

# THE VERTICAL DISTRIBUTION OF THE INVERTEBRATE FAUNA IN THE BED OF A STREAM<sup>1</sup>

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## ABSTRACT

A type of sampler is described that permits the collection of benthic fauna to a depth of 30 cm in the beds of streams. It depends on the colonization of natural substratum placed into the streambed, and invasion can occur both horizontally and vertically downward. When fully colonized, these samplers collect many times the number of animals taken by vigorous stirring of the substratum upstream of a net.

Sets of samplers in which only one of four possible horizontal layers about 7.5 cm deep was available for colonization were implanted in an Ontario stream and lifted from 1 to 28 days later.

The total numbers of many types of animals increased steadily with time in all 4 layers; more than 28 days are probably needed for full colonization. When all the catches are considered together only about 20% of the total was in the top layer, about 26% was in the bottom layer, and the rest was about evenly distributed in the two middle layers. This type of distribution was found for all the groups of animals present. Only *Simulium* appeared to be normally confined to the surface of the substratum.

It is suggested that significant numbers of animals occur deep within the substrata of stony streams, and that even samples collected down to 30 cm do not adequately represent the fauna.

## INTRODUCTION

A major problem in the study of stream benthos is that of obtaining adequate quantitative samples. This subject has been reviewed by Albrecht (1959) and Macan (1958), who discussed mainly samplers that obtain animals from, at most, the upper few centimeters of the substratum; more recently other workers (e.g., Minckley 1963; Cummins, Coffman, and Roff 1966; Sowa 1965) have used samplers that penetrate to quite shallow depths only. As it has been reported that quite ordinary aquatic animals, as opposed to truly subterranean (phreatic) ones, occur at considerable depths in the gravel below and beside streams (Angelier 1953; Schwoerbel 1961, 1967; Berthélcmy 1968), it seemed to us that a more deeply penetrating sampler was needed. We therefore designed one and

used it to obtain a year-round series of samples for study of the life histories of the insects in a stream (Coleman and Hynes, in prep.) and in an attempt to measure the annual production rate of the benthos (Hynes and Coleman 1968; Hamilton 1969). We here describe the sampler and a series of observations on the summertime depth distributions and rates of movement of the animals in the Speed River, Ontario.

## METHODS

The samplers (20 were made) were based on an extension of the ideas of Moon (1935), who placed out trays of substrate for colonization and then lifted them to collect the fauna.

Each sampler consisted of an outer cylinder of industrial aluminum sheet, 30.5 cm high and 25.5 cm diameter, in which there were closely spaced triangular holes approximately 1 cm wide (Fig. 1). Inside it fitted a cylindrical "pot" of the same material but with a bottom and an outer diameter of 21.5 cm (total capacity about 116). In the approximately 2-cm gap between the pot and the cylinder, a metal ring was

