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The Distances Travelled by Drifting Invertebrates in a Lake District Stream

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Summary. The distances travelled by drifting invertebrates of 18 taxa were investigated at sites 3 and 4 in the Wilfin Beck, a small stony stream in the English Lake District. Fifty invertebrates of the same taxon were released into the stream at increasing distances upstream from a large net which caught all invertebrates drifting downstream.

The relationship between the catch in the net (Y_x) and the distance from the release point to the net (X m) was well described by the regression equation:

$$Y_x = A e^{-RX}$$

where R is the constant relative rate of return of invertebrates to the bottom of the stream, and $A = Y_0$ = number of invertebrates released at each point = 50. Values of R, the mean drift distance ($\bar{X}$ m), and the distance (X_p m) travelled by P% (1%, 10%, 50%) of the drifting invertebrates were calculated for each taxon at different modal water velocities. Values of R, $\bar{X}$ and X_p were fairly constant for each taxon at a particular modal water velocity, and were not significantly affected by the source of the experimental animals (benthos or drift), by changes in illumination (daylight or darkness), or by seasonal changes, including water temperature.

The experimental taxa at site 4 were divided into the following three groups according to their ability to return to the bottom:

1. *Polycelis felina*, *Ancylus fluviatilis*, Chironomidae, Eliminthidae, and *Amphinemura sulcicollis*. Values of R, $\bar{X}$, X_p not significantly different from those obtained for dead invertebrates, which were removed from the drift by chance effects.

2. *Protonemura meyeri*, *Leuctra* spp., *Chloroperla* spp., *Rhithrogena semicolorata*, *Simulium* spp. Values of R, $\bar{X}$, X_p not significantly different from those obtained for dead invertebrates at modal water velocities ≥ 19 cm/sec. At low velocities (10–12 cm/sec), R was significantly greater and $\bar{X}$, X_p significantly smaller than values obtained for dead invertebrates.

3. *Erpobdella octoculata*, *Gammarus pulex*, *Hydropsyche* spp., *Ecdyonurus venosus*, *Ephemerella ignita*, *Baëtis rhodani*. Values of R, $\bar{X}$, X_p significantly different (R greater, $\bar{X}$ and X_p smaller) from those obtained for dead invertebrates.

The exponential law was not a good model for experiments with cased caddis larvae (*Agapetus fuscipes* and a mixed group of *Sericostoma personatum*, *Drusus annulatus*, *Potamophylax cingulatus*). Larvae sank rapidly after release and drifted over very short distances.

Values of R for each taxon were significantly higher at site 3 than at site 4, and the more rapid return at site 3 was presumably due to dense stands of aquatic macrophytes. The increase in R was greatest for *Simulium* spp. and *E. ignita*.

The relationship between $\bar{X}$ and modal water velocity (V cm/sec) was well described by the regression equation:

$$\bar{X} = a V^{b}$$

where a and b are constants. The relationship between R and V, or X_p and V, was described by similar equations. Values of a and b were calculated for each taxon at sites 3 and 4.

The drift distance was also investigated by blocking the total drift and taking drift samples at several stations downstream from the blockage. Drift rate was markedly reduced immediately below the blockage and then gradually increased downstream until it was similar to that recorded before blocking. The mathematical model developed from the detailed experiments was a good fit to the results of the blocking experiments.

The behaviour of the drifting invertebrates and their ability to return to the bottom are discussed. From the results of the present study and those of other workers, it is concluded that the mathematical model is a good model for invertebrate drift. The implications of the model are discussed, especially the relationship between drift rate and water velocity, and the proportion of the benthos in the drift.

Introduction

The downstream drift of stream invertebrates is a normal feature of lotic systems. Invertebrate drift provides a readily available food for fish, facilitates the colonisation of denuded areas of bottom, and may have a considerable bearing on secondary production (see references in Elliott, 1967a; Bishop and Hynes, 1969; Waters, 1969).

In assessing the importance of invertebrate drift in streams, it is clearly important to know how far the drifting invertebrates travel before they return to the bottom. The distance of drifting may vary considerably between species, between types of stream, and with conditions at the time of drifting. There are few estimates of drift distance and these are based on single experiments. Waters (1965) used a blocking technique to obtain estimates of about 50–60 m for *Baëtis vagans* McDunnough and *Gammarus pseudolimnaeus* Bousfield. In a somewhat similar experiment, Elliott (1967a) found that the maximum drift distance was only about 10 m in a stream section with dense stands of macrophytes. He concluded that the invertebrates probably spent only a short time in the drift before they returned to the bottom. A different technique was used by McLay (1970) who introduced benthic invertebrates into the stream by disturbing the substratum at increasing distances upstream from a drift sampler. This artificially induced drift travelled a maximum distance of 45.7 m and a mean distance of 10.7 m, but the mean distance varied from 0.5 to 19.3 m for different species.

In the present study, the drift distance was investigated by a blocking technique, and by introducing a known number of invertebrates into the stream. As the latter method was the most successful, it was used for all the detailed experiments. This work is part of a general study of invertebrate drift and benthos in the Wilfin Beck, a small stony stream in the English Lake District.

Description of Stream and Experimental Sites

The Wilfin Beck rises from two fishponds and flows southeast for about 4 km before entering Windermere on the west shore of the lake. The gradient is fairly steep (fall about 6%) for the first km and the bottom consists of large stones over stones and gravel with no aquatic macrophytes. The gradient decreases considerably for the next 1.5 km (fall about 1%) and the bottom is chiefly gravel and mud, with dense stands of aquatic macrophytes (chiefly *Callitriche aquatica* Sm. with some *Myriophyllum spicatum* L.). Site 3 (SD378949) is situated in this section and was used for a few experiments in June 1967. About 100 m downstream from site 3, the gradient changes abruptly to a final steep section (fall about 4%) where the bottom is again stony and macrophytes scarce. Site 4 (SD383941) is situated about 100 m upstream from the mouth of the stream and was used for most experiments. Aquatic macrophytes are limited to sparse clumps of moss on the larger stones and exposed rock. The stream is moderately shaded by deciduous trees, and leaf packets are found at the sides of the stream and between large stones in riffles. The physical conditions for each experiment are compared in Table 1. Oxygen concentration was over 85% saturation in each experiment.

Table 1. *Physical conditions for experiments at sites 3 and 4*

	Water velocity (Mode and range in cm/sec)	Water temperature (Range °C)	Modal depth (cm)	Modal width (m)
Site 4				
February	30 (17–36)	5.4–6.2	18	3.7
	46 (27–53)	5.9–7.2	18	3.7
	60 (30–70)	5.7–6.9	20	3.7
April	10 (8–15)	8.9–9.6	16	3.5
	19 (12–23)	8.7–9.4	17	3.5
	30 (20–35)	8.3–8.9	18	3.7
	50 (28–58)	8.1–9.1	18	3.7
June	12 (9–18)	13.2–14.7	16	3.5
	20 (12–25)	11.4–13.2	17	3.5
Site 3				
June	20 (15–23)	11.3–12.2	25	1.6
	40 (22–47)	11.2–12.4	40	1.6

Methods and Experimental Procedures

A large net (mesh 440 μ) with a rectangular mouth (width 120 cm, depth 45 cm) was placed across the stream. Wooden boards were arranged at the bottom and sides of the net mouth so that the stream was channelled through the net. Fifty invertebrates were placed in a cylindrical container (length 15 cm, diameter 7.5 cm) with a lid and bottom of nylon sifting cloth (mesh 440 μ). The container was placed on the bottom of the stream so that the water flowed through the cylinder and the lid faced downstream. In each experiment, the container was agitated to detach any invertebrates clinging to the sides, the lid was removed, and the invertebrates were swept into the current close to the bottom. The first group of 50 invertebrates were always released at the mouth of the net, then the net was emptied and the catch counted. This procedure was repeated at increasing distances upstream from the net, and the time interval between the release of the invertebrates and the emptying of the net was increased to allow for the greater distance of drifting. The release points were usually at 1 m intervals but shorter intervals were used for *Baëtis rhodani*, *Ephemerella ignita*, *Ecdyonurus venosus*, and *Gammarus pulex* (all 0.5 m intervals) and for caddis larvae with stony cases (0.25 m intervals).

The experiments were performed at different modal water velocities in February, April and June 1967 at site 4, and in June 1967 at site 3. At each modal water velocity, there was always an experiment with dead invertebrates and this was repeated to give 3 catches for each distance from the net. The dead invertebrates were all taxa which were frequently taken in drift samples. In the experiments with live invertebrates, the 50 invertebrates in each experiment always belonged to the same taxon, i.e. same species, genus or family. An experiment was repeated twice at each modal water velocity, first with invertebrates from drift samples and then with invertebrates from bottom samples. These experiments were all performed during daylight when drift rates were low, and it was assumed that only experimental animals were caught in the net. This assumption was checked by leaving the large net in the stream for a sampling period equal to the time interval between release of invertebrates and emptying of net. Although several terrestrial invertebrates were usually taken in these samples, no experimental taxa were taken. An experiment was repeated three times for some species (*B. rhodani*, *E. ignita*, *E. venosus*, *G. pulex*), and the third experiment was performed at night, using invertebrates obtained from drift samples. As nocturnal drift rates were high for these species, it could not be assumed that only experimental animals entered the net. Therefore the invertebrates were marked by leaving the mayfly nymphs in methylene blue or neutral red (0.5 parts/1000 water) for 12 h, and by marking *G. pulex* with cellulose paint. These marking techniques did not appear to affect the invertebrates and this conclusion was confirmed by the results of the experiments.

