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The invertebrate drift in the River Duddon, English Lake District

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Abstract

The Duddon drainage is divided into two distinct areas: an upper basin, in which Plecoptera are predominant; and a lower basin, in which Ephemeroptera are predominant, with Plecoptera common and *Gammarus pulex* common over most of the area. Drift samples were taken simultaneously at four stations: two in the upper basin and two in the lower basin.

Nearly all species taken in the bottom samples were also taken in the drift. It was concluded that the predominance of Plecoptera in the upper basin is not due to an ability to withstand detachment better than other groups. The total drift samples from December 1965 to August 1966 gave a fairly accurate list of the species present at each station, and also gave a rough estimate of the percentage contribution of each species to the total benthos. The drift samples were generally poor indices of the relative size of the standing crops at the four stations, and it was concluded that drift rate could not be used as an index of the production rate of the benthos.

Nocturnal drift rates were greater than diurnal drift rates for all groups, except the Hydrachnellae. Six species of Plecoptera and Ephemeroptera were recorded in the drift for the first time. There was a strong inverse correlation between light intensity and drift rate. More emerging Trichoptera and Chironomidae were taken at night than during the day, whereas the reverse was true for emerging Ephemeroptera. The greatest numbers of emerging Plecoptera were taken at night in the lower basin and during the day in the upper basin. Most species of Plecoptera emerged later in the upper basin than in the lower basin.

Резюме

В дренажной системе Даддона выделяют верхний бассейн, где доминируют *Plecoptera*, и нижний бассейн с преобладанием *Ephemeroptera*; *Plecoptera* там обычны, а *Gammarus pulex* встречается в большинстве участков. В 4 участках одновременно брали пробы дрифта: 2 из них находились в верхнем бассейне, и 2 – в нижнем. Даны описания участков и методов взятия проб дрифта и сбора донной фауны.

Почти все виды, найденные в донных пробах, обнаружены и в дрифте. Пробы дрифта, взятые с декабря 1965 по август 1966 г.г., содержат полный набор видов, характерных для каждого участка. Материал позволяет дать приблизительное соотношение численности отдельных видов в бентосе. Пробы дрифта не дают представления об относительных размерах продукции в 4 участках, при этом установлено, что численность дрифта не может служить показателем скорости продукции бентоса.

Ночная численность дрифта выше дневной для всех групп, кроме *Hydrachnellae*. Шесть видов *Plecoptera* и *Ephemeroptera* обнаружены в дрифте в первый раз. Имеется строгая инверсионная корреляция между интенсивностью освещения и численностью дрифта. Вылупляющиеся *Trichoptera* и *Chironomidae* более многочисленны ночью, чем днем, но для *Ephemeroptera* установлена обратная зависимость. Максимальные количества вылупляющихся *Plecoptera* собраны ночью в нижнем бассейне и днем – в верхнем. Большинство видов *Plecoptera* в верхнем бассейне появляется позже, чем в нижнем.

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1. Introduction

Studies on invertebrate drift are becoming numerous (see references in Müller 1966 and Elliott 1967 a, b), but few published results are available on the comparative aspects of this phenomenon in streams of the same and different watersheds. The results of the present study provide information on the magnitude of drift at different points in a river system, and permit a comparison with the results of previous work on the same species from different localities. They also provide information on the utility of drift measurements as suitable indices of species composition and standing crop.

This study is part of a general ecological survey of the invertebrate fauna of the River Duddon (Minshall and Kuehne, in preparation). Preliminary work showed that there is an upper basin in which Plecoptera are predominant with Ephemeroptera and *Gammarus pulex* very rare, and a lower basin in which Ephemeroptera are predominant, Plecoptera common, and *G. pulex* common over most of the area. Several explanations for the cause of this have been suggested, but the one which principally concerns the present study is a suggestion by Dr. H. B. N. Hynes (in litt.) that "one of the reasons why the Plecoptera are so much more abundant in headwaters than are the Emphemeroptera is because the habits of the stoneflies render them less likely to be swept away." Therefore drift samples were taken simultaneously at four stations: two in the upper basin, one in the lower basin where *G. pulex* was rare, and one in the lower basin where *G. pulex* was common.

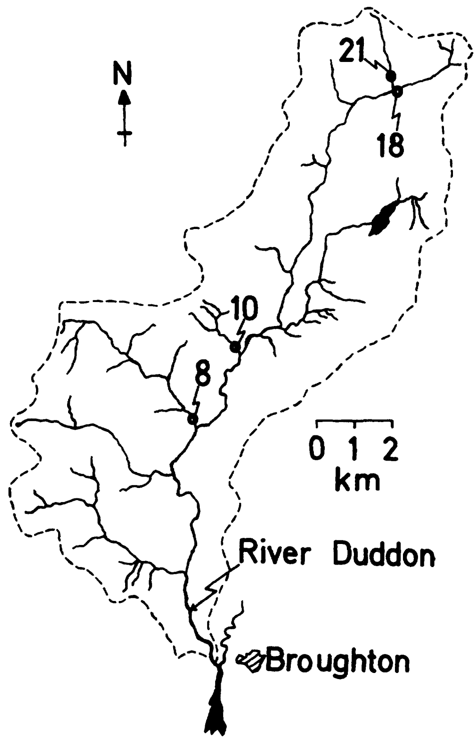


Fig. 1. Map of River Duddon, showing positions of stations 8, 10, 18, and 21.