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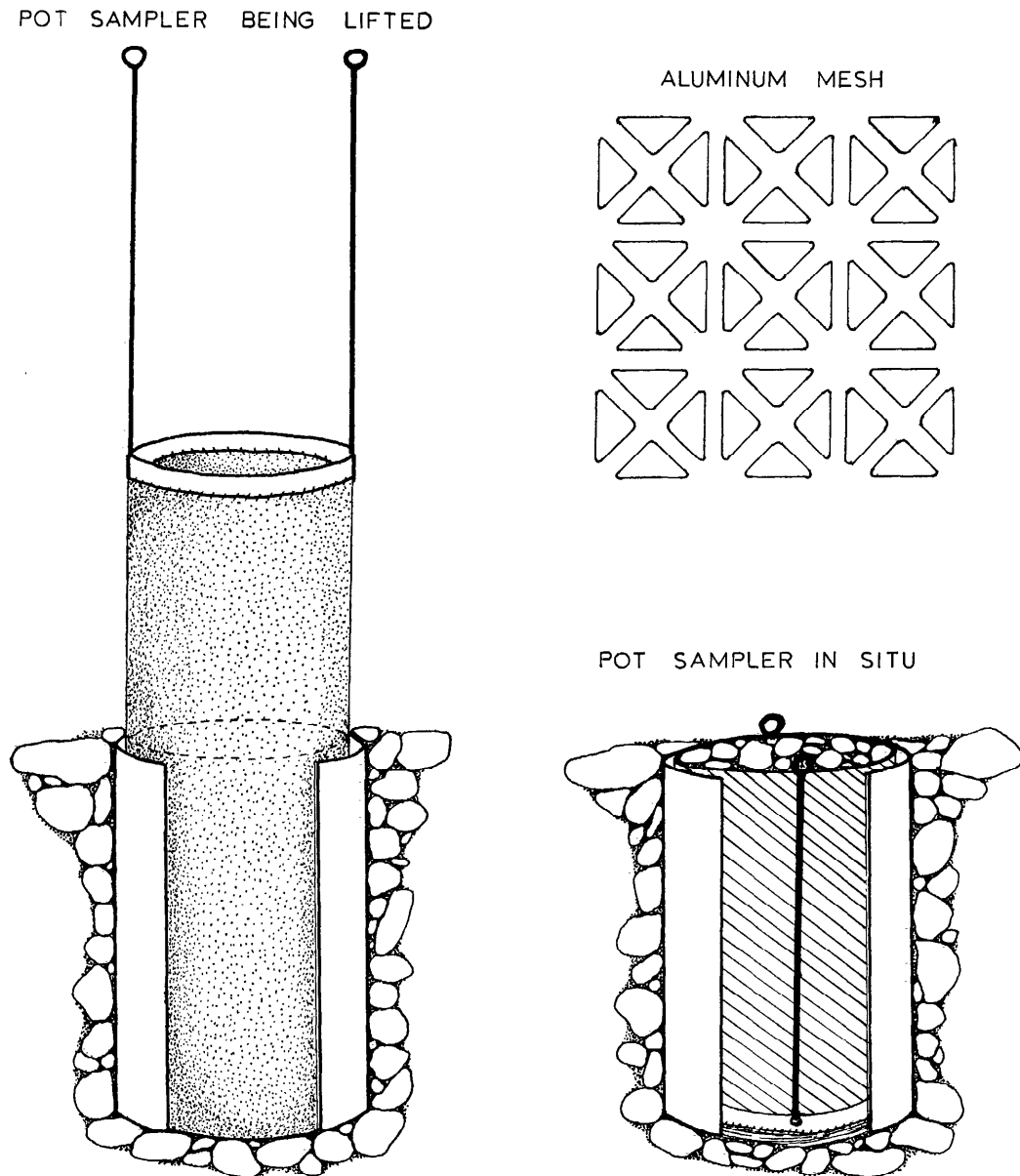


FIG. 1. Details of the mode of operation of the sampler.

loosely fitted round the pot and attached to a nylon bag 50 cm long that could completely enclose the pot. There were also two wire handles long enough to project above the pot when the ring was at the bottom. The bag was made of parachute cloth so finely woven from flattened yarn

(60 threads/cm) as to leave gaps only 30-40  $\mu$  wide.

The cylinders were buried up to their tops in the streambed and remained *in situ* throughout the study. They had been in position for more than 6 months before the observations reported here so the sub-

stratum around them had long since recovered from the disturbance caused by their emplacement. The pots were filled with sand and gravel from the streambed and fitted with their bags. They were then placed inside the cylinders, and the rings were pushed down to the bottom so that the net was folded tightly at the base of each pot. When the time came for lifting, the ring was pulled up to 20 cm above the substratum, thus isolating the pot, which was then lifted out. The gap between the pot and the cylinder became fully silted up during the first week and the ring, as it was raised, displaced the light silt into the current so that very little was retained inside the bag.