Invertebrate drift from more than one point was simulated by releasing invertebrates of the same taxon at several equidistant points from 0 to X_n m upstream from the large net. There was a 1 m interval between adjacent release points and 50 invertebrates were released at each point. These experiments were performed in April and June 1967, and there were separate day and night experiments for *G. pulex*, using marked individuals at night.

A blocking technique was also used to investigate the distances travelled by drifting invertebrates in single experiments at site 4 in February, April and June 1967. A series of nets was placed across the stream so that no drifting invertebrates passed the blocking point. Small nets (mesh 440 μ) with rectangular mouths (width 12.5 cm, depth 25 cm) were located at several stations (6 in February and April, 4 in June) downstream from the blocking point. Iron rods secured one net in midstream at each station. As the depth of the net mouth was greater than stream depth and the net rested on the bottom, the whole water column was sampled from bottom to surface. The small mouth of the net was a compromise between the disadvantages of a small catch and the need to ensure that the removal of drifting invertebrates at one station did not significantly affect the catch at the next downstream station. Drift samples were taken at each station from dusk to dawn for 3 nights before blocking in the February and April experiments, and for another night after blocking. In June, 24 h-samples were taken at each station for 3 days before blocking and for one day after blocking.

A small Ott current meter was used to measure water velocity at about 3 cm from the surface of the substratum. Five readings were taken across the stream at increasing distances from the large net or blocking point until the length of each experiment was covered. The experimental sections were carefully chosen to ensure that variations in water velocity were minimal. Maximum and minimum thermometers were read and reset under water at both sites in each experiment. Oxygen concentration was measured with a Mackereth (1964) meter.

Mathematical Model for the Analysis of the Experiments

The number of invertebrates caught in the net (ordinate: Y_x) was plotted against the distance (abscissa: X m) from the net to the point at which 50 invertebrates were introduced into the drift. As the distance from the net increased, the catch in the net decreased. The data lay approximately on a straight line when they were plotted on a semi-logarithmic scale but not on an arithmetic scale (e.g. Fig. 1). Therefore the exponential law is probably a suitable model for the data. As the value of Y_x was 0 for some values of X, it was necessary to plot

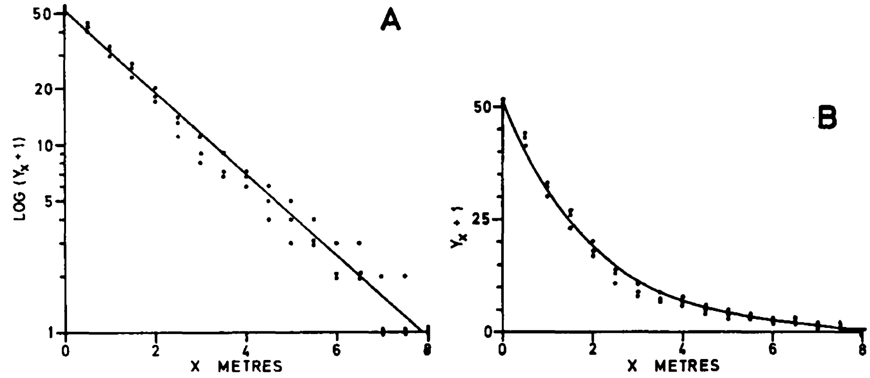

Fig. 1A and B. Relationship between catch (Y_x) and distance between net and release point (X m) for *Baëtis rhodani* at a modal water velocity of 20 cm/sec in June 1967. A On semi-logarithmic scale. B On arithmetic scale

$\log_e(Y_x+1)$ against X. The relationship between the two variables is given by the regression equation:

$$\log_e(Y_x+1)=\log_e A - RX$$

or (1)

$$(Y_x+1)=Ae^{-RX}$$

where $e=2.718$ is the base of natural logarithms, A is the value of (Y_x+1) at the intercept of the regression line and the ordinate, R is the sample regression coefficient and is also the constant *relative* rate of return of invertebrates to the bottom of the stream. Therefore the rate of return to the bottom is proportional to the numbers remaining in the drift, a result which can be expressed by calculus thus:

$$\frac{dY}{dX}=-RY$$

which leads to the relation:

$$\log_e(Y_x+1)=\log_e(Y_0+1)-RX$$

or (2)

$$(Y_x+1)=(Y_0+1)e^{-RX}$$

where Y_x is the number of invertebrates remaining in the drift at X m from the point at which Y_0 invertebrates were introduced into the drift. As $Y_0=50$ in each experiment, constant A in the regression equation should be equal to $(Y_0+1)=51$. Departures from this value were usually small, but indicated that the exponential law was not a perfect model for the data. The mean distance $(\bar{X})$ travelled by a drifting invertebrate is given by the sum of the distances travelled by individuals divided by the total number of invertebrates introduced into the drift:

$$\bar{X}=\int_0^\infty \frac{Y_0 e^{-RX}\,dX}{Y_0}=\frac{1}{R}\,. \tag{3}$$

The distance (X_p) travelled by $P\%$ of the drifting invertebrates is given by:

$$X_p=\frac{\log_e 100-\log_e P}{R}=(\log_e 100-\log_e P)\bar{X}\,. \tag{4}$$

Values of X_p were calculated for $P=1\%$, $P=10\%$, $P=50\%$. Note that X_p is also the distance over which $(100-P)\%$ of the drifting invertebrates return to the bottom.

The catch (Y_x) in the net at X m downstream from a point at which Y_0 invertebrates were introduced into the drift is given by:

$$Y_x=Y_0e^{-RX}.$$

If the same number (Y_0) of invertebrates was introduced simultaneously into the drift at several equidistant release points from 0 to X_n m upstream from the net, then the total catch (Y_T) is given by:

$$Y_T = (Y_0 e^{-RX_0}) + (Y_0 e^{-RX_1}) + (Y_0 e^{-RX_2}) + \ldots + (Y_0 e^{-RX_n})$$
$$= Y_0 \sum_{i=0}^{i=n} e^{-RX_i} = Y_0 \left[\frac{1 - e^{-RX_{n+1}}}{1 - e^{-R}} \right] \tag{5}$$

where there are $n+1$ release points and the distance between adjacent release points is the same. As X_n tends to infinity, $e^{-RX_{n+1}}$ tends to 0 and the maximum drift ($Y_{\max}$) from the area upstream from the net is given by:

$$Y_{\max} = \frac{Y_0}{1 - e^{-R}}\,. \tag{6}$$

This relationship was tested in field experiments by simultaneously releasing 50 invertebrates at several points with a 1 m interval between adjacent release points. If the distance between adjacent release points is infinitely small, then the total catch (Y_T) from all possible points upstream is given by:

$$Y_T = Y_0 \int_0^x e^{-RX} dX = \frac{Y_0 (1 - e^{-RX})}{R}\,. \tag{7}$$

As X_n tends to infinity, e^{-RX} tends to 0 and the maximum drift from the area upstream from the net is given by:

$$Y_{\max} = \frac{Y_0}{R} = Y_0 \bar{X}\,. \tag{8}$$

In the blocking experiment, the nets across the stream ensured that no drifting invertebrates passed the blocking point. If the assumptions inherent in Eq. (7) are correct, then this equation will give the catch (Y_T) at increasing distances (X m) downstream from the blocking point. Although Y_0 was unknown, $Y_{\max}$ was assumed to be equal to "normal drift", which was measured before blocking. Therefore the catch (Y_T) at X m downstream from the blocking point is given by:

$$Y_T = Y_{\max} (1 - e^{-RX}) \tag{9}$$

where $Y_{\max}$ is the normal drift at each sampling point. R was known for each taxon from the detailed experiments, and can be found directly from the blocking experiments, using the following linear regression equation:

$$\log_e \left(\frac{Y_{\max}}{Y_{\max} - Y_T} \right) = RX\,. \tag{10}$$

Expected catches obtained from Eq. (9) were compared with actual catches in the blocking experiments.

Results

a) Detailed Experiments at Site 4

The taxa used in the experiments are listed in Table 2. Eliminthidae were chiefly *Elmis aenea* Müll. with a few *Limnius volkmari* (Panzer). *Leuctra* spp. were *L. hippopus* Kempny, *L. inermis* Kempny, *L. fusca* (L.) in April and *L. fusca* in June. *Chloroperla* spp. were *C. torrentium* (Pictet) and *C. tripunctata* (Scopoli). *Hydropsyche* spp. were chiefly *H. instabilis* (Curtis). Values of A and R in Eq. (1) were calculated for each experiment. Both the correlation coefficients (modal value -0.98, range -0.89 to -1.00) and F-values from the variance ratio (comparing mean square due to regression with residual variance) were highly significant ($P < 0.001$) for all experiments except those for caddis larvae with stony cases. Therefore the regression lines were a good fit to the data and the exponential law was a good model for the experiments.

No significant differences ($P > 0.05$) were found at each modal water velocity between the results of the three experiments with different groups of dead invertebrates, or between the experiments with benthic and drifting invertebrates of the same taxon, or between night and day experiments with the same taxon (*G. pulex*, *E. venosus*, *E. ignita*, *B. rhodani*). Therefore the results of the experiments with dead invertebrates or the same taxon were pooled to give values of A and R for each modal water velocity (Table 2). Although they were not significantly different, values of R in the day experiments with *G. pulex* were consistently higher than those obtained in the night experiments (Table 2). No similar trend was shown by the values of R in the day and night experiments with mayfly nymphs. Although few comparisons could be made, no significant differences were found between values of R at similar modal water velocities in different months, i.e. 30 cm/sec in February and April, 19–20 cm/sec in April and June. Therefore the relative rate of return (R) of invertebrates of the same taxon to the bottom of the stream was fairly constant at a particular modal water velocity, and was not significantly affected by the source of the experimental animals (benthos or drift), by changes in illumination (daylight or darkness), or by seasonal changes, including water temperature (Table 1). As R was not affected by these factors, then the mean drift distance [$\bar{X}$, see Eq. (3)] and the distance [X_p, see Eq. (4)] travelled by P% of the drifting invertebrates were also not affected by the same factors.

