HOLARCTIC ECOLOGY 2: 130–136. Copenhagen 1979

The rate of downstream displacement of macroinvertebrates in the upper Wye, Wales

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Hemsworth, R. J. and Brooker, M. P. 1979. The rate of downstream displacement of macroinvertebrates in the upper Wye, Wales. – Holarct. Ecol. 2: 130–136.

Quantitative data describing drift rates and benthic density of macroinvertebrates are utilised to estimate the rates of downstream displacement of invertebrate populations in the Wye, Wales. Calculations are based upon two models, one a classical exponential relationship between drift catch and distance travelled and the other derived from a solute balance equation. Results from the two models were significantly correlated. Estimates of the rate of benthic community displacement ranged from 2.8 to 70.7 m d^{-1}, with highest rates recorded in the summer period. There were considerable differences in rates between taxa and between sites. It was estimated that a displacement of 10 km downstream could be achieved by certain taxa during a generation period.

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Introduction

The fact that upstream areas of rivers and streams are not depopulated of macroinvertebrates by drift processes (Müller 1954, Waters 1968, Pearson and Kramer 1972, Lehmkuhl and Anderson 1972) has led to the consideration of upstream migration of ovipositing adults (Müller 1954, Elliott 1967a) or benthic organisms (Elliott 1971a) as possible compensatory movements. However, there are few estimates of the distances travelled downstream by drifting organisms (McLay 1970, Elliott 1971b) and the evaluation of such movements in terms of distributional stability of populations has been limited to studies on *Gammarus* (Lehmann 1967).

As part of a broader ecological study of the River Wye in mid-Wales samples of drifting and benthic macroinvertebrates were collected during the period March 1975–February 1976 and the rate of downstream movements of macroinvertebrates estimated.

Study sites

Two study sites (W2 and W3) were selected in the upper reaches of the River Wye which drain impermeable Ordovician and Silurian mudstones and shales. W2 and W3 in this study are located respectively at W2 and about 2 km downstream of W3 described by Gee et al. (1978). The substratum at these sites, typical riffle areas, consisted of cobbles and coarse gravel. River widths varied between 12.5 and 16.9 m and between 8.2 and 17.6 m at W2 and W3 respectively. Recorded depths and water velocities when drift samples were collected ranged from 0.25 to 0.54 m and from 0.30 to 1.03 m s^{-1} respectively.

Methods

Samples of drifting macroinvertebrates were collected, generally at both sites, approximately every six weeks, with a modified high speed plankton sampler (Elliott 1970) which had a mouth aperture of 0.15 m diameter and a net mesh aperture of 440 µm. Each sampling period was 24 h and the samplers were emptied every 3 h when measurements of water velocity and river depth were recorded at the mouth of the drift samplers. In addition, the velocity of water at the exit of the sampler was measured. The relationship between the exit velocity and the flow through the sampler was established experimentally in a flume. Average flow through the

Accepted 9 February 1979

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sampler between servicing intervals was calculated from velocity measurements at the beginning and the end of the period assuming linear changes with time. Estimates of density from drift samplers were regarded as representative of the total water column.

Benthic invertebrates were collected using a cylinder sampler modified after Neill (1938). The sampler enclosed an area of $0.05\ m^2$ and had a net mesh aperture of 440 μm. Samples were collected weekly during the summer months and less frequently at other times. At each visit 14 replicate samples were taken from each site except during weekly sampling periods when the number of replicates was 7. When estimates of benthic density and drift rates were not contemporary benthic densities have been interpolated (see Fig. 1).

The rate of downstream movement of invertebrate populations was assessed in two ways:

(1) Following the model of Elliott (1971b) which described the rate of return of drifting invertebrates to the substratum, and using constants derived by Elliott (1971b) for different taxa, it was possible to calculate the number of invertebrates entering the drift from a known area upstream of the drift trap:

$$Y_t = Y_{max}\left(1 - e^{\frac{-R\,0.1}{w}}\right)$$

where Y_t = the number of invertebrates entering the drift per day from an area $0.1\ m^2$ upstream of the drift trap.

