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The Distribution of Some Stream Invertebrates in Relation  
to Current Speed<sup>1)</sup>

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Introduction

In a field investigation of the occurrence of stream animals in relation to current speed AMBÜHL (1959) collected faunal samples from sites differing, as far as he could tell, only in current speed. He found that most animals occurred in a wide range of current speeds, but that the numbers of many species, expressed as percentages of the total numbers of all kinds of animals in single samples, were clearly highest at certain speeds. MACAN (1963, p. 120) suggested that AMBÜHL's assumption that his sampling sites differed only in current speed may have been an oversimplification. He had further reservations about the validity of AMBÜHL's interpretation of his results, in terms of current speed alone, on the grounds that AMBÜHL made no allowance for possible biotic effects; that AMBÜHL recorded the current speed in the water above the bottom, not that to which the animals were directly exposed; that AMBÜHL lumped the results from several species by genera, and lastly that AMBÜHL dealt with percentages and not absolute numbers.

In this paper data collected during hydrobiological studies in the streams and rivers forming the catchment of Vaal Dam (CHUTTER and NOBLE 1966, CHUTTER 1967) have been used as a basis for a further consideration of whether or not the numbers or percentages of animals can be related to current speed under field conditions.

2. Methods

Faunal samples were collected in the field from stones-in-current biotopes with a 1 sq ft (929 sq cm) Surber sampler (SURBER 1936) whenever possible, otherwise with a hand net. The hand net was also used in stones-out-of-current biotopes. On each sampling occasion,

<sup>1)</sup> Part of a Ph.D. thesis submitted to Rhodes University.

when the Surber sampler was used, 3 samples were collected and pooled. When sampling with the hand net, stones were lifted from the water with the hand net held so that animals would wash off the stones into the net. Closely adhering animals were picked off the stones into the net. The netting used on both the hand net and the Surber sampler was bolting silk with 23 meshes/cm and an average distance between the meshes of 0.29 mm. The hand net was 35 cm deep on a strip brass ring 3 cm wide of 25 cm diameter, mounted on a handle about 2 m long. Samples were pickled in formalin in the field. In the laboratory the fauna was sorted as far as possible and counted using the sub-sampling technique described by ALLANSON and KERRICH (1961) for the smaller animals.

Current speeds were measured in the field with an Ott Laboratory Minor current meter. The propeller of the meter was mounted so that it cleared the substratum by about 2.5 cm. Several separate current speed readings were made from the sampling area on each sampling visit.

### 3. Results

#### a) Repeated sampling at one sampling point on one day

CHUTTER and NOBLE's (1966) data on the animals collected from ten separate square feet in a stony run in the Vaal River at Standerton are used here to consider the relationship between current speed and fauna. Their samples were numbered from 1 to 10 across the river and the depth of the water increased gradually from approximately 10 cm (sample 1) to approximately 23 cm (sample 10). The mean current speeds at each sampling site, which were based on three readings, ranged from 35 to 62 cm/sec. Using the KENDALL rank correlation coefficient (KENDALL 1948), it was found that the correlation between depth and current speed was significant ( $P < 0.05$ ), the deeper water being the faster flowing. The effect of depth on the correlation between current speed and densities of the various species encountered and the effect of current speed on the correlation between depth and the species densities may be eliminated by calculating the KENDALL partial correlation coefficients between current speed, depth and species densities. Partial correlation coefficients have therefore been calculated and HOFLUND's (1963) empirical probabilities for  $t_{r,zy}$  have been used to assess the probabilities of the partial correlations. As AMBÜHL presented his faunal data in percentage form, partial rank correlation coefficients between depth, current speed and species densities, expressed as a percentage of the total numbers of individuals of all species per square foot, were also calculated. Animals whose density or percentage was closely correlated with depth and current speed are shown in Table 1. This table shows that for only *Cheumatopsyche thomasseti* and *Simulium* spp. was there a significant correlation ( $P < 0.05$ ) between density and current speed when the effect of depth was eliminated. These two animals are well known inhabitants of stones-in-current biotopes and individuals are rarely found where there is no current (CHUTTER 1967). *Hydra*, *Centroptilum excisum*, *Orthotrichia* and *Burnupia* were significantly correlated with depth when current speed effects were eliminated. Larger numbers of these animals were found in shallower water. *C. excisum* is a mayfly which is found in most biotopes in South African rivers (CHUTTER 1967, HARRISON and ELSWORTH 1958). However it usually makes up a smaller part of the stones-in-current fauna than it does of the stones-out-of-current fauna. In the catchment of Vaal Dam (CHUTTER 1967) this was not due to depth as many of the stones-out-of-current biotopes were in deeper water than adjacent stones-in-

Table 1. Kendall partial rank correlation coefficients ( $t$ ) between animal numbers (1), current speed (2) and depth (3) and between animal percentages (4), current speed and depth.

