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An Ecological Study of Invertebrates of the Duddon, an English Mountain Stream

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With 4 Figures and 7 Tables in the text and on 1 Folder

Abstract

This paper concerns the relative abundance, diversity, and general distributional patterns of the benthic macroinvertrebrates of the River Duddon, Lake District, England. The drainage is divided into two distinct areas: an upper basin, in which Plecoptera are predominant and Ephemeroptera and *Gammarus* rare, and a lower basin, in which Ephemeroptera are predominant, with Plecoptera common and *Gammarus pulex* common over most of the area. Nutrients or other water quality factors appear to be the most likely explanation for the observed discontinuity of the fauna, although temperature also may be important. Other factors, such as the presence of physical barriers, substratum differences, variations in discharge and current velocity, or behavioral differences in relation to either wind or water currents, appear to be unimportant or to play only a minor role. Also included are data on hydrology, climate, and water quality of the Duddon.

Introduction

The purpose of this study is to examine the invertebrate community of an entire river system throughout a complete year. The last study of this scope conducted in England was the survey of the River Tees by Butcher, Longwell & Pentelow (1937). The River Duddon, located in the Lake District, was selected for the present study for several reasons, including: accessibility during all seasons, freedom from undue human disturbance, absence of large lakes to interrupt the stream pattern, and the existence of a considerable altitudinal gradient.

The particular ecological aspects considered in this paper are the relative abundance, diversity, and general distributional patterns of the benthic invertebrates in the mainstream and a number of tributaries. This paper also includes descriptive information on hydrology, climate, water quality, topography, and land use, all of which contribute to an understanding of the above topics. Additional information concerning stream order, invertebrate drift, life histories, and the fauna of the submerged bryophytes are being published separately.

Description of the Study Area

The River Duddon (Figs. 1 and 2) is one of several streams which form a radial drainage pattern emanating from the central Cumbrian Mountains. The headwater tributaries rise at elevations up to 735 m on the fells to the south of Crinkle Crags. The mainstream empties onto the tidal Duddon Sands approximately 18 km south-southwest of its most distant source. The basin, which comprises 8636 hectares, lies within the Lake District National Park and is largely under direct control of the Forestry Commission or the National Trust. Major tributaries of the Duddon are Tarn Beck, Crosby Gill, Holehouse Gill, and Logan Beck. The River Lickle, which joins the Duddon practically at sea level, is not included in this study.

Rocks of the basin are lower Silurian volcanic intrusives, which are acidic and resistant to weathering. Open rock faces and barren scree are

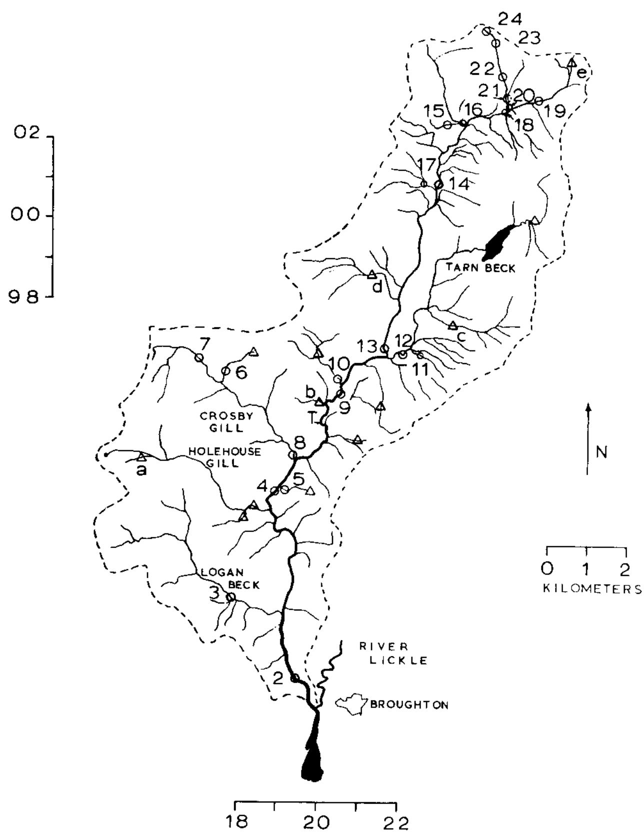

Figure 1. River Duddon and its tributaries. Numbered stations (circles) were sampled during most months of the study; lettered stations (triangles) were sampled at least twice (once in autumn and once in summer). Location of recording thermograph is designated by "T".

common around the higher peaks and restrict development of the peaty moorland soils otherwise characteristic of the rougher terrain. Patches of boulder clay and coarse alluvium occur locally, especially along the main valley.

The Duddon Valley has been modified toward a U-shape by glacial action, although only one example of a true hanging tributary exists. Typically, tributaries enter the main valley at a steep gradient, often with one or more small waterfalls. Here their courses are marked by boulders, stones, and stretches of exposed bedrock.

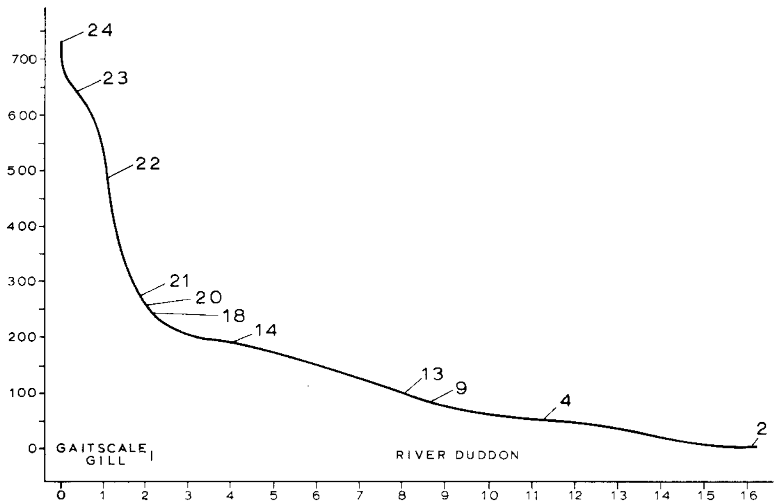

Figure 2. Profile of Gaitscale Gill and the River Duddon; elevations in meters, distances in kilometers.

In the valley the stream gradients are little more than that of the river. The highest tributary in the basin, Gaitscale Gill, has produced a braided alluvial fan of large stones at its mouth, beneath which it sinks during dry spells. Less pronounced deposition is exhibited by other tributaries as they enter the main valley. The tributaries of Tarn Beck are similar to those elsewhere in the basin, but the beck itself enters the Duddon through its own glacially scoured valley.

Away from the walls of the main valley and toward their sources, the tributaries tend to display moderate gradients with alternating pools and riffles. Some arise as becks on steep fellsides, while peat-filled pools or tarns are the sources of others. Mosses *(Fontinalis, Hypnum)* and liverworts *(Nardia)* locally form dense mats in tributaries but higher aquatic plants are common only in those few areas having slow flow and mud substratum.

A large amount of detritus is washed or blown into the Duddon and its tributaries during late autumn and winter. Dead plant material collects in mats against and beneath stones, becoming steadily more fragmented and decomposed. By late spring, floods remove most detrital material and little can be found in summer and early autumn. Leaves of deciduous trees and blades of pasture grasses appear only in some of the lower tributaries and the Lower Duddon. This detritus has been observed to fragment and disappear more quickly than the coarse vegetation originating on open fells.