2. Description of the river stations

The River Duddon lies in the southwest corner of the English Lake District along the border between Cumberland and Lancashire. The river rises near Wrynose Pass and flows south for about 17.5 km before finally entering the Irish Sea near Broughton-in-Furness (Fig. 1). The headwaters rise at heights ranging up to 732 m, but the mainstream begins at about 336 m and falls rather gradually over most of its length.

The substrate of the mainstream is relatively unstable alluvium, ranging in size up to 30 cm and interspersed occasionally with larger boulders. Very few large pools are present and the flow consists mainly of riffles and reaches. Frequent and rather rapid fluctuations in discharge are common. Rainfall is distributed throughout the year and varies from about 127 cm annually near the mouth to 305 cm near the source. A more complete description of the river and additional chemical and physical data are being published elsewhere (Minshall and Kuehne, in preparation). The positions of the four stations are shown in Fig. 1.

Station 8 (National grid reference SD201938; elevation 75 m), on Crosby Gill is located in the Ephemeroptera-predominant portion of the Duddon drainage. Crosby Gill, one of three major tributaries of the River Duddon, was one of the most productive streams examined during the survey. The flow at station 8 is torrential and the bottom reasonably stable, with many large boulders. Station 8 is the most densely shaded of the four sites.

Station 10 (SD213956, elevation 83 m) at Sling Beck can be considered as a transitional situation in which *G. pulex* is rare and Plecoptera predominant over Ephemeroptera. The stream progresses in stairstep fashion, with stretches of pools or reaches separated by shorter sections of riffles or cascades. At station 10 the substrate consists of fairly stable, flat, angular stones. The area is moderately shaded by deciduous trees.

Stations 18 and 21 are situated near the headwaters of the River Duddon in the area where Plecoptera are predominant. Both sites are located in exposed positions on boulder-strewn riffles. Grasses (*Festuca ovina* L., *Agrostis* spp., *Nardus stricta* L.), moor-rush (*Juncus squarrosus* L.), and bracken (*Pteridium aquilinium* (L.) Kuhn) are the principal kinds of vegetation in the upper basin of the Duddon and they contribute significant quantities of plant material to the river. Station 18 (NY258021, elevation 244 m) is on the mainstream of the River Duddon near the mouth of Gaitscale Gill. The bottom is more unstable than that at the other three stations. Station 21 (NY258023, elevation 275 m) at Gaitscale Gill lies about 305 m upstream from station 18. Gaitscale Gill has a relatively steep gradient (fall about 488 m in 2.4 km or 20%) and falls in a series of cascades and runs. The substrate at station 21 is chiefly large boulders interspersed with pockets of gravel or small rubble-strewn areas. This was the most difficult to sample of the four stations.

Minimum and maximum water temperatures at the four stations are compared in Tab. 1. The readings indicate the temperature conditions over 24 hours or less. Although Macan (1958 a) has shown that such isolated observations are of limited value, the table does show seasonal changes with a rise in temperature from February to April and a marked rise from April to May at all four stations. The temperatures were generally higher in the lower basin (stations 8 and 10) than in the upper basin (stations 18 and 21), but maximum temperatures in the latter were often greater than minimum temperatures in the former. Weather conditions were always more severe in the upper basin than in the lower basin and surface ice was present over most of the length of Gaitscale Gill in January and February.

Total discharge was estimated during each sampling period and was always greatest at station 8, with station 18 next, then station 10, and finally station 21 (Tab. 1). The four stations followed this same order for modal widths and for mean depths, but not for mean water velocity (Tab. 1). Although total discharge was much smaller at stations 10 and 21 than at station 18, there was a greater cross-sectional area and therefore a lower mean water velocity at station 18.

Tab. 1. Minimum and maximum water temperatures and total discharge during each sampling period; modal width, mean depth, and mean water velocity at stations 8, 10, 18, and 21.

	Maximum and minimum water temperatures (°C)				Estimated total discharge (in 1000 m³ per 24 hrs.)			
Stations: –	8	10	18	21	8	10	18	21
December 1965	1.2– 2.3	1.3– 2.5			200	11		
January 1966..	0.2– 0.5	0.4– 0.9	1.1– 1.1	0.4– 0.4	100	17	20	4
February	0.2– 0.5	0.4– 0.7	0.3– 0.5	0.0– 0.0	103	11	22	3
April.........	1.9– 5.3	2.5– 5.4	0.4– 5.8	0.4– 4.5	100	11	33	4
May	8.5–11.0	8.5–10.7	6.8– 8.7	7.9– 7.9	131	17	41	5
June	14.7–16.8	14.4–15.0	12.7–15.0	11.8–14.1	115	8	35	5
July..........	12.6–14.0	12.4–13.8	10.7–12.0	10.1–11.2	98	7	51	6
August	13.7–14.3	12.9–13.5	13.1–13.1	12.3–12.3	119	12	38	4

	Mean water velocity and range (m per sec.) across the stream				Modal width (m) and mean depth (m) at each station				
Stations: –	8	10	18	21		8	10	18	21
19 May 1966 ..	1.02	0.62	0.50	0.55	Width	7	2	3.3	1.0
	0.37–1.24	0.55–0.72	0.19–0.81	0.50–0.66	Depth	0.31	0.17	0.23	0.10

3. Methods

Bottom samples were of 2-minutes duration and were obtained by disturbing the stream bottom, either by hand-turning of stones or by kicking with the feet, and allowing the current to carry the dislodged material into a collecting net (see Macan 1958 b and Minshall and Minshall 1966 for full description). The kick method generally yielded more individuals per sample than did the hand-pick method, probably because a greater area was covered more thoroughly in a comparable time. The collecting net had a mesh of 265 microns (25 threads per cm) and was attached to a 25 cm square frame. No bottom samples were taken in February owing to ice and snow cover.