In the experiments with dead invertebrates, the animals in the drift could not actively return to the bottom and were removed from the drift by chance effects, e.g. they settled in areas of still water, were caught in leaf packets or between stones, or were caught by predatory

Table 2. *Results of experiments with*

The constants A and R ($\pm$ 95% confidence limits) in the regression equation are given for value of R for dead invertebrates, and significant differences are indicated by asterisks thus: cates that no experiment

Modal water velocity (cm/sec)		February 1967 30	 46	 60
Dead invertebrates	A	50.95	51.09	52.41
	R	0.0988 ± 0.0032	0.0668 ± 0.0020	0.0507 ± 0.0016
Group 1				
Polycelis felina (Dalyell)	A	50.97	50.91	51.60
	R	0.0973 ± 0.0058	0.0661 ± 0.0035	0.0502 ± 0.0028
Ancylus fluviatalis Müll.	A	51.95	51.07	51.43
	R	0.0990 ± 0.0191	0.0691 ± 0.0037	0.0516 ± 0.0028
Chironomidae (larvae)	A	51.10	51.05	51.57
	R	0.0967 ± 0.0060	0.0682 ± 0.0037	0.0509 ± 0.0028
Elminthidae (adults and larvae)	A	51.71	50.95	51.43
	R	0.1020 ± 0.0051	0.0661 ± 0.0039	0.0507 ± 0.0028
Agapetus fuscipes Curtis (no case)	A	—	—	—
	R			
Amphinemura sulcicollis (Stephens)	A	50.96	51.00	50.36
	R	0.0979 ± 0.0060	0.0668 ± 0.0035	0.0497 ± 0.0028
Group 2				
Protonemura meyeri (Pictet)	A	50.99	51.05	51.62
	R	0.0992 ± 0.0067	0.0672 ± 0.0037	0.0497 ± 0.0124
Leuctra spp.	A	—	—	—
	R			
Chloroperla spp.	A	—	—	—
	R			
Rhithrogena semicolorata (Curtis)	A	—	—	—
	R			
Simulium spp.	A	51.10	51.26	—
	R	0.0992 ± 0.0074	0.0682 ± 0.0035	
Group 3				
Erpobdella octoculata L.	A	—	—	—
	R			
Gammarus pulex L. (day)	A	50.95 ***	51.70 ***	52.26 ***
	R	0.3530 ± 0.0341	0.2383 ± 0.0097	0.1794 ± 0.0106
Gammarus pulex (night)	A	51.05 ***	52.02 ***	52.13 ***
	R	0.3408 ± 0.0339	0.2282 ± 0.0157	0.1743 ± 0.0106
Hydropsyche spp.	A	51.05 ***	—	—
	R	0.1481 ± 0.0147		
Ecdyonurus venosus (Fabr.)	A	50.97 ***	51.26 ***	51.62 ***
	R	0.1953 ± 0.0256	0.1290 ± 0.0097	0.0944 ± 0.0062
Ephemerella ignita (Poda)	A	—	—	—
	R			
Baëtis rhodani (Pictet)	A	52.44 ***	52.89 ***	52.63 ***
	R	0.3461 ± 0.0180	0.2344 ± 0.0078	0.1791 ± 0.0051

fish or net-spinning caddis larvae. Values of R for some live taxa (Group 1 in Table 2) were not significantly different ($P > 0.05$) from that obtained for dead invertebrates at the same modal water velocity. Therefore these taxa were probably removed from the drift simply by chance effects. This was also true for other live taxa at high modal water velocities (Group 2 in Table 2), but at low water velocities (10–12 cm/sec) these taxa *introduced invertebrates at site 4*

each taxon at each modal water velocity. Values of R in each column were compared with the
$*P < 0.05$, $**P < 0.01$, $***P < 0.001$, no asterisk $P > 0.05$ (difference not significant). A dash indi-
was performed.

April 1967				June 1967	
10	19	30	50	12	20
51.54 0.3162 ± 0.0228	51.56 0.1580 ± 0.0074	52.02 0.1041 ± 0.0044	51.12 0.0596 ± 0.0018	52.30 0.2593 ± 0.0154	51.45 0.1497 ± 0.0076
51.00 0.3157 ± 0.0403	51.05 0.1587 ± 0.0122	51.06 0.1052 ± 0.0090	50.36 0.0587 ± 0.0030	51.00 0.2602 ± 0.0276	51.04 0.1508 ± 0.0184
51.00 0.3180 ± 0.0396	51.10 0.1584 ± 0.0129	50.99 0.1015 ± 0.0074	50.36 0.0603 ± 0.0028	51.03 0.2604 ± 0.0272	51.07 0.1451 ± 0.0122
50.99 0.3178 ± 0.0396	51.18 0.1591 ± 0.0145	51.11 0.1027 ± 0.0074	51.30 0.0587 ± 0.0039	50.95 0.2581 ± 0.0329	51.05 0.1501 ± 0.0129
50.95 0.3180 ± 0.1027	50.99 0.1580 ± 0.0129	51.24 0.1043 ± 0.0083	51.58 0.0615 ± 0.0030	50.98 0.2593 ± 0.0214	51.08 0.1547 ± 0.0085
51.40 0.3157 ± 0.0408	51.32 0.1557 ± 0.0145	51.18 0.1048 ± 0.0076	51.55 0.0601 ± 0.0032	51.02 0.2602 ± 0.0272	51.06 0.1469 ± 0.0120
50.91 0.3173 ± 0.0387	50.84 0.1573 ± 0.0136	50.98 0.0990 ± 0.0090	51.64 0.0606 ± 0.0037	—	—
51.50 *** 0.5453 ± 0.0587	51.03 0.1591 ± 0.0129	51.95 0.1050 ± 0.0085	—	—	—
51.31 *** 0.5460 ± 0.0649	50.96 0.1564 ± 0.0131	51.06 0.1034 ± 0.0090	52.00 0.0580 ± 0.0030	51.40 *** 0.5501 ± 0.0578	51.00 0.1506 ± 0.0150
51.60 *** 0.5471 ± 0.0596	51.05 0.1591 ± 0.0145	51.05 0.1050 ± 0.0087	51.62 0.0590 ± 0.0042	51.44 *** 0.5517 ± 0.0463	51.31 0.1501 ± 0.0134
51.03 *** 0.5485 ± 0.0590	51.05 * 0.1722 ± 0.0129	51.04 0.0981 ± 0.0092	51.30 0.0571 ± 0.0041	—	—
51.00 *** 0.4681 ± 0.0583	51.17 0.1591 ± 0.0129	51.10 0.1048 ± 0.0074	51.40 0.0603 ± 0.0041	51.03 *** 0.5683 ± 0.0509	51.06 0.1504 ± 0.0136
—	—	—	—	50.95 *** 0.5554 ± 0.0191	51.08 *** 0.2782 ± 0.0113
50.03 *** 1.0150 ± 0.1669	51.24 *** 0.5473 ± 0.0578	51.17 *** 0.3756 ± 0.0286	51.17 *** 0.2287 ± 0.0154	50.13 *** 0.9807 ± 0.1547	50.72 *** 0.5139 ± 0.0322
50.93 *** 0.9818 ± 0.0831	51.12 *** 0.5204 ± 0.0444	51.07 *** 0.3576 ± 0.0237	52.19 *** 0.2229 ± 0.0120	50.91 *** 0.9397 ± 0.0721	50.97 *** 0.4879 ± 0.0530
51.03 *** 0.5027 ± 0.0490	50.95 *** 0.2369 ± 0.0244	51.09 *** 0.1515 ± 0.0140	51.65 *** 0.0870 ± 0.0051	51.00 *** 0.3774 ± 0.0465	51.18 *** 0.2243 ± 0.0145
51.00 *** 0.6305 ± 0.0870	51.19 *** 0.3162 ± 0.0629	51.06 *** 0.2100 ± 0.0288	51.80 *** 0.1200 ± 0.0191	51.00 *** 0.5183 ± 0.0940	—
—	—	—	—	51.73 *** 0.2888 ± 0.0136	51.14 *** 0.1732 ± 0.0279
49.80 *** 1.0026 ± 0.0592	51.98 *** 0.5383 ± 0.0242	52.23 *** 0.3657 ± 0.0150	52.78 *** 0.2266 ± 0.0076	50.37 ** 0.9176 ± 0.0652	51.55 *** 0.4999 ± 0.0228

returned to the bottom at a significantly faster rate than dead invertebrates. Although all the remaining taxa (Group 3 in Table 2) returned to the bottom at a faster rate than dead invertebrates, the relative rate of return (measured by R) greatly varied between species. This variation had a marked effect on the distances travelled by different species (Table 3).

Table 3. *Distances travelled*

Mean drift distance ($\overline{X}$ metres ± 95% confidence limits) and distances travelled
Taxa in groups 1 and 2 are listed in Table 2.

