffles (Egglishaw 1964) and to occur in equal densities in the riffles and pools of the Shelligan Burn (Egglishaw & Mackay 1967).

It is possible to give some reasonable biological explanation for most of the significant relationships between the benthic organisms and the factors examined, and as previously mentioned, experimental work has shown that plant detritus is a causal factor in the distribution of several benthic species (Egglishaw 1964). There are, however, one or two associations which appear anomalous and difficult to interpret. The numbers of *Esolus parallelopipedus* larvae are related to stone size in the River Almond, but not in the Shelligan Burn. The numbers of the adults of this species are again related to stone size in the River Almond, but to plant detritus in the Shelligan Burn. The association of *Simulium* sp. with plant detritus in the Shelligan Burn is also unexpected. It is, of course, possible that the anomalies are caused by deficiences in the sampling procedure or in the measurement of the characteristics of a site or, as is more likely, to the dependence of the organism on another unmeasured, but interrelated, factor.

In the Shelligan Burn there were only three significant regressions of organisms on stone-size or water depth, whereas in the River Almond there were eight significant regressions on these variables. This is presumably due to the relatively simpler set of environmental factors (e.g. less turbulent flow) operating within each sampling site in the latter stream.

Changes in the structure of the bottom fauna community

Since different species of bottom fauna have different quantitative relationships with plant detritus, the structure of the community at a site in a riffle depends to a large extent on the amount of detritus present there. In Fig. 3 the regressions of the numbers of several species of bottom fauna on the amounts of fine particles of plant detritus have been drawn from calculated values. The regressions on plant detritus have been calculated ignoring the partial regressions on stone size and water depth. All of the regressions given in the figure are, of course, significant. It will be seen that in Table 4, larvae of *Esolus parallelopipedus* in the River Almond are associated with stone size and not plant detritus, but that in Fig. 3 their numbers increase with increase in plant detritus.

Fig. 3 shows some of the changes that occur in the structure of the community with change in the amount of plant detritus present. The species included in the figure comprise 77% of the total individuals collected from the Shelligan Burn and 73% of those from the River Almond. Of course, for categories including more than one species (i.e. Chironomidae, possibly *Hydroptila* spp.) some of the individual species may not behave in the same way as the category does as a whole. For each increase of 0·1 g of fine particles of plant detritus there was an increase of seventy-five organisms (weighing 0·012 g) in the Shelligan Burn and an increase of thirty-seven organisms in the River Almond.

With increase in plant detritus there was also an increase in the variety of bottom fauna in the samples. In the Shelligan Burn the eight samples with the largest amounts of finer particles of plant detritus (0·702–1·622 g) contained representatives of between twenty-two and thirty-two taxonomic categories, out of a total of forty-eight distinguished from all of the samples, whereas the eight samples with the smallest amounts of plant detritus (0·117–0·239 g) contained representatives of between sixteen and twenty-three categories. Of the more common animals *Brachyptera risi* (Morton), *Protonemura meyeri* (Pictet), *Perla bipunctata* and *Hydraena gracilis* Germar were noticeably absent from these latter samples. In the River Almond the eight samples with the largest amounts of finer particles of detritus (0·971–1·656 g) contained representatives of between twenty and twenty-nine taxonomic categories, whereas the eight samples with the smallest amounts (0·159–0·302 g) contained representatives of between fourteen and twenty-one categories.