Two kinds of drift samplers were used, namely large and small surface nets. As the surface net has already been described in detail (Elliott 1967 a), only a brief account is given here. The nets floated on the water and each had a rectangular mouth with an effective sampling area of 336 cm^2 for the large nets and 125 sq cm for the small net, water being sampled to a depth of 7 cm by the large net and 5 cm by the small net. Both nets were made of nylon sifting cloth with a mesh of 440 microns (15.5 threads per cm). A small surface net was used at station 21 and one large surface net at each of the other stations. In January and February the drift sampler at station 21 was frozen solid at and above the surface of the water and had to be chipped from the ice before the catch could be removed.

A small Ott current meter was used to determine water velocity at the mouth of the net and thus an estimate could be made of the total volume of water filtered by the net. Cross-sectional area was determined at each station and water velocity was measured at 0.5 m intervals across the stream. Therefore total discharge could be estimated at each station. The ratio, total discharge: volume filtered by drift sampler, varied greatly from site to site and was about 50:1 at station 8, 9:1 at station 10, 13:1 at station 18, and 3:1 at station 21.

Because of the distance between some of the stations, it was necessary to empty the nets every 3 hours at stations 8 and 10, and every 4 hours at stations 18 and 21. Sampling periods of less than 24 hours were used in some months to reduce the quantity of material which had to be sorted, identified and counted. All samples were preserved in 70% alcohol or 10% formalin and hand sorted in the laboratory. Monthly drift samples were taken from December 1965 to August 1966, and sampling was over the following periods at each station:

Stations 8 and 10. 24 hours in December, April, June; 6 hours before and after dusk in other months.

Station 18. 4 hours before and after dusk in all months.

Station 21. 24 hours in April, June; 4 hours before and after dusk in other months.

4. Composition of drift and benthos at the four stations

Aquatic invertebrates, emerging imagines of aquatic insects, and terrestrial invertebrates were all taken in the drift samples and total

Tab. 2. Total numbers taken in the drift and bottom samples from December 1965 to August 1966 at stations 8, 10, 18, and 21. Also total volume of water passing through each drift sampler.

Stations: –	8	10	18	21
Drift samples:				
Terrestrial invertebrates	1736	899	473	604
Emerging imagines	845	224	786	725
Aquatic invertebrates	10738	1088	435	1059
Volume of water through drift sampler (m^3)	10638	6828	6151	2824
Bottom samples:				
Aquatic invertebrates	16461	5549	1269	3835

Tab. 3. Aquatic invertebrates taken in the bottom samples but not in the drift samples from December 1965 to August 1966 at stations 8, 10, 18, and 21: total numbers and percentage contribution to total benthos (a + sign indicates that the item contributes less than 0.05% to the total benthos).

Stations: –	8 Nos. (%)	10 Nos. (%)	18 Nos. (%)	21 Nos. (%)
Plecoptera				
Nemurella picteti Klap.				2 +
Perlodes microcephala (Pict.)		2 +		
Chloroperla tripunctata (Scop.)	3 +	25 (0.5)		
Ephemeroptera				
Heptagenia lateralis (Curt.)	23 (0.1)	140 (2.5)	1 +	1 +
Mollusca				
Ancylastrum fluviatile (Müll.)	3 +			
Oligochaeta	4 +			
Turbellaria				
Tricladida	232 (1.4)	4 +	7 (0.6)	7 (0.2)
	265 (1.6)	171 (3.1)	9 (0.7)	10 (0.3)

numbers for each category are given in Tab. 2. Terrestrial invertebrates were taken in large numbers at each station and formed a considerable proportion of the total drift at stations 10, 18 and 21. Over 95% of the terrestrial invertebrates were taken from April to August at station 8 and from May to August at stations 10, 18 and 21. Therefore the terrestrial component of the drift was only important during the spring and summer months. Emerging imagines of aquatic insects were also taken in large numbers and formed a large proportion of the drift at stations 18 and 21.

Nearly all species taken in the bottom samples were also taken in the drift samples and the exceptions formed a small proportion of the total benthos (Tab. 3). Two notable exceptions were *Heptagenia lateralis* and Tricladida. There was no apparent reason for the absence of *H. lateralis* from the drift since other species of Ecdyonuridae (*Rhithrogena semicolorata*, *Ecdyonurus venosus*, and *E. dispar*) were often taken in the drift samples. Tricladida were also absent from the drift in a Dartmoor stream (Elliott 1967 a) but have been taken in the drift by Müller (1966).

Tab. 4 includes all species taken in both drift and bottom samples from December 1965 to August 1966. *Gammarus pulex* was confined to station 8 and nymphs of Ephemeroptera to stations 8 and 10, apart from four nymphs of *Siphlonurus lacustris* taken in the drift at station 18 and single nymphs of *Heptagenia lateralis* taken in the bottom samples at stations 18 and 21. Some species, e.g. *Leuctra nigra*, *Capnia vidua*, *Siphlonurus lacustris*, *Helodes* sp., *Dixa* sp., were absent from the bottom samples when present in the drift and this indicates some limitations in the bottom sampling.

