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INTRODUCTION

Benthic invertebrates in lotic systems drift downstream in large numbers (see references in Bishop & Hynes 1969a; Waters 1969), but little is known about compensatory upstream movements. In amphibiotic insects the upstream flight of females may partially compensate for the drift of eggs and larvae (Roos 1957). Müller (1954) proposed the term 'Colonization Cycle' for the whole process of females migrating upstream, oviposition near the source of the stream, and larvae drifting downstream. This hypothesis is applicable to some species of Trichoptera (Roos 1957; Waters 1968; Elliott 1969), but imagines of most species fly in the same direction as the wind and show no persistent upstream movement (Elliott 1967; Bishop & Hynes 1969a).

An alternative mechanism is the upstream movement of benthic invertebrates, and this is the only possible mechanism for species which are aquatic throughout their lives. Upstream movements have been recorded for gammarid amphipods (Macan & Mackereth 1957; Minckley 1964; Müller 1966; Kureck 1967; Lehmann 1967; Hultin 1968), crayfish (Momot 1966), stonefly nymphs (Stehr & Branson 1938), and mayfly nymphs (Traver 1925; Neave 1930; Harker 1953; Macan 1957; Leonard & Leonard 1962). Ball, Wojtalik & Hooper (1963) studied the upstream dispersion of radiophosphorus in a Michigan stream and concluded that the radiophosphorus was probably carried upstream by benthic invertebrates. These upstream movements were quantitatively unknown and were not related to downstream drift. Recent studies in a Canadian river (Bishop & Hynes 1969b) and in a Swedish stream (Hultin, Svensson & Ulfstrand 1969) have shown that substantial numbers of invertebrates move upstream.

The purpose of the present study was to investigate the upstream movements of benthic invertebrates in a stony stream. 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 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 (Fig. 1a). Site A (Nat. Grid ref. SD374967) is situated just below the junction of the two tributaries. The gradient is fairly steep (fall about 6%) and the bottom consists of large stones (up to 30 cm diameter) over stones and gravel with no aquatic macrophytes. This steep gradient continues for a further kilometre and then decreases considerably for the next kilometre (fall about 1%). The bottom is now chiefly gravel and mud with dense stands of macrophytes (*Callitriche aquatica* Sm., some *Myriophyllum spicatum* L.). In the final kilometre, the gradient is again steep (fall about 4%) and the bottom is stony with macrophytes scarce. Site B (SD383941) is situated about 100 m above the mouth of the stream. Both sites are

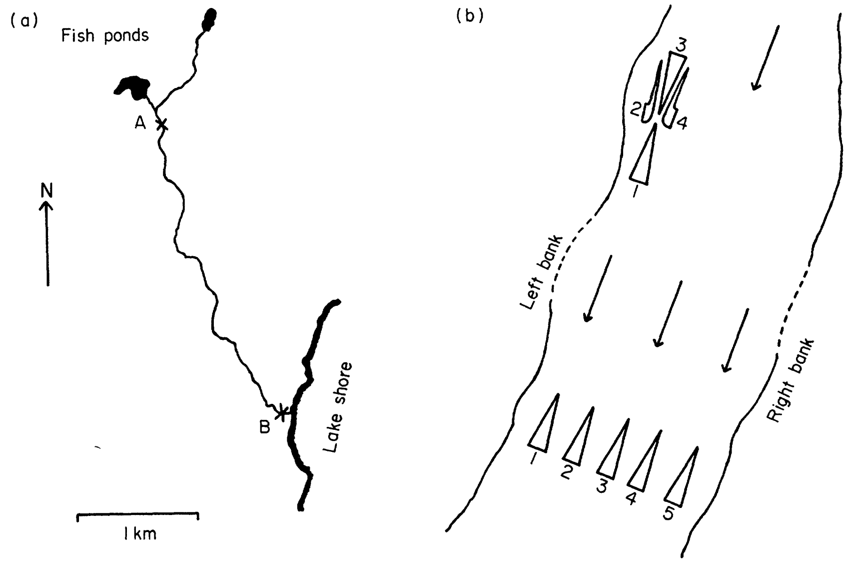

FIG. 1. (a) Map of Wilfin Beck, showing positions of sites A and B. (b) Sampling plan at one site, showing positions of traps (1–5) across the stream and in a cross formation near the bank (traps 1–4). Width of stream about 3·5 m. Arrows indicate direction of flow.

Table 1. *Range of water temperature, range of water velocity, modal width and modal depth at each site in each month (over sampling period only)*

		Nov. 1966	Feb. 1967	April	June	November
Water temperature (° C)	Site A	—	5·6–6·7	8·1–9·5	11·7–16·8	3·2–5·4
	Site B	5·3–6·8	5·4–7·2	8·1–9·6	11·7–15·4	5·3–6·4
Water velocity (cm/sec)	Site A	—	16·2–34·1	14·2–25·8	7·1–13·4	10·7–20·9
	Site B	38·9–95·0	30·1–70·1	25·1–44·8	12·2–25·8	28·1–53·1
Modal width (m)	Site A	—	3·4	3·4	3·0	3·2
	Site B	3·7	3·7	3·7	3·5	3·7
Modal depth (cm)	Site A	—	20	20	15	18
	Site B	24	20	17	16	18

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 at each site are compared in Table 1. Oxygen concentration was over 85% saturation at both sites in each month.

METHODS AND SAMPLING PROCEDURE

Various traps have been used to catch upstream-moving invertebrates (Waters 1965; Müller 1966; Lehmann 1967; Hultin 1968; Bishop & Hynes 1969b). The traps in the present study were tapered bags (100 cm long) with a rectangular mouth (30 cm wide and 15 cm deep). Each trap was double walled with an inner bag of nylon sifting cloth (mesh 440 μ, 15·5 meshes/cm) and an outer bag of 'Tygan' plastic screening (mesh about 1 mm^2).