The drainage basin is divided into an upper and lower portion, which show differences in stream fauna, physico-chemical conditions, and hydrology; these differences will be elaborated in the text. We have considered the upper basin to be the area above station 13 (Fig. 1), about where Tarn Beck enters the mainstream, and the lower basin to be the area below station 13, including the nearby stations 11 and 12. The river flows turbulently over several zones of bedrock between stations 14 and 13, forming a distinct gorge that separates the upper and lower valleys. In the lower basin the stream flows over bedrock above and again below station 4. Elsewhere the streambed is composed of stones, gravel, and scattered boulders. Pools may exceed 2 m in depth at normal levels and are separated by much longer stretches of rapids, varying between 15 cm and 60 cm deep. The stream normally is about 15 m wide at station 4, 9 m wide at station 14, and 4.5 m wide at station 19.

In the lower basin, oak forest and coniferous plantings cover many of the slopes adjacent to the main valley. Pasture grasses, such as *Poa* spp., are cut for hay but very little land is cultivated. High fells more distant from the valley are grazed by sheep. Cover is provided mainly by hardy species of grasses (*Festuca ovina* L., *Agrostis* spp., *Nardus stricta* L.) and by bracken (*Pteridium aquilinium* [L.] KUHN), which is locally abundant. Gorse (*Ulex europaeus* L.) and heather (*Erica cinerea* L.) are common along some rocky outcrops.

The upper Duddon basin is mostly open country. Scattered woodlands, primarily conifer plantations, persist about as far up the valley as station 14. The remainder of the upper basin is devoted to sheep grazing. Winter pasture and lambing quarters are in the main valley and animals range freely on the high fells during the warmer half of the year. The coarse grasses and bracken mentioned previously form the general vegetative cover, but moor-rush (*Juncus squarrosus* L.) and various sedges predominate over boggy areas.

In the upper basin there are only two farms, neither very productive and both dependent largely upon sheep grazing on the open fells for their existence. On the other hand, the lower basin contains over a dozen farms, at least one dairy, and a number of residences; the pastures commonly are fertilized and cattle are common. Therefore, it is reasonable to assume that the greater productivity and more varied and intense farm practices in the lower basin are reflected in the quality and amount of nutrients reaching the river (either as dissolved salts or as detritus). Ultimately it would seem that the observed differences in vegetation and land usage are manifestations of climatic differences between the two basins.

Old mines and quarries in the area are inactive, leaving the Duddon basin free from excessive human disturbance. Recreational usage of the basin, including sightseeing, hiking, and camping, is heavy in the summer months. The river is lightly fished for Atlantic salmon and sea trout.

Methods

The Ordnance Survey of Great Britain (1 : 63,000 series) was used in drafting Figure 1 and in measuring basin area. More detailed Ordnance Survey maps (1 : 25,000 series) were employed to determine station elevations and the vertical profile of the river (Fig. 2).

Stations that were visited at least once in every season are circled in Figure 1. These are numbered 2 through 24 and, in general, run from mouth toward source of the river. Supplementary stations, which were sampled at least twice during the study, have been designated with triangles and lettered A through E. Some additional collecting sites are shown as triangles but have been given no further designations, since they are not specifically referred to in this paper.

Collecting sites were selected on the basis of flow and substratum characteristics to be as comparable as possible. Collections were taken over stony riffles with maximum depths of 45 cm in the main river and minimum depths of 2.5 cm in the smallest becks. A net with a metal frame 25 cm square, fitted with a tapered nylon bag with mesh size of 265 microns and an open area of 44 percent, was used to make all collections. In lower numbered stations (2—13) invertebrates were collected by overturning stones by hand (Macan 1958 a), except during high water when the feet also were used to dislodge stones and disturb the bottom. In higher numbered stations (14—24) and those designated with letters the stream bottom was agitated by kicking (Hynes 1961).

For the purposes of this paper two series of collections were used: an autumn series, in which all of the numbered stations were sampled on 16—17 November 1965 and the lettered stations A, C, E and B, D were sampled in mid-October 1965 and mid-February 1966, respectively; and a summer series, in which all stations were sampled during 1—2 July 1966. The representativeness of these collections was verified by comparison with similar collections made at the numbered stations during other months of the year. The autumn samples were of 5-minutes duration at all stations except B and D; the autumn samples for B and D and all of the summer collections were of 2-minutes duration. The numbers of individuals presented in Tables 6 and 7 are expressed as numbers per 5 minutes of sampling.

Collections were preserved in formalin in the field. In the laboratory invertebrates were separated from gravel and heavier organic debris by flotation in a saturated solution of magnesium sulfate or were merely handpicked from relatively clean collections. Seventy percent ethanol was used as a final preservative.

Water temperatures were taken at the numbered stations during intensive autumn (November) and summer (July) invertebrate sampling and also were taken at many stations during other months (Table 3). These data are not strictly comparable because sites were visited at various hours, sometimes on successive days.

Additional data were obtained from maximum-minimum recording thermometers which were mounted in sections of iron pipe and lodged beneath stones in several streams. One such thermometer was lost, one was broken in a flood, and several others disappeared in a major flood of 13 August 1966. A temperature record for the lower Duddon was obtained from a continuous recording thermograph located at the Ulpha Water Works below station 9. This is the same instrument used in the studies by MACAN 1958 b) and MACAN & MAUDSLEY (1966). In Figure 3, mean temperature values for each week are given. These were determined by taking the sum of the number of hours at a given temperature (in 1° intervals) times the given temperature and dividing this product by the number of hours per "week". (In some instances a "week" was actually less than 7 days.) Because of the size of the stream at the point where the thermograph was located and because the flow below this point is regulated, the temperatures obtained from the thermograph probably are representative of those occurring in the lower reaches of the mainstream (stations 2 and 4). Water Works personnel furnished the discharge data on which Figure 2 is based. Rate of flow was measured several times at selected stations (Table 3) with a Watts-Price current meter or with an Ott C-1 miniature current meter.

Water samples from the numbered stations (Table 4) were analyzed for sodium with a flame photometer to obtain a general index of seasonal variations in dissolved solids. Six stations were analyzed more completely in the study months of December, March, and July (Table 5) by the water chemistry laboratory of the Freshwater Biological Association.

Results

Temperature

During the year for which complete thermograph records are available (1966), temperatures in the River Duddon (Fig. 3) ranged from 0° C (January) to almost 20° C (June—July). Maximum weekly variation was about 10° C (May); weekly ranges of about 8° C were recorded in April, May, July, and August. The seasonal pattern is much the same as that described by MACAN (1958 b) for Ford Wood Beck, although due to a great size difference the two streams are not strictly comparable in this respect.

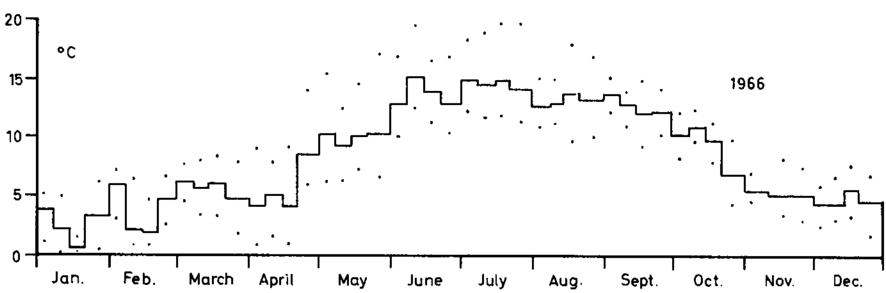

Figure 3. Weekly average stream temperature (°C) at Ulpha Water Works (station T), 1966. Weekly maxima and minima are designated by dots.

Table 1. Maximum-minimum temperature recordings (°C) from the River Duddon and some of its tributaries.