	February 1967		
Modal water velocity (cm/sec)	30	46	60
Mean drift distance ($\overline{X}$)			
Group 1	9.89 ± 0.10	15.17 ± 0.16	19.80 ± 0.21
Group 2	9.92 ± 0.10	15.37 ± 0.26	20.14 ± 0.40
Erpobdella octoculata	—	—	—
Gammarus pulex	2.88 ± 0.28	4.29 ± 0.17	5.66 ± 0.33
Hydropsyche spp.	6.75 ± 0.68	—	—
Ecdyonurus venosus	5.12 ± 0.75	7.75 ± 0.60	10.59 ± 0.70
Ephemerella ignita	—	—	—
Baëtis rhodani	2.89 ± 0.15	4.27 ± 0.14	5.58 ± 0.16
Distance travelled by 1% ($X_{p=1}$)			
Group 1	45.54 ± 0.49	69.89 ± 0.81	91.20 ± 1.09
Group 2	45.66 ± 1.50	70.75 ± 2.30	92.71 ± 3.00
Erpobdella octoculata	—	—	—
Gammarus pulex	13.26 ± 1.29	19.76 ± 0.78	26.05 ± 1.52
Hydropsyche spp.	31.09 ± 3.13	—	—
Ecdyonurus venosus	23.58 ± 3.45	35.69 ± 2.76	48.77 ± 3.22
Ephemerella ignita	—	—	—
Baëtis rhodani	13.31 ± 0.69	19.66 ± 0.65	25.70 ± 0.74
Distance travelled by 10% ($X_{p=10}$)			
Group 1	22.77 ± 0.22	34.95 ± 0.37	45.60 ± 0.50
Group 2	22.87 ± 0.20	35.43 ± 0.68	46.43 ± 1.10
Erpobdella octoculata	—	—	—
Gammarus pulex	6.63 ± 0.65	9.88 ± 0.39	13.03 ± 0.76
Hydropsyche spp.	15.54 ± 1.57	—	—
Ecdyonurus venosus	11.79 ± 1.73	17.85 ± 1.38	24.38 ± 1.61
Ephemerella ignita	—	—	—
Baëtis rhodani	6.65 ± 0.35	9.83 ± 0.32	12.85 ± 0.37
Distance travelled by 50% ($X_{p=50}$)			
Group 1	6.85 ± 0.08	10.52 ± 0.13	13.73 ± 0.17
Group 2	6.88 ± 0.04	10.66 ± 0.17	13.97 ± 0.28
Erpobdella octoculata	—	—	—
Gammarus pulex	2.00 ± 0.19	2.97 ± 0.12	3.92 ± 0.23
Hydropsyche spp.	4.68 ± 0.47	—	—
Ecdyonurus venosus	3.55 ± 0.52	5.37 ± 0.42	7.34 ± 0.49
Ephemerella ignita	—	—	—
Baëtis rhodani	2.00 ± 0.10	2.96 ± 0.10	3.87 ± 0.11

by drifting invertebrates

by 1%, 10%, and 50% ($X_p \pm 95\%$ confidence limits) of the drifting invertebrates. All taxa are given for group 3.

April 1967				June 1967	
10	19	30	50	12	20
3.28 ± 0.02	6.25 ± 0.05	9.89 ± 0.10	16.50 ± 0.18	3.94 ± 0.03	6.58 ± 0.06
1.83 ± 0.07	6.17 ± 0.01	9.92 ± 0.10	16.73 ± 0.30	1.81 ± 0.07	6.51 ± 0.01
—	—	—	—	1.80 ± 0.07	3.60 ± 0.15
1.01 ± 0.08	1.88 ± 0.17	2.73 ± 0.20	4.43 ± 0.24	1.04 ± 0.08	2.00 ± 0.13
1.99 ± 0.20	4.22 ± 0.44	6.60 ± 0.62	11.49 ± 0.67	2.65 ± 0.33	4.46 ± 0.30
1.59 ± 0.23	3.16 ± 0.66	4.76 ± 0.66	8.33 ± 0.86	1.93 ± 0.37	—
—	—	—	—	3.46 ± 0.16	5.77 ± 0.96
1.00 ± 0.06	1.86 ± 0.09	2.73 ± 0.11	4.41 ± 0.15	1.09 ± 0.08	2.00 ± 0.09
15.10 ± 0.09	28.80 ± 0.27	45.54 ± 0.49	75.98 ± 0.89	18.14 ± 0.13	30.32 ± 0.29
8.41 ± 0.31	28.40 ± 0.95	45.66 ± 1.50	77.03 ± 2.50	8.36 ± 0.37	29.97 ± 0.10
—	—	—	—	8.29 ± 0.32	16.58 ± 0.69
4.65 ± 0.37	8.66 ± 0.78	12.57 ± 0.92	20.40 ± 1.11	4.79 ± 0.37	9.21 ± 0.60
9.16 ± 0.92	19.43 ± 2.03	30.39 ± 2.86	52.91 ± 3.09	12.20 ± 1.52	20.54 ± 1.38
7.32 ± 1.06	14.55 ± 3.04	21.92 ± 3.04	38.36 ± 3.96	8.89 ± 1.70	—
—	—	—	—	15.93 ± 0.74	26.57 ± 4.42
4.61 ± 0.28	8.57 ± 0.41	12.57 ± 0.51	20.31 ± 0.69	5.02 ± 0.37	9.21 ± 0.41
7.55 ± 0.04	14.40 ± 0.12	22.77 ± 0.22	38.00 ± 0.40	9.07 ± 0.06	15.16 ± 0.13
4.21 ± 0.15	14.23 ± 0.01	22.87 ± 0.20	38.58 ± 0.90	4.18 ± 0.19	15.01 ± 0.01
—	—	—	—	4.15 ± 0.16	8.29 ± 0.35
2.33 ± 0.18	4.33 ± 0.39	6.29 ± 0.46	10.20 ± 0.55	2.40 ± 0.18	4.61 ± 0.30
4.58 ± 0.46	9.72 ± 1.01	15.20 ± 1.43	26.46 ± 1.54	6.10 ± 0.76	10.27 ± 0.69
3.66 ± 0.53	7.28 ± 1.52	10.96 ± 1.52	19.18 ± 1.98	4.44 ± 0.85	—
—	—	—	—	7.97 ± 0.37	13.29 ± 2.21
2.30 ± 0.14	4.28 ± 0.21	6.29 ± 0.25	10.15 ± 0.35	2.51 ± 0.18	4.61 ± 0.21
2.27 ± 0.02	4.33 ± 0.05	6.85 ± 0.08	11.44 ± 0.15	2.73 ± 0.03	4.56 ± 0.05
1.23 ± 0.05	4.29 ± 0.01	6.88 ± 0.04	11.61 ± 0.20	1.26 ± 0.06	4.52 ± 0.01
—	—	—	—	1.25 ± 0.05	2.50 ± 0.10
0.70 ± 0.06	1.30 ± 0.12	1.89 ± 0.14	3.07 ± 0.17	0.72 ± 0.06	1.39 ± 0.09
1.38 ± 0.14	2.93 ± 0.31	4.57 ± 0.43	7.96 ± 0.46	1.84 ± 0.23	3.09 ± 0.21
1.10 ± 0.16	2.19 ± 0.46	3.30 ± 0.46	5.77 ± 0.60	1.34 ± 0.26	—
—	—	—	—	2.40 ± 0.11	4.00 ± 0.67
0.69 ± 0.04	1.29 ± 0.06	1.89 ± 0.08	3.06 ± 0.10	0.76 ± 0.06	1.39 ± 0.06

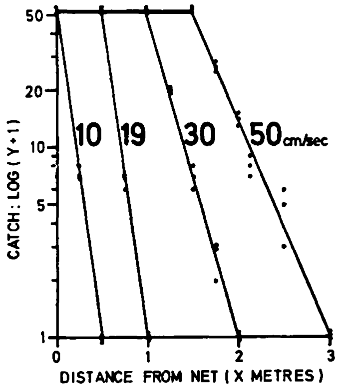

Fig. 2

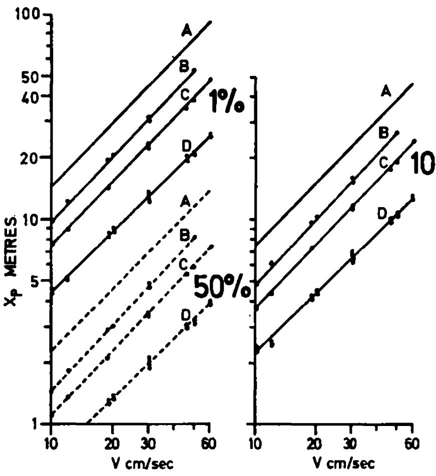

Fig. 3

Fig. 2. Relationship between catch (Y_x) and distance between net and release point (X m) for *Agapetus fuscipes* at different modal water velocities in April 1967

Fig. 3. Regression lines for the relationship between the distance (X_p) travelled by P% ($P = 1$%, 10%, 50%) of the drifting invertebrates and modal water veocityl (V cm/sec). X_p is also the distance over which $(100 - P)$% of the drifting invertebrates returned to the bottom. *A* Groups 1 and 2; *B Hydropsyche* spp.; *C Ecdyonurus venosus*, *D Gammarus pulex*, *Baëtis rhodani*. As there was a large amount of data for groups 1 and 2, the individual points are omitted for regression line *A*

The mean drift distance ($\bar{X}$ m) and the distances travelled by 1%, 10% and 50% (X_p m) of the drifting invertebrates were calculated from Eqs. (3) and (4). Values of X_p are also the distances over which 99%, 90% and 50% of the drifting invertebrates returned to the bottom. As there were no significant differences at each modal water velocity between the values of R within groups 1 and 2, values of $\bar{X}$ and X_p were not calculated for each taxon in these groups. Although taxa in group 1 did not return to the bottom at a faster rate than dead invertebrates, the drift distances were surprisingly short at low water velocities, e.g. 90% of the invertebrates had returned to the bottom after only 7.55 m at 10 cm/sec. Values of $\bar{X}$ and X_p for group 2 were not significantly different ($P > 0.05$) from those for group 1, except at 10 and 12 cm/sec. At these low water velocities, invertebrates in group 2 drifted about half the distance travelled by invertebrates in group 1. All taxa in group 3 drifted over shorter distances than taxa in group 1, but at low water velocities (10–12 cm/sec) some taxa in group 3 returned to the bottom at either a slower rate (*Ephemerella ignita* and *Hydropsyche* spp.)