Samples of upstream-moving invertebrates were taken in November 1966 at site B, and in February, April, June and November 1967 at sites A and B. In each month, five traps were placed across the stream at each site with the mouths of the traps facing downstream (Fig. 1b). Each trap was placed in the same position in each month. Stones from an area of about 1500 cm^2 of stream bottom were thoroughly washed and scraped to remove all the invertebrates, and were then spread evenly in a trap. The mouth of the trap was closed with a clip, and the trap was buried to a depth of about 13 cm in the bottom of the stream. After 72 h, the trap was lifted and emptied to check the extent of colonization by drifting invertebrates. Small chironomid larvae were the only invertebrates to drift through the walls of the traps and were taken in small numbers. The trap was then refilled with the same stones and replaced in the stream bottom with the trap mouth open. As the upper edge of the trap mouth was about 2 cm above the stream bottom, an invertebrate could enter the trap by moving in the substratum (to depth of about 13 cm), by crawling over the surface of the substratum, or by swimming just above the substratum. At the end of a 72 h sampling period, the trap was lifted and the total catch was removed.

This sampling procedure was slightly modified to compare day and night catches at site B in April, June and November 1967. Instead of leaving the traps open for 72 h, the traps were left open only during daylight for the first 3 days and only during darkness for the next 3 days. The traps were lifted at the end of each 3-day period, and the day or night catch was removed. Ratios of day to night sampling periods were 1 : 1 in April, 5 : 1 in June, and 1 : 3 in November. The traps were closed or opened at dusk and dawn (light intensity <1 lux). To close a trap, the upper and lower edges of the mouth were brought together, folded over, and secured with a clip. This operation necessitated a slight disturbance of the stones in the trap mouth, but care was taken that no invertebrates escaped from the trap.

A second experiment was designed to discover if the invertebrates moved randomly over the bottom. Four traps were arranged in a cross formation about 15 m above the five traps at site B (Fig. 1b). The traps were left open for 3 days in November 1966, April and June 1967. A similar experiment was performed at site A in June 1967, but the four traps were placed near the opposite bank (i.e. trap 4 nearest right bank). At both sites, a canopy was fixed over the mouth of trap 3 to prevent invertebrates drifting into the trap.

A small Ott current meter was used to measure water velocity over each trap. No quantitative comparisons were made between water movements inside and outside a trap, but small volumes of Pararosaniline dye were pipetted into the upstream end of a trap about 5 cm below the surface of the substratum. The dye rapidly diffused throughout the whole length of the trap, and through the side walls and mouth of the trap. Although the rate of diffusion was not measured, the dye tests demonstrated a rapid flow of water through the traps in a predominantly downstream direction. Maximum and minimum thermometers were read and reset under water at both sites in each month. Oxygen concentration was measured over each trap with a Mackereth (1964) meter.

Two methods were used to measure the distance covered by upstream-moving invertebrates in April and June 1967. Large individuals of eleven species were marked with cellulose paint and then released near the bank. Care was taken that the marked invertebrates clung to the stones and did not drift away. After 24 h, the invertebrates were recaptured by disturbing the substratum, either by hand-turning of stones or by kicking with the feet, and allowing the current to carry dislodged invertebrates into a dip net. This procedure was continued at increasing distance from the release point, and the distance from recapture point to release point was measured to the nearest metre for each marked invertebrate. Upstream movements of fourteen species and two genera were also studied in a trough at site B. There were separate day and night experiments for each species and the experiments were not limited to large individuals. The invertebrates were placed in a small nylon bag (mesh 440 μ) at the downstream end of the trough (600 cm long and 10 cm wide) which was closed with a nylon sieve at the upstream end. The trough was situated in the stream and was filled with small stones and gravel. Twenty invertebrates of the same species were put into the bag at dusk or dawn, and their positions were recorded after the corresponding period of night or day.

RESULTS

(a) *Composition of total catch at each site*

A large number of invertebrates moved upstream into the traps (Table 2). The total catch was 3432 at site A for the 4 months and 5665 at site B for the 5 months, with five traps sampling across each site for 72 h in each month. Most larvae of Diptera were not identified to species, but last-instar larvae of Simuliidae were chiefly *Simulium monticola* Friederichs, *S. tuberosum* Lundstroem and *S. nitidifrons* Edwards. *Ancylus fluviatilis* Müller, the river limpet, was the only species which was common in the benthos but was not taken in the traps.

Table 2. *Total numbers of invertebrates taken by five traps at site A in February, April, June and November* 1967; *and at site B in November* 1966, *February, April, June and November* 1967

	Site A			Site B		
	< Half size	> Half size	Total	< Half size	> Half size	Total
Plecoptera (nymphs)						
Protonemura meyeri (Pictet)	15	0	15	189	68	257
P. praecox (Morton)			0	6	0	6
Amphinemura sulcicollis (Stephens)	13	0	13	117	25	142
Nemoura cambrica Stephens			0	22	5	27
Leuctra inermis Kempny	20	4	24	36	7	43
L. hippopus Kempny	47	16	63	15	1	16
L. fusca (L.)	22	38	60	49	10	59
L. nigra (Olivier)	0	2	2			0
L. moselyi Morton	3	5	8	6	0	6
Chloroperla torrentium (Pictet)	122	149	271	108	59	167
C. tripunctata (Scopoli)	9	10	19	11	0	11
Isoperla grammatica (Poda)	31	15	46	10	6	16
Perlodes microcephala (Pictet)	3	4	7	4	3	7
Total Plecoptera	285	243	528	573	184	757
Ephemeroptera (nymphs)						
Baetis rhodani (Pictet)	959	63	1022	1999	118	2117
B. pumilus (Burmeister)	0	4	4	26	0	26
Ephemerella ignita (Poda)	28	8	36	140	26	166
Ecdyonurus torrentis Kimmins	68	39	107			0
E. venosus (Fabricius)			0	72	71	143
Heptagenia lateralis (Curtis)	81	45	126	36	4	40
Rhithrogena semicolorata (Curtis)	106	41	147	89	24	113
Caenis rivulorum Eaton			0	0	12	12
Paraleptophlebia submarginata (Stephens)	2	0	2			0
Total Ephemeroptera	1244	200	1444	2362	255	2617

Table 2 (*contd*)

