

STUDENT INVESTIGATIONS ON THE FAUNA OF AN EXMOOR STREAM

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ABSTRACT

Eighty-eight sets of student data (collected between 1970 and 1988) describing the distribution patterns shown by 8 taxa of stream invertebrates, have been analysed. Despite the well-known errors inherent in student data, repeatable patterns emerge. Some taxa are always taken more often in the headwaters and others further downstream: some are more common in pools and others in riffles. Many of the patterns can be related to the distribution of other organisms. Others appear related to maximum velocities or temperatures. Simple associations with pools or riffles are easier to appreciate than precise regressions. The most significant finding, however, is the stability shown by many of the patterns over an extended period that included the floods of May 1983 as well as the drought of 1975/76. The results would have been much more useful if identification had been taken to a lower level.

INTRODUCTION

ARNOLD AND MACAN (1969) describe and interpret a student investigation into the distribution of invertebrate stream animals down Ashes Hollow, in the Long Mynd, Shropshire. This paper describes and analyses the results of a comparable study along the Exmoor stream variously known as Embercombe Water, Chetsford Water and Nutscale Water (NGR SS8540: Fig. 1). Biology students from the Leonard Wills Field Centre at Nettlecombe Court, of all ages from 8 to 80, have used this stream. Some of the data they collected between 1970 and 1988 are summarised and discussed here.

The stream rises at an altitude of 430 m and flows north to enter the Bristol Channel in Porlock Bay. The section under investigation runs from the bog at Embercombe Head (NGR SS859406) to the fence below Nutscale Rocks (NGR SS858429). Away from the water's edge, the surrounding moorland is dominated by heathers, *Calluna vulgaris* and *Erica cinerea*, or bracken, *Pteridium aquilinum*, but with increasing numbers of trees (at first mostly hawthorn, *Crataegus monogyna*, but later replaced by alder, *Alnus glutinosa*) on the valley floor.

METHODS

Collections of invertebrate animals were made at six stations; three along Embercombe Water and three along Nutscale Water (Fig. 1). Interest was concentrated on eight taxa: freshwater shrimps, flatworms, mayfly nymphs, stonefly nymphs, cased caddis larvae, caseless caddis larvae, blackfly larvae and water beetle adults. Each group of students collected, identified and counted the number of individual animals (in each of these taxa) associated with nine stones, at each station. When sampling, a net was placed in the water downstream of a chosen stone, which was then lifted out so that anything sheltering underneath was caught in the net. The catch was sorted in a white plastic tray, partially filled with clear water. The stones were later returned to the stream, the "correct" way up.