Table 4. *Results of experiments with cased caddis larvae at site 4*

Values of C (in metres), A and R, mean drift distance ($\bar{X}$ metres ± 95% confidence limits), and distances travelled by 1% ($X_{p=1}$) and 10% ($X_{p=10}$) of the drifting larvae are given for each modal water velocity.

		April 1967				June 1967	
Modal water velocity	(cm/sec)	10	19	30	50	12	20
Agapetus fuscipes	C	0.0	0.50	1.0	1.51	0.0	0.50
	A	51.43	2540.40	2705.90	2536.30	51.48	2542.20
	R	7.8650	7.8401	3.9584	2.5874	7.8645	7.8650
	$\bar{X}$	0.13 ± 0.001	0.63 ± 0.003	1.25 ± 0.011	1.90 ± 0.035	0.13 ± 0.002	0.63 ± 0.003
	$X_{p=1}$	0.60 ± 0.002	1.10 ± 0.010	2.15 ± 0.050	3.31 ± 0.160	0.60 ± 0.010	1.10 ± 0.010
	$X_{p=10}$	0.30 ± 0.001	0.80 ± 0.007	1.58 ± 0.020	2.41 ± 0.080	0.30 ± 0.005	0.80 ± 0.007
Other species	C	0.0	0.54	1.09	1.70	0.0	0.54
	A	51.19	3478.6	3809.0	4083.2	51.30	3557.1
	R	7.8800	7.8779	3.9681	2.5817	7.9258	7.9005
	$\bar{X}$	0.13 ± 0.013	0.67 ± 0.012	1.34 ± 0.025	2.09 ± 0.035	0.13 ± 0.012	0.67 ± 0.013
	$X_{p=1}$	0.60 ± 0.060	1.14 ± 0.055	2.24 ± 0.010	3.50 ± 0.160	0.60 ± 0.055	1.14 ± 0.060
	$X_{p=10}$	0.30 ± 0.030	0.84 ± 0.028	1.67 ± 0.050	2.60 ± 0.080	0.30 ± 0.028	0.84 ± 0.030

or about the same rate (*Erpobdella octoculata* and *Ecdyonurus venosus*) as the taxa in group 2. *Gammarus pulex* and *Baëtis rhodani* drifted over very short distances, and both species were capable of a rapid return to the bottom, even at high water velocities.

The exponential law did not fit the results of the experiments with cased caddis larvae. There were separated experiments for *Agapetus fuscipes*, but the less numerous species (*Sericostoma personatum* Spence, *Drusus annulatus* Stephens, *Potamophylax cingulatus* Stephens) were treated as one group. As all these larvae had stony cases, they sank rapidly after release and drifted over a short distance. No larvae returned to the bottom for a short distance (C m) which increased with increasing water velocity, and then a rapid return to the bottom followed the exponential law (e.g. Fig. 2). As the maximum catch for these experiments was 50 larvae, C was defined as the value of X for which $(Y_x + 1) = 51$. Values of C, A and R were calculated for each experiment, together with the mean drift distance and the distances travelled by 1% and 10% of the drifting larvae (Table 4). Caddis larvae with stony cases were rarely taken in drift samples but larvae of *A. fuscipes* were often taken without their cases. Unlike cased larvae, these caseless larvae were incapable of a rapid return to the bottom (cf. Tables 2 and 4).

Although the results of other experiments did not show a significant departure from the exponential law, values of A often departed from the expected value of 51 [cf. Eqs. (1) and (2)]. The value of A was generally, but not always, higher than expected at high water velocities and lower than expected at low water velocities (Table 2). These differences were always small and were never significant. Too high a value of A indicates a slightly delayed return to the bottom at short distances from the net, whereas too low a value of A indicates that the rate of return to the bottom at short distances from the net was slightly faster than that given by R. Therefore the exponential law was a very good, but not a perfect, model for the experiments.

b) Experiments at Site 3

These experiments were limited to two modal water velocities in June. As there was no significant difference ($P > 0.05$) between the results of experiments with benthic and drifting invertebrates, or between the results of day and night experiments with drifting invertebrates of *Gammarus pulex*, *Ephemerella ignita*, and *Baëtis rhodani*, results for the same taxon were pooled to give values of A and R [Eq. (1)], $\bar{X}$ and X_p for each modal water velocity (Table 5).

The rate of return to the bottom of each taxon was significantly faster ($P < 0.05$) at site 3 than at site 4 (cf. values of R in Tables 2 and 5), and the more rapid return at site 3 was presumably due to the dense

Table 5. *Results of experiments with introduced invertebrates at modal water velocities of 20 and 40 cm/sec at site 3 in June 1967*

A and R are constants in regression Eq. (1). $\bar{X}$ is mean drift distance and X_p is the distance travelled by 1% or 10% of the drifting invertebrates. 95% confidence limits are given for each value. See Table 2 for explanation of asterisks.

	cm/sec	A	R	$\bar{X}$	$X_{p=1}$	$X_{p=10}$
Dead invertebrates	20	51.16	0.3947 ± 0.0283	2.53 ± 0.15	11.65 ± 0.69	5.83 ± 0.35
	40	51.04	0.1907 ± 0.0078	5.24 ± 0.22	24.13 ± 1.01	12.07 ± 0.51
Polycelis felina	20	50.99	0.3954 ± 0.0594	2.53 ± 0.39	11.65 ± 1.80	5.83 ± 0.90
	40	51.03	0.1895 ± 0.0143	5.28 ± 0.40	24.32 ± 1.84	12.16 ± 0.92
Chironomidae (larvae)	20	51.04	0.3940 ± 0.0465	2.54 ± 0.30	11.70 ± 1.38	5.85 ± 0.69
	40	51.07	0.1902 ± 0.0141	5.26 ± 0.39	24.22 ± 1.80	12.11 ± 0.90
Elminthidae (adults and larvae)	20	50.95	0.3944 ± 0.0649	2.54 ± 0.42	11.70 ± 1.93	5.85 ± 0.96
	40	51.05	0.1914 ± 0.0138	5.23 ± 0.38	24.09 ± 1.75	12.04 ± 0.87
Leuctra spp.	20	51.05	0.3956 ± 0.0649	2.53 ± 0.42	11.65 ± 1.93	5.83 ± 0.96
	40	51.60	0.1907 ± 0.0141	5.24 ± 0.39	24.13 ± 1.80	12.07 ± 0.90
Chloroperla spp.	20	50.95	0.3951 ± 0.0500	2.53 ± 0.32	11.65 ± 1.47	5.83 ± 0.73
	40	51.04	0.1902 ± 0.0143	5.26 ± 0.40	24.22 ± 1.84	12.11 ± 0.92
Simulium spp.	20	51.10	$\overset{***}{0.7903}$ ± 0.0905	1.27 ± 0.15	5.85 ± 0.69	2.92 ± 0.34
	40	51.31	$\overset{***}{0.3838}$ ± 0.0283	2.61 ± 0.20	12.02 ± 0.92	6.01 ± 0.46
Erpobdella octoculata	20	51.05	$\overset{***}{0.7675}$ ± 0.0721	1.30 ± 0.14	5.99 ± 0.65	2.99 ± 0.32
	40	51.24	$\overset{***}{0.3806}$ ± 0.0267	2.63 ± 0.20	12.11 ± 0.92	6.06 ± 0.46
Gammarus pulex	20	50.01	$\overset{***}{1.0306}$ ± 0.1117	0.97 ± 0.12	4.49 ± 0.58	2.24 ± 0.29
	40	51.31	$\overset{***}{0.5395}$ ± 0.0571	1.88 ± 0.20	8.64 ± 0.92	4.31 ± 0.46
Ephemerella ignita	20	47.69	$\overset{***}{0.9597}$ ± 0.0647	1.04 ± 0.07	4.79 ± 0.32	2.40 ± 0.16
	40	50.98	$\overset{***}{0.4797}$ ± 0.0283	2.08 ± 0.14	9.58 ± 0.65	4.79 ± 0.32
Baëtis rhodani	20	48.74	$\overset{***}{1.0102}$ ± 0.0764	0.99 ± 0.08	4.56 ± 0.37	2.28 ± 0.18
	40	51.12	$\overset{***}{0.5061}$ ± 0.0313	1.98 ± 0.13	9.12 ± 0.60	4.56 ± 0.30

stands of aquatic macrophytes which provided a natural sieve for the detached animals. As expected, taxa included in group 3 at site 4 also returned to the bottom at a faster rate than dead invertebrates at site 3. Larvae of *Simulium* spp. were the noteable exceptions and were able to rapidly return to the bottom at high modal water velocities (> 12 cm/sec) at site 3 but not at site 4. *Ephemerella ignita* showed the largest increase in the rate of return to the bottom when comparisons were made between sites. Nymphs of *E. ignita* drifted over large distances at site 4, whereas drift distances at site 3 were almost as short as those covered by *B. rhodani* and *G. pulex* (cf. Tables 3 and 5). Although the exponential law was an adequate model for the experiments at site 3 (correlation coefficients —0.98 to —0.99, and $P < 0.001$ for F-values from variance ratio), the values of A indicate that it was an inaccurate model at short distances from the net for nymphs of *E. ignita* and *B. rhodani* at 20 cm/sec.

c) Relationship between Distance Travelled by Drifting Invertebrates and Modal Water Velocity

The relative rate of return of invertebrates to the bottom (ordinate: R) was plotted against modal water velocity (abscissa: V cm/sec). A linear relationship was obtained when the data were plotted on a double logarithmic scale (i.e. log R against log V), but not on an arithmetic

