AN INVESTIGATION OF THE DISTRIBUTION OF THE MAYFLY FAUNA OF A LANCASHIRE STREAM

BY JANET E. HARKER

*Department of Zoology, University of Manchester**

(With 3 Figures in the Text)

This investigation was designed to study in detail the movements and variation in numbers of the mayfly fauna of a small section of a stream.

The stream chosen was Broadhead Brook at Entwistle, Lancashire (Fig. 1), which runs from its source at an altitude of 900 ft. to Wayoh Reservoir (550 ft.), a distance of about two miles. The surrounding country is agricultural farm land, except for the first half mile where moorland conditions still exist. In the lower reaches of the stream artificial falls have been built to prevent undue damage when flooding occurs. The width of the stream is fairly constant at about 30 ft., but the whole stream bed is very seldom covered. The bed is stony, or in places sandy, with little mud; and the main flow is such as to prevent blockage with leaves.

The stream is a fast filling one, and during the September floods of 1950 the whole bed of the stream changed its form; the artificial falls were in many places completely dislodged, and the large concrete slabs so displaced blocked the flow, causing a new course to be taken.

The area of the stream selected for detailed work was bounded at the upper end by an artificial fall, and at the lower by an incline leading to a second fall. This region of the stream was fairly straight and could be easily marked off into a number of stations by a series of parallel lines. The stream was divided longitudinally into ten regions, each 3 ft. apart, and transversely into fourteen regions, chosen so as to include various habitats and to keep one type of habitat only within each station. One hundred and forty stations were thus marked, covering approximately 30×150 sq. ft.

In May 1950 the mayfly fauna of the stream completely disappeared in this area. The disappearance seemed to be associated in some way with an extraordinary increase in the number of blue-green algae and diatoms, which practically blocked the stream at that point. Large numbers of dead nymphs were found under the algae, but whether they were killed by some toxic product, a lack of oxygen (there was no fall in the day-time oxygen content) or perhaps an increase in temperature is not known. Mayflies were still abundant in a region just below the experimental area where no increase in the amount of algae occurred.

The original stream was still kept under observation, but when the nymphs disappeared another stream was included in the survey. This stream, Wayoh Stream, joins Broadhead Brook nearly a quarter of a mile below the experimental area, and at the chosen area runs parallel to it. The two are separated by a small rise, and are about 500 yards apart, but there is no connexion between them until they finally unite. A similar area to the original experimental area was selected and divided in like manner

* Present address: Girton College, Cambridge.

into a number of stations by longitudinal and transverse lines, giving 100 stations in all.

Wayoh Stream is narrower than Broadhead Brook, and the marked stations covered an area of approximately 15 × 200 sq. ft. The stream bed is stonier than that of Broadhead Brook, and the banks are wooded.

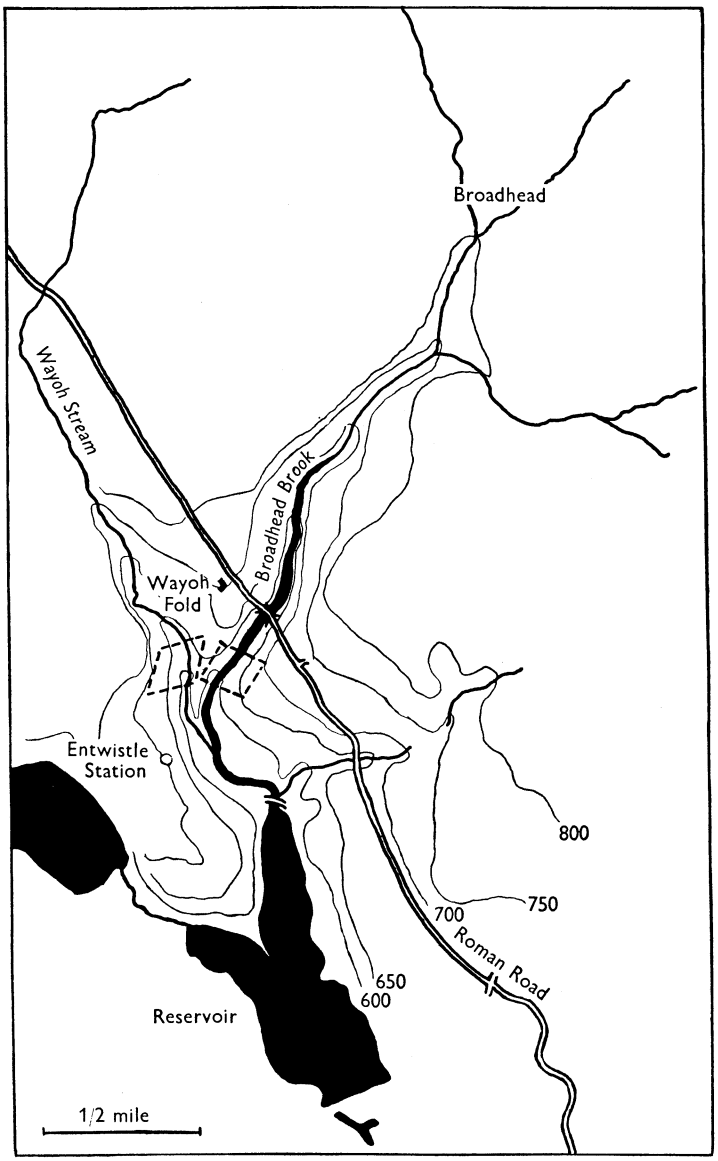

Fig. 1. Map showing the positions of the areas investigated, marked by dotted lines.