Trichoptera (larvae)						
Rhyacophila dorsalis (Curtis)			0	0	2	2
Agapetus fuscipes Curtis	6	6	12	2	5	7
Hydropsyche instabilis (Curtis)	151	45	196	35	37	72
H. fulvipes (Curtis)			0	3	5	8
Plectrocnemia geniculata McLachlan	10	7	17			0
Potamophylax cingulatus (Stephens)	13	7	20	13	48	61
Drusus annulatus Stephens	0	17	17	0	21	21
Chaetopteryx villosa (Fabricius)	0	3	3			0
Sericostoma personatum (Spence)	21	15	36	0	11	11
Silo pallipes (Fabricius)	20	0	20			0
Odontocerum albicorne (Scopoli)	8	8	16	0	9	9
Total Trichoptera	229	108	337	53	138	191
Coleoptera (larvae and adults)						
Hydraena gracilis Germar (adults only)	0	4	4	0	51	51
Elmis aenea Müller	22	1	23	42	24	66
Limnius volckmari (Panzer)	0	2	2	10	5	15
Oulimnius tuberculatus (Müller)			0	0	2	2
Elodes sp. (larvae only)			0	9	0	9
Total Coleoptera	22	7	29	61	82	143
Diptera (larvae)						
Simuliidae	10	0	10	85	41	126
Chironomidae	40	0	40	813	251	1064
Tipulidae	0	36	36	0	2	2
Total Diptera	50	36	86	898	294	1192
Neuroptera: *Sialis fuliginosa* Pictet	0	4	4			0
Non-Insecta						
Gammarus pulex L.	581	406	987	193	156	349
Polycelis felina (Dalyell)			14			351
Erpobdella octoculata (L.)			1			50
Glossiphonia complanata (L.)			1			12
Hydrachnellae			0			3
Total non-Insecta			1003			765

The number of invertebrates less than and greater than half size is also given for each species, genus or family of insects (except Coleoptera) and for *Gammarus pulex*. Catches of Coleoptera were divided into larvae (in $<$half size column) and adults (in $>$half size column).

All insects, except Coleoptera, were measured from the front of the head to the tip of the abdomen (to nearest millimetre), and total catches were divided into small (less than half size) and large (greater than half size) larvae or nymphs. Half size was half the mean length of last instar larvae or nymphs, and varied from 3 mm for *Caenis rivulorum* to 9 mm for *Perlodes microcephala*. The catches of Coleoptera were divided into larvae and adults, and catches of *Gammarus pulex* were divided into individuals less or greater than half the maximum size.

Small individuals were more numerous than large individuals in the total catches of most taxa (Table 2), and the exceptions were chiefly Trichoptera with case-building larvae (*Drusus annulatus* at both sites; *Potamophylax cingulatus*, *Sericostoma personatum* and *Odontocerum albicorne* at site B). Small individuals were also predominant in the monthly catches of most taxa, and the exceptions were Plecoptera at site A in June (chiefly *Chloroperla torrentium* and *Leuctra fusca*), Trichoptera at site B in April and June (case-building species), and *Gammarus pulex* at both sites in April. In all these exceptions, the predominance of large individuals in the catches corresponded to their predominance in the benthos; e.g. in both benthos and traps at site A in June, the Plecoptera were chiefly full-grown nymphs which were ready to emerge. Therefore, apart from these few exceptions, the invertebrates moving upstream into the traps were chiefly small nymphs of Plecoptera and Ephemeroptera, small larvae of *Hydropsyche instabilis* and Diptera, larvae of Coleoptera and small individuals of *Gammarus pulex*.

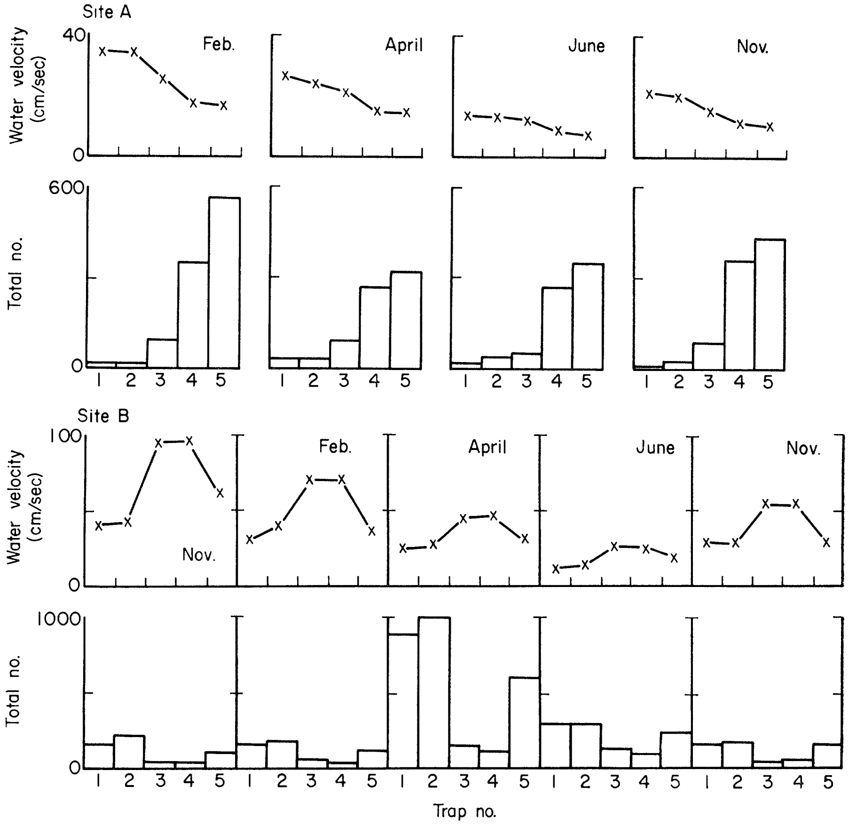

FIG. 2. Comparison of catches across the stream at sites A and B. Five traps were used in each month. Trap 1 was close to left bank and trap 5 was close to right bank (see Fig. 1b). Readings of water velocity over each trap are given at the top of the figure. Each column is the total catch for 72 h.