	Mainstream				Lower Basin Tributaries			Upper Basin Tributaries		
Station	Ulpha W.Wrks.	13	14	18	5	6	8	17	20	23
Date (1966)										
19 Jan.—	0	0	—	0	3.9	2.2	5.6	0	3.3	0
7 Mar.*	7.8	7.2	—	6.7	8.3	10.0	8.9	7.8	5.6	5.0
7 Mar.—	0.9	0	0	0	2.2	1.7	1.1	0.6	0	0
29 Apr.**	11.9	11.7	12.2	10.6	12.8	14.4	12.8	12.2	9.4	9.4
29 Apr.—	6.4	5.0	5.0	4.4	7.2	3.9	7.2	6.1	2.8	1.7
19 May***	15.6	15.0	17.2	14.4	15.6	18.9	15.6	16.1	12.8	13.3
19 May—	6.5	6.1	5.0	5.0	7.8	5.6	4.4	4.4	5.0	3.3
21 June	19.6	18.9	21.7	18.9	20.6	21.1	18.9	20.6	15.6	15.6
21 June—	10.5	10.0	?	broken	11.7	8.9	10.6	9.4	10.6	7.2
19 July	18.3	22.8	—	—	20.0	19.4	17.2	20.0	15.6	15.0
19 July—	9.9	lost	lost	—	11.3	8.9	10.1	lost	lost	7.2
16 Aug.	19.8	—	—	—	20.2	21.7	17.9	—	—	17.2

* Stations 5 and 6 installed 24 February.
** Station 14 installed 13 April.
*** Station 23 read 24 May.

Records of maximum-minimum temperatures for certain regular sampling stations (Table 1) are incomplete but they do encompass the coldest and warmest periods of the year (Fig. 3 and Macan 1958 b). Maximum-minimum temperatures from the recording thermograph have also been included for comparable periods as an indication of conditions in the lower sections of the mainstream. The lowest temperatures (minima) consistently were recorded at station 23, and during periods when all stations were near 0° C (January-March) the maxima at station 23 were the lowest of the series. For every interval the maximum recorded at station 6 (a small, exposed stream, located on a southwest facing slope) was among the highest. The period of greatest fluctuation at all stations was during 19 May to 21 June.

Temperatures generally were warmer and persisted near the maximum values longer in the lower basin tributaries than in those of the upper basin (Table 1). The principal exception was station 17, which was often as warm or warmer than some of the lower basin tributaries. Except for the maxima at station 14, a similar pattern is evident when the upper and lower mainstream records are compared. Although the values for station 14 cannot be ignored, it is clear that the duration of time spent at or near the maxima is as much a factor in survival as is the particular temperature value, and further, that the smaller streams are more likely to reflect local climatic differences than are large streams (Ross 1963).

In general, our findings tend to support the observation that conditions in the upper basin are harsher than those in the lower basin. Among other things snowfall was greater and persisted longer in the upper basin (beginning about station 13 and becoming progressively more severe to stations 23, 24, and E), and the growing season for terrestrial vegetation was shorter and later.

Precipitation, Discharge, Flow

Precipitation in the Duddon Valley is relatively abundant throughout the year (Table 2). In general, February through July is the driest period; values in August through January average 5 to 7 cm per month higher. As might be expected, actual values during the study do not show such a clear pattern. The wettest months during the study were December and February; October and August were the driest. Mean annual precipitation at Ulpha Water Works is 203 cm (range 149—278). But the variation within the

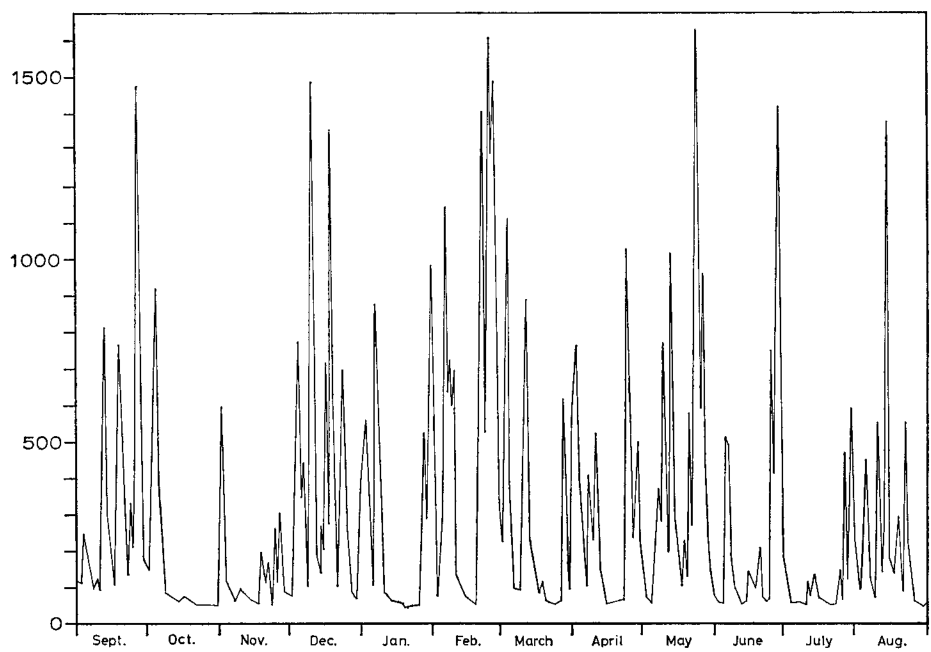

Figure 4. Total daily stream discharge (m^3/day × 1000) at Ulpha Water Works (station T), during the study period (1965—1966).

Table 2. Monthly precipitation and discharge values for the River Duddon at Ulpha Water Works.

	1965				1966								
	S	O	N	D	J	F	M	A	M	J	J	A	Total
	Precipitation (cm)												
Mean (1940—1965)	22	20	22	23	21	14	13	13	11	12	16	19	203 (mean)
1965—1966	20	8	17	32	18	31	16	14	19	19	11	13	216
	Discharge (1000 m^3)												
1965—1966	10,151	3,778	3,977	12,427	7,619	13,714	8,328	8,872	11,523	7,442	3,942	6,968	—

drainage basin is quite pronounced, from about 125 cm at Duddon Bridge (station 2) to 250—300 cm at Seathwaite Tarn. Periods as long as two weeks without precipitation are unusual. Snow melts rather quickly at lower elevations, but above 600 m it may persist for most of the winter.

The Duddon is a clear, swift stream which is subject to rapid fluctuations (Fig. 4). Daily variations in discharge in the River Duddon closely followed fluctuations in local precipitation. Likewise, the seasonal pattern of discharge was quite similar to monthly variations in precipitation (Table 2). Discharge at the Ulpha Water Works ranged from 41,760 m^3/day to 1,612,000 m^3/day. Natural flow of the stream has been slightly modified in that the Ulpha Water Works takes its supply from the lower Duddon (Fig. 1, station T) and controls the discharge from Seathwaite Tarn, to assure a specified minimum flow below the intake. In general, most of the regular sampling sites had similar mean velocities (Table 3). With the exception of station 4, the range of conditions between the upper (0.16—1.0 m/sec) and lower (0.16—0.95 m/sec) mainstream and the upper (0.17—0.88 m/sec) and lower (0.20—0.86 m/sec) tributaries was about the same.

Water Quality

Sodium values were used as a convenient index of total ions (Table 4) at such times and places where more complete water analyses (Table 5) were not made. According to Gorham (1961), rainfall is the primary source of sodium, potassium, chloride, and sulphate in this portion of the English Lake District, and more than half of the dissolved magnesium and calcium also is derived from rainfall, especially that produced by westerly storms. The remainder of the latter two ions is supplied as bicarbonate by soil weathering. Our values for sodium are notably higher in the months of November-January than at other times of the year. With the exceptions of pH, calcium, and bicarbonate, the other ions tested in December, May, and July show a downward trend.

In the mainstream sodium concentrations increase steadily from source to mouth. Highest values generally occur in lower tributaries and lowest values in the upper tributaries. Expressed as milli-equivalents per liter, sodium comprises less than half of the total ions in the lower basin samples (Table 5), but it makes up half or more of the total ions in samples from the upper basin, where weathering seems to contribute little dissolved material.