Animals	$t_{12.3}$ (density & current speed, depth held)	$t_{13.2}$ (density & depth, current speed held)	$t_{42.3}$ (percentage & current speed, depth held)	$t_{43.2}$ (percentage & depth, current speed held)
<i>Hydra</i> spp.	-0.24	-0.59	-0.34	-0.53
<i>Centropitium excisum</i> BARNARD	-0.35	-0.51	-0.48	-0.40
<i>Choroterpes</i> ( <i>Euthraulus</i> ) sp.	0.44	0.49	0.16	0.14
<i>Aethaloptera maxima</i> ULMER	0.35	0.28	0.32	0.58
<i>Amphipsyche scottae</i> KIMMINS	0.43	0.83	-0.04	0.74
<i>Cheumatopsyche thomasseti</i> (ULMER)	0.51	0.00	0.36	0.24
<i>Macronema capense</i> WALKER	0.35	0.14	0.09	0.52
<i>Orthotrichia</i> sp.	0.15	-0.74	-0.17	-0.66
<i>Stenelmis</i> sp.	0.04	0.48	0.16	0.70
<i>Simulium</i> spp.	0.55	0.05	0.27	0.37
<i>Barnupia</i> spp.	-0.07	-0.60	0.28	0.47

Notes 1. From HOELUND 1963 when  $p = 0.05$ ,  $t_{xy.z} = 0.49$ , when  $p = 0.01$ ,  $t_{xy.z} = 0.62$ , when  $p = 0.001$ ,  $t_{xy.z} = 0.74$ .

2. Some species names have changed since CHURTER & NOBLE's Table I was compiled. *Euthraulus* sp., *Macronema* sp. and Elmidae type H are now *Choroterpes* (*Euthraulus*) sp., *Macronema capense* and *Stenelmis* spp.

current biotopes. It therefore seems reasonable to conclude that in spite of the lack of confirmation from the Standerton data, the occurrence of this animal is related to current speed. In *Choroterpes (Euthraulus)* sp. and *Amphipsyche scottae* there was also a significant correlation between numbers and depth, but in these species the greater numbers were found in the deeper water. *Choroterpes (Euthraulus)* sp. is found in day-time in cavities under stones where it is protected from the current (CHUTTER, in press). It is usually more abundant under stones out of the current than under stones in the current (CHUTTER 1967). At Standerton it was found in greater numbers in deeper water possibly because the stones in the deeper water were larger and had larger cavities under them. *A. scottae* is a Hydropsychid caddis which does not live in biotopes where there is no current. While depth was obviously a more important factor governing the numbers of *A. scottae* at Standerton, the rather large coefficient for numbers and current speed with depth held (Table 1) does suggest that its numbers may also be related to current speed.

Turning now to the correlations between percentages and current speed and depth (Table 1) it is obvious that the percentage transformation resulted in some spuriously significant correlations (*Aethaloptera maxima*, *Macronema capense* and *Stenelmis* and depth) while masking some genuine correlations (*C. thomasseti*, *Simulium* and current speed; *Choroterpes (Euthraulus)* sp., *Burnupia* and depth).

Examination of CHUTTER and NOBLE's data for species other than those discussed above failed to reveal any species whose peak densities appeared to be in the middle of the range of current speeds or depths recorded from the 10 samples. Among the species found in only a few of the 10 samples, the Glossiphonidae, *Ecnomus* sp. and *Simulium nigratarsis* COQUILLET pupae were found mainly in the shallower, slower flowing water, while a large number of Elmid larvae "type 7" (which are probably *Stenelmis* larvae) were in the sample where the current speed was greatest (see CHUTTER and NOBLE's Table 1).