Y_{max} = the number of invertebrates estimated to be caught in a column of water, w d, per day, d being the river depth where the drift sampler was placed (m) and w being the width of water column considered (m).

R = constant, depending on water velocity, taxon and physical characteristics of the river.

From Elliott (1971b) the average distance travelled by those invertebrates entering the drift, $\bar{X}$ (m), was calculated from:

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

where a_2 and b_2 = constants, depending on the taxon and physical characteristics of the river.

and V = velocity ($cm\ s^{-1}$) of water in front of the drift sampler.

The cumulative distance travelled by invertebrate populations per day is $Y_t \bar{X}$ and the mean rate of travel of the population, Vp_1 ($m\ d^{-1}$), is:

$$Vp_1 = \frac{Y_t \bar{X}}{D_B} \qquad \text{(Eq. 1)}$$

where D_B = average density of benthic invertebrates ($n\ 0.1\ m^{-2}$)

Tab. 1. A. The proportion (%) of total benthos entering the drift per day $\frac{Y_t\,1000}{N_B}$ and

B. The proportion (%) of the total benthos in the drift at any instant $\frac{D_D\,d\,100}{N_B}$

	1975 Mar W2	Mar W3	Apr W2	Apr W3	May W2	May W3	Jul W2	Jul W3	Aug W2	Aug W3	Oct W2	Oct W3	Dec W2	Dec W3	1976 Feb W2	Feb W3
A	13	12	153	197	53	52	76	51	204	97	27	28	27	18	18	×
B	0.0090	0.0060	0.0705	0.1096	0.0254	0.0227	0.0408	0.0296	0.1050	0.0488	0.0108	0.0119	0.0099	0.0071	0.0080	×

× = Not sampled.

(2) Adapting the basic solute balance equation described by Hem (1970), and assuming that drifting invertebrates travel at the same rate as the water velocity, density components of benthic invertebrate populations can be resolved in the following way:

$$(V_D\, N_D) + (V_B\, N_B) = (N_D + N_B)\, Vp_2$$

where V_D = velocity of the drift (m s^{-1})
V_B = velocity of the benthos $\rightarrow 0$
N_D = number of invertebrates in the drift (n m^{-2})
N_B = number of invertebrates associated with the benthos (n m^{-2})
Vp_2 = average velocity of the invertebrate population (m s^{-1})

Therefore,

$$Vp_2 = \frac{(V_D\, N_D + V_B\, N_B)}{(N_D + N_B)}$$

Since V_B approaches zero and N_D is small compared with N_B then:

$$Vp_2 = \frac{V_D\, N_D}{N_B}$$

However, $N_D = D_D\, d$
where D_D = drift density (n m^{-3})
and d = depth of water (m)

so

$$Vp_2 = \frac{V_D\, D_D\, d}{N_B} \qquad \text{(Eq. 2)}$$

The expression

$$\frac{D_D\, d}{N_B}$$

is the same as that used for calculating the proportion of the benthos in the drift at any instant (Ulfstrand 1968).

Results

Total numbers of invertebrates drifting in the River Wye ranged from 34000 to 798000 d^{-1} and peaks were recorded in April and August at W2 and W3 (Fig. 1). In contrast, maximum densities of invertebrates collected from the river substratum were generally in June and July, mean density reaching peaks of 3057 and 2230 m^{-2} at W2 and W3 respectively.