Table 6. *Relationships between R and modal water velocity (Vcm/sec), and between mean drift distance ($\bar{X}m$) and modal water velocity. Constants a_1b_1 and a_2b_2 in the regression equations are given for groups 1 and 2, and different taxa in group 3, together with the 95% confidence limits for b, correlation coefficient (r), and number of paired observations (n). Values of A_p and b_2 are given for the relationships between the distances (X_p) travelled by P% of the drifting invertebrates and modal water velocity*

R and V	a_1	b_1	95% C.L.	r	n
Group 1	3.2277	−1.0174	±0.0106	−0.999	58
Group 2 ($V \geq 19$ cm/sec)	3.2502	−1.0205	±0.0349	−0.997	22
Gammarus pulex	9.8538	−0.9770	±0.0705	−0.997	9
Hydropsyche spp.	5.5094	−1.0625	±0.0620	−0.999	7
Ecdyonurus venosus	6.9150	−1.0414	±0.0382	−0.999	8
Baëtis rhodani	9.3972	−0.9631	±0.0535	−0.998	9
$\bar{X}$ and V	a_2	b_2			
Group 1	0.3098	1.0174	±0.0106	0.999	58
Group 2	0.3077	1.0205	±0.0349	0.997	22
Gammarus pulex	0.1015	0.9770	±0.0705	0.997	9
Hydropsyche spp.	0.1815	1.0625	±0.0620	0.999	7
Ecdyonurus venosus	0.1446	1.0414	±0.0382	0.999	8
Baëtis rhodani	0.1064	0.9631	±0.0535	0.998	9
X_p and V	A_p ($P = 1\%$)	A_p ($P = 10\%$)	A_p ($P = 50\%$)	b_2 ($P = 1\%$, 10%, 50%)	
Group 1	1.4267	0.7134	0.2148	1.0174	
Group 2	1.4170	0.7085	0.2133	1.0205	
Gammarus pulex	0.4674	0.2337	0.0704	0.9770	
Hydropsyche spp.	0.8358	0.4179	0.1258	1.0625	
Ecdyonurus venosus	0.6659	0.3330	0.1002	1.0414	
Baëtis rhodani	0.4900	0.2450	0.0738	0.9631	

Table 7. *Relationship between R and V, $\bar{X}$ and V, X_p and V for taxa limited to experiments at only two modal water velocities (see Table 6 and text for explanation of symbols)*

General group at site 3 includes all taxa for which the values of R were not significantly different from dead invertebrates (see Table 5).

	R and V		$\bar{X}$ and V		X_p and V	
	a_1	b_1	a_2	b_2	A_p ($P=1\%$)	A_p ($P=10\%$)
Site 4						
Erpobdella octoculata	16.043	−1.3535	0.0623	1.3535	0.2896	0.1435
Ephemerella ignita	3.474	−1.0010	0.2878	1.0010	1.3254	0.6627
Site 3						
General group	9.238	−1.0524	0.1082	1.0524	0.4983	0.2491
Simulium spp.	17.918	−1.0419	0.0558	1.0419	0.2570	0.1285
E. octoculata	15.892	−1.0116	0.0629	1.0116	0.2897	0.1448
Gammarus pulex	16.935	−0.9342	0.0590	0.9342	0.2717	0.1359
E. ignita	19.191	−1.0000	0.0521	1.0000	0.2399	0.1200
Baetis rhodani	19.999	−0.9967	0.0500	0.9967	0.2303	0.1151

scale or a semi-logarithmic scale. Therefore the relationship between the two variables is given by the regression equation:

$$\log R = \log a_1 - b_1 \log V$$

or

$$R = a_1 V^{-b_1} \tag{11}$$

where a_1 and b_1 are constants. As $\bar{X} = 1/R$ [Eq. (3)], the relationship between mean drift distance ($\bar{X}$ m) and modal water velocity is given by:

$$\bar{X} = a_2 V^{b_2} \tag{12}$$

where a_2 and b_2 are constants. Values of $a_1 b_1$ and $a_2 b_2$ were calculated for group 1, group 2 ($V \geqq 19$ cm/sec), and each taxon with more than two readings in group 3, i.e. not *Erpobdella octoculata* and *Ephemerella ignita* (Table 6). The relationship between the distance (X_p) travelled by P% of the drifting invertebrates and modal water velocity is easily derived from Eqs. (4) and (12) thus:

$$X_p = (\log_e 100 - \log_e P) a_2 V^{b_2} = A_p V^{b_2} \tag{13}$$

where $A_p = (\log_e 100 - \log_e P) a_2$. Values of A_p and b_2 were calculated for $P = 1\%$, $P = 10\%$, $P = 50\%$ (Table 6), and the relationship between X_p and V is illustrated by Fig. 3.

Therefore estimates can be made of the rate of return to the bottom (R), the distance travelled by drifting invertebrates ($\bar{X}$, X_p), and the distance over which $(100-P)$% of the drifting invertebrates returned to the bottom for all water velocities between 10 and 60 cm/sec. These estimates are only suitable for the bottom conditions at site 4, i.e. a stony bottom with very few macrophytes. It was assumed that the relationships given by Eqs. (11), (12) and (13) were also correct for *E. octoculata* and *E. ignita* at site 4 and for all experimental taxa at site 3. As these experiments were limited to two modal water velocities for each taxon, this assumption could not be checked. Therefore the estimates of a_1b_1, a_2b_2, and A_p (Table 7) must be treated with caution.

d) Simulated Drift and Blocking Experiments

There was good agreement between the actual catches in the simulated drift experiments and the catches predicted from Eq. (6) ($P > 0.05$ for all χ^2 values in Table 8). Therefore the exponential law was also a good model for these experiments. There was no significant difference between the day and night catches of *Gammarus pulex*, as also found in the detailed experiments at sites 3 and 4. The catch of *Baëtis rhodani* was not significantly increased by the release of more nymphs at dis-

Table 8. *Simulated drift experiments at site 4*

V = modal water velocity (cm/sec), $\sum Y_0$ = total number of introduced invertebrates, Y_0 = number of invertebrates introduced at each release point (Y_0 = 50 in each experiment), X_n = distance in metres of farthest release point from the net (there was a 1 metre interval between adjacent release points), R = rate of return of invertebrates to bottom (value of R obtained from Table 2), Exp. Y_T = expected catch predicted from equation 6, Act. Y_T = actual catch obtained in an experiment. χ^2 was used to compare expected and actual catches.

	V	$\sum Y_0$	X_n	R	Exp. Y_T	Act. Y_T	χ^2
April 1967							
Gammarus pulex (day)	10	300	5	1.02	78.1	79	0.01
Gammarus pulex (night)	10	300	5	0.98	80.7	81	0.001
Rhithrogena semicolorata	10	500	10	0.55	119.1	116	0.08
June 1967							
Chironomidae	20	1300	25	0.15	357.1	348	0.23
Baëtis rhodani	12	300	5	0.92	83.3	82	0.02
Baëtis rhodani	12	550	10	0.92	83.3	84	0.01

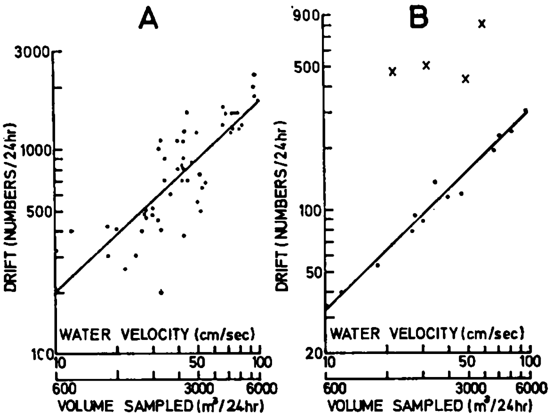

Fig. 4A and B. Examples of the relationship between invertebrate drift and water velocity. A Total catches of all taxa at 3 sites. B Total catches of nymphs of *Baëtis rhodani* at one site. Data from Walla Brook, Dartmoor (see Elliott, 1967a). Ordinate: total number of invertebrates taken in drift samples over 24 h. Abscissa: water velocity (cm/sec) and total volume of water sampled (m^3/24 h)

tances beyond the distance travelled by 1% of the drifting nymphs, i.e. 5 m (see Table 3).

The sections for the blocking experiment were carefully chosen to ensure that variations in substratum, water velocity and the volume of water sampled by each net were minimal. Model water velocities were 60 cm/sec in February, 19 cm/sec in April and 12 cm/sec in June. As the catches of some taxa were very small, only total catches were compared for groups 1 and 2 (Table 9). Taxa in group 1 were *Polycelis felina*, *Ancylus fluviatilis*, Chironomidae, Eliminthidae, and *Amphinemura sulcicollis* (not in June experiment). Taxa in group 2 were *Simulium* spp. in all experiments, *Protonemura meyeri* in February, *Leuctra inermis* and *Rhithrogena semicolorata* in April, and *Chloroperla torrentium* in April and June. A few species (Others category in Table 9) were not listed in the experimental taxa (Table 2) and included *Nemoura cambrica* Stephens, *Baëtis pumilus* (Burm.), *Hydraena gracilis* Germar, and *Elodes* sp. *Baëtis scambus* Eaton was also in this category, but was listed separately because of the relatively high catches.

The χ^2 test for homogeneity (see Elliott, 1970a, Chapter 7) was applied to the samples taken before blocking in each experiment, and no significant differences ($P > 0.05$) were found between samples taken at the same station, or between samples taken at different stations.

Table 9. *Results of blocking*

$Y_{\max}$ (± 95% confidence limits) = estimate of normal drift at each station before
at one of 6 stations) and 12 samples in June (each sample over 24h at one of 4 sta-
(Y_T) calculated from Eq. (9), using values of R from Table 2. χ^2 was used to test for
from Eq. (10) and compared with expected values of R from Table 2. A dash indicates
calculated.