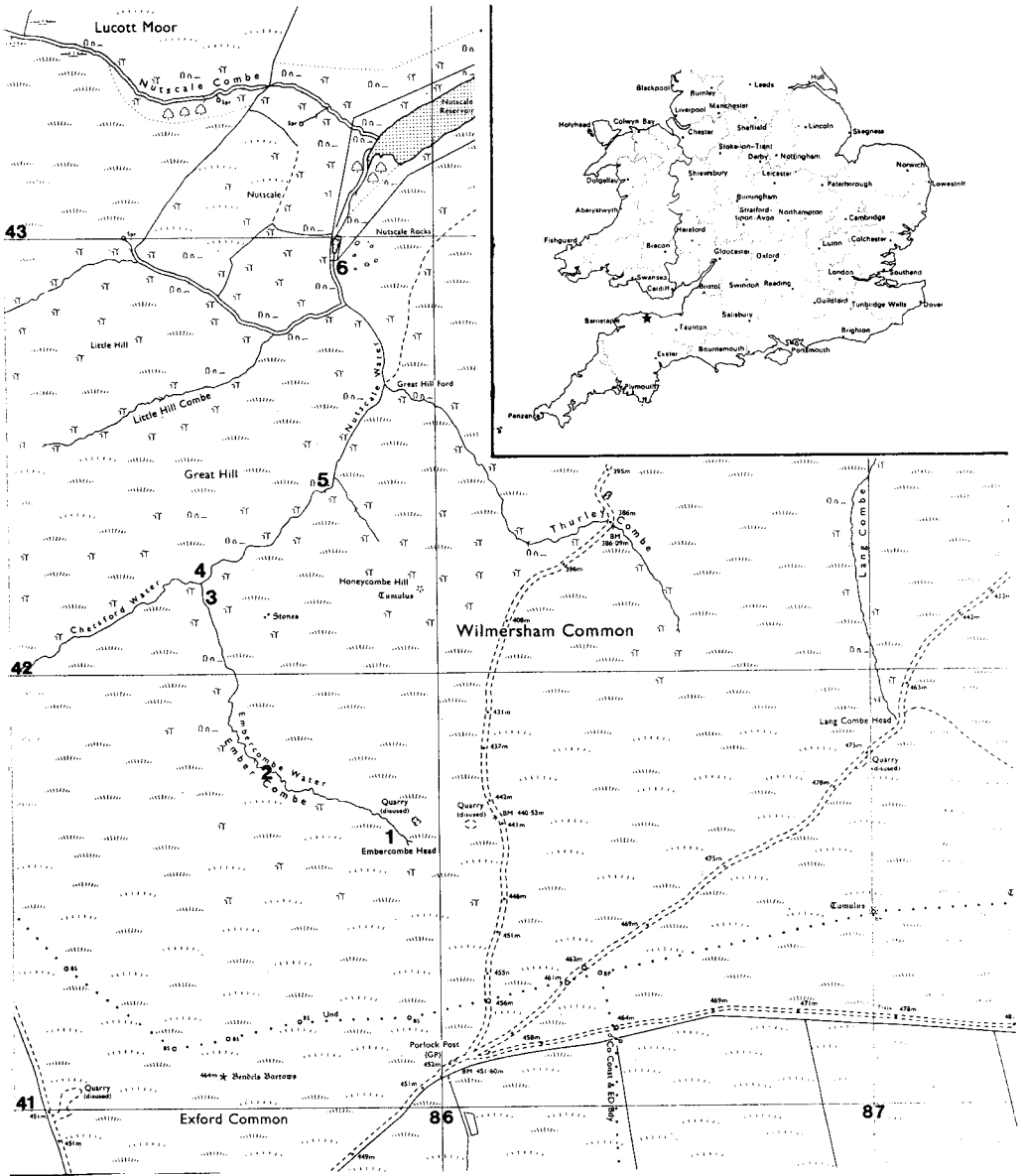


FIG. 1.

Part of Grid Square SS84 showing the approximate locations of the six sampling sites. Station 1, below the disused quarry at Embercombe Head, marks the upper limit of the stony hill stream; station 3 is just above the junction with Chetsford Water; whilst station 2 is at a convenient spot in between. Station 4 is just below the junction; station 6 is just above the reservoir boundary fence; whilst station 5 is at a convenient point in between. The double dashed line (passing through the "e" of Wilmersham Common) marks the road. Spot heights are in metres.

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Half the data were collected from pools, and half from riffles. Group data were subsequently added together to produce a class total (or, occasionally, a class average when an uneven number of groups were involved). Records were kept of water temperature (using a thermometer) and of velocity (using a Braystoke meter). Occasional measurements of pH, conductivity and oxygen concentration were also taken.

STUDENT DATA

Most of the data considered here were collected by GCE A-level or undergraduate students, whose only common factor was that they had not attempted the survey before. Undoubtedly, there are errors—both in identification and in counting—especially with the very small insects found in summer. Some data were taken in heavy rain (when it is very difficult to do anything accurately) and others in sub-zero temperatures. Not all the people concerned were highly motivated. Nevertheless, consistent patterns do emerge which are “explicable” in terms of the known biology of the animals.

Field courses vary in size. The smallest group contributing data to this set comprised five people, and the largest sixty-six. Most included between 15 and 30 individuals. Not surprisingly, the larger classes caught more animals, and it was necessary to transform the raw data to eliminate this bias. Thus, the numbers of (say) freshwater shrimps in pools and riffles at the six sites were expressed as percentages of the total number caught on that day. The monthly, annual or overall means discussed in this paper are derived from these percentage catches (Appendices).

It must also be remembered throughout the paper that the records are of the number of individuals *counted* and not of the number *present*. Changes in the figures reflect both the ease of capture and alterations in abundance. This is especially true of catches from the deeper pools in the lower reaches.

RESULTS

A recent set of data is reproduced in Table 1.