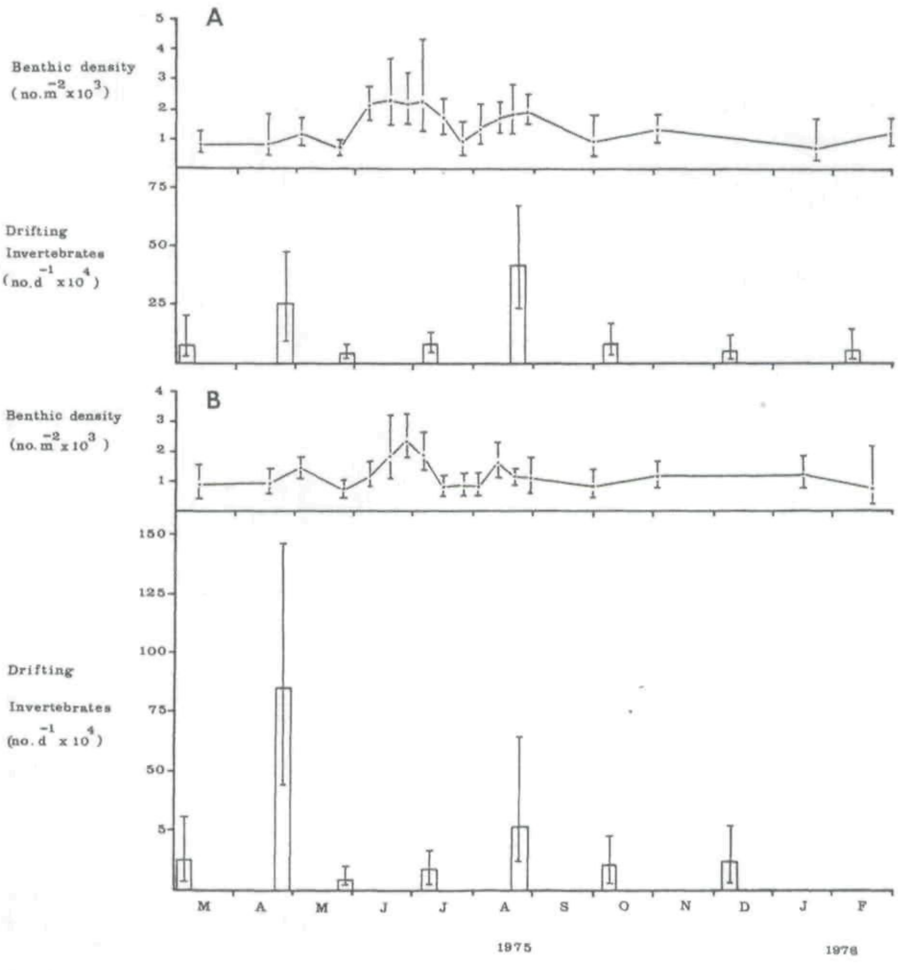

Fig. 1. Seasonal changes in the density (geometric mean and 95% confidence limits) of benthic macroinvertebrates and the total number of macroinvertebrates drifting at (A) W2 and (B) W3 Confidence limits (95%) for single samples of drifting invertebrates were established from published tables for Poisson variables after suitable transformation of the data (unpublished information).

Considering total numbers of macroinvertebrates, the proportion (%) of the benthos entering the drift per day per m^2

$$\frac{Y_t\ 1000}{N_B}$$

ranged from 13–204% at W2 and 12–197% at W3 (Tab. 1). These estimates are much larger than the proportion (%) of benthos in the drift at any instant

$$\frac{D_D\ d\ 100}{N_B}$$

(Ulfstrand 1968), ranging from 0.0060 to 0.1096% (Tab. 1). The high proportion of benthos entering the drift suggests that, at certain times of the year, benthic organisms drifted between one and two times per day. Maximum rates of such turn over for populations of *Baetis rhodani* (Pictet) were estimated to be 20 and 6 times per day at W2 and W3 respectively.

Estimates of the rate of benthic community displacement (total macroinvertebrates), using Elliott's model (Eq. 1), ranged from 4.3 – 53.3 m d^{-1} and 2.8 – 39.5 m d^{-1} at W2 and W3 (Tab. 2). There were considerable differences in rates between taxa. Generally, of the taxa considered, the Baetidae and Chironomidae had highest rates of displacement and the Plecoptera and *Rhithrogena semicolorata* (Curtis) the lowest (Tab. 2). Seasonal changes in displacement rates were generally similar at both sites although substantial differences in magnitude were often recorded e.g. *Baetis rhodani* (Tab. 2).