Apart from a few larger stones at the surface, the gravel did not vary greatly with depth, so there was little difficulty in constructing a facsimile of the streambed within the pots; and, of course, the holes in the walls of the cylinder allowed free access of water and animals at all levels. For long-term observations, therefore, the pots were simply filled with gravel from the stream and left in place for several months before lifting. For the study reported in detail here, however, the gravel was carefully washed and kept dry for some time before use, so that it was initially free of animals. The pots were divided into 4 levels: 1) surface to 7.6 cm; 2) 7.6 to 15.2 cm; 3) 15.2 to 22.9 cm; and 4) 22.9 to 30.5 cm. In each pot the gravel in three of the levels was enclosed in polyethylene bags, so that animals had access to only 1 level, and then only horizontally. A series of 4 pots was, therefore, needed to represent the 4 levels. Two such series were set out and lifted between 8 June and 20 July 1966 in such a way that one whole series of stratified samples was lifted after being in place for 1, 2, 3, 4, 5, 6, 7, 14, and 28 days respectively. The dates of lifting were 9, 15, 16, 13, 13, 22, and 22 June and 6 and 20 July respectively.

After the pots were lifted, the gravel was washed in small portions and the animals and debris were retained in a fine sieve (40 meshes/cm, mesh size ca.  $170 \mu^2$ ). The gravel was searched for molluscs and cased

trichopteran larvae before being discarded, and the whole sample was preserved in formalin. Later the animals were floated from the silt and other debris in a saturated solution of calcium chloride (Hynes 1961). Many samples contained large numbers of small invertebrates, and, while all the specimens over 5 mm long were counted individually, the rest were subsampled as described by Hynes (1961); only a fourth of the small specimens were actually counted and measured. In five instances all four subsamples were counted and the results agreed remarkably well. The figures given here are for the whole sample, on the assumption that the subsamples accurately represented a fourth of the small animals present.

#### THE SPEED RIVER

The samples were all collected from an area about 3 km from the source of the Speed River, which flows into the Grand River and rises at  $80^\circ 13' 18''$  W,  $43^\circ 45' 40''$  N in Wellington County, Ontario. The stream drains mainly agricultural land on glacial till and has hard water, many creek chub [*Semotilus atromaculatus* (Mitchill)] and hogsuckers [*Hypentelium nigricans* (Le Sueur)], and a few brook trout [*Salvelinus fontinalis* (Mitchill)]. At the sampling site the stream is about 7 m wide and normally 20–35 cm deep, flowing over a 100 m long, uniform riffle composed of fine and coarse silty gravel intermixed with stones ranging up to 10 cm diameter.

#### RESULTS

##### *Depth distribution*

The series taken on day 7 is not included in this part of the calculations, because the sample from level 3 was lost. When the total numbers of animals taken in the remaining 8 sets of stratified samples were considered together, only about 20% of the total catch had been collected from level 1 (Table 1). In all groups the animals were more or less evenly distributed in depth; if anything, the top layer, where most stream investigators have taken their samples, was the least populated, and there was

TABLE 1. *The numbers and percentage vertical distribution of those groups of animals of which more than 200 specimens were collected, and of the total collections (not including day 7)*

Group	Total catch	Total nonchironomids (%)	% of each group at each level			
			1	2	3	4
Oligochaeta	4,732	13.4	21.1	25.1	25.2	28.6
Mollusca	577	1.6	17.7	25.1	16.1	41.1
Copepoda	5,288	14.8	23.4	35.6	19.4	21.6
Plecoptera	403	1.1	29.3	35.5	19.1	16.1
Ephemeroptera	11,275	32.0	21.0	27.5	25.2	26.2
Trichoptera	4,214	12.0	29.3	14.1	25.5	31.0
Coleoptera	1,798	5.1	18.0	32.3	32.5	17.2
Chironomidae	128,285	—	19.7	26.8	26.6	25.7
Other Diptera	2,078	5.9	14.3	30.0	33.4	22.2
Hydracarina	4,424	12.6	18.7	26.9	25.5	28.8
Total	163,074		20.25	26.95	26.45	25.96

little evidence of any falling off in numbers in the lowest layer.