Table 1. *An example of a class data set. These data were obtained on 16 May 1988 by Open University students, working in 10 groups. They are the totalled catches of the animals, and the means of temperature and velocity readings from pools (P) and riffles (R) at the six stations marked in Figure 1*

	1		2		3		4		5		6		TOTALS
	P	R	P	R	P	R	P	R	P	R	P	R	
FW Shrimps	27	85	39	16	43	80	2	18	0	3	1	5	319
Flatworms	105	127	14	9	17	14	0	14	0	0	1	0	301
Swimming Mayflies	52	39	11	0	5	12	4	11	24	46	22	41	267
Flattened Mayflies	2	5	2	9	25	14	46	61	47	38	76	40	365
Stoneflies	38	149	40	34	21	85	14	59	20	24	17	13	514
Cased Caddis	9	25	14	39	42	13	24	13	24	7	67	8	285
Caseless Caddis	11	15	5	12	3	23	1	19	3	8	1	15	116
Blackfly	6	64	13	76	18	51	4	36	13	48	18	66	413
Water Beetles	15	0	34	2	28	2	84	8	48	11	22	3	257
Total	265	509	172	197	202	294	179	239	179	185	225	191	2837
mean:-													
Temperature °C	12	11	11	11	12	13	14	14	16	16	16	16	
Flow cm.s ⁻¹	12	54	12	55	5	61	6	56	14	31	9	47	

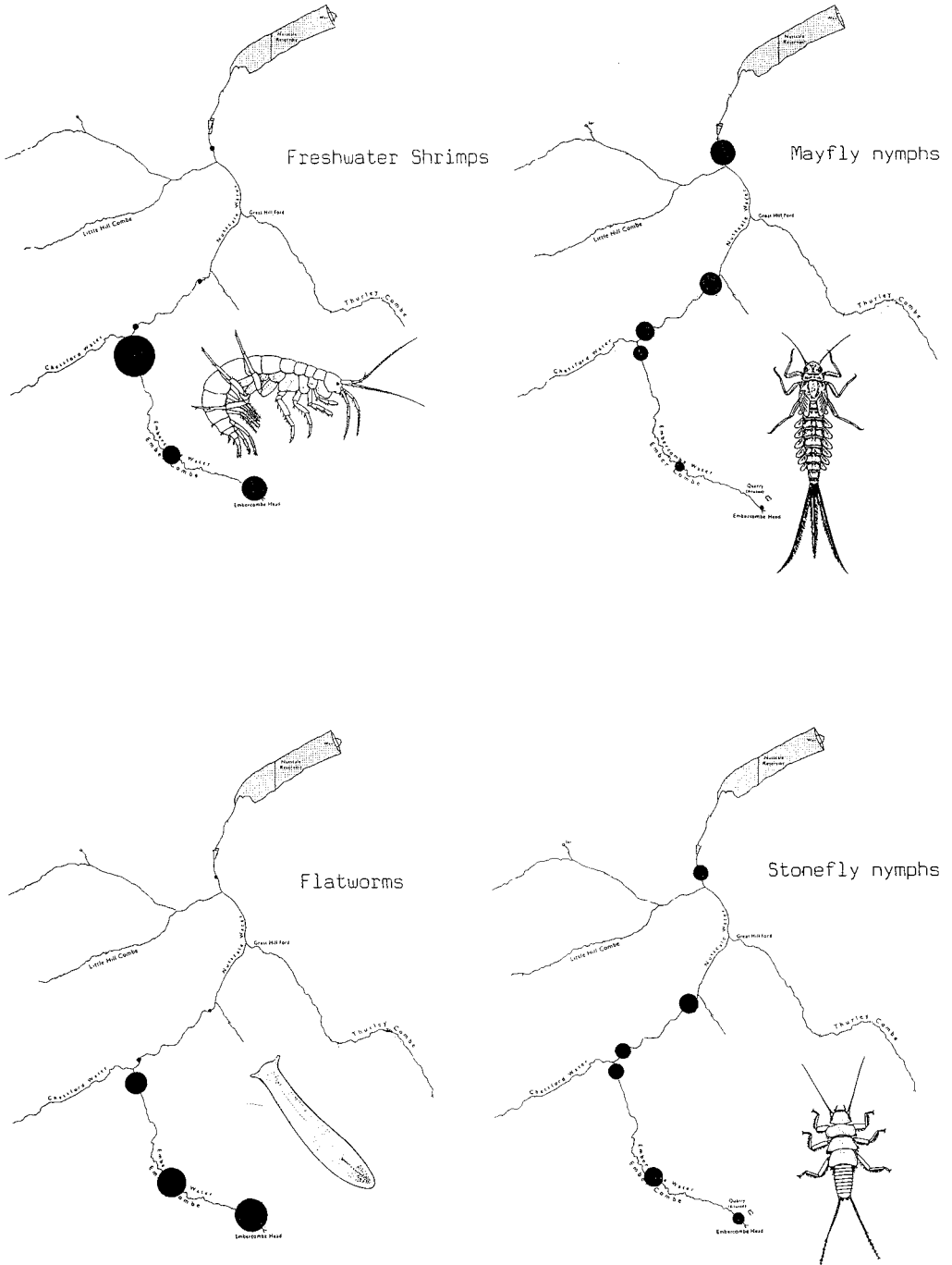


FIG. 2.