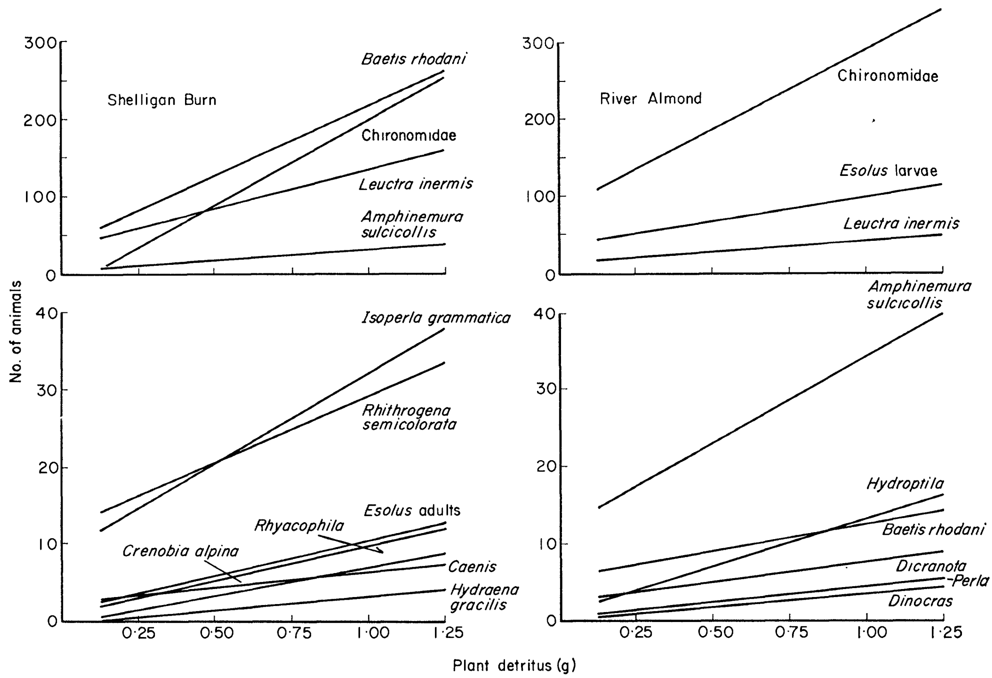

FIG. 3. The regressions of some of the chief species in the riffles of the two streams to show changes in the composition of the benthic community with change in the amount of finer particles of plant detritus.

BOTTOM FAUNA IN MOSS

The dry weights of the twenty-four samples of moss ranged from 1·116 g to 7·183 g with half between 2·0 g and 3·8 g. The mean numbers of the commonest species and the mean dry weights of invertebrates per 1 g of moss in the six samples from each of the four streams examined are given in Table 5. It can be seen from the relatively small standard deviations that, within the clumps of moss the animals were less aggregated than they were in the under-stone habitat. Within each stream the total weights of animals per 1 g of moss did not vary much.

The composition of the fauna occurring in the moss samples and the fauna collected with plant detritus in the Surber-type samples taken on the same day from each stream is given in Table 6. *Amphinemura sulcicollis* was much the commonest species in moss in all four streams. Some species, such as *Chloroperla torrentium*, *Rhithrogena semicolorata* and also *Ecdyonurus venosus* (Fabricius), which made up a significant part of the community collected by the Surber sampler were rare or absent from the community living in moss. Conversely there were some species, such as *Protonemura meyeri*, *Limnius tuberculatus* adults, *Hemerodromia sp.* and *Pericoma* sp., which comprised a much greater part of the community living in moss than that collected in the Surber samples. Some similar observations have been made by Hynes (1961), who has recorded the absence of *Chloroperla tripunctata* and *Ecdyonurus venosus* from moss, and the larger contribution *Protonemura meyeri* makes to the invertebrate community living in moss, compared with the community living on the stony bed of a Welsh mountain stream.

Table 5. *The numbers of the commonest species, and the total dry weight of invertebrates per* 1 *g* (*dry*) *of moss in four streams* (*the figures are the means and standard deviations of six samples*)

	Shelligan	Dos Mhuicarain	Menach	Fender
Amphinemura sulcicollis	20·2 ± 2·86	23·3 ± 6·96	33·5 ± 8·43	15·3 ± 4·68
Leuctra inermis	8·3 ± 1·97	–	5·3 ± 2·25	2·8 ± 1·17
Protonemura meyeri	6·7 ± 1·63	2·5 ± 0·55	5·8 ± 2·14	–
Isoperla grammatica	3·8 ± 1·72	–	10·3 ± 2·07	11·0 ± 2·83
Baetis rhodani	3·3 ± 1·37	–	9·8 ± 4·17	4·7 ± 1·63
Limnius tuberculatus Müller a	–	–	5·3 ± 4·37	–
Total weight (dry) (g) of organisms	0·012 ± 0·0022	0·012 ± 0·0026	0·017 ± 0·0032	0·016 ± 0·0024

Table 6. *The percentage composition of the fauna collected with* (*A*) *plant detritus among stones and* (*B*) *moss*