Estimates of the rate of downstream displacement of the benthic community (total macroinvertebrates), calculated using (Eq. 2), ranged from 4.4 – 70.7 m d^{-1} and 2.9 – 55.9 m d^{-1} at W2 and W3 respectively (Tab. 3). Estimates of displacement for the selected taxa, calculated using (Eq. 1) and (Eq. 2), were significantly correlated at W2 ($r = 0.99$, $p < 0.001$) and W3 ($r = 0.99$, p

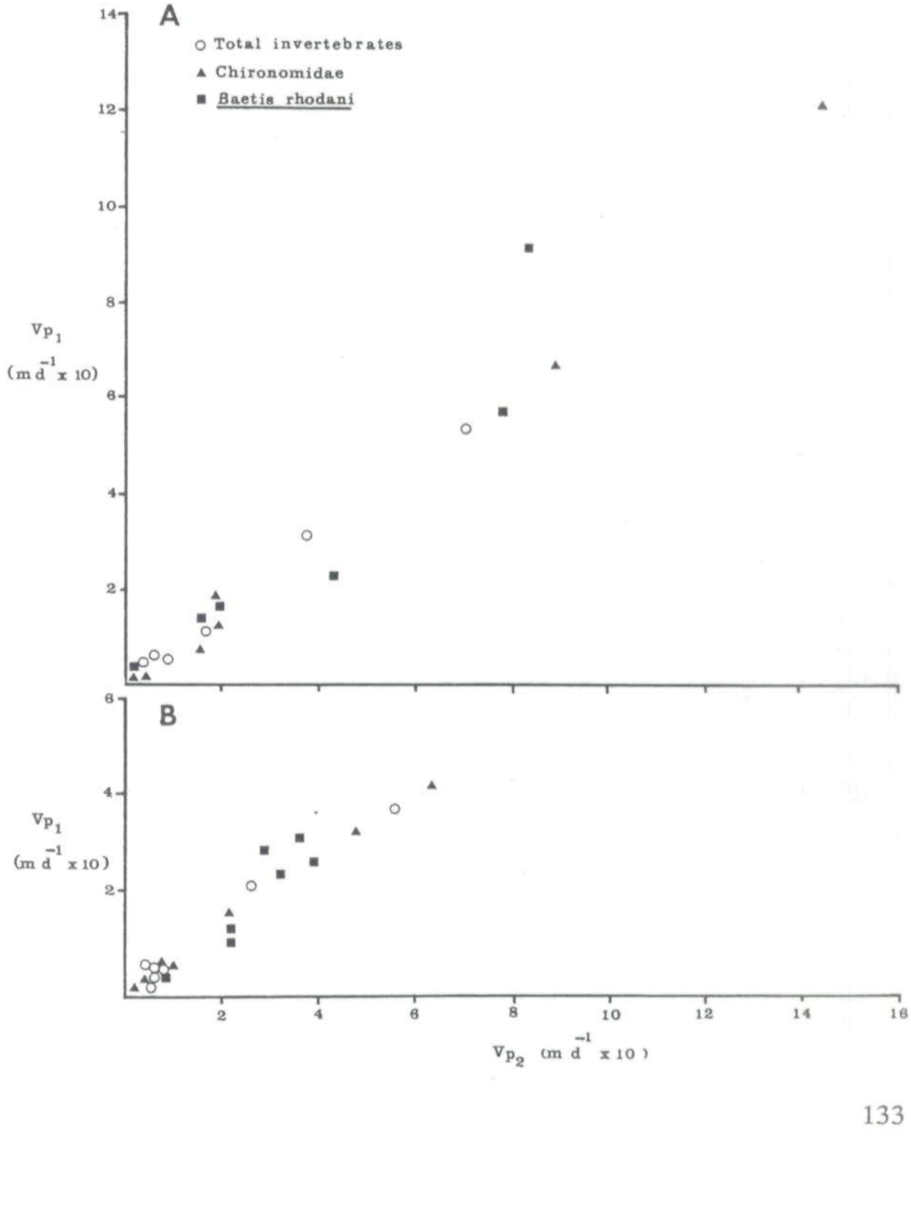

Fig. 2. Relationship between the population displacement rates Vp_1 and Vp_2 at (A) W2 and (B) W3.