	$Y_{\max}$ (± 95% C. L.)	Distance from Block Nets (Xm)					
		5 m		10 m		20 m	
		Act.	(Exp.)	Act.	(Exp.)	Act.	(Exp.)
February							
Group 1	34 ± 2.9	7	(7.5)	13	(13.3)	21	(21.4)
Group 2	4 ± 1.0	0	(0.9)	1	(1.6)	2	(2.5)
Others	7 ± 1.3	1		2		4	
Gammarus pulex	10 ± 1.6	6	(5.7)	8	(8.2)	10	(9.7)
Hydropsyche spp.	1 ± 0.5	0		1		0	
Ecdyonurus venosus	14 ± 1.9	5	(5.0)	8	(8.3)	11	(11.6)
Baëtis rhodani	254 ± 7.93	146	(149.9)	214	(210.8)	247	(246.4)
April		1 m		5 m		10 m	
Group 1	24 ± 2.4	3	(3.6)	13	(13.2)	19	(19.2)
Group 2	21 ± 2.3	3	(3.2)	11	(11.6)	17	(16.8)
Others	6 ± 1.2	1		4		5	
Gammarus pulex	24 ± 2.4	9	(9.8)	22	(22.3)	24	(23.9)
Hydropsyche spp.	5 ± 1.1	1	(1.1)	4	(3.5)	5	(4.6)
Ecdyonurus venosus	6 ± 1.2	2	(1.6)	5	(4.8)	6	(5.8)
Baëtis rhodani	194 ± 6.9	81	(81.5)	182	(180.4)	193	(192.8)
June		1 m		5 m		10 m	
Group 1	24 ± 3.1	5	(5.5)	17	(16.1)	22	(22.3)
Group 2	10 ± 2.0	4	(4.2)	9	(9.4)	10	(10.0)
Gammarus pulex	9 ± 1.9	6	(5.6)	9	(8.9)	8	(9.0)
Ephemerella ignita	13 ± 2.3	3	(3.3)	9	(10.0)	12	(12.2)
Baëtis rhodani	58 ± 4.8	34	(34.8)	58	(57.4)	60	(58.0)
Baëtis scambus	13 ± 2.3	5		11		12	
Hydropsyche spp.	3 ± 1.1	1	(1.0)	2	(2.6)	3	(2.9)

Therefore the mean catch for these samples was used to estimate the "normal drift" [$Y_{\max}$ in Eq. (9) and Table 9] at each station before blocking. The effect of blocking was to markedly reduce the drift rate at stations immediately below the blockage, and the catches gradually increased downstream until they were similar to those obtained before blocking (cf. $Y_{\max}$ and Act. catches in Table 9). A rough estimate of the distance travelled by drifting invertebrates was given by the distance *experiments at site 4*

blocking = mean of 18 samples in February and April (each sample over one night tions). Act. = actual catch at each station after blocking. Exp. = expected catch agreement between actual and expected catches. Actual values of R were determined that the catches were too low or too few (< 3 values of Y_T) for values of R to be

						χ^2	R	
40 m		70 m		100 m				
Act.	(Exp.)	Act.	(Exp.)	Act.	(Exp.)		Act.	(Exp.)
28	(29.2)	34	(33.0)	33	(33.8)	0.15	0.05	0.05
3	(3.4)	4	(3.9)	5	(4.0)	0.74	0.03	0.05
6		7		6		—	0.05	—
10	(10.0)	9	(10.0)	11	(10.0)	0.23	0.16	0.17
1		0		0		—	—	—
13	(13.6)	14	(14.0)	13	(14.0)	0.15	0.08	0.09
258	(254.0)	253	(254.0)	260	(254.0)	0.36	0.18	0.18
20 m		30 m		35 m				
23	(23.0)	23	(23.8)	25	(24.0)	0.19	0.15	0.16
20	(20.2)	21	(20.8)	22	(21.0)	0.10	0.15	0.16
5		7		6		—	0.13	—
22	(24.0)	26	(24.0)	24	(24.0)	0.41	0.47	0.52
6	(5.0)	5	(5.0)	4	(5.0)	0.52	0.21	0.24
5	(6.0)	6	(6.0)	7	(6.0)	0.44	0.25	0.32
196	(194.0)	194	(194.0)	189	(194.0)	0.17	0.55	0.54
20 m								
24	(23.9)					0.10	0.26	0.26
10	(10.0)					0.03	—	0.55
10	(9.0)					0.25	—	0.96
14	(13.0)					0.22	0.26	0.29
58	(58.0)					0.09	—	0.92
12						—	0.35	—
3	(3.0)					0.18	—	0.38

from the block nets to the station at which the blockage did not significantly affect "normal drift rates". As it was difficult to choose the latter station, no accurate estimates of drift distance could be made, e.g. estimated drift distance was 20–40 m for *Baëtis rhodani* in February.

An alternative approach was to compare the catches obtained at each station with the catches predicted from Eq. (9), using values of R obtained from the detailed experiments. Expected catches were calculated for all taxa except the "Others" category and *B. scambus*. There was good agreement between the actual and expected catches of all taxa ($P > 0.05$ for all χ^2 values in Table 9). Estimates of R were also obtained directly from the blocking experiments, using Eq. (10) and values of Y_T less than or equal to $Y_{\max}$. Although only 3 or 4 values of Y_T were available to estimate R for each taxon, the estimates were not significantly different from those obtained from the detailed experiments (cf. Act. and Exp. values of R in Table 9). Therefore the mathematical model developed from the detailed experiments was a good fit to the results of the blocking experiments.

Discussion

a) The Behaviour of the Drifting Invertebrates

The results of the detailed experiments demonstrate that drifting invertebrates vary considerably in their ability to return to the bottom. All taxa in group 1 were usually small, were poor swimmers, and were incapable of rapid attachment when they came into contact with a stone or plant. Taxa in group 2 swam at all water velocities, but were capable of rapid attachment only at low water velocities (10–12 cm/sec). Drifting nymphs of Plecoptera in group 2 and *Rhithrogena semicolorata* were unable to make a firm contact with an exposed substratum in turbulent water, and touched the substratum (or plants at site 3) several times whilst travelling downstream. The nymphs usually returned to the bottom when they landed in a zone of comparatively low water velocity, e.g. near the banks, within leaf packets, between and at the rear of large stones. Madsen (1968) has observed similar behaviour in nymphs of *Heptagenia fuscogrisea* (Retz.) in a stream tank. As *R. semicolorata* is well adapted to live on large stones in swift-flowing streams (cf. Ambuhl, 1959), the inability of nymphs to return rapidly to the bottom is surprising.

At first, there appeared to be no obvious explanation for the rapid return of *Simulium* spp. at low water velocities at site 4, and at both water velocities at site 3. The larva is a poor swimmer, but can produce a long silk thread which is attached to the substratum before the larva releases its hold (Miall, 1895). As larvae are frequently taken in drift samples, it must be assumed that these mooring threads often snap. The broken threads trail behind the drifting larvae and stick to stones and plants. This effect was clearly seen at site 3 and the drifting of the larvae was soon checked when the threads became tangled in the aquatic macrophytes. Each larva slowly crawled up the thread and finally became attached to the plant. This method of returning to the bottom was obviously less successful on a stony bottom with few macrophytes.

As the stream was shallow and turbulent, most invertebrates drifted throughout the whole water column and the only exceptions were in group 3. After a brief period of swimming, nymphs of *Ecdyonurus venosus* and *Ephemerella ignita* became rigid and drifted passively with the current. The nymphs were frequently carried to the bottom by turbulent currents and rapidly regained contact with the substratum in areas of low water velocity. In swift-flowing sections at site 4, a firm contact was made occasionally by *E. venosus* but rarely by *E. ignita*, except when nymphs came into contact with a clump of moss. At site 3, nymphs of *E. ignita* made a secure contact as soon as they touched a leaf or stem of *Callitriche aquatica*. Therefore *E. ignita* is well adapted for a rapid return to the bottom when aquatic macrophytes are present, but not when the bottom is stony and macrophytes scarce. Passive drifting was also observed in nymphs of *Heptagenia sulphurea* (Müll.) and *Brachyptera risi* (Morton) by Madsen (1968, 1969), but the nymphs regained a firm foothold as soon as turbulence brought them into contact with the substratum of a stream tank, even in a strong current (about 30 cm/sec).

The remaining taxa in group 3 drifted downstream either near the water surface (*Hydropsyche* spp., *Baëtis rhodani*) or near the bottom (*Erpobdella octoculata, Gammarus pulex*). *E. octoculata* maintained its position near the bottom by swimming continuously. The leeches soon found an area of low water velocity and then rapidly regained contact with the stones at site 4, or the stones and plants at site 3. When larvae of *Hydropsyche* spp. were released into the drift, they immediately swam to the water surface with strong side-to-side movements (cf. Edington, 1965). The larvae did not swim continuously in the drift and returned to the bottom when they drifted into an area of low water velocity. A firm contact was sometimes made in swift-flowing areas, especially when the larvae came into contact with moss. Larvae of *Hydropsyche* are found predominantly in rapids (Edington, 1968) and upstream movements of the larvae (Elliott, 1971) ensure that larvae settling in areas of low water velocity move back into rapids.