The fauna of both streams consists of fairly typical brook forms such as Planarians *Dendrocoelum*, *Hydropsyche*, *Rhyacophila*, *Simulium*, *Cottus*, etc.

During the period September 1949 to August 1951 a sample of the mayfly fauna was taken at each station at regular monthly intervals. In addition to this, measurements

of the current-rate, temperature, concentration of dissolved oxygen, and the depth were made at each station.

PHYSICAL AND CHEMICAL CHARACTERISTICS

(*a*) *Current*

A simple right-angled pitot tube (Dodds & Hisaw 1924) was used to measure the current. The main disadvantage of the method was the necessity of taking readings of the water-level at the surface of the stream. In turbulent water this became almost impossible, but the difficulty was partly overcome by surrounding the pitot tube at the stream water-level by a glass tube of larger diameter, and thus eliminating the ripples. The slowest movement which could be measured was 0·15 m./sec. Measurements were made at the surface of the stream as the water was in parts too deep for readings at the bottom to be taken.

The maximum and minimum current-rates for each month are given in Table 1. Throughout the year the average rate of flow varied from 0·1 to 2·5 m./sec. or from

Table 1. *The physical and chemical conditions each month in Broadhead Brook* (B) *and Wayoh Stream* (S)

	Average depth (cm.)		Current (m./sec.) Max.	Current (m./sec.) Min.		pH		Average dissolved oxygen (% sat.)		Average temperature (° C.)	
	B	S	B	B	S	B	S	B	S	B	S
13 Sept. 1949	8	—	1·5	0	—	7·4	—	—	—	13	—
11 Oct.	43	—	0·9	0	—	7·4	—	—	—	13	—
8 Nov.	43	—	0·9	0	—	7·4	—	99	—	13	—
2 Dec.	27	—	2·0	0	—	7·6	—	70	—	4	—
12 Jan. 1950	32	—	1·3	0	—	7·8	—	60	—	2·5	—
13 Feb.	49	—	0·5	0	—	7·4	—	76	—	2·5	—
10 Mar.	18	—	0·5	0·1	—	7·4	—	74	—	6	—
8 Apr.	28	—	0·3	0·1	—	7·4	—	75	—	8	—
9 May	—	31	—	—	0·1	—	7·4	—	101	—	15
8 June	—	27	—	—	0·1	—	7·5	—	97	—	11
5 July	—	32	—	—	0·1	—	7·6	—	112	—	14
14 Aug.	—	28	—	—	0·3	—	7·4	—	114	—	15
11 Sept.	—	31	—	—	0·1	—	7·5	—	100	—	12
6 Oct.	10	53	3·0	1·6	0·6	7·5	7·5	92	90	8	8
2 Nov.	48	16	2·0	1·3	0·2	7·5	7·5	74	79	4	4
6 Dec.	48	23	1·5	0	0·1	7·5	7·5	69	66	2	2
14 Jan. 1951	33	22	1·4	0·1	0·1	7·5	7·4	63	65	2	2
1 Feb.	14	17	0·9	0·2	0·2	7·4	7·4	77	79	5	5
1 Mar.	16	19	1·0	0·2	0·2	7·4	7·4	74	76	7	7
2 Apr.	16	20	0·9	0·1	0·1	7·4	7·4	75	78	7	7
1 May	15	19	0·8	0	0·1	7·4	7·4	69	72	12	12
2 June	17	18	1·0	0·1	0·1	7·4	7·4	93	104	11	11
1 July	19	23	0·7	0·1	0·1	7·4	7·4	79	82	10	10
1 Aug.	16	20	0·4	0	0	7·5	7·4	74	76	10	9

a very slow current to a very strong current. During some months of the year the same range could be found within the stream at any one time; for instance in September 1950 the rate varied from 0·1 to 2·5 m./sec., in December from 0 to 2·0 m./sec. But in some months the readings showed very little variation anywhere, for example from March to July the fastest current was 0·4 m./sec. The regions of greatest velocity altered throughout the year, particularly after the January and October floods.