Alkalinity was so low at our headwater station as to be undetectable. Values for bicarbonate generally were several times greater in the lower than in the upper basin. One moderately high value (station 7, July 1966) was obtained just after nearby pastures were limed. Highest pH values were recorded in the lower basin, reaching neutrality in one instance (station 7 in May). Gaitscale Gill (station 22) remained below pH 6.0.

Table 3. Comparison of current velocities, mean and range (m/sec) in the mainstream and representative tributaries of the River Duddon.

A. Mainstream

Station	2	4	9	13	14	18
22 December 1965	1.4	1.1	1.1	0.81	0.60	0.61
19 May 1966	—	—	0.55	0.38	0.60	0.50
			(0.26—1.1)	(0.17—0.55)	(0.38—0.88)	(0.19—0.81)
23 June 1966	0.70	0.84	0.54	0.44	0.31	0.70
	(0.22—0.93)	(0.52—1.46)	(0.16—1.0)	(0.17—0.59)	(0.16—0.45)	(0.45—0.95)

B. Lower basin tributaries

Station	3	5	7	6	10	11	12	8
22 December 1965	1.1	0.49	0.89	0.65	0.66	0.49	0.91	1.3
23 June 1966	0.35	0.38	0.44	0.33	0.44	0.48	0.49	0.55
	(0.24—0.44)	(0.30—0.45)	(0.20—0.58)	(0.21—0.58)	(0.27—0.51)	(0.25—0.80)	(0.43—0.56)	(0.35—0.86)

C. Upper basin tributaries

Station	17	15	16	20	21
22 December 1965	—	—	—	0.65	1.1
23 June 1966	0.36	0.56	0.36	0.60	0.60
	(0.23—0.43)	(0.38—0.65)	(0.17—0.52)	(0.54—0.66)	(0.44—0.88)

Table 4. Values for water temperature (° C) and sodium ion (ppm) in the River Duddon and tributaries during 11 monthly trips in 1965—66. Temperatures were taken at various times of the day. Sodium values are not always identical with those shown in Table 5. Station elevations in meters are estimated from maps with 25 foot (7.62 m) contour lines.

	Sta.	Elev.	S	O	N	D	J	M	A	M	J	J	A
Temperature													
Lower Duddon	2	3	10.2	9.9	2.2	5.1	2.3	7.2	9.7	—	—	13.2	—
	4	53	10.0	10.4	2.3	4.9	2.3	6.9	9.2	9.5	—	13.3	14.5
	9	84	9.9	9.9	2.1	4.9	2.5	6.7	6.7	—	—	13.8	—
	13	99	—	8.7	1.3	5.1	2.2	6.6	9.6	8.9	12.9	13.8	—
Upper Duddon	14	191	9.8	8.2	1.4	—	1.4	6.4	11.3	8.9	13.4	18.6	—
	18	244	9.4	7.8	1.4	4.7	—	5.9	10.6	8.2	12.7	17.2	13.1
	19	247	—	8.0	0.6	4.8	1.7	6.0	—	7.9	—	17.4	—
Lower tribs.	3	130	—	9.9	1.7	4.4	1.9	6.6	—	—	—	13.0	—
	5	53	—	10.6	3.8	5.4	3.3	7.0	11.1	9.8	16.7	15.0	15.7
	6	236	—	10.9	0.7	3.9	2.2	6.5	9.8	—	16.3	16.2	17.2
	7	236	—	9.6	1.2	4.1	1.1	6.5	—	—	—	14.0	—
	8	69	—	9.3	1.4	4.7	2.1	6.8	9.8	—	13.8	13.6	13.9
	10	84	—	9.4	2.2	4.7	2.2	6.7	—	—	—	14.0	13.1
	11	114	—	8.9	2.1	5.0	2.1	6.8	—	—	—	16.5	—
	12	107	—	9.6	1.4	4.8	2.0	6.2	—	8.9	—	14.6	—
Upper tribs.	15	244	—	10.4	0.8	—	1.7	6.2	—	—	—	16.9	—
	16	214	—	10.2	1.5	—	1.7	6.3	—	—	—	15.5	—
	17	206	—	8.3	1.6	—	2.1	6.2	11.5	8.5	12.9	17.9	—
	20	259	9.2	9.6	2.6	4.3	1.5	6.4	9.2	8.2	12.0	15.0	—
	21	274	8.5	8.8	0.7	4.2	1.5	6.3	—	7.4	—	15.0	12.3
	22	488	—	9.4	0.1	3.3	—	4.9	—	—	—	11.6	—
	23	640	7.6	8.8	0.9	2.4	0.4	4.2	—	5.6	9.6	11.0	11.7
	24	732	6.3	—	—	—	—	4.0	—	—	—	12.2	—
Sodium													
Lower Duddon	2	3	4.7	—	6.0	5.1	5.8	4.4	—	4.3	—	4.2	—
	4	53	4.1	—	5.5	4.8	4.8	4.1	—	3.7	—	3.8	—
	9	84	—	—	4.6	4.3	4.3	3.7	—	—	—	3.5	—
	13	99	3.7	—	4.4	4.4	4.3	3.6	—	3.6	—	3.4	—
Upper Duddon	14	191	—	—	4.6	4.0	3.8	3.3	—	3.4	—	3.0	—
	18	244	—	—	3.9	3.9	—	3.3	—	2.9	—	3.0	—
	19	247	3.1	—	3.9	3.9	3.9	3.3	—	3.0	—	3.1	—
Lower tribs.	3	130	5.2	—	7.4	5.2	5.8	4.9	—	—	—	4.6	—
	5	53	5.2	—	6.7	5.5	5.5	4.8	—	4.4	—	4.7	—
	6	236	—	4.3	6.4	5.2	6.1	4.2	—	3.3	—	4.0	—
	7	236	—	4.8	6.9	5.3	5.2	5.0	—	3.4	—	4.9	—
	8	69	—	—	6.7	5.1	5.6	4.6	—	—	—	4.5	—
	10	84	—	4.0	6.7	5.1	4.8	4.0	—	—	—	3.5	—
	11	114	3.8	—	6.2	4.6	4.7	4.0	—	—	—	3.7	—
	12	107	—	—	5.9	4.2	4.0	3.5	—	3.4	—	3.5	—
Upper tribs.	15	244	—	—	4.1	4.0	3.9	3.3	—	—	—	2.9	—
	16	214	—	—	3.9	3.8	3.7	3.3	—	—	—	3.1	—
	17	206	—	3.4	3.9	4.7	4.5	3.7	—	3.5	—	3.3	—
	20	259	—	—	4.1	4.0	4.0	3.3	—	3.0	—	2.9	—
	21	274	3.0	3.1	3.9	3.7	4.0	3.3	—	3.0	—	2.9	—
	22	488	—	—	3.9	3.7	—	3.1	—	—	—	2.9	—
	23	640	—	—	3.9	3.5	3.7	3.0	—	—	—	2.8	—
	24	732	—	—	—	3.7	—	2.9	—	—	—	2.2	—

Table 5. Water quality at selected stations in the River Duddon and tributaries taken 21—23 Dec. 1965, 19 May, and 4 July 1966. Except for pH, values are expressed as milli-equivalents per liter (mel) and parts per million (ppm). Data for station 22 were taken nearer station 23 in Dec. and nearer station 21 in May.