At each station the percentage composition of the aquatic component of the drift was generally similar to that of the total benthos (see Tab. 4). The proportions of Plecoptera and Ephemeroptera in the drift were greater than those in the benthos, whereas the reverse was true for Diptera. Trichoptera were chiefly the net-spinning and free-living forms, and they and Coleoptera formed only a small proportion of drift and benthos. At station 8, Ephemeroptera were definitely predominant over Plecoptera in both drift and benthos, whereas at station 10 the reverse was true in the benthos with the two groups contributing similar proportions to the drift. Plecoptera formed over 80% of the total drift at stations 18 and 21, and were clearly drifting in large numbers in both upper and lower basins.

It is concluded from this comparison of drift and benthos that the total drift samples give a fairly accurate list of the species present at each station and also a rough estimate of the percentage contribution of each species to

Tab. 4. Aquatic invertebrates taken in the drift and bottom samples from December 1965 to August 1966
indicates that an item contributes less

	STATION 8			
	Drift		Benthos	
	No.	(%)	No.	(%)
Plecoptera				
Brachyptera risi (Mort.)	1	+	1	+
Protonemura meyeri (Pict.)	20	(0.2)	51	(0.3)
P. praecox (Mort.)				
Amphinemura sulcicollis (Steph.)	577	(5.4)	1033	(6.3)
Nemoura cambrica Steph.	1	+	3	+
Leuctra fusca (L.)	696	(6.5)	402	(2.4)
L. hippopus Kemp.	24	(0.2)	9	(0.1)
L. inermis Kemp.	38	(0.4)	17	(0.1)
L. moselyi Mort.	12	(0.1)	12	(0.1)
L. nigra (Ol.)	4	+		
Capnia vidua Klap.				
Isoperla grammatica (Poda)	5	+	7	+
Chloroperla torrentium (Pict.)	15	(0.1)	7	+
Total Plecoptera	1393	(13.0)	1542	(9.4)
Ephemeroptera				
Leptophlebia vespertina (L.)	1	+		
Ephemerella ignita (Poda)	112	(1.0)	307	(1.9)
Baetis pumilus (Burm.)	24	(0.2)	59	(0.4)
B. rhodani (Pict.)	6749	(62.9)	6146	(37.3)
B. scambus Eat.	82	(0.8)	40	(0.2)
Siphlonurus lacustris Eat.				
Rhithrogena semicolorata (Curt.)	14	(0.1)	36	(0.2)
Ecdyonurus dispar (Curt.)	4	+		
E. venosus (F.)	14	(0.1)	98	(0.6)
Total Ephemeroptera	7000	(65.2)	6686	(40.6)
Trichoptera				
Rhyacophila dorsalis (Curt.)	10	(0.1)	42	(0.3)
Philopotamidae				
Plectrocnemia conspersa (Curt.)	2	+	2	+
P. geniculata McL.			1	+
Hydropsyche instabilis (Curt.)	13	(0.1)	28	(0.2)
Limnephilidae	10	(0.1)	1	+
Total Trichoptera	35	(0.3)	74	(0.5)
Coleoptera				
Helmis maugei Bedel	194	(1.8)	557	(3.4)
Limnius tuberculatus Müll.	59	(0.6)	11	(0.1)
Hydraena sp.	4	+	2	+
Helodes sp.	2	+		
Dytiscidae	1	+		
Total Coleoptera	260	(2.4)	570	(3.5)
Diptera				
Tipulidae	2	+	5	+
Chironomidae	257	(2.4)	2351	(14.3)
Simulium spp.	1479	(13.8)	4114	(25)
Dixa sp.	17	(0.1)		
Total Diptera	1755	(16.3)	6470	(39.3)
Gammarus pulex L.	265	(2.5)	829	(5)
Hydrachnellae	30	(0.3)	25	(0.2)
Only in bottom samples			265	(1.6)

at stations 8, 10, 18 and 21: total numbers and percentage contribution to total drift and benthos (a + sign than 0.05 % to the total drift or benthos).