(b) *Comparison of catches across the stream*

In each month, there was an inverse relationship between numbers in a trap and water velocity over the trap (Fig. 2), but this relationship was not seen when the catches for the various months were collated. For example, although similar water velocities were recorded at site A over traps 4 and 5 in April and traps 1 and 2 in June, the five catches followed a similar pattern in both months with low catches in traps 1 and 2, and high catches in traps 4 and 5. Water velocity was probably an important indirect factor on account of its effect on the substratum. The stones in each trap generally reflected variations in substratum across the stream. Stones in traps 1 and 2 at site A and traps 3 and 4 at site B were large (up to 30 cm diameter) with a few small stones and a small amount of gravel. The other traps contained smaller stones (up to 15 cm diameter) with a larger quantity of small stones and gravel. Total catches were always highest in the traps containing small stones and gravel (traps 4 and 5 at site A, and traps 1, 2 and 5 at site B). Therefore, in spite of monthly fluctuations in water velocity, most invertebrates moved upstream in the small stones and gravel near the banks.

This relationship was shown by most species at site A, and by *G. pulex* and small larvae (or nymphs) of Plecoptera, Ephemeroptera, *Hydropsyche instabilis* and Diptera at site B. Catches of all these taxa were significantly different from each other ($P<0{\cdot}05$), when χ^2 analysis was used to test for significant differences among the five catches across the stream (Table 3). Large nymphs of *Baetis rhodani* at site B in April and June were the only invertebrates with significantly higher catches in midstream (traps 3 and 4) where

Table 3. χ^2 *values for comparisons of catches across the stream at site B (see Fig.* 4)

		Nov. 1966	Feb. 1967	April	June	November
Plecoptera	> Half-size	—	7·7 (NS)	2·3 (NS)	2·3 (NS)	—
	< Half-size	89·0***	22·5***	29·4***	8·0 (NS)	24·2***
Ephemeroptera	> Half-size	1·1 (NS)	2·1 (NS)	11·4*	20·4***	—
	< Half-size	77·3***	116·1***	1128·5***	282·4***	45·2***
Trichoptera	All sizes	4·8 (NS)	0·8 (NS)	8·2 (NS)	3·2 (NS)	21·0***
Coleoptera	Adults + larvae	—	—	22·3***	9·4 (NS)	4·5 (NS)
Diptera	> Half-size	—	—	44·9***	1·5 (NS)	—
	< Half-size	43·4***	16·0**	139·3***	17·8**	35·0***
Gammarus pulex	> Half-size	—	—	64·4***	—	—
	< Half-size	19·2***	11·3*	27·5***	62·8***	28·3***

Levels of significance are indicated by asterisks: * = $P<0{\cdot}05$, ** = $P<0{\cdot}01$, *** = $P<0{\cdot}001$, NS, not significant ($P>0{\cdot}05$). —, Indicates that the catches were too low (total catch for five traps < 20) for χ^2 test to be applied.

the substratum was chiefly large stones, i.e. exactly the opposite to the usual pattern across site B. No significant differences were found at site B among the five catches of large nymphs of Plecoptera (chiefly *Protonemura meyeri* and *Amphinemura sulcicollis* in April, *Leuctra fusca* in June, and *Chloroperla torrentium* in April and June), large nymphs of Ephemeroptera in November 1966 and February 1967 (chiefly *Ecdyonurus venosus* and *Rhithrogena semicolorata*), Trichoptera in most months (case-building species) and Coleoptera in 2 months (NS in Table 3). Monthly catches of non-Insecta usually followed the general pattern of the total catches, but there were no significant differences at site B among the five catches of *Erpobdella octoculata* in April and *Polycelis felina* in June. Therefore most invertebrates moved upstream in the small stones and gravel near the banks, but large nymphs of *Baetis rhodani* showed greater upstream movement in midstream and other upstream-moving invertebrates, including large nymphs (or larvae) of Plecoptera, Ephemeroptera and Trichoptera, showed no preference for a particular type of substratum.

(c) *Comparison of day and night catches at site B*

More invertebrates were taken by night than by day, and the only exceptions were *Nemoura cambrica*, *Leuctra hippopus*, *L. moselyi* (all < half size) and Hydrachnellae (Table 4). Although most species moved upstream in greatest numbers at night, day catches were often quite high for small nymphs of *Ephemerella ignita* (taken only in June)

Table 4. *Total numbers of invertebrates taken in the night and day samples at site B in April, June and November* 1967 (*for sampling procedures, see section on Methods*)

	Less than half-size		Greater than half-size	
	Night	Day	Night	Day
Plecoptera				
Protonemura meyeri	47	17	39	0
P. praecox	2	0		
Amphinemura sulcicollis	63	21	25	0
Nemoura cambrica	5	6	3	0
Leuctra inermis	14	7	6	0
L. hippopus	3	4		
L. fusca	31	18	9	0
L. moselyi	2	2		
Chloroperla torrentium	46	24	54	3
C. tripunctata	6	2		
Isoperla grammatica	3	1	6	0
Perlodes microcephala	1	0	2	0
Ephemeroptera				
Baetis rhodani	1147	669	108	10
B. pumilus	8	3		
Ephemerella ignita	78	62	23	3
Ecdyonurus venosus	23	3	25	3
Rhithrogena semicolorata	18	8	23	0
Heptagenia lateralis	7	2	4	0
Caenis rivulorum			9	2
Trichoptera				
Agapetus fuscipes			3	2
Hydropsyche instabilis	13	8	25	2
H. fulvipes	1	0	2	1
Potamophylax cingulatus	6	2	40	8
Drusus annulatus			6	2
Sericostoma personatum			5	2
Odontocerum albicorne			9	0
Coleoptera				
Hydraena gracilis			39	10
Elmis aenea	23	9	12	4
Limnius volckmari	7	2	4	0
Oulimnius tuberculatus			2	0
Elodes sp.	5	1		
Diptera				
Simulium spp.	50	28	30	7
Chironomidae	356	201	132	99
Gammarus pulex	89	46	119	12
	All sizes			
Polycelis felina	267	56		
Erpobdella octoculata	44	3		
Glossiphonia complanata	9	1		
Hydrachnellae	0	3		

and *Baetis rhodani*, larvae of Chironomidae, small *Gammarus pulex* and *Polycelis felina*.