	Shelligan		Dos Mhuicarain		Menach		Fender	
	A	B	A	B	A	B	A	B
Amphinemura sulcicollis	20·5	21·1	37·0	46·6	8·3	26·0	9·5	21·1
Leuctra inermis	15·6	8·3	1·2	0·2	9·0	4·2	21·0	3·6
Isoperla grammatica	7·7	3·4	4·6	3·1	2·6	8·0	2·6	16·0
Protonemura meyeri	1·4	7·1	0·6	5·1	0·6	3·7	0·1	0·9
Chloroperla torrentium	2·7	0·0	4·6	1·6	1·6	0·0	0·9	0·0
Baetis rhodani	19·4	2·4	0·0	0·0	29·8	7·9	25·3	6·5
Rhithrogena semicolorata	10·4	0·0	0·2	0·0	10·6	0·0	6·4	0·0
Hydropsyche sp.	0·5	2·7	0·3	0·0	1·0	2·4	0·2	0·5
Limnius tuberculatus a	0·0	0·8	0·0	0·0	0·2	4·8	0·0	4·3
Chironomidae (several species)	6·8	41·4	31·8	35·5	2·9	32·9	7·5	26·3
Pericoma sp.	0·0	0·5	0·0	0·0	0·0	1·2	0·0	0·9
Simulium sp.	3·6	5·3	5·2	2·3	8·3	1·3	13·9	0·3
Hemerodromia sp.	0·0	1·5	0·0	0·0	0·1	2·5	0·0	1·4
Total	88·6	94·5	85·5	94·4	75·0	94·9	87·4	81·3

As well as differences in the species composition of moss samples and Surber samples there were noticeable differences in the sizes of some of the species that were fairly common in both types of sample. Fig. 4 shows the length frequency distributions of four species in the samples from the Shelligan Burn. There are obvious differences in the diagrams for *Leuctra inermis*, *Baetis rhodani* and particularly *Isoperla grammatica*. In each case there was a higher proportion of smaller animals in moss than there was among the stones of the riffle. In contrast, the two length frequency diagrams for *Amphinemura sulcicollis* are very similar. Hynes (1961) found that all stages of *Isoperla grammatica* occurred in moss and in the stony bed of the stream he studied, although there was a tendency for 2 mm and 3 mm size groups to congregate in the moss. The data from the Shelligan Burn show that the bulk of the *I. grammatica* population in moss is also of the 2 mm and 3 mm size groups.

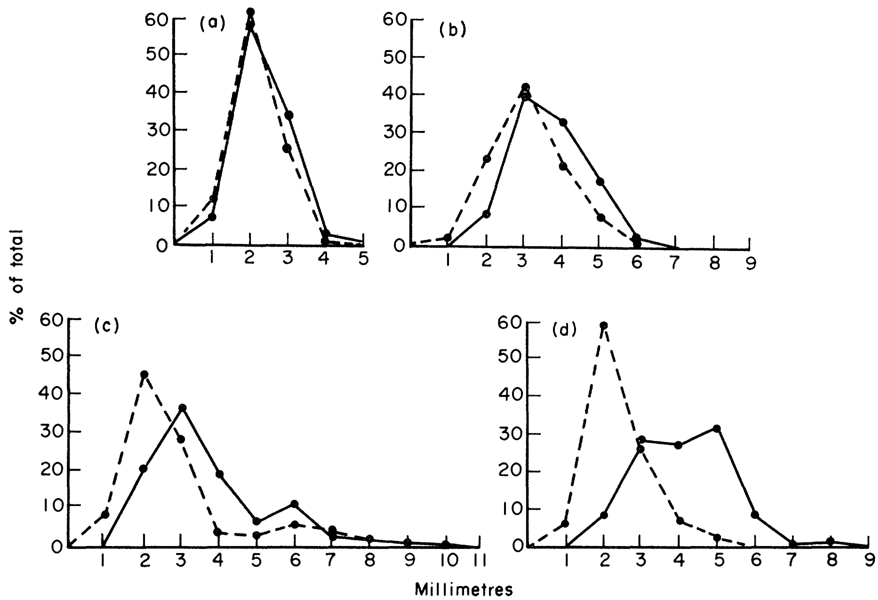

FIG. 4. The length–frequency distributions of four of the commonest species occurring among stones at moss-free sites (————) and in clumps of moss (– – – –). (a) *Amphinemura sulcicollis,* (b) *Leuctra inermis,* (c) *Baetis rhodani* and (d) *Isoperla grammatica.*