STATION 10		STATION 18		STATION 21	
Drift	Benthos	Drift	Benthos	Drift	Benthos
No. (%)	No. (%)	No. (%)	No. (%)	No. (%)	No. (%)
12 (1)	30 (0.5)		1 (0.1)	27 (2.5)	46 (1.2)
43 (4)	666 (12)	18 (4.1)	27 (2.1)	113 (10.7)	149 (3.9)
6 (0.6)	43 (0.8)				
44 (4)	60 (1.1)	161 (37.1)	205 (16.2)	262 (24.7)	747 (19.5)
	1 +	2 (0.5)		2 (0.2)	
10 (0.8)	154 (2.8)				
16 (1.5)	46 (0.8)	21 (4.8)	182 (14.3)	53 (5)	181 (4.7)
118 (10.9)	204 (3.7)	118 (27.1)	494 (38.9)	391 (36.9)	1404 (36.5)
4 (0.4)	111 (2)				
3 (0.3)				7 (0.7)	
3 (0.3)				24 (2.3)	26 (0.7)
28 (2.6)	168 (3)	6 (1.4)	16 (1.3)		
118 (10.9)	59 (1.1)	28 (6.4)	21 (1.7)	9 (0.8)	75 (2)
405 (37.3)	1542 (27.8)	354 (81.4)	946 (74.6)	888 (83.8)	2628 (68.5)
1 (0.1)	1 +				
1 (0.1)					
1 (0.1)	12 (0.2)				
383 (35.1)	686 (12.4)				
29 (2.7)	59 (1.1)				
		4 (0.9)			
	2 +				
1 (0.1)	1 +				
416 (38.2)	761 (13.7)	4 (0.9)			
4 (0.4)	46 (0.8)		3 (0.2)	6 (0.6)	13 (0.4)
6 (0.5)	35 (0.6)		1 (0.1)		
6 (0.5)	12 (0.2)	6 (1.4)	8 (0.6)	16 (1.5)	30 (0.8)
	21 (0.4)	2 (0.5)	6 (0.5)		1 +
	6 (0.1)				
3 (0.3)	3 +	1 (0.2)		1 (0.1)	
19 (1.7)	123 (2.2)	9 (2.1)	18 (1.4)	23 (2.2)	44 (1.2)
4 (0.4)	16 (0.3)	1 (0.2)			
		1 (0.2)			
	4 +				
8 (0.7)	4 +				
3 (0.3)		4 (0.9)	4 (0.3)	8 (0.8)	1 +
15 (1.4)	24 (0.4)	6 (1.4)	4 (0.3)	8 (0.8)	1 +
2 (0.2)	4 +	3 (0.6)	3 (0.2)		11 (0.3)
90 (8.3)	1813 (32.7)	52 (12)	245 (19.3)	46 (4.3)	579 (15.1)
119 (10.9)	1103 (19.9)	6 (1.4)	44 (3.5)	94 (8.9)	562 (14.6)
20 (1.9)	4 +				
231 (21.3)	2924 (52.7)	61 (14)	292 (23)	140 (13.2)	1152 (30)
2 (0.2)	4 +	1 (0.2)			1 +
	171 (3.1)		9 (0.7)		10 (0.3)

the total benthos. Therefore, in the absence of bottom samples, drift samples could be used as an index of species composition.

The total numbers in the bottom samples varied considerably from station to station (Tab. 2), and the ratio of these totals gives an indication of the relative size of the standing crop at each station (Tab. 5). Similar ratios have been calculated for the major groups in the benthos and these ratios are compared with those for the corresponding groups in the drift (Tab. 5). If the volume of water flowing through a drift sampler increases, the size of the catch increases; therefore comparisons of numbers per unit volume (i.e. density of animals in the drift) are preferable to comparisons of numbers per unit time (Elliott 1967 a, b). The total volume of water passing through each drift sampler varied from station to station and was greatest at station 8 and smallest at station 21 (Tab. 2). Therefore ratios are given for both numbers per unit time (24 hours) and density (numbers per 1,000 m^3) of animals in the drift.

The ratio of total benthos indicates that the standing crop was greatest at station 8, followed by stations 10, 21, and 18 respectively (Tab. 5). The stations did not follow this order for ratios of either numbers per unit time or density in the drift. In the Plecoptera the order of stations was identical for ratios of benthos and density of nymphs in the drift, whereas in the Coleoptera and Diptera the order was the same for the ratios of drift per unit time and benthos. The order of stations was different for all three ratios in the Trichoptera. Even when the order of stations was the same, there was little similarity between the size of the ratios in benthos and drift.

Therefore, although the drift did reflect some quantitative differences in the benthos, it was generally a poor index of the relative size of the standing crop at each station.

5. Comparison of nocturnal and diurnal drift rates

At all stations, the total number of animals

Tab. 5. Ratios of numbers per unit time (24 hours) and density (numbers per 1000 m^3) of aquatic invertebrates in the drift samples, and total numbers of invertebrates in the bottom samples.

Stations: –	8	10	18	21	Order of stations from highest to lowest ratio			
Total aquatic invertebrates								
Drift per 24 hrs	11.2	: 1.1	: 1	: 1.7	8	21	10	18
Density in drift	14.2	: 2.2	: 1	: 5.3	8	21	10	18
Total benthos	13	: 4.4	: 1	: 3	8	10	21	18
Plecoptera								
Drift per 24 hrs	3.4	: 1	: 1.9	: 3.3	8	21	18	10
Density in drift	2.3	: 1.1	: 1	: 5.4	21	8	10	18
Total benthos	1.6	: 1.6	: 1	: 2.8	21	8/10		18
Ephemeroptera								
Drift per 24 hrs	16.8	: 1						
Density in drift	10.8	: 1						
Total benthos	8.8	: 1						
Trichoptera								
Drift per 24 hrs	1.8	: 1	: 1	: 1.7	8	21	10/18	
Density in drift	2.3	: 1.9	: 1	: 5.6	21	8	10	18
Total benthos	4.1	: 6.8	: 1	: 2.4	10	8	21	18
Coleoptera								
Drift per 24 hrs	22	: 1.3	: 1.1	: 1	8	10	18	21
Density in drift	24	: 2	: 1	: 3	8	21	10	18
Total benthos	570	:24	: 4	: 1	8	10	18	21
Diptera								
Drift per 24 hrs	13.1	: 1.7	: 1	: 1.6	8	10	18	21
Density in drift	16.5	: 3.4	: 1	: 5	8	21	10	18
Total benthos	22.2	:10	: 1	: 4	8	10	21	18

Tab. 6. Total numbers of aquatic invertebrates and trout fry taken in the night and day drift samples from December 1965 to August 1966 at stations 8, 10, 18, and 21.