An extra trap was placed near the bank about 20 cm upstream from the traps at site B, and was emptied every 2 h over 24 h in April and June. The catches of *Baetis rhodani* and *Gammarus pulex* were large enough to show a definite diel variation in upstream movement with a distinct nocturnal peak in the catches of both species (Fig. 3). Small individuals were predominant in all catches except those of *G. pulex* in April, the only

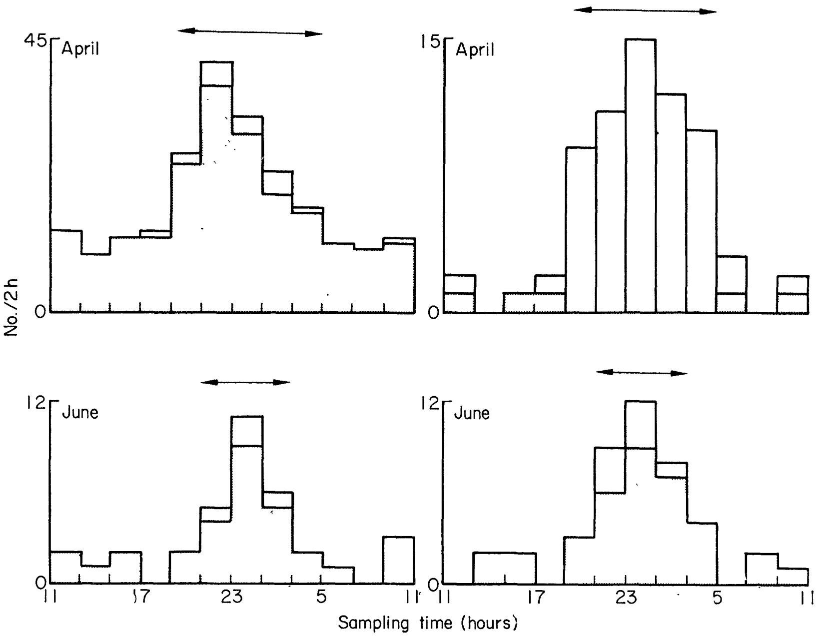

FIG. 3. Diel variation in upstream movement of *Baetis rhodani* (left) and *Gammarus pulex* (right) in April and June. Ordinate: numbers of invertebrates taken in a trap over a 2 h period; stippled portion of a column indicates the number of invertebrates less than half size. Abscissa: time in hours G.M.T. Arrow at top of each figure indicates period of darkness (<1 lux).

month when large individuals of this species were predominant in the catches at site B. Catches of other species were small and added no more information to the results of the day and night catches at site B.

(d) *Random versus upstream movements*

If the invertebrates moved randomly over the bottom of the stream, there should be no significant differences among the catches of the four traps arranged in a cross formation

Table 5. *Total numbers of invertebrates taken in four traps at site B in November* 1966, *April and June* 1967 *and at site A in June* 1967 (*traps were arranged in a cross formation: trap* 1 *downstream, trap* 3 *upstream, traps* 2 *and* 4 *across stream*)

	Site B												Site A			
	Nov. 1966				April 1967				June 1967				June 1967			
Trap no.	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Plecoptera	62	48	1	10	68	34	0	9	18	3	0	4	39	11	0	15
Ephemeroptera	58	47	2	8	458	134	8	52	168	86	4	64	93	30	1	50
Hydropsyche spp.	7	0	0	1	5	0	0	2	7	1	0	0	6	4	0	0
Case-building spp.	4	3	5	1	17	14	11	16	9	7	6	2	5	3	6	3
Coleoptera	7	2	0	0	18	14	7	4	8	3	0	1	1	0	0	0
Diptera	28	26	5	8	192	67	32	41	81	55	40	44	5	1	2	3
Gammarus pulex	27	21	1	4	50	27	0	14	26	21	0	4	124	11	0	38
Polycelis felina	5	2	2	3	38	21	18	19	37	27	19	21	0	0	0	0
Erpobdella octoculata	2	0	0	0	4	1	0	1	3	1	0	0	0	0	0	0
Total numbers	200	149	16	35	850	312	76	158	357	204	69	140	273	60	9	109

Table 6. *Marking experiments*

		Upstream movement			Downstream movement	
		No. marked	No. recaptured	Modal distance (and range) (m)	No. recaptured	Modal distance (and range) (m)
Plecoptera						
Isoperla grammatica	Site A, April	20	14	6(2–6)	1	< 1
	Site B, April	20	12	6(3–8)	0	
	Site B, June	10	7	4(4–6)	0	
Perlodes microcephala	Site A, April	20	18	4(2–8)	0	
	Site B, April	10	8	4(2–6)	0	
Ephemeroptera						
Ecdyonurus torrentis	Site A, April	50	29	2(0–6)	3	5(5–6)
E. venosus	Site B, April	50	34	3(1–5)	1	10
Heptagenia lateralis	Site A, April	30	21	4(1–6)	0	
	Site A, June	20	17	2(0–3)	0	
Rhithrogena semicolorata	Site A, April	40	21	4(0–4)	1	2
	Site A, June	20	8	4(0–4)	4	4
	Site B, April	30	15	5(2–6)	5	6(3–9)
	Site B, June	10	6	4(1–4)	1	5
Gammarus pulex	Site A, April	100	32	4(0–14)	28	4(2–10)
	Site A, June	100	24	4(0–12)	20	2(1–7)
	Site B, April	100	28	4(0–14)	26	5(1–8)
	Site B, June	50	12	4(0–10)	16	3(1–8)
Trichoptera						
Potamophylax cingulatus	Site B, April	20	20	< 1(0–1)	0	
	Site B, June	20	20	< 1(0–1)	0	
Drusus annulatus	Site B, April	20	20	< 1(0–1)	0	
Sericostoma personatum	Site B, April	20	20	< 1(0–1)	0	
Odontocerum albicorne	Site B, June	20	14	4(2–10)	1	1

Distances moved upstream and downstream by invertebrates in 24 h. Modal distance and range (in parentheses) are given to nearest metre.