Proportional circles to display the overall distribution of freshwater shrimps (*Gammarus pulex*); flatworms (*Polycelis felina*); mayfly nymphs; stonefly nymphs; blackfly larvae; water beetles (*Oreodytes sanmarkii*); cased caddis larvae and caseless caddis larvae between the six stations, 1970-1987.

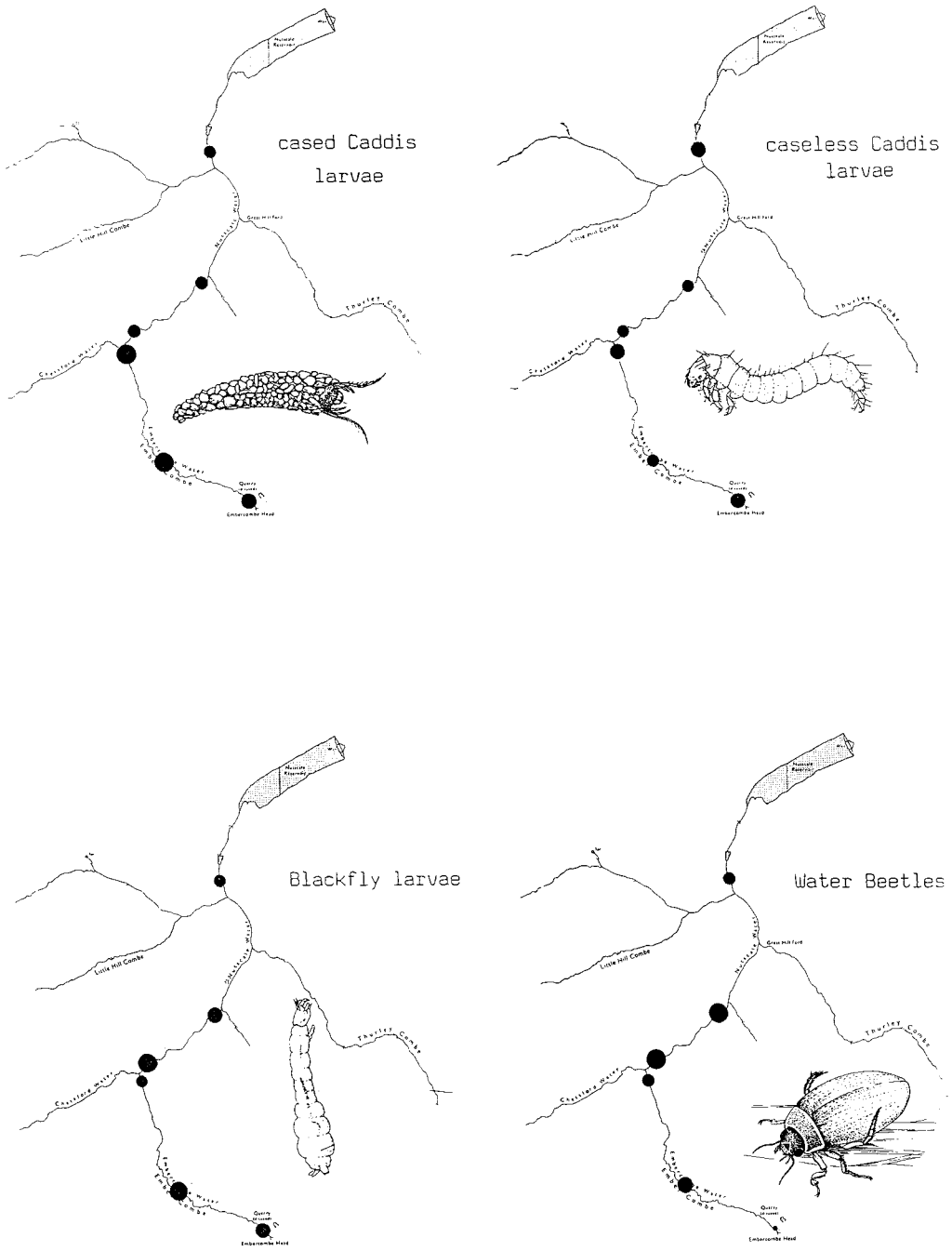


FIG. 2

Table 2. *The 1988 data tabled to show the percentage composition of the stream fauna at the six sites shown in Figure 1. It will be noted that freshwater shrimps and flatworms together represent very nearly half the total caught at site 1, but only 4% at sites 5 and 6. Overall they constitute 22% of the total catch*