Stations: –	8 Drift		10 Drift		18 Drift		21 Drift	
	Night	Day	Night	Day	Night	Day	Night	Day
Plecoptera								
Brachyptera risi		1	9	3			26	1
Protonemura meyeri	19	1	38	5	18		103	10
P. praecox			5	1				
Amphinemura sulcicollis	521	56	38	6	158	3	238	24
Nemoura cambrica	1				2		2	
Leuctra fusca	696		10					
L. hippopus	23	1	15	1	18	3	43	10
L. inermis	37	1	112	6	105	13	355	36
L. moselyi	12		4					
L. nigra	3	1	3				4	3
Capnia vidua			3				20	4
Isoperla grammatica	4	1	23	5	6			
Chloroperla torrentium	14	1	116	2	26	2	4	5
Ephemeroptera								
Ephemerella ignita	106	6	1					
Baetis pumilus	24			1				
B. rhodani	6658	91	359	24				
B. scambus	76	6	24	5				
Rhithrogena semicolorata	14							
Ecdyonurus dispar	4							
E. venosus	12	2	1					
Trichoptera								
Rhyacophila dorsalis	10		4					6
Plectrocnemia conspersa		2	6		6		12	4
Hydropsyche instabilis	10	3						
Coleoptera								
Helmis maugei	156	38	2	2	1			
Limnius tuberculatus	57	2			1			
Diptera								
Chironomidae	182	75	60	30	36	16	10	36
Simulium spp.	1316	163	88	31	4	2	54	40
Dixa spp.	14	3	18	2				
Gammarus pulex	249	16						
Hydrachnellae	4	26	1	1		1		
Trout fry (May)	8		11		6			
Trout fry (June)	1				36	1		

taken in the drift was far greater in the night samples than in the day samples (Tab. 6). This was also true for all species and groups in the drift except the Hydrachnellae. Although the total numbers in the day samples were often large for the more abundant species in the drift, they were always less than the total numbers in the corresponding night samples. The very low water temperatures of January and February (Tab. 1) did not inhibit the nocturnal increase in drift rate, and drifting nymphs of Plecoptera were taken under the ice at station 21. Müller (1966) found that if the water temperature falls to about 0°C, drift rates of *Baetis* spp. are higher in the day than at night. This was not the case for nymphs of *Baetis rhodani* in the River Duddon and the normal nocturnal increase in drift rate still occurred at 0.2°C.

Trout fry (*Salmo trutta* L.) were taken in the drift samples for May and June at stations 8, 10 and 18 (Tab. 6). The fry were about 2.5 cm long and all except one were taken at night. These observations agree with those on downstream movements of trout fry in a Dartmoor stream (Elliott 1966). In the Dartmoor stream, however, the fry were taken in the March and April drift samples with greatest numbers in April, whereas in the River Duddon maximum numbers were taken during May in the lower basin (stations 8, 10) and during June in the upper basin (station 18). Therefore the time of these nocturnal downstream movements can vary considerably from one locality to another.

The daily fluctuations of the more abundant species in the drift are compared in Fig. 2. Numbers in the drift are shown separately for stations 8, 10, and 21; and where possible, December, April, and June figures have been included to illustrate the effect of different periods of darkness. The volume of water passing through each drift sampler (in m^3 per sample) are given for each month at the top of Fig. 2. Discharge through each sampler remained constant during the 24-hour sampling period in April and June, but decreased with time in December. This was due to the December samples being taken just after the peak of a severe spate. Readings of light intensity (in lux) at station 8 are also given for each month and the periods of darkness (shaded) and daylight (unshaded) are shown for each species. As there was no correlation between variations in water temperature and drift rate, readings of water temperature are omitted from Fig. 2.

There was a strong correlation between decreasing light intensity and drift rate, a relationship also recorded by Tanaka (1960), Waters (1962), Södergren (1963), Levanidova and Levanidov (1965), Müller (1966), and Elliott (1965 a, b, 1967 a). In December and April, the drift rates of most species were at a maximum in the early hours of the night, but in June the maxima often occurred just before dawn. There were also secondary peaks in drift rate, especially in winter (see December column in Fig. 2). Waters (1962) suggested that these secondary peaks could be due to the occlusion of moonlight and Anderson (1966) concluded that moonlight had a depressant effect on the nocturnal drift rate. In December, the drift samples in the River Duddon were taken just before full moon and the night was clear and bright until the moon set at 3.15 hrs. The moonlight appeared to have no depressant effect on drift rate and there was no marked increase in drift rate after the moon had set. Elliott (1967 a) found that secondary peaks in the drift occurred even on nights when skies were overcast with no moon visible.

Hydrachnellae were usually taken in small numbers in the drift but in April the numbers were large enough to be compared over 24 hours at station 8. Maximum numbers were taken in the afternoon, with a smaller peak in the morning and minimum numbers at night (Fig. 2). This pattern is very similar to the activity pattern of a water-mite *Hygrobates naicus* in a lake (Moon 1940).

6. Emerging imagines in the drift

Emerging imagines were frequently taken in the drift samples and Chironomidae were by far the most abundant at all stations (Tab. 7). Greater numbers of Trichoptera and Chironomidae were taken at night than during the day, whereas the reverse was true for Ephemeroptera. The greatest numbers of emerging Plecoptera were taken at night in the lower basin and during the day in the upper basin. All species of Plecoptera, except *Amphinemura sulcicollis*, followed this pattern. *Taeniopteryx nebulosa*, *Philopotamus montanus*, *Polycentropus flavomaculatus*, *Beraea maurus* and *Halesus radiatus* were taken as emerging imagines but were not recorded in the drift and bottom samples. Nymphs of *T. nebulosa* were taken in bottom samples above station 8 and presumably the single imago taken at station 8 had drifted from upstream.