(*b*) *Depth*

The depth of the water was measured monthly at each station. Particularly in Broadhead Brook, it varied markedly from month to month, so that from one month to the next the two extremes of depth found within the stream may appear in the one station. Fig. 2 and Table 1 show the depth and rate of flow of the water in both streams

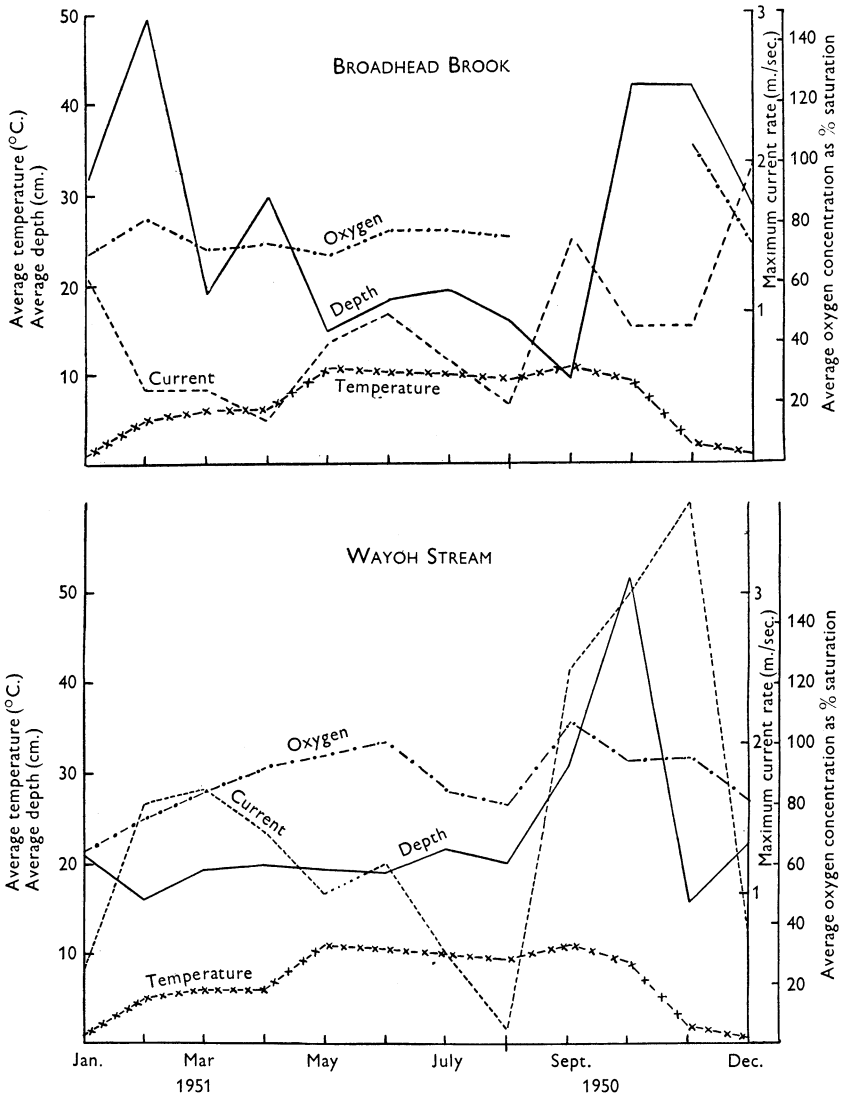

Fig. 2. The monthly maximum flow, average depth, oxygen concentration, and temperature in Broadhead Brook and Wayoh Stream.

over 12 months. The years have not been shown in order because of the break in readings in Broadhead Brook, but even so the picture given may be assumed to show approximately the conditions over a year.

In Broadhead Brook there is an almost complete inverse correlation between depth and speed, obvious in particular in December, January, April and September. The

rate of flow will depend on the quantity of water coming downstream, the drainage below the experimental area, and the width of the stream. In September there is an increase in the rate of flow due to the autumn rains, but the water at first drains away quickly, so that there is no increase in depth. Later, flow is less rapid because the drainage from the surrounding areas into the lower reaches increases, causing the level to rise and the flow to slacken. During the summer months the stream has been flowing through a narrow channel, giving in April and May a relatively fast rate of flow, but after the autumn rain the water flows through the whole channel causing again a decrease in depth. In February the snow begins to melt and causes another increase in depth, but probably because of the slow rate of the process there is little effect on the speed.

Wayoh Stream is narrower and on more of a slope, so that a slightly different relationship is found between the depth and flow. There appears to be what might be termed a basic depth at which the water can run off quite fast, and yet fluctuations about this depth do not directly affect the current-rate. In general, in this stream a decrease in speed only occurs at the beginning of an increase in depth, and then the depth builds up to a point where the water runs away fast.

(*c*) *Dissolved oxygen*

The dissolved oxygen concentration of the water was measured by the Winkler method, using a portable apparatus (Whitney 1938). The percentage saturation of the water has been calculated from Ricker's nomogram (1934). The average saturation varied between 60 and 114% during the 24 months, so that even when the stream was frozen the concentration was not very low. An oxygen gradient occurred during the summer months between some of the stations. Beneath the fall at the upper end of Broadhead Brook supersaturation to the extent of 114% saturation was measured. Although this appears to be a very high reading, water from this region, when kept at constant temperature, retained this degree of supersaturation for some hours. When few algae were present at the side of the stream the concentration fell to 58% saturation if the temperature was high.