G. pulex and *B. rhodani* travelled very short distances in the drift and were able to return to the bottom at a faster rate than all other taxa. When released into the drift, *G. pulex* swam to the bottom and soon disappeared under or between stones. *G. pulex* also secured a firm hold as soon as it contacted macrophytes at site 3. Nymphs of *B. rhodani* were remarkable in their ability to attach to a stone or plant, even in turbulent water or a strong current. When released into the drift, the nymphs swam to the water surface and then ceased swimming whilst they turned a somersault which brought them back to the substratum ventral surface downwards. This procedure was repeated on the rare occasions when the nymphs did not successfully attach to the substratum on their first contact. Similar behaviour was observed in *Baëtis harrisoni* Barnard by Hughes (1966) who concluded that this "somersaulting" behaviour was caused by a dorsal light response. As nymphs of *B. rhodani* showed the same behaviour in the night experiments at site 4, it cannot be concluded that a dorsal light response was also responsible for the somersaulting behaviour in *B. rhodani*. Madsen (1966) also noted the rapid return to the bottom of *Baëtis* sp., and found that most nymphs re-attached within 2–3 sec, whereas nymphs of *Ephemerella ignita* took 5–6 sec when released into a stream tank (water velocity c. 30 cm/sec).

The experiments with benthic and drifting invertebrates of the same taxon demonstrated that there were no noticeable differences in the ability of these two groups to return to the bottom. Hughes (1966) has suggested that the dorsal light response may be a mechanism for maintaining orientation in drifting invertebrates, and that the invertebrates are unable to return efficiently to the bottom in the absence of the orienting light source at night. This hypothesis would explain the high nocturnal drift rates of mayfly nymphs that are known to be more active at night (Elliott, 1968). Unfortunately, the results of the day and night experiments in the present study do not support this hypothesis, apart from the non-significant trend towards a higher rate of return to the bottom during the day for *G. pulex*.

b) *The Adequacy and Implications of the Mathematical Model*

The results of the detailed experiments at sites 3 and 4, the simulated drift experiments, and the blocking experiments demonstrate that the mathematical model developed in Eqs. (1) to (10) is a good model for invertebrate drift. Cased caddis larvae were the only exceptions, but some taxa showed slight departures from the model at short distances from the point of entry into the drift. In a single experiment in a New Zealand stream, McLay (1970) introduced invertebrates into the drift by disturbing the bottom at increasing distances upstream from a drift sampler. He found that the exponential law was a good model for this experiment, and also for the blocking experiment of Waters (1965) and the re-attachment experiments of Madsen (1966, 1968). Some implications of the mathematical model are now discussed.

The relationship between the total drift ($Y_{\max}$) reaching a sampling point in unit time (i.e. drift rate) and modal water velocity (V cm/sec) is easily derived from Eqs. (8) and (12) thus:

$$Y_{\max} = Y_0 X = Y_0 a_2 V^{b_2} \tag{14}$$

where Y_0 is the number of invertebrates entering the drift at each of an infinite number of points upstream from the sampling point. The results of the present study suggest that a_2 and b_2 remain fairly constant for a particular taxon. If Y_0 also remains constant, then the relationship between $Y_{\max}$ and V will be linear when the data are plotted on a double logarithmic scale. Some results from a previous study (Elliott, 1967a) were used to test this hypothesis.

In the first example (Fig. 4A), catches of all taxa (numbers/24 h) were compared with modal water velocity near the mouths of the drift samplers, and also with the total volume of water passing through the drift samplers (m³/24 h). As the 54 catches contained many taxa and were from 3 sites over 17 months, it is not surprising that there was a large scatter of points around the regression line. In spite of this scatter, the regression line was a good fit to the data ($Y_0 a_2 = 24.10$, $b_2 = 0.9228$, correlation coefficient $r = 0.81$, variance ratio $F = 98.00$, $P < 0.01$). Catches in the second example (Fig. 4B) were limited to *Baëtis rhodani* and were from one site over 17 months. As 4 catches (crosses in Fig. 4B) were far higher than the others, they were not included in the calculation of the regression equation. The remaining catches lay very close to the regression line which was thus an excellent fit to the data ($Y_0 a_2 = 3.56$, $b_2 = 0.9583$, $r = 0.99$, $F = 627.42$, $P < 0.01$). Therefore Y_0 was fairly constant in most months, and an increase in total drift at the sampling point was due to an increase in drift distance, which was related to an increase in water velocity. The high catches demonstrate a marked increase in Y_0 in 4 months when the nymphs were growing rapidly (Elliott, 1967b). Similar results were obtained for other taxa from the same stream (Walla Brook, Dartmoor). In both these examples, the values of b_2 were very similar to those obtained in the present study (cf. Table 6). Values of b_2 were the same for the relationship between catch and volume of water sampled, but values of $Y_0 a_2$ were different (0.40 for all taxa, 0.06 for *B. rhodani*). As values of b_2 were close to one in these examples and also in the detailed experiments at sites 3 and 4 (Tables 6 and 7), a linear relationship on arithmetic scales will be an approximate model. When the data of the first example were plotted on an arithmetic scale, the regression line was a good fit (Elliott, 1970b), but was not such a good fit as on a double logarithmic scale.

Although drift rate usually decreases with decreasing water velocity, there may be an increase in drift rate at low water velocities (< 10 cm/sec) when stream discharge is reduced to very low levels (Pearson and Franklin, 1968; Minshall and Winger, 1968; Hughes, 1970). This increased drifting is probably an escape mechanism from streams that are drying up (cf. Elliott, 1968).

Table 10. *A summary of factors affecting the mean drift distance ($\bar{X}$) and the number of invertebrates (Y_0) entering the drift*

$\bar{X}$	1. Specific for each taxon (Tables 3 and 5).
	2. Varies with water velocity ($\bar{X} = aV^b$).
	3. Varies with type of bottom (e.g. stony or weedy) and stream characteristics (e.g. depth, leaf packets, pools).
	4. Does not significantly vary from day to night, or from month to month.
Y_0	1. Usually low in day and high at night, and usually varies considerably through the night.
	2. Mean value for day or night may be fairly constant for each taxon over long periods (e.g. Fig. 4B).
	3. may increase considerably during periods of rapid growth (e.g. crosses on Fig. 4B).
	4. May increase as a response to exceptionally low water velocities-escape mechanism.
	5. May be affected by numerous other factors, including crowding, competition between invertebrates for food and space (both intra- and inter-specific), and escape from predators.

The results of the present study will also affect methods of calculating the proportion of the benthos in the drift. Elliott (1965, 1967a) and Ulfstrand (1968) have proposed similar equations which compare the number of invertebrates in the column of water above a square metre of bottom at an instant in time with the number of invertebrates in the square metre of substratum. This method assumes that each square metre of bottom contributes the same proportion to the total catch. A similar assumption is made when drift rate per unit area is estimated as the quotient of total catch and the area of bottom upstream from the sampling point for a discrete distance (Waters, 1962, 1966). The results of the present study demonstrate that this assumption is erroneous. As the distance upstream from the sampling point increase, each square metre of bottom contributes a progressively smaller proportions of drifting invertebrates to the total catch. The mathematical model assumes that a constant number of invertebrates (Y_0) enters the drift at each of an infinite number of points upstream from the sampling point, but that very few of these invertebrates actually reach the sampling point. The following method is derived from the model and estimates the proportion of the benthos in the drift in unit time.

In April 1967, nets were placed across the stream so that all drifting invertebrates were caught in a night (dawn to dusk = 10 h, modal water velocity = 10 cm/sec, mean depth = 17 cm, stream width = 3.7 m at sampling point). The total catch of *Baëtis rhodani* was 3880 ($= Y_{\max}$). A square metre of bottom immediately upstream from the nets was 3.7 m wide and 0.27 m long. The estimate of total drift (Y_T) of *B. rhodani* from this m^2 was 524 nymphs [using Eq. (7) with $Y_0/R = Y_{\max} = 3880$, $R = 0.5383$ from Table 2, $X = 0.27$). The estimate of Y_T for 2 m^2 was 978 nymphs ($X = 0.54$). Therefore 454 nymphs came from the second m^2 of bottom. The model assumes that 524 nymphs entered the drift from the second m^2 and 70 nymphs returned to the bottom before the drifting nymphs reached the nets. Similar estimates can be made for each m^2 of bottom upstream from the nets. As the distance from the nets increases, the number of nymphs returning to the bottom will also increase until no drifting nymphs reach the nets. Therefore, 524 was the best estimate of the number of nymphs entering the drift from each m^2 of bottom during the night. The mean number (±95% confidence limits) of nymphs per m^2 of bottom was 2462 ± 213 (estimated from large random sample of 50 sampling units; each unit from 0.05 m^2). Therefore the proportion of the population/m^2 entering the drift in a night was $524(100)/2462 = 21.3\%$, and the proportion entering the drift/m^2/sec was $21.3/36000 = 0.00059\%$. At a modal water velocity of 19 cm/sec, most nymphs taken in the nets had drifted from an area of bottom 3.7 m wide and 10 m long (see drift distances for 19 cm/sec in Table 3). The total population of *B. rhodani* in this area was estimated to be 91094 nymphs. Therefore the proportion of the population lost as drift in a night was $3880(100)/91094 = 4.3\%$, which was considerably less than the proportion entering the drift in a night. If the mathematical model was ignored and it was assumed that each m^2 of bottom contributed the same proportion to the total catch, then the drift rate of *B. rhodani* would be 105 nymphs/m^2/night and the proportion of the population entering the drift/sec would be 0.00012%. These estimates are much lower than those obtained from the mathematical model.

The total drift ($Y_{\max}$) at a sampling point can be resolved into two components, the mean distance ($\bar{X}$) travelled by the invertebrates and the number of invertebrates (Y_0) entering the drift at each of an infinite number of points upstream from the sampling point [see Eq. (8)]. A large number of factor affect these components, and Table 10 lists all known factors. The present study has examined the various factors which affect $\bar{X}$, but more work is needed on factors affecting Y_0 before a complete model can be developed for invertebrate drift.

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