Emerging Trichoptera were taken from May to August and emerging Plecoptera and Ephemeroptera were scarce before May (Tab. 8). There was a steady succession of *Leuctra* spp., as found by Hynes (1961) in the Afon Hirnant. *L. hippopus* emerged first, followed by *L. inermis*, *L. moselyi*, and finally *L. fusca*, which presumably continued to emerge until December. The emergence periods of *Protonemura meyeri*, *Amphinemura sulcicollis*, *Leuc-*

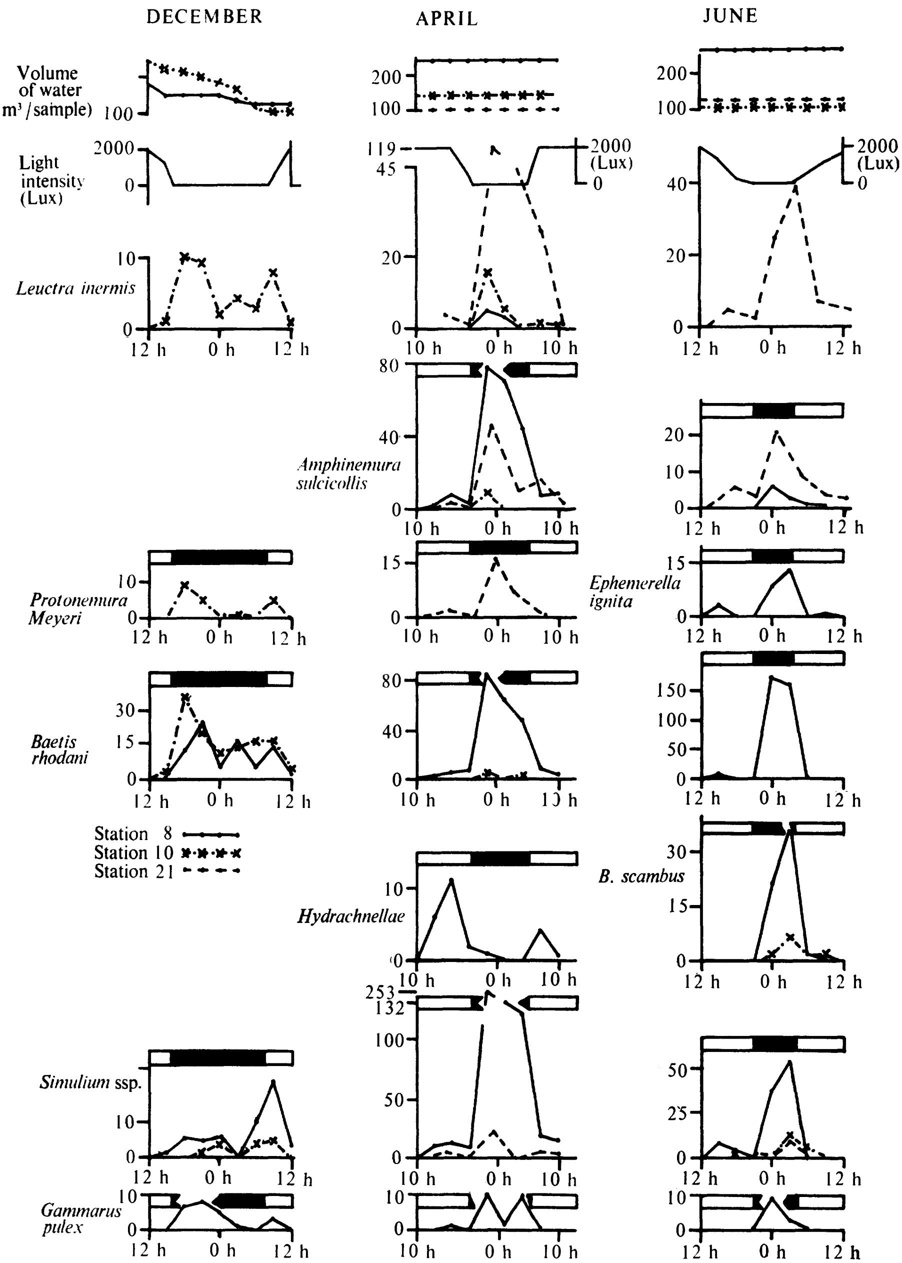


Fig. 2. Daily fluctuations in the numbers of the more abundant species in the drift (ordinate: numbers taken in each sample; abscissa: time in hours with Oh. indicating midnight). Variations in light intensity (lux) and volumes of water passing through each drift sampler (cu.m per sample) are shown at the top of the figure.

Tab. 7. Total numbers of emerging imagines taken in the night and day drift samples from December 1965 to August 1966 at stations 8, 10, 18, and 21.