(*d*) *Temperature*

The annual range in temperature is about 18° C., as measured by the monthly readings. The edges of the stream froze from December 1949 to March 1950, and all but a stream about 10 in. wide froze in January 1950 when the ice near the banks was 3 in. thick. In December 1950 and January 1951 the whole stream froze over, but the water was flowing quite freely underneath the ice in the central part of the stream.

A temperature gradient was present across the stream during the summer months when the temperature of the shallow side regions often rose to 20° C., as compared with 11–14° C. in the central region. No vertical temperature gradient was present.

(*e*) *Chemical properties*

The hydrogen-ion concentration of the water was measured each month colorimetrically. The pH was found to range from 7·4 to 7·8 from September 1949 to February 1951.

As the fields which were under cultivation near part of Broadhead Brook were limed during the year, calcium determinations were made to ascertain whether the lime was being washed into the stream. The calcium content did not vary to any appreciable extent over the year, and was very low, averaging 1·0 p.p.m.

THE DISTRIBUTION OF THE FAUNA

(*a*) *Sampling technique*

Samples were obtained of the fauna at each station using the following method. A galvanized iron square, enclosing an area of 530 sq.cm. was plunged into the water and pushed well down into the stream bed. The stones within the area were turned over, and the number of nymphs present was counted. Most nymphs were found clinging to the bottom of larger stones; these stones were removed with the nymphs still attached, and piled carefully outside the square, later to be replaced. The nymphs which were washed off or free swimming, were caught in a very small hand-net and held there until the counting was finished. All the nymphs were replaced, and the stones as nearly as possible returned to their original positions.

There are at least two obvious sources of error involved in this method. Possible numbers of nymphs were either overlooked or counted twice, and each count involved disturbance of the habitat. Any method of sampling the population of a fauna living mainly beneath stones must of necessity involve the disturbance of the habitat; the method had, of all the methods tried, the least effect on the habitat. Also each station was at least 3 sq.yd. in area, so that a period of 4–5 months elapsed between sampling of exactly the same position. It may be objected that the sampling of slightly different areas each month is another source of error. It will be remembered that each station consisted, as far as possible, of only one type of habitat, and preliminary counts showed that the numbers from any area within each of the stations were very similar. These preliminary counts were compared with results obtained from other sampling methods; collecting for a definite period of time in each area, and in another part of the stream dredging the bottom and sorting the material in the laboratory. While these methods are not suitable for the type of work which was being done, they served as a check on the standard method used, and showed that very little double counting or omission of the nymphs can have taken place. When the water was very deep and the current fast there may have been more nymphs washed away; when the nymphs were more numerous there may have been some double counting. These errors emphasize the scarcity or abundance, as the case may be, but should give a fairly accurate picture.

After each count a sample of the nymphs of each of the species counted was retained and further examined in the laboratory to check the identifications. The four species counted were *Ecdyonurus torrentis* Kimm., *Heptagenia lateralis* (Curt.), *Rithrogena semicolorata* (Curt.) and *Baëtis rhodani* (Pict.). The only other nymphs found in the stream were *Ephemerella* and *Paraleptophlebia*, neither of which was likely to be confused with the ones under observation. No other species of the four observed genera was present, and each could be easily distinguished from the others by the body shape, markings, and the type of movement.

(*b*) *Seasonal variations*

Ecdyonurus torrentis. Two sizes of nymph were recognized in this species, as they appeared to be separately distributed. Large nymphs were those with fully developed gills, with the metathoracic pair of wing pads completely hidden by the mesothoracic pair, and the lateral margins of the wing pads sloping inwards (stages XIV–XVII of Rawlinson 1939). Small nymphs were those which did not fall into the large class and consisted of those nymphs without gill pads (stages IX–XIV of Rawlinson). Stages smaller than this, that is less than about 3 mm., were too small to be counted. The results are expressed as the average number of nymphs per station, which gives an appearance of very few nymphs per count as there were frequently no nymphs at all present in some of the very deep stations. The results of the counts are shown in Fig. 3 and Table 2.

E. torrentis disappeared completely in Broadhead Brook during May 1950 when the previously described algal growth occurred, and no trace of re-establishment was found.

The life-cycle of this species as it occurs in this stream has been described elsewhere (Harker 1952). Three broods develop, approximately in March–July, July–May and May–March. Nymphs of two different broods are thus always present in the stream at any one time. The increase in numbers of large nymphs from February to June 1950 is due to the growth of the overwintering nymphs. In February and March the May–March brood nymphs were nearing their full size, and in April and May the July–May brood were reaching their penultimate instar. By July all the nymphs from the March–July brood had emerged as adults. Therefore only small nymphs were left, except for a few nymphs from the May-March brood which entered the larger group in August, causing the increase in that month. Other increases caused by the growth during the summer will be masked by emergence of some nymphs as adults, so that the total population of large nymphs does not alter appreciably. Decreases in the number of large nymphs were seen to occur in November 1949 and 1950, and in July 1950. The decreases in November 1949–50 appear to be due to migration upstream; the reasons for this supposition will be discussed in a later paper. The decrease in July 1950 can be explained on the basis of the emergence of the adults of the March–July brood which left only the small nymphs which hatched in May.