Tab. 2. Estimated rate of population displacement Vp_1 ($m\ d^{-1}$), for selected taxa. From (Eq. 1).

	1975														1976	
	Mar		Apr		May		Jul		Aug		Oct		Dec		Feb	
	W2	W3	W2	W3	W2	W3	W2	W3	W2	W3	W2	W3	W2	W3	W2	W3
Total invertebrates	4.3	2.9	31.1	39.5	5.2	5.1	12.7	5.4	53.3	20.3	4.9	5.7	4.5	2.8	4.8	×
Amphinemura sulcicollis (Plecoptera)	5.1	3.6	10.8	12.7	5.1	–	–	–	–	–	1.5	1.0	2.4	7.9	16.4	×
Chloroperla torrentium (Plecoptera)	0.1	1.1	12.4	16.2	0.3	3.4	–	2.5	–	0.5	1.6	–	3.5	0.1	3.2	×
Rhithrogena semicolorata (Ephemeroptera)	1.5	0.6	0.4	0.2	–	0.7	–	–	–	–	0.5	2.5	0.1	0.2	3.2	×
Baetis rhodani (Ephemeroptera)	22.8	14.0	14.6	20.0	–	4.8	92.7	12.5	57.2	28.1	16.8	32.5	2.7	25.0	–	×
Hydropsyche siltalai (Trichoptera)	3.9	2.2	63.8	71.7	–	3.5	7.8	2.7	3.1	1.6	14.3	7.5	7.8	2.3	1.4	×
Chironomidae (Diptera)	8.4	6.8	121.2	43.8	2.7	0.9	13.9	6.1	66.5	35.1	18.0	17.9	1.0	3.4	3.6	×

– = Not recorded in the drift or benthos.
× = Not sampled.

Tab. 3. Estimated rate of population displacement, Vp_2 ($m\ d^{-1}$), for selected taxa. From (Eq. 2).

	1975														1976	
	Mar		Apr		May		Jul		Aug		Oct		Dec		Feb	
	W2	W3	W2	W3	W2	W3	W2	W3	W2	W3	W2	W3	W2	W3	W2	W3
Total invertebrates	8.0	3.7	37.1	55.9	6.5	5.9	17.3	8.4	70.7	26.5	5.0	6.4	4.4	2.9	5.1	×
Amphinemura sulcicollis	9.2	4.6	18.9	18.1	9.6	–	–	–	–	–	1.5	1.0	2.3	8.1	17.3	×
Chloroperla torrentium	0.4	2.0	19.5	30.2	0.4	3.7	–	4.3	–	0.9	2.3	–	3.4	0.2	3.5	×
Rhithrogena semicolorata	8.4	2.0	1.1	0.9	–	1.5	–	–	–	–	1.1	2.8	0.1	0.5	10.0	×
Baetis rhodani	42.8	21.4	15.1	29.0	–	8.8	136.7	20.1	78.4	39.1	17.8	37.5	2.6	27.2	–	×
Hydropsyche siltalai	7.0	2.7	75.8	101.5	–	4.1	17.6	4.1	4.2	2.1	15.9	9.9	7.5	2.4	1.5	×
Chironomidae	15.5	8.7	144.4	62.3	3.5	1.0	19.7	9.4	89.0	47.1	18.3	20.1	1.0	3.5	3.8	×

– = Not recorded in drift or benthos.
× = Not sampled.

< 0.001) (Fig. 2). Displacement rates calculated from (Eq. 2) were generally higher than those from (Eq. 1) (Tabs 2, and 3).