BOTTOM FAUNA ON THE UPPER SURFACE OF STONES

The bottom fauna collected from the upper surface of stones in riffles was separated into fifty-one taxonomic categories of which there were representatives of between twelve and twenty in the samples from the River Almond, between nineteen and twenty-six in the samples from the Shelligan Burn, and between eleven and twenty-three in those from the Fender Burn. Unlike samples of bottom fauna collected with plant detritus from under and among stones, the samples from the upper surface of stones were made up largely of only one or two groups. The most common organisms in the River Almond were several species of Chironomidae and a species of *Hydroptila* which together comprised between 90% and 96% of the animals in each sample. Chironomidae comprised between 75% and 86% of the upper stone surface fauna in the Shelligan Burn, and between 73% and 86% of the upper stone surface fauna in the Fender Burn. The next commonest taxa were *Clinocera* sp. (1·1% of the total fauna) and *Esolus parallelopipedus* larvae (0·9%) in the River Almond, *Nais elinguis* Müller, (5·7%), *Clinocera* sp. (2·6%), *Baetis* sp. (1·7%) and *Elmis maugei* larvae (1·5%) in the Shelligan Burn, and *Baetis* sp. (8·2%), *Clinocera* sp. (1·9%), *Nais elinguis* (1·9%) and *Elmis maugei* larvae (1·9%) in the Fender Burn.

The frequency distributions of the amounts of bottom fauna in the samples from the upper surface of stones were less skewed than the frequency distributions of the amounts in the samples collected with detritus from under stones. The values of the mean numbers and mean total weights of organisms per sample were only slightly higher than the median values for all three streams (Table 7).

The quantitative relationships between the bottom fauna and the algae and the size of stones at sampling sites are given in Table 8. The table includes all taxa that had a mean value of thirty or more per sample. The size of the stones at a site was expressed by summing the squares of the lengths of stones greater than 15 cm. The amounts of algae in the three streams differed greatly, the mean amounts per sample being 5·72 g for the River Almond, 0·598 g for the Shelligan Burn and 0·181 g for the Fender Burn. These amounts include small quantities of silt which was not separated from the algae.

Table 7. *The mean and median numbers and total weights of organisms in samples taken from the upper surface of stones in riffles*

	Almond		Shelligan		Fender	
	No.	Weight (g)	No.	Weight (g)	No.	Weight (g)
Median values	715	0·035	1766	0·062	489	0·018
Mean values	723	0·037	1819	0·065	522	0·019

Table 8. *The estimated partial regressions of the amounts of bottom fauna from the upper surface of stones in riffles on the amounts of algae present and the size of the stones*

	Mean	Animals/algae b_1	Animals/stones b_2
RIVER ALMOND			
Chironomidae	471	5·4	34·4
Hydroptila sp.	204	21·9	**33·0**
Weight of bottom fauna (g)	0·037	0·00042	**0·00445**
SHELLIGAN BURN			
Chironomidae	1507	376·0	40·6
Nais elinguis	103	−89·9	10·2
Clinocera sp.	46	−54·9	6·1
Baetis sp.	31	11·2	3·4
Weight of bottom fauna (g)	0·065	**0·07040**	0·00236
FENDER BURN			
Chironomidae	424	152·59	14·2
Baetis sp.	43	14·06	4·1
Weight of bottom fauna (g)	0·019	−0·00101	−0·00048

Algae are measured in 1 g units, stone size in units of 100 cm. The three significant regressions are given in bold type.

It is surprising that, of the eleven calculated partial regressions of the quantities of benthic organisms on the amounts of algae at sampling sites, only the total weights of bottom fauna in the Shelligan Burn are shown to be significantly associated with the amounts of algae. It might have been expected that some species would have fed directly on the algae and have occurred in greater numbers where the largest quantities of it occurred. Of the eleven partial regressions of the quantities of bottom fauna on the size of the stones at a site only those of the total weight of bottom fauna and the number of *Hydroptila* sp. in the River Almond are significant. A greater number of samples might have demonstrated significant associations between a few more taxa and either or both algal abundance or stone size but it is clear that the majority are not associated with either factor.

DISCUSSION

The results given in the present paper are, to some extent, dependent on the sampling techniques used and, because it is necessary, when using Surber-type techniques to sample in water that is not deeper than the height of the net, there is an artificial limit to the 'habitat' examined. The results are based on the assumption that the collecting techniques were equally efficient at all sites sampled. It is believed that the long, fine-mesh net used on the Surber-type sampler caught all the bottom fauna and plant detritus disturbed.

The chief sources of plant food available for the invertebrates in fast-flowing streams are plant detritus trapped among stones, clumps of moss and the covering of algae on the upper surfaces of stones. The sampling techniques used in the present work separate the benthic organisms into the communities that are found with each of these food supplies. The present work has shown that the structure of a community can change with change in certain factors, such as the amount of plant detritus present, and it is of considerable interest that the invertebrate communities associated with the three sources of food or the positions where it is found, differ so clearly among each other in species composition, community dominants and in the size-frequency distribution of certain species. Because of the factors tending to prevent the isolation of 'habitats', e.g. the turbulent nature of riffles, the diurnal activities of many species and the ease with which organisms can drift in the stream current, it might be expected that the separation of the bottom fauna of a riffle into smaller community groups would be less distinct. As most of the benthic species that show a clumped distribution, aggregate in response to local differences in the substratum there is a great need for the better description and analysis of the environment in studies on stream ecology.