Apart from the major increases and decreases caused by the life-cycles of the nymphs there are those caused by the environment. Flooding of the stream was a factor which appeared to have a marked effect on *E. torrentis*. Evidence for this was gained rather by an examination of the stream than by the counted number of nymphs. This is due to the difficulty in separating the decreases in number due to the life-cycle from those resulting from the environment. After a flood crushed nymphs were invariably found in any drift, and the very fact that nymphs were previously found associated with stones which were swept away or ground together supports this evidence. In December 1949 the stream flooded slightly. The numbers did not decrease appreciably, but this may be due to the fact that very few nymphs were present anyway. Two other minor floods occurred in August and September 1950. Although the numbers had increased in August, it may be supposed that they had not in fact increased as much as

they would have done had the flood not occurred. The slight decrease in numbers in September supports this supposition, and increase in numbers would be expected in September as the nymphs hatching in July would then be appearing in the larger

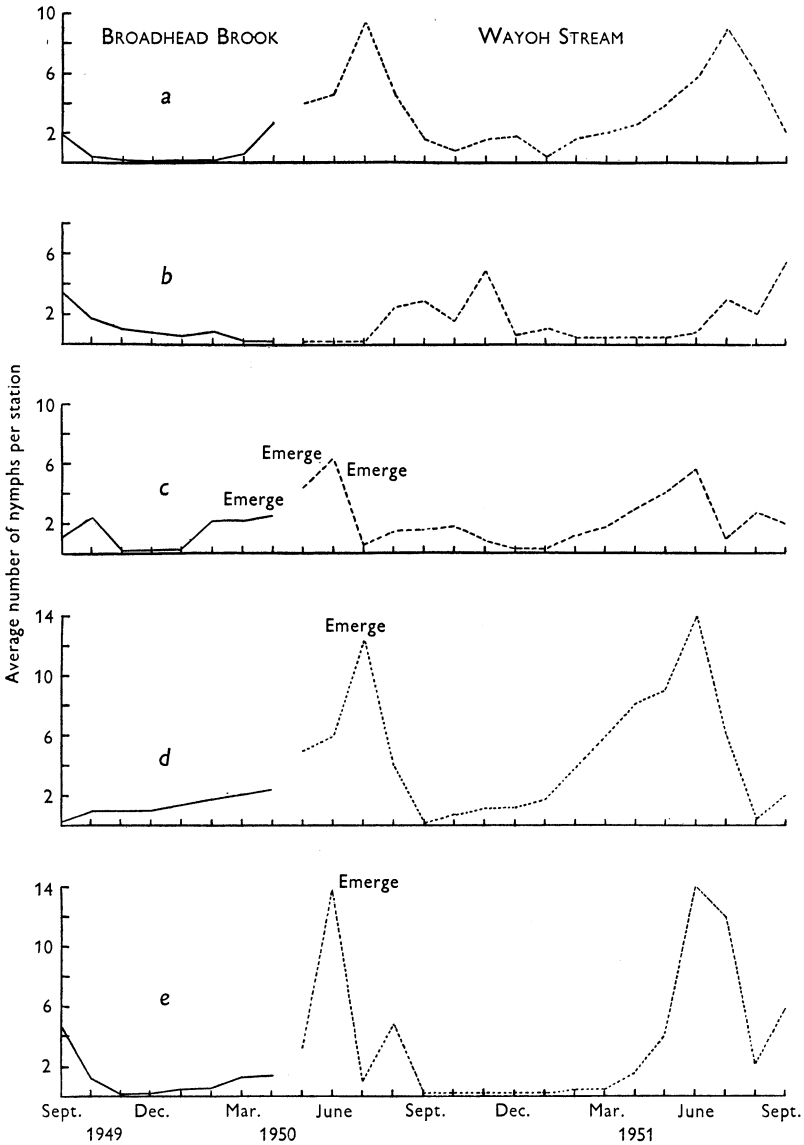

Fig. 3. The monthly average number of nymphs collected in a 530 sq.cm. area at 140 stations in Broadhead Brook and 100 stations in Wayoh Stream. (*a*) *Baëtis rhodani*; (*b*) *Ecdyonurus torrentis*, small nymphs; (*c*) *E. torrentis*, large nymphs; (*d*) *Rithrogena semicolorata*; (*e*) *Heptagenia lateralis*.

classes in which they overwinter. In August 1951, when no flooding occurred, a much greater increase in numbers is shown. The bad flood in October 1950 does not seem to have affected the nymphs any more than the smaller floods. Probably all the nymphs attached to small rocks had by that time already been swept away, or had moved to more secure stones which had not been moved by the flood waters.

The slow decrease in numbers of small *E. torrentis* nymphs from September 1949 to February 1950 may be due to gradual growth during the winter causing nymphs to enter the 'large' class at this time. The sudden decrease in March coincides with a period of rapid growth taking many nymphs into the larger class. The nymphs hatching out in March do not appear in great numbers, probably because the increase in numbers is masked by the decrease of small nymphs at the upper size level. But the nymphs hatching in July, and some of the later May brood, both appear in August counts, causing a sudden increase in numbers. The increase in February 1950 and 1951 is again thought to be related to migration.