	1	2	3	4	5	6	Mean
FW Shrimps	20	15	26	5	1	3	12
Flatworms	29	9	8	3	3	1	10
Swimming Mayflies	17	18	13	18	28	22	19
Flattened Mayflies	2	3	11	18	19	17	11
Stoneflies	9	12	12	10	11	7	10
Cased Caddis	6	9	7	6	7	11	8
Caseless Caddis	5	5	5	3	5	5	5
Blackfly	10	23	10	25	17	28	19
Water Beetles	1	6	7	11	9	6	6

Table 2 displays information about the community composition of the stream fauna in 1988. Other years would have given very similar patterns. It will be noted that the catch in Nutscale Water (stations 4–6) is dominated by mayfly nymphs whilst in Embercombe Water (stations 1–3) this position is held by freshwater shrimps and flatworms. Their failure to extend downstream is one reason why the total catch is smaller lower down.

Fig. 2 displays the overall mean distributions of the taxa sampled.

Environmental factors

1. Velocity

Table 3 summarises the stream velocity data collected by the student groups. The figures, which have been averaged month by month, relate to mid-column flow and do not

Table 3. *Monthly means of the recorded velocities (cm.s^{-1}) in pools and riffles at the six sites, together with the highest and lowest values recorded*

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
March	13	56	28	86	13	79	18	63	10	107	13	86
April	22	63	24	79	17	80	17	72	19	93	23	79
May	13	46	10	54	12	53	18	70	15	59	9	60
June	16	57	16	68	8	58	15	87	15	46	11	73
July	7	32	4	36	7	40	18	43	14	49	8	54
August	21	42	24	66	10	70	23	72	13	72	46	73
September	8	34	12	56	10	59	14	76	18	67	11	70
October	21	61	20	68	16	72	33	80	20	86	34	96
Average velocity in pools	16				Average velocity in riffles				65			
overall												
Maximum values	33	115	57	104	33	125	56	143	38	136	68	141
Minimum values	2	7	3	18	0	19	3	20	4	42	2	7

Table 4. The mean data for 1987 and 1988 tabulated to show the proportion of the catch taken in riffles

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
1987												
Average catch	293	390	239	447	300	414	322	313	204	285	160	267
% in riffles		57		65		58		49		58		63
Overall proportion in riffles	58											
1988												
Average catch	226	277	130	259	154	211	139	245	134	203	132	222
% in riffles		55		67		58		64		60		63
Overall proportion in riffles	61											

indicate the true conditions experienced by the animals (except when they are drifting). They are used as the best available indication of *differences* between the sites. Also, the real maxima and minima will be higher and lower than those given in the table, for it is most unlikely that our visits coincided with the occurrence of extreme velocities.

The sampling technique depends upon a flow of water to wash the animals into a net. It might be expected, therefore, that catches would be higher from riffles than from pools, even if the fauna was evenly distributed. Table 4 summarises the 1987 and 1988 data. Catches from riffles represented 58% and 61% respectively—figures notably similar to the 60% quoted by Hynes (1970) from Black River, Missouri.

Nevertheless, when the long-term data for the individual taxa are considered, each is seen to adopt one of three patterns. (Fig. 3). Water beetles are caught far more often in pools than in riffles. With blackfly larvae it is the other way round. Whilst freshwater shrimps appear to show little preference for one habitat over the other.

2. Temperature

Temperatures also change (slightly) from day to day and (much more significantly) between summer and winter (Table 5). As with the velocity data, this table records the

Table 5. Monthly mean values for water temperature ($^{\circ}\text{C}$) recorded in pools and riffles at the six sites, and the highest and lowest figures obtained

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
March	6	6	7	6	7	8	7	8	8	8	8	8
April	7	8	8	8	8	8	9	9	10	10	10	10
May	10	10	10	11	11	12	13	12	13	13	13	14
June	11	11	12	12	13	12	15	14	15	15	16	16
July	12	12	13	12	14	13	15	15	17	17	17	17
August	10	11	11	11	11	11	12	12	12	12	12	12
September	11	11	11	11	11	11	12	12	13	12	13	12
October	9	9	9	9	9	9	10	10	10	10	11	11
November	11	11	11	11	11	11	11	11	11	11	12	11
Maximum values	14	14	15	15	17	17	19	19	21	21	21	21
Minimum values	4	4	4	4	5	5	4	4	4	4	5	5