The range of current speeds in CHUTTER and NOBLE's data was rather narrower than that in AMBÜHL's field studies. However, this analysis of the 10 Surber sample data does lend some support to AMBÜHL's finding that, even in field samples, the numbers of some species can be shown to be related to current speed.

#### b) Repeated sampling at single sampling points at monthly intervals

Of a large number of sampling points on the streams and rivers of the Vaal Dam Catchment (CHUTTER 1967) there were only two, Stations 2a and 21, where there were a suitable number of successive quantitative (Surber) samples and current speed measurements to investigate whether the density of species or groups of animals was related to the current speed from month to month. At Station 21 *C. excisum* and *A. scottae* were too rare to compare their densities and percentages with current speed. Of the common animals found at this sampling point, only the numbers of *Cheumatopsyche thomasseti* and the closely related *C. afra* (MOSELY) followed current speed fluctuations (Fig. 1a). Taking all quantitative data for these species at this sampling point, and not only the successive monthly data shown in Fig. 1a, into consideration (Fig. 1b) shows that in both species there was little increase in the numbers of individuals as the current rose from 20 to 50 cm/sec, but that the density increased sharply

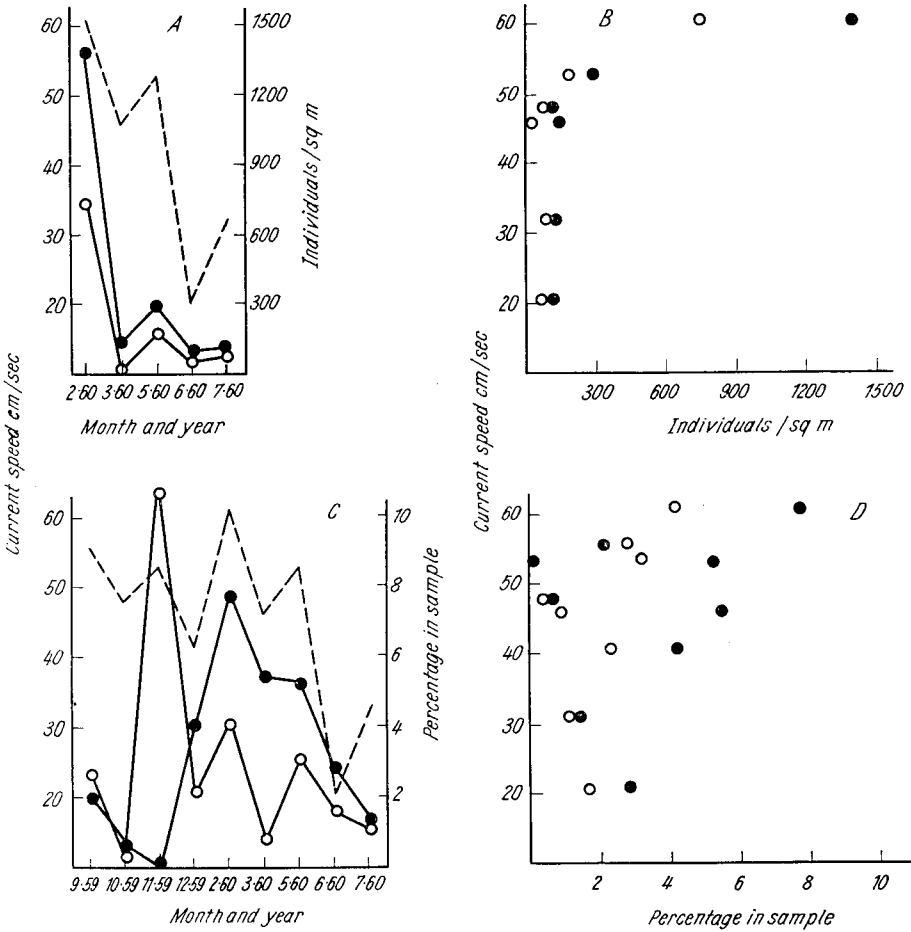


Fig. 1. *Cheumatopsyche afra*, *C. thomasseti* and current speeds from the stones in current at Station 21.