This applied also to animals not numerous enough to be included in the table, such as the triclad *Cura formanii* (Girard), the crayfish *Orconectes propinquus* Girard, and even the darter *Etheostoma flabellare* (Rafinesque) of which 7 out of a total of 28 specimens were taken in level 4.

The Chironomidae so dominated the fauna that in summed statistics they tend to overshadow the other groups, so it is more revealing to consider the artificial category of nonchironomids separately.

Among the Chironomidae the larvae of Orthocladiinae comprised 55.7% of the total numbers of larvae and pupae, Chironominae 38.1%, and Tanypodinae 4.1%; 2.1% were pupae. All, including the pupae, were fairly evenly distributed at all depths, and there was no marked correlation between larval size and depth of occurrence (Fig. 2). The last point also applied to the nonchironomids, although this was not always true in detail, as is discussed below.

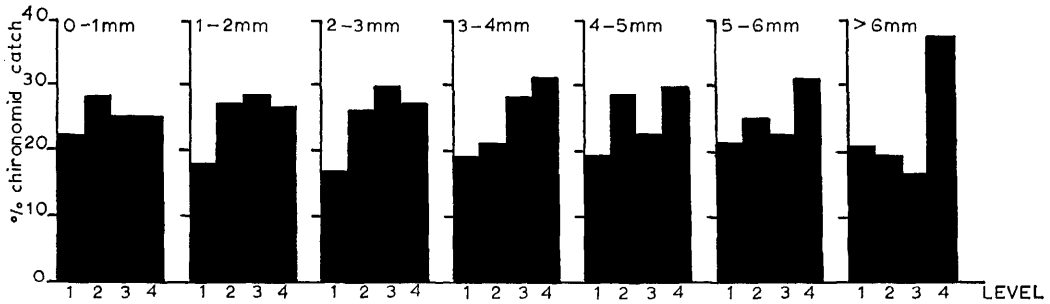
Most of the oligochaetes were *Pristina longiseta leidyi* (Smith) whose tendency to break up into small reproductive fragments in formalin makes any discussion meaningless. The commonest molluscs were *Sphaerium striatinum* (Lamarck) together with a few *S. simile* (Say); all sizes occurred at all levels. The Copepoda and Hydracarina were not studied in detail but both groups, of course, fall in the 0-1-mm size group. By far

the commonest stonefly during the period of the experiment was *Allocaenia pygmaea* (Burmeister), the nymphs of which were in early instars and in process of going into diapause (Khoo 1964). The still active nymphs were most abundant in levels 1 and 2, while those actually in the characteristic diapausing condition tended to be in the deeper levels.

Several families of Ephemeroptera were well represented, and in all except the abundant Caenidae each of the lower levels contained more specimens than the top one. Moreover, in the Leptophlebiidae (mostly *Paraleptophlebia*), Heptageniidae (mostly *Stenonema*), Ephemerellidae and Baetidae, there seemed to be an increasing percentage of specimens in the lower levels, especially 2 and 3, the larger the nymphs.

The commonest Trichoptera were very small specimens of Hydroptilidae and Leptoceridae; both families showed peaks of occurrence in both levels 1 and 4. Many of the Leptoceridae in level 1 were actually in the process of emerging from their eggs, so that possibly the two peaks represent eclosion at the surface followed by deep penetration downwards. Small Hydropsychidae and Rhyacophilidae were also fairly abundant. Both were most common in levels 3 and 4, and such few larger specimens as were taken were also deep in the gravel. This is particularly surprising when it is recalled that Hydropsychidae are net spinners. Also surprising is the occurrence