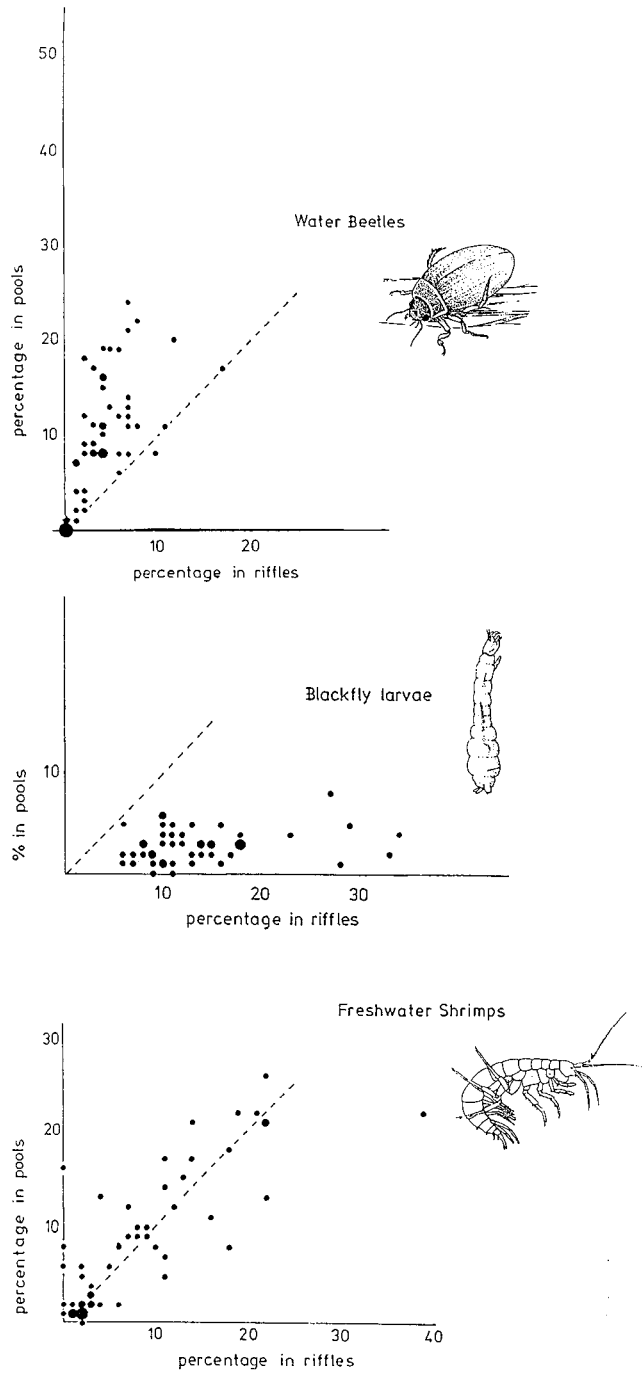


FIG. 3.

The mean distribution of (a) water beetles (*Oreodytes sanmarkii*), (b) blackfly larvae (Simuliidae) and (c) freshwater shrimps (*Gammarus pulex*) between pools and riffles (1970–1987). This figure uses monthly (February–October) means, plotting mean February station 1 pools against mean February station 1 riffles, and so on. The dashed line indicates the equilateral about which the dots would fall if there was no preference shown for either habitat.

Table 6. Values of pH measured at the six stations on ten occasions between 1975 and 1985. nd = no data

	1	2	3	4	5	6
16 June 1975	6.5	6.5	6.5	7.5	7.0	7.5
20 June 1977	6.5	6.5	6.5	6.5	6.5	6.5
20 June 1978	7.0	7.2	8.1	nd	8.3	8.0
18 June 1979	6.5	6.5	7.4	7.5	7.6	7.6
17 June 1980	6.5	6.5	6.6	6.8	6.8	nd
21 June 1981	6.8	5.9	5.8	5.8	5.8	5.8
21 June 1983	7.4	7.4	6.2	7.4	7.0	7.0
21 June 1984	7.0	7.1	7.1	7.1	7.3	8.0
3 May 1985	6.5	6.7	6.9	7.0	7.0	7.1
11 October 1985	7.4	7.3	7.1	7.2	7.4	nd
Mean	6.8	6.8	6.8	7.0	7.1	7.2

measurements taken whilst sampling. The true maxima and minima will be more extreme. There is so little difference between the minima that they are unlikely to have influenced any of the distribution patterns. The maxima, however, could have relevance for several of the taxa. In general, warmer temperatures encourage activity in invertebrates (although this is not invariably true—see below) and speed-up incubation of their developing eggs. But, warmer water is able to hold less oxygen in solution; which may present problems for some species.