Station		4		7		12		14		17		22	
	D	6.8		6.7		6.6		6.0		5.0		4.9	
pH	M	6.9		6.7		6.8		6.2		6.1		5.7	
	J	6.9		7.0		6.9		6.7		6.3		5.9	
		mel	ppm	mel	ppm	mel	ppm	mel	ppm	mel	ppm	mel	ppm
Anions													
	D	.076		.076		.036		.008		nil		nil	
alkalinity	M	.096		.078		.044		.016		.012		nil	
(HCO_3^-)	J	.107		.320		.058		.016		.016		nil	
	D		3.8		3.8		1.8		.4		nil		nil
alkalinity	M		4.8		3.9		2.2		.8		.6		nil
as $CaCO_3$	J		5.4		16.0		2.9		.8		.8		nil
	D	.217	7.7	.235	8.4	.207	7.4	.186	6.6	.207	7.4	.177	6.3
chlorides	M	.162	5.8	.162	5.8	.163	5.8	.146	5.2	.165	5.9	.144	5.1
(Cl^-)	J	.165	5.9	.198	7.0	.159	5.6	.119	4.2	.142	5.0	.112	4.0
	D	.150	7.2	.164	7.9	.122	5.9	.109	5.2	.136	6.5	.077	3.7
sulphate	M	.130	6.3	.136	6.5	.128	6.1	.115	5.5	.131	6.3	.100	4.8
($SO_4^=$)	J	.128	6.1	.151	7.3	.113	5.4	.102	4.9	.116	5.6	.086	4.1
nitrate	D	.015	.20	.003	.05	.016	.23	.014	.20	.016	.23	.012	.17
nitrogen	M	.008	.12	.002	.03	.012	.17	.007	.10	.009	.12	.006	.09
(NO_3^-)	J	.005	.06	.007	.10	.007	.09	.002	.02	.003	.04	.002	.03
Cations													
	D	.175	3.50	.165	3.30	.103	2.05	.073	1.45	.065	1.30	.029	.57
calcium	M	.175	3.50	.145	2.90	.115	2.30	.089	1.78	.098	1.95	.055	1.10
(Ca^{++})	J	.187	3.74	.355	7.10	.128	2.55	.082	1.63	.088	1.76	.042	.84
	D	.073	.88	.080	.97	.091	1.10	.068	.82	.075	.91	.085	1.05
magnesium	M	.055	.67	.081	.98	.081	.98	.044	.53	.058	.70	.035	.43
(Mg^{++})	J	.060	.73	.124	1.51	.073	.89	.029	.35	.045	.54	.024	.29
	D	.187	4.3	.213	4.9	.174	4.0	.161	3.7	.191	4.4	.148	3.4
sodium	M	.152	3.5	.148	3.4	.148	3.4	.148	3.4	.135	3.1	.130	3.0
(Na^+)	J	.157	3.6	.204	4.7	.139	3.2	.126	2.9	.135	3.1	.117	2.7
	D	.012	.45	.012	.45	.009	.35	.004	.15	.004	.15	.004	.15
potassium	M	.010	.4	.005	.2	.008	.3	.005	.2	.005	.2	.010	.4
(K^+)	J	.005	.2	.008	.3	.008	.3	.005	.2	.003	.1	.003	.1
	D	.447		.470		.377		.306		.335		.266	
Sum of	M	.392		.379		.352		.286		.296		.230	
Cations	J	.409		.691		.348		.242		.271		.186	
	D	.458		.478		.381		.317		.359		.266	
Total ions	M	.396		.378		.347		.284		.317		.250	
	J	.405		.676		.337		.239		.277		.200	

Fauna

All of the benthic macroinvertebrates collected during this study are listed in Table 6. Sixty-two taxa are represented, most of which (44) are at the species level.

Leuctra inermis was the most abundant; it together with *Simulium* spp., Chironomidae, *Amphinemura sulcicollis, Baetis rhodani, Leuctra hippopus, Gammarus pulex,* and *Protonemura meyeri* made up the bulk (71 %) of the total collected during the autumn and summer. Only the Chironomidae and *Simulium* spp. occurred at all 28 stations; but *A. sulcicollis, P. meyeri, L. inermis,* and *L. hippopus* all were found at more than 25 of the sites.

Distribution

With the exception of two specimens of *Siphlonurus lacustris* (stations 15 and 18) and four of *B. rhodani,* no Ephemeroptera were collected above station D. *G. pulex* was confined mostly to tributaries of the lower basin. *Isoperla grammatica* is unusual in that is was the only species found throughout the mainstream and lower tributaries yet absent from most of the upper tributaries. Many of the rare forms were found only in the tributaries; none was taken solely in the mainstream.

The data in Table 6 are arranged to emphasize differences in community composition between the Upper and Lower Duddon. These differences are due mainly to the addition of species in the lower reaches rather than the existence of two distinct community types. For the most part, those taxa which are present in the upper basin also are present lower down. Excluding the rare forms, only three taxa, all plecopterans, are restricted primarily to the Upper Duddon. The greater diversity of the benthic fauna in the lower basin is due to the occurrence of 36 additional taxa, of which 16 are common or abundant. The predominant forms in the upper basin are those which were abundant and widespread throughout the drainage; these are mainly plecopterans. The principal exceptions are those Plecoptera which require cool conditions and hence are restricted to the upper basin (Minshall 1969). Cursory observations, as well as collections from different micro-habitats, indicate that most of the animals tended to aggregate in packets of terrestrial plant debris found in the stream. There is good reason to believe that this detritus provides a major food base for invertebrates in the River Duddon as well as in other streams (Egglishaw 1964, Minshall 1967).

Seasonal Abundance

An insight into the seasonal occurrence of some of the more common species may be gained from Table 7. In general the differences are a reflection of life history phenomena, the autumn species growing mainly

Table 6. Benthic macroinvertebrates of the River Duddon and its tributaries. Values given are totals of the actual numbers taken in the autumn 1965 and summer 1966 collections; taxa collected at some other time are indicated by a +.