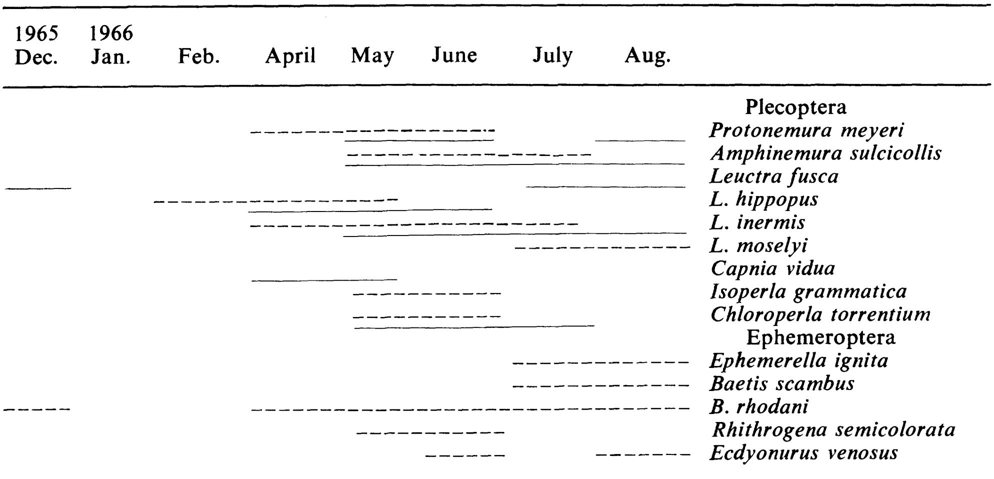
Stations	8		10		18		21	
	Night	Day	Night	Day	Night	Day	Night	Day
Taeniopteryx nebulosa (L.)		1						
Protonemura meyeri	4	4	1		2		3	3
Amphinemura sulcicollis	9	22			5	13	3	2
Leuctra fusca	93	15	5	1				
L. hippopus		2	1	2	2	8	21	31
L. inermis	4	2	3	3	8	28	10	27
L. moselyi	3		2					
L. nigra	1						1	
Capnia vidua							2	4
Isoperla grammatica	1	1						
Chloroperla torrentium	2	2	4	8	2	8		4
Total Plecoptera	117	49	16	14	19	57	40	71
Ephemerella ignita	1	24						
Baetis pumilus		1						
B. rhodani	7	77		7				
B. scambus	1	2		2				
Siphlonurus lacustris						1		
Rhithrogena semicolorata		14						
Ecdyonurus venosus		2						
Total Ephemeroptera	9	120		9		1		
Rhyacophila dorsalis	7	1	1		3		1	
Philopotamus montanus (Don.)				1				
Plectrocnemia conspersa					2		2	
Plectrocnemia geniculata					9		1	
Polycentr. flavomaculatus (Pict.)			2					
Polycentropidae		1			2		3	
Hydropsyche instabilis	13	2						
Beraea maurus (Curt.)		1						
Halesus radiatus (Curt.)					1			
Tinodes sp.			1					
Total Trichoptera	20	5	4	1	17		7	
Chironomidae	331	194	92	88	371	321	351	256

tra hippopus, *L. inermis*, and *Chloroperla torrentium* were later in the upper basin than in the lower basin (Tab. 8). These same species in a Dartmoor stream emerged much later after a severe winter than in a normal year and the normal nocturnal increase in emerging Plecoptera was reversed (Elliott 1967 b). These changes after a severe winter are very similar to those recorded from lower to upper basin of the River Duddon. The growth of the nymphs was not studied in the Duddon, but in the Dartmoor stream the late emergence appeared to be due to a marked retardation in growth rate by the very low winter temperatures. This could also be the reason for the later emergence of Plecoptera in the upper basin, where the water temperatures were generally lower than in the lower basin.

7. Discussion

Invertebrate drift is clearly an integral part of the ecology of the River Duddon and all the more abundant species in the benthos also occur in the drift. Nymphs of Plecoptera appear to be swept into the drift just as easily as nymphs of Ephemeroptera; therefore

Tab. 8. The emergence periods of the more abundant species of Plecoptera and Ephemeroptera.



- - - - - - - - - Lower basin (stations 8 and 10)
__________ Upper basin (stations 18 and 21)

their predominance in the upper basin is not due to an ability to withstand detachment. Elliott (1967 b) lists all those species of Plecoptera and Ephemeroptera which have been taken in the drift by various workers. The following species from the River Duddon are not included in this list and therefore are recorded in the drift for the first time: *Protonemura praecox*, *Leuctra moselyi*, *L. nigra*, *Capnia vidua*, *Siphlonurus lacustris*, and *Ecdyonurus dispar*.

Waters (1961, 1966) concluded that drift is a mechanism for removing excess production and therefore drift rate can be used as an index of the production rate of the benthos. Waters (1961) also found that when standing-crop samples of five streams were "limited to groups of similar longevity", the distribution of standing crops was similar to the ranking of expected productivities and close to the distribution of drift rates. Although the invertebrates at the four stations in the River Duddon were of similar longevity, there was little similarity between ratios of standing crop and those of drift. Therefore drift rates would probably be of little use as indices of production rate in the River Duddon. Müller (1966) and Elliott (1967 a) also concluded that drift could not be used as an index of the production rate of the benthos.

Levanidova and Levanidov (1965) concluded "that the duration of the individual migration of larvae is much less than the total duration of the nocturnal migration (8–9h)", Waters (1965) estimated the distance of daily drift and found that "this seems a surprisingly short distance considering normal current velocities and the fact that organisms are well represented in the upper strata of water", and Elliott (1967 a) concluded that most of the aquatic invertebrates in the drift returned to the benthos after travelling only a short distance. Therefore, the animals in the drift are not necessarily removed from a section of stream and cannot be regarded as excess production. A drift sampler catches the animals in the drift before they can return to the bottom and accrual takes place in the sampler over a period of time. Although there is usually less than one animal per cubic metre of water, a large volume of water passes through the sampler in 24 hours and, therefore, large numbers are taken in the drift. This may explain why the drift rate over an area of bottom is often many times greater than the standing crop of that area.

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