- A. Monthly variation in current speed and numbers of individuals/sq m.
  - B. The relationship between numbers/sq m and current speed.
  - C. Monthly variation in current speed and numbers of individuals expressed as a percentage of the total number of animals in each sample.
  - D. The relationship between percentages and current speed.
- Symbols: --- current speed, ○ *C. afra*, ● *C. thomasseti*

at speeds above 50 cm/sec. In *C. afra*, percentage peaks followed current speed peaks fairly closely, but in *C. thomasseti* they did not do so (Fig. 1c). (There are more percentage data than quantitative data as hand net results have been included). In both species the higher percentages were found at the higher current speeds (Fig. 1d).

At Station 2a the species whose numbers and percentages followed current speed changes were *Centroptilum excisum* and *Cheumatopsyche thomasseti* (Fig. 2).

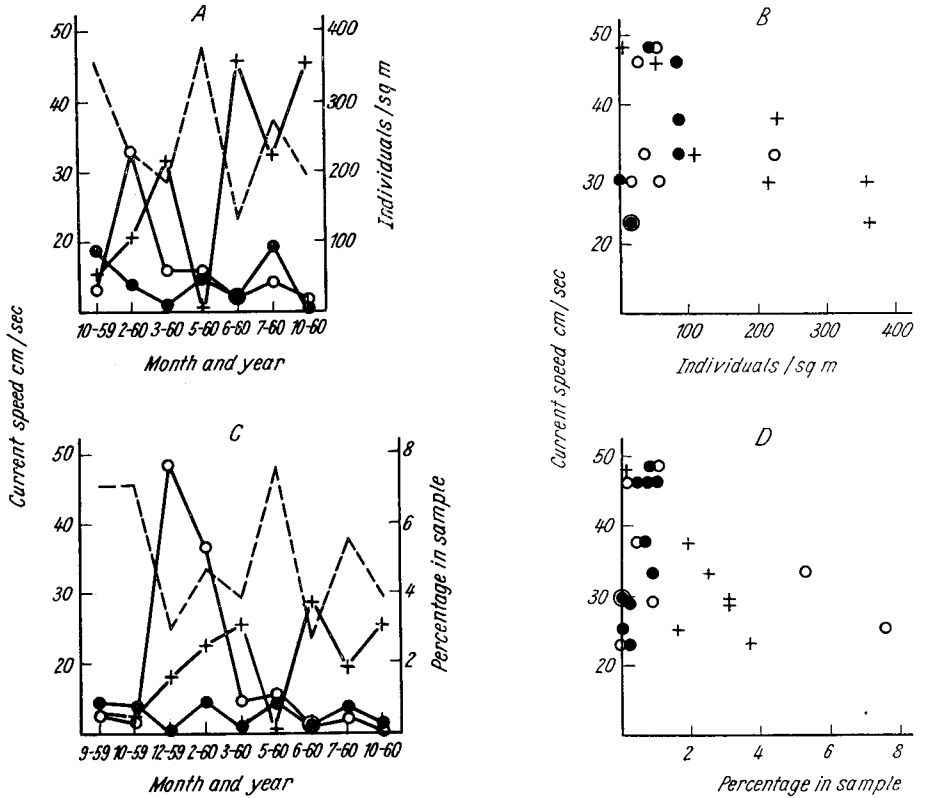


Fig. 2. *Centropitulum excisum*, *Cheumatopsyche afra* and *C. thomasseti* and current speeds from the stones in current at Station 2a. A, B, C & D as in Fig. 1  
 Symbols: --- current speed, + *C. excisum* ○ *C. afra*, ● *C. thomasseti*

The numbers and percentages of *C. afra* were not nearly as closely related to current speed as were those of the other two species (Fig. 2b, d). The inverse correlation between *C. excisum* percentages and current speed was remarkably close.

### e) Results from a number of different sampling points

In order to find out whether the density of any species followed current speed variation from sampling point to sampling point, it is advisable to eliminate possible spurious correlations due to seasonal variation in density. This has been done by comparing data for three months from several sampling points for *C. excisum* (Fig. 3) and *C. thomasseti* (Fig. 4). In *C. excisum* both the density and the percentage were very low at high current speeds in summer. Summer is a clearly defined rainy season in the catchment of Vaal Dam and there was consequently only one sampling point where a moderately low current speed was measured in the summer. The density and percentage of *C. excisum* were greater at this sampling point than at the other sampling points used in this