Table 2. *Monthly collections*

(The figures give the average number of nymphs per station collected each month followed by the standard deviation.)

	Heptagenia lateralis	*Ecdyonurus torrentis* (large)	*Ecdyonurus torrentis* (small)	*Baëtis rhodani*	*Rithrogena semicolorata*
BROADHEAD BROOK					
Sept. 1949	10·2 ± 3·1	1·1 ± 0·3	3·3 ± 0·7	1·8 ± 0·07	0·4 ± 0·03
Oct.	1·3 ± 0·2	2·3 ± 0·4	1·9 ± 0·8	0·5 ± 0·05	1·0 ± 0·02
Nov.	1·3 ± 0·1	0·1 ± 0·01	0·9 ± 0·01	0·3 ± 0·03	1·0 ± 0·02
Dec.	0·1 ± 0·01	0·1 ± 0·01	0·8 ± 0·04	0·4 ± 0·02	1·0 ± 0·03
Jan. 1950	0·3 ± 0·1	0·3 ± 0·02	0·6 ± 0·07	0·1 ± 0·01	1·3 ± 0·07
Feb.	0·5 ± 0·2	2·0 ± 0·1	0·8 ± 0·06	0·1 ± 0·01	1·8 ± 0·9
Mar.	1·4 ± 0·1	2·1 ± 0·9	0·2 ± 0·02	0·5 ± 0·02	2·1 ± 0·8
Apr.	1·5 ± 0·3	2·6 ± 0·5	0·1 ± 0·03	2·8 ± 0·02	2·3 ± 0·8
WAYOH STREAM					
May	3·2 ± 0·5	4·5 ± 1·0	0·1 ± 0·03	4·1 ± 0·09	5·0 ± 1·1
June	12·8 ± 1·3	6·3 ± 0·9	0·08 ± 0·05	4·6 ± 0·2	6·0 ± 0·1
July	1·1 ± 0·2	0·6 ± 0·1	0·08 ± 0·07	9·7 ± 0·3	12·5 ± 0·5
Aug.	5·0 ± 0·3	1·6 ± 0·2	2·5 ± 0·09	4·5 ± 0·02	3·9 ± 0·6
Sept.	0·3 ± 0·1	1·5 ± 0·1	2·8 ± 1·01	1·6 ± 0·3	0·2 ± 0·01
Oct.	0·2 ± 0·01	1·9 ± 0·2	1·5 ± 0·9	1·0 ± 0·9	0·9 ± 0·07
Nov.	0·2 ± 0·01	0·8 ± 0·01	4·7 ± 0·8	1·6 ± 0·7	1·0 ± 0·02
Dec.	0·2 ± 0·01	0·3 ± 0·03	0·6 ± 0·04	1·7 ± 0·6	1·2 ± 0·09
Jan. 1951	0·3 ± 0·01	0·2 ± 0·05	0·9 ± 0·02	0·3 ± 0·02	1·7 ± 0·08
Feb.	0·4 ± 0·02	1·3 ± 0·3	0·4 ± 0·03	1·6 ± 0·03	3·8 ± 0·1
Mar.	0·5 ± 0·05	1·9 ± 0·1	0·4 ± 0·02	2·0 ± 0·9	5·9 ± 0·2
Apr.	1·6 ± 0·09	3·0 ± 0·4	0·4 ± 0·02	2·6 ± 0·9	8·0 ± 2·0
May	4·0 ± 0·8	4·1 ± 0·9	0·5 ± 0·03	3·9 ± 0·2	9·1 ± 1·1
June	14·0 ± 2·1	5·6 ± 1·1	0·8 ± 0·08	5·8 ± 0·9	13·9 ± 1·9
July	12·1 ± 2·4	1·0 ± 0·07	2·9 ± 0·1	9·0 ± 1·3	6·0 ± 1·0
Aug.	2·2 ± 1·0	2·8 ± 0·09	2·0 ± 0·2	6·0 ± 1·8	0·6 ± 0·03
Sept.	5·9 ± 0·8	2·0 ± 0·07	5·4 ± 0·2	2·1 ± 0·9	2·0 ± 0·2

Flooding does not seem to have affected the small nymphs as much as the larger ones. The dead nymphs found at these times were very seldom of the small nymph class. The major flood in October 1950 coincided with a natural decrease in numbers as can be seen by reference to the figures for the same month in 1949. Freezing of the stream may have affected *E. torrentis* slightly, as the numbers in December 1950 and January 1951, when the stream was frozen, decreased slightly more than in the same months of the previous year.

Rithrogena semicolorata. Owing to the limitations imposed by the inability of the observer to count more than a certain number of nymphs during any one counting

period, the nymphs of this species were treated as a whole and not divided into small and large nymphs. Preliminary counts showed no distinctive distribution in August and September of the small and large nymphs, as was found for those of *Ecdyonurus torrentis*. The results of the monthly counts are shown in Fig. 3.