3. Water Chemistry

On the occasions when pH has been measured, little variation was found between the sites (Table 6). Likewise conductivity readings were always between 7 and 8×10^{-4} siemens. Oxygen concentrations were generally high and, whilst decreasing slightly downstream, can rarely have been limiting except in the warmest weather and at the lowest flows.

DISCUSSION

Freshwater shrimps, *Gammarus pulex**

Overall, freshwater shrimps peaked at station 3 and were rarely caught at the three lower stations (Figs. 2 and 4). *G. pulex* is predominantly a detritivore, depending largely for its food on the dead leaves of terrestrial plants that fall into the stream, although it will also eat a wide range of other decomposing matter. Detritus tends to accumulate in pools and, presumably, greater quantities will be available as distance from the headwaters increases and more material enters the stream. (Dead leaves cannot move upstream!). In this stream system, the abundance of bankside trees also increased downstream. Countering this, small headwater streams may be more retentive of leaf litter than larger channels because there are more obstructions and a lower discharge of water. Nevertheless, if availability of food was the controlling influence on their distribution, freshwater shrimps should increase in abundance in pools, downstream; this is clearly not the case here. In Embercombe

*No other species has been identified in this stream system, so we have assumed that all animals recorded as "freshwater shrimps" are of this species.

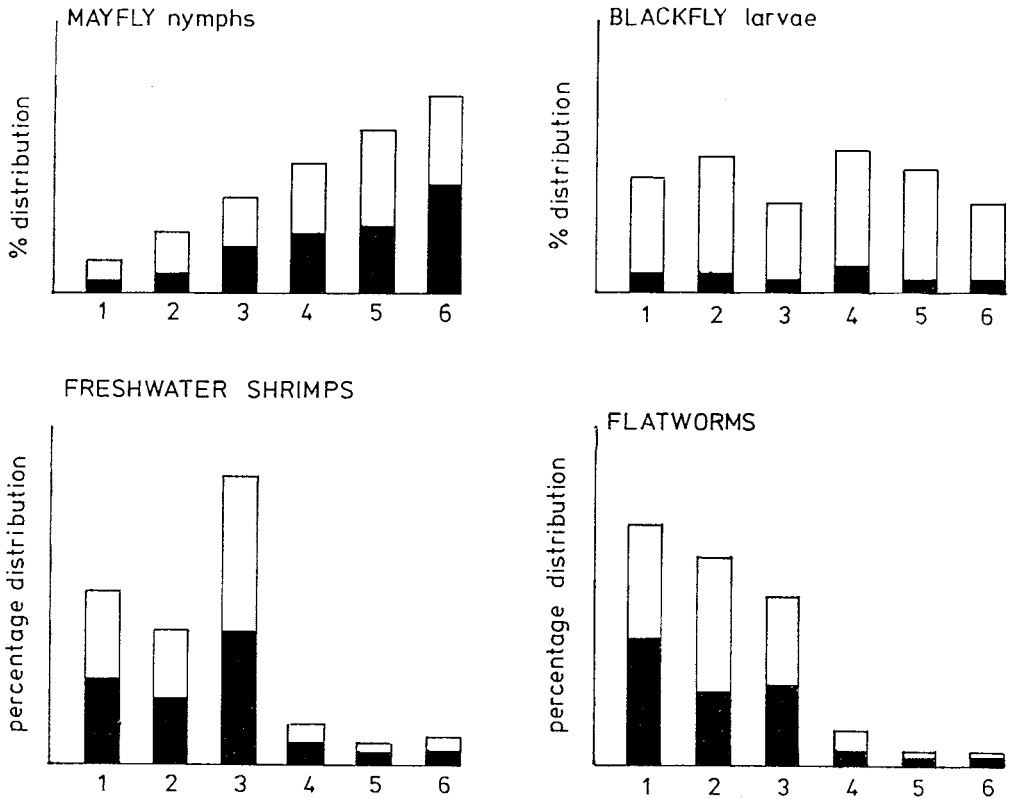


FIG. 4.

Bar charts to display the mean distribution patterns of four selected taxa in pools and riffles at the six stations, 1970–1987. Flatworms represent groups that are commoner in the headwaters and decrease downstream: Mayflies represent groups that increase downstream: and Blackfly larvae represent groups for which the distinction between pools and riffles is more important than position within the stream. Freshwater shrimps are unusual in that they build up from station 1 to 3 and then fall sharply.

Water/Nutscale Water, they are commonest in the headwaters and there is little overall difference between the numbers caught in pools and riffles (Fig. 3), although seasonal variations are apparent (Fig. 5: Appendix 1).