	Mainstream							Tributaries																				
								Lower											Upper									
Station	2	4	9	13	14	18	19	5	8	10	B	12	11	3	C	6	7	A	D	17	16	15	20	21	22	E	23	24
Elevation (m)	3	53	84	99	191	244	247	53	69	84	92	107	114	130	183	236	236	351	214	206	214	244	259	274	488	488	640	732
I. Abundant to common																												
A. Taxa with a generally widespread distribution																												
Abundant																												
Chironomidae	57	113	56	60	61	24	11	5	175	45	1242	60	111	65	25	19	61	14	216	22	80	178	163	16	104	371	148	659
Simulium spp.	14	12	15	72	91	7	9	31	961	78	290	6	121	312	+	43	53	643	114	106	262	118	134	288	193	315	115	5
Amphinemura sulcicollis (Stephens)	331	207	33	233	111	28	19	3	39	4	3	49	53	432	105	13	28	7	1239	377	83	2	398	232	72	38	4	--
Protonemura meyeri (Pictet)	25	39	9	83	34	6	6	17	17	34	45	29	10	31	123	5	13	228	105	33	58	3	11	148	1	44	16	--
Leuctra inermis Kempny	1	8	1	173	227	430	128	31	1	23	31	17	--	60	449	12	4	43	798	230	208	32	1060	695	408	176	1014	--
Leuctra hippopus (Kempny)	5	13	8	44	134	53	48	57	--	5	17	32	--	18	27	29	9	111	25	53	292	85	50	26	207	163	195	460
Common																												
Chloroperla torrentium (Pictet)	1	5	--	10	17	10	16	1	--	3	520	2	2	32	7	--	2	10	17	19	19	2	22	23	45	14	43	--
Tipulidae	--	2	2	5	--	5	4	32	--	--	95	3	5	7	4	6	--	9	2	--	7	5	8	5	5	19	19	10
Rhyacophila dorsalis Curtis	2	15	1	4	--	--	--	6	8	7	3	8	8	38	1	1	--	--	24	7	3	--	11	12	9	--	--	--
Oligochaeta	2	6	3	2	--	--	1	9	1	--	84	2	14	4	--	--	21	3	--	1	2	2	--	1	1	--	4	35
Plectrocnemia conspersa Curtis	2	--	--	4	--	--	--	1	--	--	200	3	4	--	+	3	2	10	8	2	1	1	3	--	4	18	15	19
Limnephilidae	5	1	1	--	2	--	1	1	--	3	110	8	--	2	--	--	11	1	--	--	--	--	--	1	2	1	19	9
Plectrocnemia geniculata McLachlan	--	--	1	1	1	5	5	--	--	--	--	2	--	--	--	--	2	--	--	5	--	--	7	9	4	18	15	1
Polycelis felina (Dalyell) – Crenobia alpina (Dana)	8	--	5	3	4	2	--	--	8	1	395	2	--	1	--	--	391	--	--	1	2	3	--	--	--	--	--	--
Isoperla grammatica (Poda)	7	3	1	6	3	15	9	55	--	29	27	16	--	+	38	18	--	40	8	--	--	--	--	--	--	--	--	--
B. Taxa which, in general, are restricted to the Lower Duddon or its tributaries																												
Baetis rhodani (Pictet)[1]	95	67	2	1	--	--	--	248	241	136	705	26	6	609	+	25	190	364	2	+	--	--	--	+	--	--	1	1
Chloroperla tripunctata (Scopoli)	2	9	6	13	--	--	--	--	--	2	--	3	1	7	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Leuctra moselyi Morton	--	28	8	1	--	--	--	5	1	5	--	2	9	18	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Leuctra fusca (L.)	11	23	--	--	--	--	--	15	29	--	7	--	1	15	--	--	26	--	114	--	--	--	--	--	--	--	--	--
Protonemura praecox (Morton)	3	1	--	--	--	--	--	--	--	44	--	6	--	1	32	---	--	--	3	--	--	--	--	--	--	--	--	--
Ephemerella ignita (Poda)	49	4	--	--	--	--	--	16	53	--	--	--	--	41	1	--	23	16	--	--	--	--	--	--	--	--	--	--
Gammarus pulex (L.)	--	5	--	--	--	--	--	132	133	--	1317	--	--	3	1	1	393	53	1	--	--	--	--	--	--	--	--	--
Elmidae (adults and larvae)	8	--	--	--	--	--	--	3	74	--	55	--	1	2	15	--	169	181	--	--	--	--	--	--	--	--	--	--
Baetis scambus Eaton	32	--	--	--	--	--	--	2	5	18	--	--	6	18	+	1	--	--	--	--	--	--	--	--	--	--	--	--
Wormaldia sp.	--	--	--	--	--	--	--	18	--	--	11	5	11	1	+	25	--	21	--	--	--	--	--	--	--	--	--	--
Hydropsyche instabilis Curtis	89	7	--	--	--	--	2	--	4	--	--	6	--	8	--	13	4	--	--	--	--	--	--	--	--	--	--	--
Rhithrogena semicolorata (Curtis)	58	41	--	--	--	--	--	39	--	6	50	1	--	30	--	18	--	--	--	--	--	--	--	--	--	--	--	--
Ecdyonurus venosus (Fabricius)	8	8	--	--	--	--	--	--	--	3	--	11	--	2	--	6	1	--	--	--	--	--	--	--	--	--	--	--
Ancylastrum fluviatile (Müller)	5	1	--	--	--	--	--	1	--	--	14	--	--	2	--	--	6	--	--	--	--	--	--	--	--	--	--	--
Baetis pumilus Burmeister	1	--	--	--	--	--	--	4	38	6	53	--	--	8	--	6	6	--	--	--	--	--	--	--	--	--	--	--
Heptagenia lateralis (Curtis)	--	--	1	--	--	--	--	16	--	14	136	--	--	1	--	3	--	--	--	--	--	--	--	--	--	--	--	--
C. Taxa which, in general, are restricted to the Upper Duddon or its tributaries																												
Leuctra nigra (Olivier)	--	--	--	--	5	1	--	--	--	--	744	4	--	--	1	--	--	4	1	1	--	--	4	1	1	112	5	35
Nemoura cambrica (Stephens)	--	--	--	--	25	--	1	--	--	--	87	--	--	--	1	--	--	6	3	--	--	1	--	--	1	--	2	254
Capnia vidua Klapálek	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	35	--	--	--	21	55	234	--	443	63

II. Rare. Found at 5 stations or less; the number of stations is given in parenthesis. U - restricted to upper basin; L - restricted to lower basin. (Based on records from the entire study period including both qualitative and quantitative collections).

A. Found in both the mainstream and its tributaries.

Siphlonurus lacustris Eaton (2) U.

Perlodes microcephala (Pictet) (5) L.
Sphaerium sp. (3) L.
Polycentropus flavomaculatus Pictet (2) L.

Hydrachnellae (5)

Hirudinea (2) L.
Rheotanytarsus sp. (2) L.
Ecdyonurus dispar (Curtis) L.

Thaumaleidae (4)

B. Found only in the tributaries

Brachyptera risi (Morton) (3) U.
Diura bicaudata (L.) (2) U.
Nemoura avicularis Morton (1) U.

Dytiscidae (adults and larvae) (5) L.
Helodidae (5) L.
Noteridae (3) L.
Leptophlebia marginata (L.) (2) L.
Pericoma sp. (2) L.
Dinocras cephalotes (Curtis) (1) L.
Perla bipunctata Pictet (1) L.

Nemurella picteti Klapálek (3)

Taeniopteryx nebulosa (L.) (1) L.
Baetis tenax Eaton (1) L.
Agapetus fuscipes Curtis (1) L.
Diplectrona felix McLachlan (1) L.
Rhyacophila obliterata McLachlan (1) L.
Silo sp. (1) L.
Haplidae (1) L.

[1] Very small nymphs of Baetis that could not be named with certainty were all assigned to B. rhodani for purposes of tabulation.

Table 7. Seasonal differences in numbers of the more common benthic macroinvertebrates from the River Duddon and its tributaries. Totals for all stations; all values given as numbers per 5-minute sample.

	Autumn 1965	Summer 1966
1. Present only in autumn collection		
Capnia vidua (Plecoptera)	830	
Ecdyonurus venosus (Ephemeroptera)	39	
2. Present only in summer collection		
Leuctra fusca (Plecoptera)		321
Leuctra moselyi (Plecoptera)		177
Ephemerella ignita (Ephemeroptera)		510
Baetis pumilus (Ephemeroptera)		304
Baetis scambus (Ephemeroptera)		206
3. Present year round		
a) Most abundant in autumn collection		
Leuctra hippopus (Plecoptera)	2132	29
Nemoura cambrica (Plecoptera)	323	10
Protonemura praecox (Plecoptera)	87	3
Leuctra nigra (Plecoptera)	464	37
Rhithrogena semicolorata (Ephemeroptera)	212	18
Chloroperla tripunctata (Plecoptera)	41	5
Leuctra inermis (Plecoptera)	5458	745
Isoperla grammatica (Plecoptera)	240	36
Amphinemura sulcicollis (Plecoptera)	3173	571
Protonemura meyeri (Plecoptera)	1028	249
Hydropsyche instabilis (Trichoptera)	118	39
Chloroperla torrentium (Plecoptera)	456	190
Gammarus pulex (Amphipoda)	1683	892

		Autumn 1965	Summer 1966
Heptagenia lateralis (Ephemeroptera)		76	55
b) Most abundant in summer collection			
Simulium spp. (Diptera)		901	8723
Chironomidae (Diptera)		1058	6806
Elmidae	larvae	136	727
(Coleoptera)	adults	8	86
Ancylastrum fluviatile (Gastropoda)		10	49
Wormaldia sp. (Trichoptera)		34	147
Plectrocnemia geniculata (Trichoptera)		40	92
Baetis rhodani (Ephemeroptera)		1509	2167
Rhyacophila dorsalis (Trichoptera)		98	136
Plectrocnemia conspersa (Trichoptera)		112	152
Limnephilidae (Trichoptera)		74	99
Tipulidae (Diptera)		140	184
Polycelis felina-Crenobia alpina (Turbellaria)		411	448
Oligochaeta		106	113

in the cooler months, the remainder chiefly during the summer. Important exceptions are those taxa which occur in limited numbers at all stations. In these cases the seasonal pattern may be obscured by the sparsity of individuals during all seasons.