Rithrogena semicolorata was one of the two species which returned to Broadhead Brook after the algal growth in May 1950. In October 1950 an average number of 0·08 nymph per station was found and this number increased to 2·2 by February 1951. Since the new appearance in October coincides with the hatching of eggs in Wayoh Stream it seems likely that the two nymphs in Broadhead Brook are the offspring of adults emerging from Wayoh in August 1950. The slow increase in numbers from October to March is probably due to the gradual growth of nymphs from eggs hatched in May, June and July, which are reaching a countable size. The increase to 6·5 nymphs per station in July corresponds with the period shown in the life cycle when the nymphs from the June hatching become large enough to count, and before the occurrence of the major emergence in July itself. The drop in numbers in August coincides with the end of the emergence period and is a common feature in 1-year life cycles.

Flood has affected *R. semicolorata* less than any other species. Again this is concluded rather from observation than from the numbers counted. No crushed *Rithrogena* nymphs were collected after floods, and the sucker-like arrangement of the gills gives a greater adhesive power than is found in other species (Harker 1951). A decrease in numbers occurred in August and September 1950 coinciding with floods, but also coinciding with the annual emergence which must cause a decrease in numbers. In October 1950 when the worst flood occurred the number actually increased, and in December 1949 after a flood no decrease in numbers was found. Freezing of the stream did not affect the numbers of nymphs. The stream was frozen in December 1950 and January 1951 and yet the numbers increased more than they did in the same months of the previous year.

Heptagenia lateralis. The results of the monthly counts are given in Fig. 3. The main emergence in June would account for the drop in numbers in July and the following increase in August, as the nymphs hatching from the eggs laid in June began to enter the counts.

H. lateralis lives in very similar habitats to those of *Ecdyonurus torrentis*. The main peaks in the totals of *E. torrentis* occur in June and October, while a peak appears in the numbers of *Heptagenia* in June, August or September. Floods affected *H. lateralis* more than any other species, the numbers dropping after every flood. The very low numbers in Broadhead Brook may be associated with the unstable bottom as compared with that of Wayoh Stream.

Baëtis rhodani. The nymphs of this species are often found on the tops of stones and swimming freely in the water, so that it was the most difficult species to count, and the results (Fig. 3) are probably less accurate than for those of other species. The numbers for the total population do not indicate the complexity of the life cycle, nor the presence of the two different sizes of nymphs (Harker 1952).

B. rhodani reappeared in Broadhead Brook in November 1950, an average of 0·2 nymph per station being present. This number increased to 1·1 per station by February 1951. Although no separate counts of small and large nymphs were made

it was noted that the very small nymphs, which do not appear in the counts, were present in the water just below the overhanging grasses and weeds at the edges of the deeper parts of the stream.

B. rhodani was only slightly more affected by floods than *Rithrogena*. Again the totals were dropping owing to emergence at the times of the floods, and the numbers do not indicate the resistance of these nymphs to fast-flowing currents.

(*c*) *Micro-distribution*

The nymphs of each species were found to follow a Poisson distribution over the experimental area in the following months: *R. semicolorata* December 1950, January and February 1951; *Ecdyonurus torrentis*, small nymphs, and *Baëtis rhodani*, August, September and October 1950, *Ecdyonurus torrentis*, large nymphs, February 1951; *Heptagenia lateralis* July 1950. In other months between September 1949 and February 1951 distribution was not random. Some difficulty has been experienced in relating the counts at each station to the depth or current since the total number of nymphs, the frequency of each type of habitat, and the total number of habitats actually covered by the stream varied each month. Using Spearman's rank correlation coefficient no significant correlation has been found between the depth at each station and the number of nymphs. However, correlating the relative depths (in groupings of 25% of the greatest depths) with the number of nymphs, using the same coefficient, shows a significant correlation at the 1% level in some months, Bessel's correction having been applied for the small sample size (Table 3). That is, the nymphs in general do not show a distribution correlated with absolute depth, but are associated with the relative degrees of depth.

Ecdyonurus torrentis large nymphs showed a correlation at the 5% level in December 1950 and January 1950–51, with the greatest number in depths above 75% of the deepest area. From March to August 1950 the correlation was at the 1% level with the majority of nymphs in the 0–25% depth area. No correlation was found between the relative depths and the number of small *E. torrentis* nymphs. The number of *Baëtis rhodani* nymphs showed a direct correlation with the relative depths at the 1% level in autumn from September to December 1949 and 1950. There was no significant correlation in other months of the year. *Heptagenia lateralis* nymphs were in the majority in the shallow areas from December to March and showed a significant correlation with the relative depth at the 1% level. In summer the correlation was significant at the 5% level, with the greatest number of nymphs in the shallow areas. The number of nymphs of *Rithrogena semicolorata* shows a correlation at the 1% level with the relative depth from June to August when the nymphs were in depths above 75% of the deepest area.