Discussion

The invertebrate fauna recorded from the upper reaches of the River Wye is generally similar to that recorded in other upland rivers and streams (Hynes 1961, Egglishaw and Mackay 1967, Armitage et al. 1975). Estimates of the rate of total invertebrate drift (34000–798000 d^{-1}) are similar to those recorded in the River Duddon, Lake District (Elliott and Minshall 1968), Speed River, Canada (Bishop and Hynes 1969) and a stream in Lapland (Ulfstrand 1968).

The proportion (%) of total benthos drifting in the River Wye at any instant (0.0060–0.1096%) was similar to values recorded by other workers (Tab. 4).

Estimates of the proportion of invertebrates entering the drift in the River Wye and the calculation of population displacement using (Eq. 1) depend upon the assumption that conditions in the upper reaches of this river fulfill the requirements of Elliott's (1971b) model. It seems likely that this assumption is reasonable (Elliott, pers. comm.) and that results reported from the Wye are realistic.

Elliott (1971b) calculated that the proportion of *Baetis rhodani* entering the drift in a Lake District stream in April (water velocity, 0.19 $m\ s^{-1}$) was 0.00059% $m^{-2}\ s^{-1}$ (calculated over a 10 h night-time period). Rates for total invertebrates in the River Wye ranged from 0.00014–0.00236% $m^{-2}\ s^{-1}$ (calculated over a 24 h period), equivalent to 12–204% $m^{-2}\ d^{-1}$. Using basic data collected by Elliott (1965) the proportion of *Baetis* sp. and total macroinvertebrates entering the drift in a Norwegian stream (water velocity 0.90 m s^{-1}) was 0.01987 and 0.00015% $m^{-2}\ s^{-1}$ respectively, equivalent to 1716 and 13% $m^{-2}\ d^{-1}$. Such rates indicate a high degree of turn over of certain benthic invertebrates. The highest turn over rate in the River Wye (*Baetis rhodani*, 20 times per day) was similar to the rate calculated, using basic data from Elliott (1965), for a similar species in a Norwegian stream (17 times per day).

For the same Norwegian stream it has been calculated, using (Eq. 1), that the average rates of downstream displacement of *Baetis* sp. and total inver-

Tab. 4. The proportion (%) of total benthos in the drift at any instant at various sites.

Location	Proportion	Reference
Small mountain stream, Norway	0.0057	Elliott (1965)
Walla Brook, England	0.0006–0.0086	Elliott (1967)
Tjulån stream, Lapland, Sweden	0.0100–0.3400	Ulfstrand (1968)
Speed River, Canada	0.0002–0.0037	Bishop and Hynes (1969)
Kananaskis River, Canada	0.0100–0.6600	Radford and Hartland-Rowe (1971)
Lusk Creek, Canada	0.0500–0.3500	Radford and Hartland-Rowe (1971)

tebrates were 31.3 and 3.9 m d^{-1} respectively. Results obtained from the River Wye over a longer study period are broadly similar though maximum rates are substantially higher (see Tab. 2).

Crisp and Gledhill (1970) calculated that the downstream shift of benthos in East Stoke mill stream and the Bere stream was 0.6 and 1.9 m d^{-1} respectively. These estimates were made by multiplying the proportion of invertebrates in the drift

$$\frac{D_D\ d}{N_B}$$

by the water velocity (V_D) and give the same results as (Eq. 2). Lehmann (1967) studied the upstream and downstream movements of *Gammarus* in a stream using labelled specimens and estimated drift velocity to be 2 m d^{-1}.

The assumption in (Eq. 2), that organisms travel downstream at the same rate as the water velocity, probably leads to generally higher estimates of downstream displacement compared with results derived from (Eq. 1). The full use of (Eq. 1), derived from the model of Elliott (1971b), allows some description of the probability of distribution of velocities within an invertebrate population, based upon the distribution around the mean distance travelled ($\bar{X}$). (Eq. 2) provides estimates of mean velocity only but has the advantage of simplicity. In both models errors associated with assessing benthic density using conventional samplers are likely to lead to overestimates of average population displacement. Results from a site on the River Wye, nearby to W3, indicate that a substantial proportion of the sampled fauna is not available to conventional methods of collection (0–10 cm) and that benthic density may be underestimated by 8–45% (Tab. 5). However, such an assessment takes no account of those organisms which are not collected by samplers with a mesh size less than 440 μm. Some workers have recorded aggregations of different size classes of some invertebrates at different depths (Coleman and Hynes 1970, Poole and Stewart 1976) and Ulfstrand (1968) found that there was a greater proportion of large ephemeropterans in the drift compared with the surface benthos. Elliott (1967a, b) also reported that invertebrates drifted more during late instar stages and periods of high growth rate. Clearly without information on size distributions and those animals not collected by the sampling methods available it is not possible to estimate relative rates of displacement of all size classes of total populations in the River Wye.