The majority of the animals were taken in both the autumn and summer collections. Those having their greatest abundance in the summer were the most diverse taxonomically. Except for *Gammarus pulex* and *Hydropsyche instabilis,* all of the animals which were most abundant or present exclusively in the autumn collection were either Ephemeroptera or Plecoptera.

Macan (1957) has shown that at least two collections a year, preferably during the winter and summer, are necessary for a reliable picture of the fauna. With the exception of *Ecdyonurus venosus* and *Capnia vidua,* all of the species listed were taken in the summer collection, whereas five species would have been missed if only an autumn collection had been taken.

Comparison with Other Local Streams

The only studies in the Lake District available for comparison with the River Duddon are those on Ford Wood Beck (MACAN 1957, MACKERETH 1957) and Whelpside Ghyll (MACAN 1957, GLEDHILL 1960 and unpublished field notes). There is a great deal of similarity between the mayfly fauna of Ford Wood Beck (MACAN 1957) and that of the Lower Duddon. Six species (*Baetis pumilus, B. rhodani, Ecdyonurus venosus, Ephemerella ignita, Heptagenia lateralis,* and *Rhithrogena semicolorata)* were common-to-abundant at both locations. Excluding the casual or accidental forms, the only species found in Ford Wood Beck and not in the Lower Duddon were *Ecdyonurus torrentis* Kimmins, *Habrophlebia fusca* (CURTIS), and *Paraleptophlebia submarginata* (STEPHENS). *Baetis tenax, Ecdyonurus dispar,* and *Leptophlebia marginata* were absent from Ford Wood Beck, but occurred sporadically in the tributaries of the River Duddon. *Baetis scambus,* a river species, was taken from several sites in the lower Duddon but was rare in Ford Wood Beck.

A high degree of similarity also exists between the Plecoptera of Ford Wood Beck and that of the River Duddon. MACKERETH (1957) recorded 16 species of Plecoptera from Ford Wood Beck. Of these all but *Nemoura erratica* Claassen were taken in the River Duddon. In addition *Dinocras cephalotes, Diura bicaudata, Capnia vidua, Nemoura avicularis, Nemurella picteti,* and *Taeniopteryx nebulosa* were collected in the River Duddon. As with the Ephemeroptera, most of the Plecoptera not found in Ford Wood Beck occurred only at scattered locations and in limited numbers in the River Duddon. *Diura bicaudata* and *Capnia vidua* normally are restricted to streams at high elevations and therefore are to be expected in the Upper Duddon and not in Ford Wood Beck. *Nemoura avicularis, Nemurella picteti,* and *Taeniopteryx nebulosa* occur in slow water; it is likely that a few suitable biotopes for these species would be found in the Duddon drainage basin though not in the more restricted Ford Wood Beck.

GLEDHILL (1960) reported four species of Ephemeroptera from Whelpside Ghyll (*Baetis pumilus, B. rhodani, B. tenax,* and *Ameletus inopinatus* Eaton), although *Ecdyonurus venosus, Ephemerella ignita, Heptagenia lateralis,* and *Rhithrogena semicolorata* also are known to occur there (MACAN 1957). Except for *Ameletus* the species list is similar to both that of the Lower Duddon and Ford Wood Beck. One notable difference is that in Whelpside Ghyll all the Ephemeroptera except *Ameletus* and *Baetis rhodani* were so scarce that they were not taken on every occasion. However, Whelpside Ghyll is a high, headwater stream and therefore the most meaningful comparisons are between it and Gaitscale Gill (Upper Duddon headwaters). Except for *Baetis rhodani* (which was extremely rare) no mayflies were found in Gaitscale Gill; not even *Ameletus* was taken although it was sought and might have been expected, being a typically montane species (Macan 1957, Gledhill 1959). *Diura bicaudata, Isoperla grammatica, Amphinemura sulcicollis,* and *Capnia (bifrons?)* were abundant; and *Protonemoura praecox, Leuctra hippopus, L. inermis,* and *Chloroperla torrentium* were common in Whelpside Ghyll at an elevation of 670 m (Gledhill unpublished field notes). *Gammarus pulex,* which is restricted to the lower basin of the Duddon, occurs in both Whelpside Ghyll and Ford Wood Beck.

Thus, Whelpside Ghyll contains some elements characteristic of the Upper Duddon (e. g., *Capnia*) and some elements characteristic of the Lower Duddon (e.g., Ephemeroptera spp. and *Gammarus*). *Diura bicaudata* and *Isoperla grammatica* are much more abundant in Whelpside Ghyll than at any location sampled in the River Duddon; but, in general, the Plecoptera fauna of Whelpside Ghyll resembles that of the Upper Duddon, and especially that of Gaitscale Gill, while the mayfly fauna is taxonomically similar to that of the lower Duddon.

Discussion

As suggested in Results the most striking feature revealed by this study is the distinct difference in the fauna of the Upper and Lower Duddon. The main purpose of the Discussion is to examine several possible explanations for this phenomenon and to suggest likely areas for future intensive study. Those explanations that seem less plausible to us are discussed first.

The Duddon basin lacks sharp changes in lithology which might cause the observed faunal break, and there are no apparent physical barries for invertebrates. The occasional records of Ephemeroptera and *Gammarus* in the upper basin support the idea of physical continuity between the Upper and Lower Duddon.

Rapid variations in discharge (Fig. 4) probably have an important influence on any stream fauna (Minshall & Winger 1968) and may help explain the relatively low concentrations of invertebrates in the mainstream in contrast to the relatively high numbers in tributaries. A similar situation exists in regard to bottom materials. The substratum of the mainstream is typically unstable, while that of the tributaries generally is more firmly fixed. Therefore, although rapid oscillation of discharge or an unstable bottom may result in low biomass in the mainstream in contrast with the tributaries, neither factor offers a suitable explanation for differences between the two basins.

The possibility that differences in current velocity may exclude some groups from the upper basin does not gain much support from our data (Table 3). As noted earlier, stream velocity varies as much within as between the two basins, and the faunal distributions seem to be independent of the variation. For example, the highest velocities in the mainstream occur at stations

2 (lower basin) and 18 (upper basin) but Ephemeroptera and *Gammarus* are common at 2 and absent at 18. Highest velocities in tributaries were recorded at stations 8 (lower basin) and 21 (upper basin) but the taxa mentioned are common at 8 and absent at 21. In addition, no relationship appears to exist between the predominant forms in the two basins and their ability to keep from being swept away as drift (ELLIOTT & MINSHALL 1968).

It has been suggested that adult Ephemeroptera and other weak fliers may be excluded from the upper basin by strong winds through interference with mating or oviposition (T. T. MACAN, personal communication). Although strong winds are more frequent in the upper basin than in the lower basin, one of the most wind swept areas was the upper reaches of Crosby Gill (stations 6 and 7), a location where several species of mayflies were common to abundant. Also, this explanation fails to account for the corresponding absence of *Gammarus*, whose distribution parallels that of the mayflies.