The samples of organisms and detritus taken by the Surber-type technique and the samples of organisms found on the upper surface of stones were each collected from a delineated area of 0·093 m^2 of the bed of the streams. Several species of invertebrates found under the stones feed on the plant detritus, and their numbers increase with increase in the amount of plant detritus present, but no similar significant increase in the number of any species was found with increase in the amount of algae on the upper surface of the stones. It is probable that not many species of invertebrates can make use of the living algae for food. Some species have been found with small pieces of algae among their gut contents but the extent to which they can digest the algae is not known. It may be that the algae become of value as food only when they have died and begun to break down.

Because of the variety of places in which the common organisms live in fast-flowing streams and because within the same kind of place different species have different patterns of distribution any estimation of the production of the total bottom fauna would require such an extensive sampling programme as to be impracticable. It is likely that production studies will be carried out instead on selected species or groups. The data in the present paper allow species to be selected more appropriately than has previously been possible. From a known distribution the number of samples required to give the desired precision can be determined. Those species whose populations are more aggregated require more extensive sampling programmes and sometimes a greater variety of techniques, than those whose populations are less aggregated. The distribution pattern of *Chloroperla torrentium*—usually random among Surber samples and not present in moss—would suggest this species as a possible choice for investigations on the productivity of a benthic organism. However, if studies of fish production are also being carried out it may be necessary to take into consideration the fact that for some fish (carp, roach and bleak (Ivlev 1961), salmon and trout (Egglishaw 1967)) the more even the distribution of food the less there is eaten in a given time compared with a patchy distribution of food.

Whilst for some productivity investigations estimates of the biomass of bottom fauna per unit area will be needed, the biomass per unit weight of plant detritus, algae or moss may have more ecological significance in accounting for the standing stock. If the amounts of plant detritus, algae and moss per unit area are also known the data can be converted easily from one form to another.

Of the many associations found between benthic species populations and gradients in the amounts of plant detritus, water depth or the size of the largest stones at a site (Tables 3 and 4) only for the associations between certain common species and plant detritus has there been shown to be a causal connection (Egglishaw 1964). The results presented here suggest the need for more experimental work to discover which are the real factors determining the behaviour and pattern of distribution of the different components of the bottom fauna.

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SUMMARY

1. The paper deals with the distribution of benthic invertebrates in stream riffles, with particular reference to the three main sources of plant food—plant detritus under stones in the bed of streams, clumps of moss growing on stones and the algal covering on the upper surface of stones.

2. The frequency distributions of the numbers of the commonest invertebrate species collected with plant detritus in samples from the stony beds of two streams of different character (Shelligan Burn and River Almond) were positively skewed. A logarithmic transformation made the distributions more normal. The ranked variances on the log scale of the commonest species present in both streams were significantly correlated. In the River Almond, where the samples were taken systematically, the populations of certain organisms (*Isoperla grammatica*, *Rhithrogena semicolorata* and *Leuctra inermis*) were fairly evenly distributed across the width of the stream, whilst others (*Latelmis volkmari* larvae, *Esolus parallelopipedus* larvae, *Hydroptila* spp. and *Perla bipunctata*) were clearly more dense in the centre of the stream. The numbers of twelve species in the Shelligan Burn and six in the River Almond increased with increase in the amount of detritus at sampling sites, and the numbers of two species in the Shelligan Burn and five in the River Almond increased with increase in the size of the largest stones at the sites. Of twenty-nine significant associations between different species and the environmental factors measured only one was negative. Since different species of bottom fauna had different quantitative relationships with plant detritus, the structure of the community at a site depended to a large extent on the amount of detritus present there. With increase in plant detritus there was also an increase in the variety of bottom fauna.

3. The populations of most species of bottom fauna were less aggregated in clumps of moss growing on stones than were populations in the under-stone habitat. There were differences in the species composition and in the length–frequency distributions of

certain species of the fauna from both habitats. The numbers of no species living on the upper surface of stones and only the weight of bottom fauna in one of three streams examined was found to be significantly associated with the amount of algae present.

4. The bearing of the results on future work in stream ecology is discussed.

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