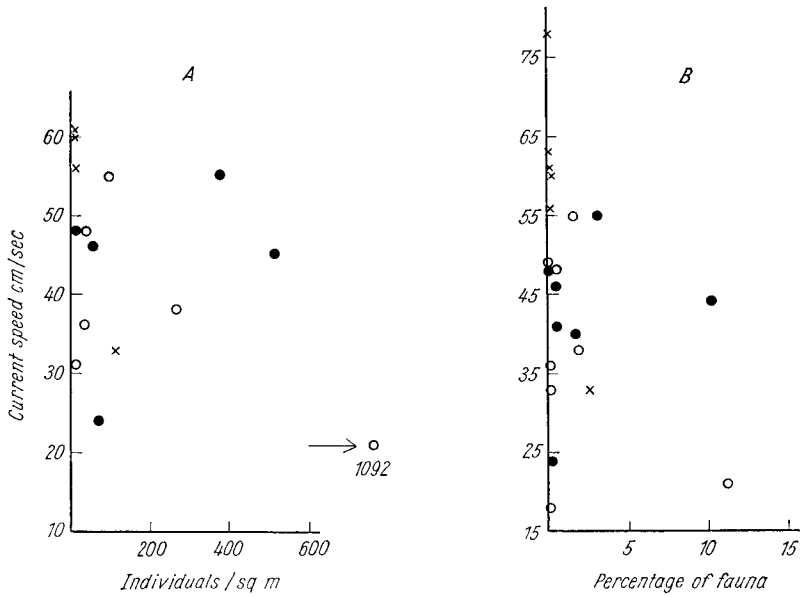


Fig. 3. The numbers of individuals/sq m (A) and the percentage of the whole fauna (B) of *C. excisum* in relation to current speed at sampling points in the catchment of Vaal Dam. Symbols: ○ July 1960 (winter), ● October 1959 (dry early summer), × January 1960 (summer).

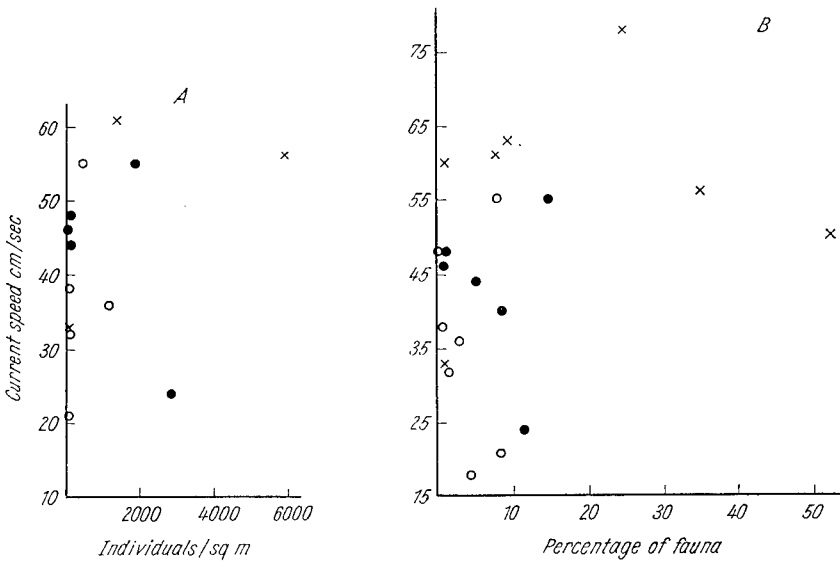


Fig. 4. The numbers of individuals/sq m (A) and the percentage of the whole fauna (B) of *C. thomasseti* in relation to current speed at sampling points in the catchment of Vaal Dam. Symbols as in Figure 3

season. There was otherwise no evidence, in summer or in the other two seasons, that the density of *C. excisum* at the various sampling points was inversely correlated with the current speeds recorded at those sampling points. The data for *C. thomasseti* (Fig. 4) fail to show that the greatest numbers or the highest percentages were found at the greatest current speeds.

It may therefore be concluded that the numbers and percentages of *C. excisum* and *C. thomasseti* do not follow current speed in series of samples taken in the same month from a number of different sampling points.

#### 4. Discussion

CHUTTER and NOBLE's data show that the percentage transformation produces spurious correlations between the occurrence of animals and current speed. MACAN's reservation about the validity of AMBÜHL's interpretation based on percentage data is therefore reasonable. Moreover the percentage transformation masked several significant correlations between the density of animals and current speed and depth. Not only may AMBÜHL's data have shown spurious correlations but they may have masked some real correlations.