## THE VERTICAL DISTRIBUTION OF THE CHIRONOMIDAE



## THE VERTICAL DISTRIBUTION OF THE NONCHIRONOMIDS

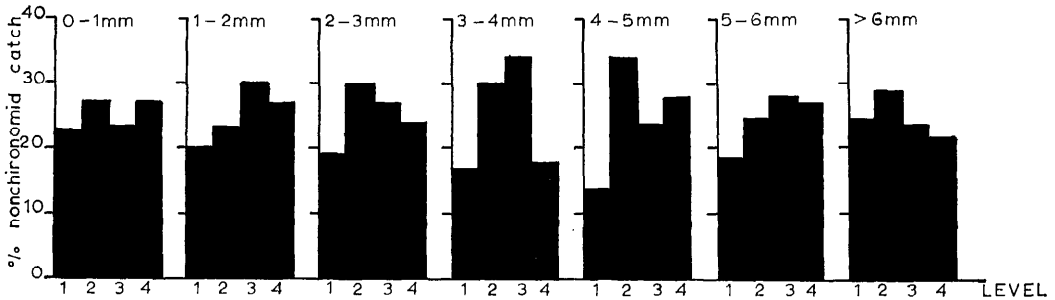


FIG. 2. The size distributions of the Chironomidae and of the nonchironomids taken in all levels in all samples except those of day 7.

of some trichopteran pupae in the lower levels.

The beetles, including Elminthid adults and larvae and the larvae of *Psephenus*, all occurred most commonly in level 2 or 3. However, very small larvae (0-1 mm) and larvae of *Ectopria* were most common at the surface, indicating, for the former, that perhaps hatching occurs there.

Other Diptera included several types of Limoniinae, *Culicoides*, and *Simulium*. Most of these, including *Simulium*, were most common in the deeper levels, and level 4 contained the most species. However, it should be stressed that *Simulium* was found below the surface only up to day 7, after which it disappeared from the lower levels. It is probable that the larvae had attached themselves to the sides of the pots and were projecting into the spaces between them

and the outer cylinder, spaces they had to vacate as they became silted up. This illustrates a weakness in short-term work using this pattern of sampler, which is discussed below. Nevertheless, no other organism showed this change of distribution, and the percentage distribution of the fauna on days 14 and 28 resembled that based on the total catch (Table 2). Indeed, an even smaller proportion of the animals collected then occurred in the top 7 cm.

#### Rate of colonization

The numbers of animals collected in all the levels increased fairly steadily throughout the sampling period except for a peak in the numbers of small Chironomidae in the pots that had been in place for 7 days (Fig. 3). Level 1, however, showed greater fluctuations than the others. This was probably