(see Fig. 1b). This hypothesis was tested by χ^2 analysis (applied to monthly catches in Table 5). No significant differences ($P > 0{\cdot}05$) were found for case-building species of Trichoptera in all months. Significant differences ($P < 0{\cdot}05$) were found for the remaining catches which usually decreased in the following order: downstream trap 1, trap nearest bank (trap 2 at site B, trap 4 at site A), trap near midstream (trap 4 at site B, trap 2 at site A), and upstream trap 3. Monthly catches of different species of Plecoptera, Ephemeroptera and Coleoptera also followed this order at both sites. Although *Polycelis felina* and larvae of Diptera moved upstream in greatest numbers, the numbers moving downstream were quite high in April and June (Table 5). Therefore a definite upstream movement was shown by all taxa except case-building species of Trichoptera.

(e) *Distances covered by upstream-moving invertebrates*

Modal distances covered by the marked invertebrates were similar in April and June for each species, but there was a large variation in the distances covered by individuals of the same species (Table 6). A small number of mayfly nymphs and a large number of gammarids were recaptured below the release point. The downstream movement was probably due to drifting rather than movements on the bottom of the stream. This hypothesis was supported by the high catches of the same species in drift samples, and by the low catches of trap 3 in the experiments on random movements (see Table 5). All species of Trichoptera, except *Odontocerum albicorne*, were recaptured at or near the release point. Although these larvae did not appear to move far in 24 h, they crawled up to 4 m upstream or downstream at night and usually returned to the release point before dawn (see also Elliott 1969, 1970a).

In the trough experiments, all species moved further upstream at night than during the day (Table 7), but high modal values were recorded during the day for some species, e.g. *Baetis rhodani* and *Ephemerella ignita* in June. Although there was a large variation in the distances covered by individuals of each species, modal values varied considerably between species, especially at night. There was good agreement between modal values for the same species in the trough and marking experiments (five species in April, three species in June). Therefore the results of the marking and trough experiments provide estimates of the distances moved upstream by twenty species and two genera. These estimates were limited to April and June, and may be quite different for the same species in other months of the year.

The modal distances in the marking and trough experiments were a measure of the rate (= relative speed) of upstream movement, i.e. the distance covered in unit time (24 h in marking experiments, length of night or day in trough experiments). As the rate of upstream movement for a particular species increases, the number of invertebrates passing a width transect, or portion thereof, in unit time will also increase. Therefore the number of invertebrates entering a trap in unit time depends upon both the rate of upstream movement of a particular species and its density (numbers per unit area) in the benthos downstream from the traps. As the rate of upstream movement increases, the catch in a trap will come from a greater area of bottom and the ratio of catch per unit time to density in the benthos will increase. Although it is impossible to calculate the actual rate of upstream movement from the catch and density of a particular species, an index of the rate of upstream movement is given by C/D. The numerator (C) was the mean catch for five traps across the stream at site B, and the denominator (D) was the mean density (numbers/$0{\cdot}05$ m^2) for a random sample of five sampling units taken with a shovel sampler downstream from the traps. Separate night and day indices were calculated for all species used in the trough experiments (Table 8). Spearman's rank correlation coefficient (r_s) was used to measure the degree of concordance between modal values from the trough experiments and indices of the rate of upstream movement. The rankings of modal values and indices were in almost complete concordance for the night comparisons (April $r_s = 0{\cdot}99$, $P<0{\cdot}01$; June $r_s = 0{\cdot}96$, $P<0{\cdot}01$), and were significantly correlated for the day comparisons (April $r_s = 0{\cdot}77$, $P<0{\cdot}01$; June $r_s = 0{\cdot}81$, $P<0{\cdot}01$). These significant correlations increased confidence in the order in which species were ranked according to their rate of upstream movement (Table 8). It was therefore concluded that modal values obtained in the trough experiments reflected the rates of upstream movement on the bottom of the stream.

Table 7. *Trough experiments at site B*

	April Modal distance (and range) (cm)		June Modal distance (and range) (cm)	
	Night	Day	Night	Day
Plecoptera				
Protonemura meyeri	600 (125–600)	25 (0–75)	400 (125–450)	50 (0–125)
Amphinemura sulcicollis	225 (75–300)	25 (0–75)	175 (50–225)	25 (25–75)
Nemoura cambrica	125 (25–200)	50 (0–75)		
Leuctra spp.	475 (200–600)	100 (25–150)	275 (100–325)	75 (50–125)
Chloroperla torrentium	525 (200–600)	75 (50–125)	350 (150–450)	75 (50–150)
Isoperla grammatica	600 (375–600)	25 (0–100)	375 (175–450)	25 (0–150)
Perlodes microcephala	450 (200–600)	25 (0–125)		
Ephemeroptera				
Baetis rhodani	475 (175–600)	150 (25–250)	325 (150–450)	150 (50–275)
Ephemerella ignita			325 (75–350)	125 (50–200)
Ecdyonurus venosus	325 (125–425)	25 (0–75)	175 (25–225)	25 (25–75)
Rhithrogena semicolorata	575 (175–600)	50 (25–75)	350 (150–375)	50 (25–75)
Trichoptera				
Hydropsyche instabilis	75 (25–125)	25 (25–75)	50 (25–100)	25 (25–100)
Diptera				
Simulium spp.	50 (25–100)	0 (0–25)	50 (25–75)	25 (0–50)
Non-Insecta				
Gammarus pulex	400 (0–600)	50 (0–200)	275 (75–325)	100 (25–150)
Polycelis felina	200 (25–325)	50 (0–125)	175 (25–300)	50 (0–200)
Erpobdella octoculata	225 (25–400)	25 (0–50)	200 (25–300)	25 (0–50)

Distances moved upstream by twenty invertebrates of the same species during the night and day; modal distance and range (in parentheses) given to nearest 25 cm. *Leuctra* spp. were *L. inermis* and *L. fusca*. Modal water velocity in the trough was 27 cm/sec in April and 19 cm/sec in June.