*Choroterpes (Euthraulius)* sp. is a useful example of the difficulties that may be involved in interpreting field data. It has been suggested that this animal was correlated with depth because there was more shelter from the current for it where the water was deepest, because stones and the cavities under them may have been larger there.

It is surprising that so many species appeared to be responding to depth changes of the small range (10 to 23 cm) recorded at Standerton. There are, however, some factors which could help to explain the correlations. For instance it may be that there were more algae in the shallower water, or that predators such as fish are affected by the depth of the water.

It should be remembered that the current speeds reported for the various sampling points apply only to the areas from which the samples were drawn. The Standerton data show how the current speed may vary at any one time at a sampling point. Much of the month to month variation in current speeds at Stations 21 and 2a may therefore be due to the fact that samples were not drawn from precisely the same area at each sampling point every month. In these circumstances there are two possible explanations when the density of a species apparently follows current speed from month to month. Firstly the correlation could be the spurious outcome of independent seasonal changes in the animal density. However, this is an unlikely explanation when, as at Station 2a (Fig. 2A), the current speed rises and falls from month to month without showing any distinct trend of change. The second possibility is that the correlation is real, but this requires that the size of the aquatic stage population of the species remains reasonably constant from month to month. In insects with an aquatic developmental stage there are often striking changes in abundance of the aquatic stage over a year, and this severely restricts the number of species which can be shown, on a month to month basis, to follow current speed changes. The density of the Simuliidae was related to current speed in CHUTTER and NOBLE's data (Table 1) and studies in other parts of the world (GRENIER 1949, PHILIPSON 1956) have shown that Simuliidae do respond to current speed. Changes in population size were almost undoubtedly responsible



for the failure of Simuliid densities to follow current speed changes from month to month at sampling points in the catchment of Vaal Dam. Another factor affecting the density of the Simuliidae is that there were several species involved, which, as MACAN points out, may easily conceal a current speed effect.

The comparison of species density and current speed data from different sampling points (Fig. 3 and 4) is important in several respects. It shows that while current speed may be an important factor regulating the density of certain animals at single sampling points (Figs. 1 and 2), current speed has no obvious effect on variation in density from sampling point to sampling point. This is because the size of the whole population of a species at a particular place is the outcome of the inter-play of many variables. Some of these variables, such as the amount of food available, would be particularly likely to mask the effect of current speed when densities are compared from station to station. This has important implications for the interpretation of data resulting from general studies of the fauna of rivers, such as the studies made by HARRISON and ELSWORTH (1958), OLIFF (1960) and CHUTTER (1967). Differences between the fauna collected from different sampling points may be ascribed to current speed differences only in exceptional circumstances. Then again many of the sharpest changes in the occurrence of species which AMBÜHL found to be correlated with current speed took place in the current speed range 0 to 10 cm/sec (AMBÜHL, figs. 23, 24, 25). Mean current speeds as low as this were not recorded in places from which the Vaal Dam Catchment stones-in-current samples were drawn.

Finally, the data presented in this paper do show that in many instances MACAN's reservations about AMBÜHL's interpretation of his field data are justified. Spurious correlations between current speed and fauna have been found — sometimes due to the percentage transformation, at other times due to subtle changes in the biotope. However, taken with observations made in stones out of the current, data from the catchment of Vaal Dam do show that, in certain circumstances, the numbers and percentages of a few species from stones-in-current biotopes appear to be directly related to the speed of the current. These results provide yet another instance of animals living among stones reacting to the speed of the water above the stones. This is an aspect of the current speed/fauna relationship which puzzled MACAN, but until the movement of water among stones has been measured at varying current speeds in the water above the stones there is little point in discussing this problem.

#### Acknowledgements

The author would like to thank Mr R. G. NOBLE for drawing his attention to the KENDALL partial rank correlation coefficient and to HOFELUND's (1963) paper.

#### 5. Summary

In stones-in-current biotopes in the streams and rivers of the Vaal Dam Catchment the density of some aquatic invertebrates appeared to be related to current speed in a series of samples collected from one biotope in one day and also from month to month at single sampling points. However, the density of these animals was not related to current speed changes from sampling point to sampling point. An attempt is made to explain these field observations.

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