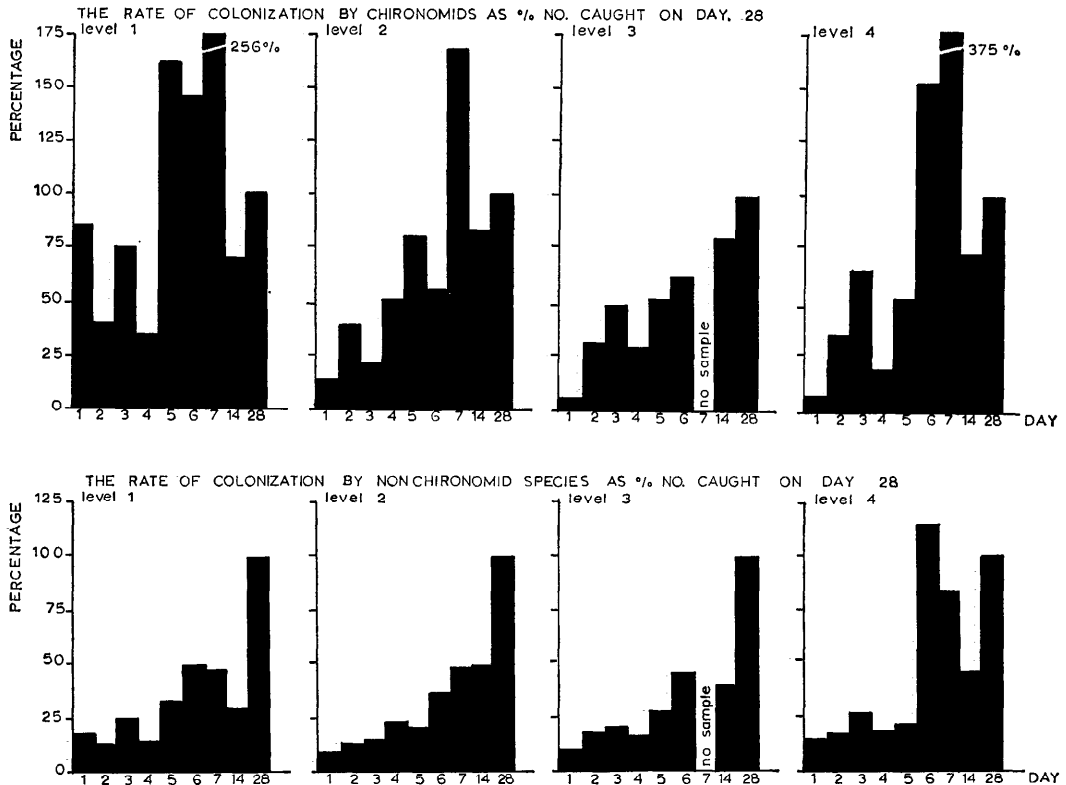


FIG. 3. The rate of colonization of all levels by Chironomidae and nonchironomids during the 28 days, shown as percentages of the number caught at each level on the last day.

because it is more subject to extrinsic factors and such things as drift and eclosion of eggs deposited on the gravel surface. The numbers of most organisms were clearly still increasing at the end of the experiment, indicating that 28 days is not long enough for full stable occupancy of a vacant space, even so small a one as that enclosed by the sampler.

Within each group of animals the catches increased in much the same way as did the totals, although more irregularly because of the smaller numbers involved. The data are, therefore, far from conclusive, but a few interesting trends were noted.

Some eggs of *Allocapnia pygmaea* were still hatching during the experiment, and this seems to have led to wide fluctuations in numbers in level 1 and to some extent in level 2. In levels 3 and 4, however, the

numbers were more steady, indicating, perhaps, lateral movement of slightly older nymphs that had already dispersed more evenly deep into the gravel.

Among the Ephemeroptera, while the numbers continued to rise irregularly in the upper three levels, there was some indication of stabilization in the bottom layer after day 6, caused primarily by *Ephemerella* spp. and Caenidae. *Baetis vagans* McDunnough and *B. near herodes* Burks (possibly an undescribed species) moved in rapidly and seemed to attain fair stability of numbers after only about 4 days, as did the Coleoptera. At least some animals therefore move into an empty area rapidly and seem to do so laterally through the gravel. This statement must be qualified by the point already made—that for the first few days it was possible for animals to move

TABLE 2. The numbers and percentage vertical distributions of the catches on the two last days of sampling

	Total catch	% of each category at each level			
		1	2	3	4
Day 14					
Chironomidae	20,393	12.2	31.1	33.2	23.6
Non-Chironomidae	5,049	16.0	35.2	25.4	23.3
Total	25,442	12.9	31.9	31.6	23.5
Day 28					
Chironomidae	26,247	13.5	29.1	32.3	25.1
Non-Chironomidae	11,949	22.7	30.1	25.8	21.4
Total	38,196	16.4	29.4	30.3	24.0

downwards in the gap between pot and cylinder. This did not apply to increases after day 7, by which time silt had completely filled the space.

It is also noteworthy that representatives of nearly all taxa were present in the samples at all levels after only 1 day, and all, even *Sphaerium*, were present by day 3.