(f) *Estimates of total numbers moving upstream*

The mean catch of the five traps across the stream (mean $= \bar{x}$) was an estimate of the number of invertebrates moving upstream in 72 h for a section 30 cm wide (the width of the mouth of a trap). As the width of the stream (W cm) was measured in each month (Table 1), an estimate of total numbers moving upstream in 24 h was given by $(\bar{x}W)/90$.

Confidence limits for the mean are usually calculated by multiplying the standard error by an appropriate value from Student's t-distribution. This method results from the central limit theorem (Snedecor & Cochran 1967) and is applicable to large random samples from any population with finite variance, to small samples from normally-distributed populations, to small samples from a Poisson series when the mean is fairly high, but not to small samples from other non-normal populations. Counts of the latter samples must be transformed before confidence limits are calculated, and the transformation should bring the data close to normality (see Chapter 6 in Elliott 1970b).

Table 8. *Comparison of results of trough experiments, marking experiments and indices of the rate of upstream movement at site B (species are ranked according to the modal distance moved by each species in the trough experiments at night)*

	April					June				
	Trough experiments modal distance (cm)		Marking experiments modal distance (m/24 h)	Index of rate of upstream movement		Trough experiments modal distance (cm)		Marking experiments modal distance (m/24 h)	Index of rate of upstream movement	
	Night	Day		Night	Day	Night	Day		Night	Day
Protonemura meyeri	600	25		5·5	0·3	400	50		4·0	0
Isoperla grammatica	600	25	6	4·0	0	375	25	4	3·0	0
Rhithrogena semicolorata	575	50	5	3·3	0·5	350	50	4	2·5	0
Chloroperla torrentium	525	75		2·6	0·7	350	75		2·0	0·3
Ephemerella ignita						325	125		1·5	1·0
Baetis rhodani	475	150		2·1	1·2	325	150		1·5	0·8
Leuctra spp.	475	100		2·0	0·9	275	75		0·9	0·3
Perlodes microcephala	450	25	4	2·0	0·0					
Gammarus pulex	400	50	4	1·8	0·4	275	100	4	1·1	0·6
Ecdyonurus venosus	325	25	3	1·3	0·3	175	25		0·7	0
Amphinemura sulcicollis	225	25		1·2	0·3	175	25		1·0	0
Erpobdella octoculata	225	25		1·0	0·1	200	25		1·3	0·1
Polycelis felina	200	50		0·8	0·2	175	50		0·8	0·2
Nemoura cambrica	125	50		0·7	0·2					
Simulium spp.	50	0		0·2	0·1	50	25		0·7	0·2
Hydropsyche instabilis	75	25		0·2	0	50	25		0·3	0

Table 9. *Estimates of total numbers of invertebrates moving upstream at each site in 24 h*

		November 1966	February 1967	April 1967	June 1967	November 1967
Site A						
Plecoptera	> Half-size		11 (2–33)	70 (50–91)	61*(31–118)	23 (12–35)
	< Half-size		43*(9–219)	23*(0–194)	5*(0–24)	25*(0–232)
Ephemeroptera	> Half-size		10*(0–41)	48*(15–155)	42*(17–105)	9 (0–33)
	< Half-size		72*(0–1580)	26*(0–339)	31*(0–444)	110*(4–1751)
Trichoptera	> Half-size		11 (2–33)	33 (19–47)	28*(14–58)	
	< Half-size		27*(0–341)	13*(1–51)	5 (0–24)	32*(1–249)
Coleoptera			9 (2–30)	4*(0–23)		
Diptera			7*(0–45)	6*(0–28)	11*(0–87)	4*(0–27)
Gammarus	> Half-size		41*(6–219)	92*(17–499)	22*(7–68)	9*(0–53)
	< Half-size		31*(0–392)	14*(0–124)	25*(0–552)	26*(0–412)
Total numbers			287*(30–2744)	367*(94–1430)	280*(60–1311)	270*(30–2411)
Site B						
Plecoptera	> Half-size	8*(1–28)	19 (5–45)	83 (60–106)	23 (9–51)	13 (3–36)
	< Half-size	82*(22–303)	74*(40–137)	105*(58–191)	25 (13–37)	113*(59–216)
Ephemeroptera	> Half-size	19 (5–45)	18 (5–42)	98 (73–123)	55*(25–118)	7 (1–30)
	< Half-size	78*(15–398)	91*(18–463)	343*(15–7885)	120*(10–1446)	56*(14–225)
Trichoptera		20 (7–48)	24 (9–54)	56 (37–75)	34 (20–48)	15*(4–53)
Coleoptera		12 (3–36)	8 (1–30)	48*(16–144)	18 (5–43)	16 (5–42)
Diptera		79*(32–192)	132*(80–218)	345*(130–911)	202 (167–237)	86*(38–191)
Gammarus	> Half-size	12 (3–36)	9 (1–30)	51*(11–248)	16 (4–40)	7 (1–30)
	< Half-size	28*(10–76)	12 (3–36)	16*(1–78)	24*(0–165)	16*(0–114)
Total numbers		366*(133–1007)	415*(192–899)	1690*(509–5608)	800*(465–1381)	427*(192–950)
Total numbers in drift		950	1115	15840	11237	1312
Numbers moving upstream as % of numbers in drift		38·5%	37·2%	10·7%	7·1%	32·6%

95% confidence limits for these estimates are given in parentheses. Estimates based on geometric means are indicated by asterisks. Estimates of total numbers drifting downstream at site B in 24 h are also given.

All estimates of total numbers moving upstream (Table 9) were made from samples of five sampling units. When agreement with a Poisson series was accepted, the arithmetic mean was used to estimate total numbers moving upstream (estimates not marked with asterisks in Table 9) and 95% confidence limits were either calculated from normal theory (when $\bar{x} > 6$) or obtained from tables (when $\bar{x} < 6$). When agreement with a Poisson series was rejected ($P < 0{\cdot}05$), the counts were transformed to logarithms before the mean and 95% limits were calculated. The antilog of the mean gave a derived mean (= geometric mean), and antilogs of the confidence limits gave asymmetrical limits which were large for many samples. The geometric mean was used to estimate total numbers moving upstream (estimates marked with asterisks in Table 9).