Tab. 5. The average vertical distribution (%) of selected taxa in the River Wye during the period June 1976–September 1977.

	Depth (cm)		
	0–11	12–22	23–33
Total invertebrates	61	23	16
Plecoptera	64	23	13
Ephemeroptera	92	7	1
Trichoptera	63	19	18
Diptera (Chironomidae)	55	26	19

The differences in displacement rates calculated from data collected at W2 and W3 on the River Wye indicate considerable variability. In addition, the nature of the sites chosen for sampling is likely to bias these estimates considerably since no account has been taken of slower flowing pool areas. Nor has within site variability been assessed. Nevertheless such estimates probably reflect the order of displacement rates which may be achieved in upland rivers.

It is known that many benthic macroinvertebrates are capable of upstream movements (Lehmann 1967, Elliott 1971a) and in order to estimate net rates of downstream displacement some account must be taken of such movements. Hayden and Clifford (1974) reported that nymphs of *Leptophlebia cupida* (Say) were capable of moving upstream at 10 m h^{-1} at certain times of the year. However, Elliott (1971a) studied 16 taxa in trough experiments and recorded that the modal distance moved upstream by invertebrates did not exceed 6.3 m d^{-1}, substantially less than the maximum downstream rates achieved by invertebrate populations in the River Wye. In addition, the number of invertebrates moving upstream was less than 30% of the total numbers caught in drift traps (Elliott 1971a). Therefore, assuming all stages of invertebrates behave as the sampled organisms in the present study, net downstream displacement of invertebrate populations in the upper Wye is not likely to exceed 10 km per generation (Tab. 6). Roos (1957) recorded ovipositing adults up to 5 km from the nearest water source and it has been shown for some taxa that such movements are orientated upstream (Ross 1957, Pearson and Kramer 1972, Madsen et al. 1973, Madsen and Butz 1976).

Tab. 6. Estimates of the net movement downstream of invertebrate populations between egg hatch and adult emergence.

Taxa	Time of egg hatch	Time of adult emergence	Average population displacement ($m\ d^{-1}$)	Modal upstream movement ($m\ d^{-1}$)*	Net distance travelled downstream (km)
*Baetis rhodani***	Aug	June	30	<5	8.3–10.0
*Baetis rhodani***	Apr	Aug	51	<5	6.4– 7.0
Amphinemura sulcicollis (Stephens)	Aug	May	11	<2	2.7– 3.3
Rhithrogena semicolorata	Aug	Mar	3	<5	0– 0.7
Hydropsyche siltalai (Dohler)	Aug	June	11	<1	3.0– 3.3

* Calculated from rates reported in Elliott (1971a).
** *Baetis rhodani* has two generations per year.

Since there is evidence of rapid dispersion of small nymphs from areas of high population density (Macan 1957, Swanson 1967) which tends to restore spatial equitability of densities when egg deposition is localised it seems probable that net rates of downstream movement would not lead to general depopulation of invertebrate communities in river systems like the River Wye.

Acknowledgements – This work formed part of a contract sponsored by the Welsh Water Authority and supported by funds from the Craig Goch Joint Committee and Central Water Planning Unit. Dr J. M. Elliott and Prof. R. W. Edwards suggested the models described in this paper and commented on the manuscript. The authors wish to thank the Llysdinam Trust, Dr R. Abel and Dr J. M. Hellawell.

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