Data from the Afon Hirnant (HYNES 1961) and Whelpside Ghyll (GLEDHILL unpublished field notes) show that Plecoptera become more abundant in relation to Ephemeroptera at higher elevations. KAMLER (1965) suggested that the ratio of Plecoptera to Ephemeroptera in a stream may be controlled by temperature viz. more species of Ephemeroptera and fewer species of Plecoptera were found in streams with the greatest thermal variability; the number of species and the density of Plecoptera decreased as the degree of temperature instability increased. The proportion of Plecoptera in Ford Wood Beck (elevation about 45 m) is small relative to the Ephemeroptera, as is true of the Lower Duddon. In the Upper Duddon, however, stoneflies far outnumber the mayflies.

Several investigators (VERRIER 1953, GLEDHILL 1960, CRISP & NELSON 1965) have found that with increasing altitude *Ecdyonurus, Rhithrogena,* and *Ephemerella* become less abundant in relation to *Baetis. Ecdyonurus* and *Rhithrogena* were much more abundant in Ford Wood Beck than at any site in the River Duddon. At all of the Duddon stations where Ephemeroptera were found, *Baetis rhodani* was the predominant form. In the mainstream, *B. rhodani* persisted upstream further than any of the others; yet even this species occurred only rarely in the upper basin.

Temperature is an appealing explanation for the observed distributional differences between the two basins. Temperatures of the upper basin generally were cooler and the cool periods persisted longer than in the lower basin. Species found in both basins generally had life cycles which were several weeks longer in the upper than in the lower basin (MINSHALL 1969); this suggests that temperature may affect growth and development. However, all of the mayflies found in the Lower Duddon are known to occur up to elevations of 550 m or greater in other English streams (CRISP & NELSON 1965). In particular, Whelpside Ghyll supports a varied fauna of Ephemeroptera and *Gammarus* (GLEDHILL 1960), whereas the Upper Duddon does not. Since these high altitude streams could be expected to be equally as cold as the Upper Duddon, temperature does not appear to be the factor involved.

Water quality, nutrient value of detritus and other foods, or both could be important factors limiting distribution of many invertebrates in the Duddon basin. Water analyses (Tables 4 and 5) show a general decrease of all dissolved materials toward the headwaters. A marked reduction in the bicarbonate ion (Table 5) is seen in the upper basin and samples from Gaitscale Gill lack measurable amounts. Thus, bicarbonate or some equally rare ion could be limiting to Ephemeroptera, *Gammarus*, or other taxa.

EGGLISHAW & MORGAN (1965) reported differences in the amount and composition of the bottom fauna from streams having different degress of chemical richness. They found that the bottom fauna was much poorer in streams having a concentration of less than .400 milli-equivalents of total cations per liter (range .224—.375) than in streams having amounts in excess of .400 (range .412—3.608). In the River Duddon there was a marked difference in total cations between the two basins. Values in the upper basin usually were .300 milli-equivalents per liter or less (range .186—.335) whereas total cations in the lower basin commonly were .400 or more (range .348—.691). SUTCLIFFE (1967) found that low concentrations of sodium may limit the distribution of *Gammarus duebeni* LILLJEBORG.

Lack of nutrients, either alone or together with temperature, may also limit the variety and nutritive quality of the terrestrial plants, which as detritus are the major food source for stream herbivores. WELCH & RAWES (1965) reported low plant production (559 to 915 kg dry-wt/ha/yr) on pennine sheep pastures at or about 678 m elevation, and higher production (1788 to 1947 kg dry-wt/ha/yr) on nearby pastures lying at approximately 500 m elevation..

The coarse grass *Festuca ovina* was the principal form present in the high pastures but shared dominance with other species at the lower elevation. It seems reasonable that similar differences in the type and nutritive value of detritus in the two portions of the Duddon could explain the observed faunal differences. Coarse detritus, low in nutritive value or difficult to digest, could preclude many invertebrates from the upper basin.

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Summary

The River Duddon is a mountain stream located in the English Lake District. The stream is about 18 km long and drains an area of 8636 hectares. Rate of discharge near the mouth ranges from 41,000 to 1,600,000 m^3/day and is marked by rapid and frequent fluctuations. The substratum is composed of stones, gravel, and some boulders. Temperatures range from 0° C (January) to almost 20° C (June—July). Maximum weekly variation was about 10° C (May), but weekly ranges of about 8° C are common from April through August. Concentrations of the major ions showed seasonal variations, as well as a tendency to increase from source to mouth (e.g., total ions averaged about .240 milli-equivalents per liter near the source and .420 near the mouth).

Emphasis in this study was placed on determination of the relative abundance, diversity, and general distributional patterns of the benthic macroinvertebrates. *Leuctra inermis* was most abundant; it together with *Simulium* spp., *Chironomidae, Amphinemura sulcicollis, Baetis rhodani, Leuctra hippopus, Gammarus pulex,* and *Protonemura meyeri* made up the bulk (71 %) of the total collected during the autumn and summer.

The Duddon drainage basin is divided into an upper and lower portion, which show differences in stream fauna, physico-chemical conditions, and hydrology. In the upper basin Plecoptera are predominant and Ephemeroptera and *Gammarus* rare, while in the lower basin Ephemeroptera are predominant, Plecoptera common, and *Gammarus pulex* common over most of the area. Differences in nutrients or other water quality factors appear to be the most likely explanation for the observed discontinuity of the fauna, although temperature also may be important. Other factors, such as the presence of physical barriers, substratum differences, variations in discharge and current velocity, or behavioral differences in relation to either wind or water currents appear to be unimportant or to play only a minor role.

Zusammenfassung

Der Duddon-Fluß liegt in der Bergregion des englischen Seengebietes. Er besitzt eine Länge von 18 km und ein Einzugsgebiet von 8636 ha. Die Abflußmengen des Flusses betragen nahe seiner Mündung 41 000 bis 1,6 Millionen m^3 pro Tag, und zwar mit schnellen und häufigen Änderungen. Das Flußbett weist Steine, Kies und Steinblöcke auf. Die Temperaturen des Wassers wechseln von Januar bis Juli zwischen 0 und 20° C. Die maximale wöchentliche Temperaturvariation kann im Mai 10° betragen, und in den Monaten April bis August sind 8° Unterschied normal. Von der Quelle bis zur Mündung steigt der Elektrolytgehalt von 0,24 auf 0,42 mval/l an, zugleich verbunden mit jahreszeitlichen Änderungen.

Die relative Häufigkeit, die Artenmannigfaltigkeit und das allgemeine Verteilungsmuster der benthischen Macro-Wirbellosen wurden untersucht. Am häufigsten kommt *Leuctra inermis* vor und stellt mit *Simulium, Chironomidae, Amphinemura sulcicollis, Baetis rhodani, Leuctra hippopus, Gammarus pulex* und *Protonemura meyeri* die Masse (71 %) der vom Sommer bis zum Herbst gesammelten Fauna dar.

Das Einzugsgebiet des Duddon-Flusses läßt sich in einen oberen und einen unteren Teil trennen, die sich faunistisch und chemisch-physikalisch sowie hydrolo-

gisch voneinander unterscheiden. Im oberen Teil des Einzugsbeckens herrschen Plecopteren vor, während Ephemeropteren und *Gammarus* als selten zu bezeichnen sind; im unteren Teil des Einzugsgebietes dagegen dominieren Ephemeropteren, Plecopteren und *Gammarus pulex*. Unterschiede in der Ernährung und in der Wasserbeschaffenheit sind offenbar die Ursache jener Unterschiede; aber die Wassertemperaturen scheinen die wichtigste Rolle zu spielen. Vom Flußwasser zu überwindende Schwellen, ebenso Unterschiede in der Untergrundbeschaffenheit sowie in der Strömungsgeschwindigkeit oder Änderungen der Verhaltensweise der Fauna in Abhängigkeit vom Wind oder von Wasserströmungen scheinen dagegen unbedeutende Faktoren darzustellen, die höchstens einen schwachen Einfluß ausüben können.

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