The number of nymphs was found to be correlated with the current-rate, using the rank correlation, in the same months in which a correlation was shown between depths and numbers. The current-rates were taken at the surface of the stream, and the current at the bottom will be related to the depth; it is impossible to separate the two factors in considering the micro-distribution of the nymphs.

From the results it appears that the nymphs of *Ecdyonurus torrentis* and *Heptagenia lateralis* are present in the shallow regions during the emergence periods, but *Rithro-*

gena semicolorata is in the deeper areas during this period. *Baëtis rhodani*, which emerges from the top of the water without crawling up a stone, is randomly distributed when emergence is at a maximum. The movement of nymphs of *B. rhodani*, *Heptagenia lateralis* and *Ecdyonurus torrentis* into shallow water seems to be associated with the floods. Whether this is actually movement to the shallow parts or whether the relative numbers are lowered in the deeper parts by nymphs being swept away is not known.

Table 3. *Correlation of relative depths, in ranks of 25% of the total depth, with the number of nymphs*

(S = level of *t*-value (%). D = the relative depth at which the majority of nymphs were found.)

	Ecdyonurus torrentis (large)		*Heptagenia lateralis*		*Rithrogena semicolorata*		*Baëtis rhodani*	
	S	D	S	D	S	D	S	D
Sept. 1949	0	—	5	25	0	—	1	75
Oct.	0	—	0	—	0	—	1	75
Nov.	0	—	0	—	0	—	1	75
Dec.	5	75	1	25	0	—	1	75
Jan. 1950	5	75	1	25	0	—	0	—
Feb.	5	75	1	25	0	—	0	—
Mar.	1	25	1	25	0	—	0	—
Apr.	1	25	0	—	0	—	0	—
May	1	25	0	—	0	—	0	—
June	1	25	0	—	1	75	0	—
July	1	25	5	25	1	75	0	—
Aug.	1	25	5	25	1	75	0	—
Sept.	0	—	5	25	0	—	1	75
Oct.	0	—	0	—	0	—	1	75
Nov.	0	—	0	—	0	—	1	75
Dec.	5	75	1	25	0	—	1	75
Jan. 1951	1	75	1	25	0	—	1	75
Feb.	5	75	1	25	0	—	0	—
Mar.	1	25	1	25	0	—	0	—
Apr.	1	25	1	25	0	—	0	—
May	1	25	0	—	0	—	0	—
June	1	25	0	—	1	75	0	—
July	1	25	1	25	1	75	0	—
Aug.	1	25	5	25	1	75	0	—

It has been shown for every species that distribution is neither random, nor correlated with the depth or current in some months of the year. These months are as follows: *E. torrentis*, large nymphs, September, October, November; *Baëtis rhodani*, January to May; *Heptagenia lateralis*, April to June, October to December; *Rithrogena semicolorata*, March to June, September to December. What factors are influencing the distribution at these times is not apparent.

ACKNOWLEDGEMENTS

This work was carried out while the author was the holder of the Grisedale Research Scholarship and the Philip Buckle Studentship of Manchester University.

SUMMARY

1. The numbers of nymphs of *Ecdyonurus torrentis*, *Heptagenia lateralis*, *Baëtis rhodani*, and *Rithrogena semicolorata* in a 530 sq.cm. area at each of 140 stations in Broadhead Brook and 100 stations in Wayoh Stream, Lancashire, were counted every month from September 1949 to August 1951.

2. At each station the current and depth were measured. The temperature, pH, calcium concentration and oxygen concentration were measured at various points.

3. The seasonal variations in the numbers of *Ecdyonurus torrentis* followed the course of the life-cycle and were also affected by flood. Freezing of the stream caused a decrease in numbers. The numbers of *Rithrogena semicolorata* followed the life-cycle closely. *Heptagenia lateralis* was found to be very much affected by floods. *Baëtis rhodani* was little affected by floods, and together with *Rithrogena semicolorata* re-populated Broadhead Brook after the fauna had disappeared during an excessive growth of algae.

4. *Ecdyonurus torrentis* and *Heptagenia lateralis* moved to shallow regions at the emergence periods and during floods. *Rithrogena semicolorata* moved to deeper water at the time of emergence. *Baëtis rhodani* is randomly distributed most of the year.

REFERENCES

Dodds, G. S. and Hisaw, F. L. (1924). Ecological studies of aquatic insects. I. Adaptations of mayfly nymphs to swift streams. *Ecology*, **5**, 137–48.

Harker, J. E. (1951). Unpublished thesis in Manchester University Library.

Harker, J. E. (1952). A study of the life cycles and growth-rates of four species of mayflies. *Proc. R. Ent. Soc. Lond.* (A), **27**, 77–85.

Rawlinson, R. (1939). Studies on the life-history and breeding of *Ecdyonurus venosus* (Ephemeroptera). *Proc. Zool. Soc. London.* **109** (B), 377–450.

Ricker, W. E. (1934). A critical discussion of various measures of oxygen saturation in lakes. *Ecology*, **15**, 348–63.

Whitney, R. J. (1938). A syringe pipette method for the determination of oxygen in the field. *J. Exp. Biol.* **15**, 564–70.