#### DISCUSSION

This study has, despite some weaknesses in the sampler, clearly indicated that stream animals can occur in significant numbers deep in the substratum in stony streams, and that they are capable of considerable lateral movement. Moreover, there is no significant decrease in numbers even at the depth of 23–30 cm, where even fish may occur. These are, to some extent, not new findings, as Schwoerbel (1961) has already stressed the importance of the hyporheic habitat, Phillips and Claire (1966) reported that *Cottus* can penetrate to a depth of 36 cm in coarse gravel, and Berthélemy (1968) has found that the normal habitat of *Leuctra major* Brinck is deep down in the substratum. They do, however, lead to considerable mistrust of the results of the quantitative studies which have so far been made on stream benthos. The possible shortcomings of the sampler are:

1. The gap between the pot and the cylinder may have provided a downward route for movement to the lower levels for the first few days. This may account for some of the earlier colonization of the lower

levels, but it does not explain the continuing increase in numbers after day 7. As can be seen in Fig. 3 and Table 2 the general trend of numbers continued upwards to day 28, except for the perturbation caused by the peak in numbers of Chironomidae on day 7, and a particularly high catch of nonchironomids at level 4 on day 6. One must therefore assume that there is lateral movement through the substratum at depth and that considerable numbers of invertebrates are normally present there. The alternative explanation, that animals moving near the surface of the substratum, and arriving at a sampler in which the upper levels were enclosed in plastic, were deflected downwards into the one exposed level, seems most improbable. Were this correct it would imply that stream invertebrates, moving horizontally in the upper layers of the substratum pass *under* deeply embedded boulders that lie in their path rather than around or over them. There would seem to be no reason for such a behavior pattern, and the simple assumption of lateral movement at all depths is clearly preferable.

2. A small amount of the silt that collected between the cylinder and the pot was probably incorporated into the samples. We have seen that *Simulium* was recorded as occurring in the early days at lower levels because, presumably, it was occupying the gap before it became silted up. It is also possible that some of the unexpected records from lower levels (e.g., of trichopteran

TABLE 3. *The total numbers of animals and of animals other than Chironomidae collected by kick samples and complete pot samples from the Speed River during 10 months of 1966*

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Totals
<b>Total catch</b>											
Kicks	3,113	2,360	1,564	1,994	2,191	4,743	372	936	396	568	18,237
Pots	2,058	8,230	1,338	3,688	34,521	2,766	10,923	5,778	16,526	5,552	91,380
<b>Non-Chironomidae</b>											
Kicks	1,217	836	1,136	301	284	2,251	164	292	176	164	6,821
Pots	496	1,660	385	1,619	8,274	1,161	2,681	2,238	5,585	1,388	25,487

pupae) occurred in this way. However, because the ring was closer to the pot than to the cylinder it displaced most of the silt outwards as it was raised, and most was washed away by the current and not retained in the bag. This was especially true of pots containing deeper level samples, as the top surface was then smooth polyethylene sheet which was immediately scoured clear. The small amounts that did enter the bag could not have contained any but a very small proportion of the large numbers of invertebrates included in the samples. Indeed had they done so the uppermost layers, which retained silt more readily than the others since it could lodge among the stones, would always have given the highest yields, and they manifestly did not (Tables 1 and 2).

3. It is possible that the substratum in the pots, having recently been disturbed, and for this experiment washed and dried, may have provided a particularly favorable habitat. For the first few days this may have been true, although only the silt had been removed by the washing. The silt was, however, rapidly replaced into the gap and presumably into the interstices in the gravel as well. Also, as is shown below, this pattern of sampler caught very high numbers even when it had been in place for months, indicating that there was no initial high attractiveness followed by a decline as the substratum reverted to its original undisturbed state.

There remain, however, the unexplained peak in numbers of Chironomidae on day 7 and the less marked peak of nonchironomids on day 6 at level 4 (Fig. 3), which could both have been caused by initial

attractiveness followed by decline as the substratum became silted up. The peak of nonchironomids is so small as to be probably merely a sampling error; that of chironomids also occurred in the top layer, indicating that it was a general phenomenon. It seems most likely therefore to have been caused either by the hatching of large numbers of eggs or by a mass movement. The numbers of Chironomidae in the stream became very high in July (Table 3) and this must have resulted from massive hatching in late June and early July.