There was no significant difference between total numbers of invertebrates moving upstream at site A in February, June and November, and at site B in November 1966, February and November 1967. Significantly higher numbers moved upstream at both sites in April and at site B in June. Comparisons were made with the total numbers of invertebrates drifting downstream at site B (using methods described by Elliott 1967). Numbers in the drift were fairly constant in November and February, but increased markedly in April and June. In winter, when both upstream movement and drift were at a minimum level, the numbers moving upstream compensated for about 30% of the numbers in the drift over 24 h. Although upstream movement and drift were high in spring and summer, numbers moving upstream compensated for only 7–10% of the downstream drift. Therefore upstream movement of invertebrates was probably an important compensatory mechanism for downstream drifting in the winter months when drift rates were usually low, but not during high drift periods in spring and summer. Further comparisons between upstream movement and drift will be made in a later paper on drift rates of different species.

DISCUSSION

The positive rheotaxis of stream invertebrates is well known (see references in Müller 1966; Bishop & Hynes 1969b) and Neave (1930) showed that dead nymphs and even exuviae orientate positively with the current. As a result of this rheotaxis, all movements, including foraging, will tend to carry an invertebrate upstream. Upstream movements are therefore positive rheotactic responses and were shown by all species in the present study, except three species of Trichoptera (*Potamophylax cingulatus*, *Drusus annulatus* and *Sericostoma personatum*). As most species moved upstream in greatest numbers at night, it was difficult to discover whether upstream movement occurred above, on, or in the substratum. A red light was used for several observations at night, but only a small number of upstream-moving invertebrates were seen near the mouths of the traps. *Gammarus pulex* and large nymphs of *Baetis rhodani* were the only invertebrates which were observed swimming upstream just above the substratum at night. Large nymphs of Plecoptera and Ephemeroptera, larvae of *Hydropsyche* spp., *Erpobdella octoculata* and *Polycelis felina* were occasionally seen moving upstream over the substratum. Therefore some invertebrates probably moved upstream into the traps by swimming and by moving over the bottom of the stream. As few invertebrates were seen to enter the traps in these two ways, it was concluded that large numbers of invertebrates, especially small nymphs and larvae, probably entered the traps by moving upstream in the substratum. The dye experiments demonstrated a downstream flow between the stones in a trap, and this flow would ensure the positive rheotactic responses of the invertebrates in the substratum.

Other workers have found that interstitial currents deliver oxygen and food particles (Wickett & Pollard 1954; Pollard 1955; Vaux 1962), but the effect of these currents on the invertebrates is not known. Nor is it known why most of the smaller invertebrates moved upstream in the small stones and gravel near the banks. The simplest explanation is that the small invertebrates were more abundant near the banks, but little is known about the spatial distribution of stream invertebrates.

Little is known about the effect of upstream movements on benthic populations. Hultin *et al.* (1969) found that the upstream movements of several species in a Swedish stream were restricted to a limited part of the year, which was frequently the period before pupation or emergence. No comparisons were made in the present paper between monthly catches and life histories, but the catches of upstream-moving insects were certainly not limited to mature larvae and pre-emergent nymphs. Lehmann (1967) concluded that both drift and upstream movements of *Gammarus pulex* are caused by the males searching for females during the breeding period, but this was not confirmed in the present study. It is clearly important to discover if the whole, or only a part, of the population of each species is moving upstream. The ecological significance of upstream movements will probably vary between species and more detailed studies on each species are clearly needed.

The importance of upstream movements as a compensatory mechanism for downstream drift has been investigated in only one other locality. Estimates of total numbers moving up a Canadian river (width 5 m) ranged from 2617/day in December to 25 483/day in August (Bishop & Hynes 1969b). Although these estimates are far higher than those for the Wilfin Beck (Table 9), the upstream movement compensated for only 1·6–14·9% of the numbers drifting downstream (cf. range of 7·1–38·5% in Table 9). Therefore, in both localities, upstream movements only partially compensated for downstream drift, and did not seem to be a serious compensatory mechanism during high drift periods in spring and summer. These comparisons between upstream movements and drift may be misleading as they do not take into account the relative rates of movement in each direction. The rates of upstream movement in the Wilfin Beck varied between species, and drift rates may show a similar variation. When estimates of the distances travelled by drifting invertebrates are available, further comparisons can be made between upstream movements and drift.

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SUMMARY

(1) Monthly samples of upstream-moving invertebrates were taken at two sites in the Wilfin Beck, a small stony stream in the English Lake District.

(2) A large number of invertebrates moved upstream into traps at both sites and were chiefly small nymphs of Plecoptera and Ephemeroptera, small larvae of Diptera, larvae of Coleoptera, and small individuals of *Gammarus pulex*. Large individuals were predominant in the catches of a few species of Trichoptera with case-building larvae, and *G. pulex* in spring. Case-building larvae of Trichoptera did not show a definite upstream movement.

(3) Most invertebrates moved upstream in the small stones and gravel near the banks. Large nymphs of *Baetis rhodani* were the only invertebrates to show greater upstream movement in midstream where the substratum was chiefly large stones. Other invertebrates, including large larvae (or nymphs) of Plecoptera, Ephemeroptera and Trichoptera, moved upstream in similar numbers at different points across the stream.

(4) More invertebrates moved upstream at night than during the day, and the catches of *B. rhodani* and *Gammarus pulex* were large enough to show a definite diel periodicity in upstream movement with a distinct nocturnal peak.

(5) Measurements were made of the distances moved upstream by marked invertebrates or by invertebrates in a trough (twenty species and two genera). There were significant correlations between modal values obtained in these experiments and indices of the rate of upstream movement into traps. All species moved further upstream at night than during the day, but high modal values were recorded during the day for some species, e.g. *Baetis rhodani* and *Ephemerella ignita.*

(6) Estimates were made of the total numbers of invertebrates moving upstream in 24 h, and ranged from 366 in November to 1690 in April at one site. Upstream movement compensated for about 30% of the numbers of invertebrates drifting downstream in winter (upstream movement and drift at a minimal level), and for only 7–10% of the drift in spring and summer when both upstream movement and drift were high.

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