We have, however, no explanation as to why the peaks occurred only in the 7-day samples and were less manifest in the 6-day ones, although present to some extent at levels 1 and 4 (Fig. 3). Both sets of samples were lifted on 22 June and they were only 20 m apart.

In connection with the last possible shortcoming, it is interesting to compare the numbers of animals obtained by whole unstratified pots lifted during certain months with the "kick samples" collected during the same months. The latter were obtained as described by Hynes (1961) and considered at some length by Morgan and Egglshaw (1965). They were collected by placing a flat-ended handnet of bolting cloth with 20 meshes/cm (mesh size,  $340 \mu^2$ ) vertically on the streambed. An area estimated to be about 900 cm<sup>2</sup>, just upstream of the net, was then vigorously disturbed down to a depth of 5-7 cm. The dislodged debris and some small stones were swept into the net by the current. The net was then emptied and the process repeated twice more. The 3 netfuls constituted 1 kick sample, and represented about the equivalent of a Sur-

ber sample taken from an area of about 2,700 cm<sup>2</sup>. However, in using a Surber sampler the stones are brushed off individually into the mouth of the net, so that closely attached animals, such as some Trichoptera, are more thoroughly collected. On the other hand the mesh size used in a Surber sampler is usually much larger (20 meshes/inch), and it cannot be operated with a fine mesh comparable with those used in this study because of loss by eddy currents. Macan (1958) and Albrecht (1959) have shown that the available quantitative sampling methods for stream benthos are all to some extent selective, and as Morgan and Egglisshaw (1965) have demonstrated that kick samples are more efficient than might be supposed, it seemed valid to use them (they had been collected for work on life histories) as a rough check on the efficiency of the pot samplers.

As might be expected from comparison between the techniques, the kick samples contained proportionately fewer very small animals, and some adherent animals were under-represented. This was also noted by Macan (1958) and Hynes (1961) and is quite understandable, but when the total numbers taken by the two methods are compared (Table 3), the differences are striking. The area enclosed by a pot was 363 cm<sup>2</sup>, so that the 2,700 cm<sup>2</sup> covered by the kick samples was about 7.5 times as great; yet the latter nearly always contained fewer specimens. Indeed if one divides the totals taken by the pot samples by 10, to allow generously for the fact that the kick samples, which extended down to only 5-7 cm in the gravel, sampled only the superficial layers, the total numbers in the kick samples, for both the complete samples and for their nonchironomid portions, are only 2-3 times as great, instead of 7.5 times. Part of this discrepancy can undoubtedly be explained by the differences in mesh size and part by the failure of the kick samples to obtain all the closely adherent animals. But superficial sampling with nets, shovels, boxes, and similar devices (Albrecht 1959; Macan 1958) is likely to be considerably less efficient than the

samplers used in this study. Moreover, as the stratified samples revealed no marked falling off in numbers below 23 cm of gravel, it is clear that even our own samplers were not collecting the entire fauna. We may also point out that pot samples can be taken even when there is thick ice. Only 10 months are shown in Table 3 because no kick samples could be obtained during January and February, when, however, we were able to lift pots.

We have already pointed out the weaknesses which our pot sampler has for short-term studies. These problems would not, of course, have affected the results shown in Table 3, as all the pots there had been in place for several months before lifting. The fact that, even so, the numbers of animals were so much higher than they were in the kick samples indicates that the lower levels continued to be inhabited long after the gaps had been filled up, and the disturbed substratum had settled down. Moreover, comparison of the long-term July catch in Table 3 with the short-term catches recorded in Table 2 shows no marked decline such as would be expected if the lower levels cease to be inhabitable some time after they have been disturbed. An additional weakness is that even 30 cm is not deep enough. We have, in fact, succeeded in locating ordinary benthic animals as far down as 70 cm below the gravel surface during summer, by pumping water up through standpipes similar to those used by Berthélemy (1968), and they seem always to be present at 50 cm. Work is continuing here on the problems of depth distribution and sampling; both must be solved if we are to obtain any really reliable information on the density and production rate of the benthos in streams.

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