Most student groups began to catch fish (bullheads, *Cottus scorpio*, and trout *Salmo trutta*), at station 3 and found significant numbers of them from station 4 onwards. In aquaria, these fish feed readily on freshwater shrimps. Their abundance in Nutscale Water doubtless contributes to the low catches of *G. pulex*. In Czechoslovakia, Straskrabe (1965), quoted by Hynes (1970), described a similar sudden diminution in the number of *Gammarus* below a weir that marked the upstream limit of trout.

The pattern described here is complicated by the low catches at station 2. The food-availability/fish-predation model presupposes that *G. pulex* numbers should rise steadily from station 1 to 3 before being depressed by predation. Table 7 shows that catches at station 2 are, on average, lower than those at stations 1 and 3. But this was not always the case, and nor were freshwater shrimps always so scarce in Nutscale Water. In the 1970s, catches at station 2 usually lay in between those of stations 1 and 3—and they were higher than either in 1978 and 1981. It is only in the last decade (1978–1988) that the consistent shortfall at station 2 has been apparent.

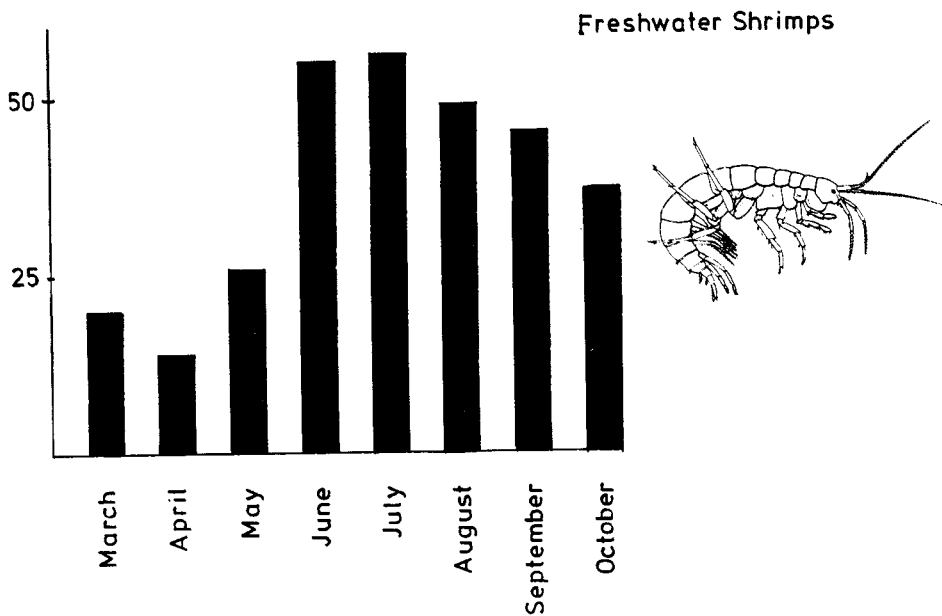


FIG. 5.

Seasonal changes in the proportions of the freshwater shrimp catch taken from pools, 1970-1987.

Studies by Gee (1982) and by Adams *et al.* (1987) suggest that the size composition of the substrate is more important than the availability of detritus in controlling the microdistribution of this species. No data on the composition of the stream bed are available for Embercombe Water or Nutscale Water. Quint (1987) found no differences in water quality within the stream system but suggested a negative association between the abundance of *G. pulex* and the presence of the green alga, *Cladophora* sp., but observations during 1988 suggested that this was coincidental: in that year *Cladophora* was common in Embercombe Water as well as in Chetsford Water.

Flatworms, *Polycelis felina**

Flatworms were much more common in Embercombe Water than in Nutscale Water and appeared to show little preference between pools and riffles (Figs 2 and 4). Overall, 46% of the catch was taken in pools, but the percentage was higher in the colder months and lower in high summer. The stability of this species' distribution pattern from season to season and from year to year is apparent from Appendix 2.

Polycelis felina is carnivorous, feeding particularly on freshwater shrimps but also upon stonefly nymphs and caddis larvae (Ball and Reynoldson, 1981). Its coincidence with freshwater shrimps in Embercombe Water was, therefore, not surprising. But the relationship is not close and catches of the two taxa rarely peaked together. It is likely that the effect of temperature was much more important, for *P. felina* is known to favour cooler water. According to Pattee, quoted by Ball and Reynoldson (1981) and Macan (1983), the upper

*No other species of *Polycelis* has been identified in this stream system, and only once have we found another flatworm—*Phagocatta biguttata*—so we have assumed that all animals recorded here as "flatworms" are *Polycelis felina*.

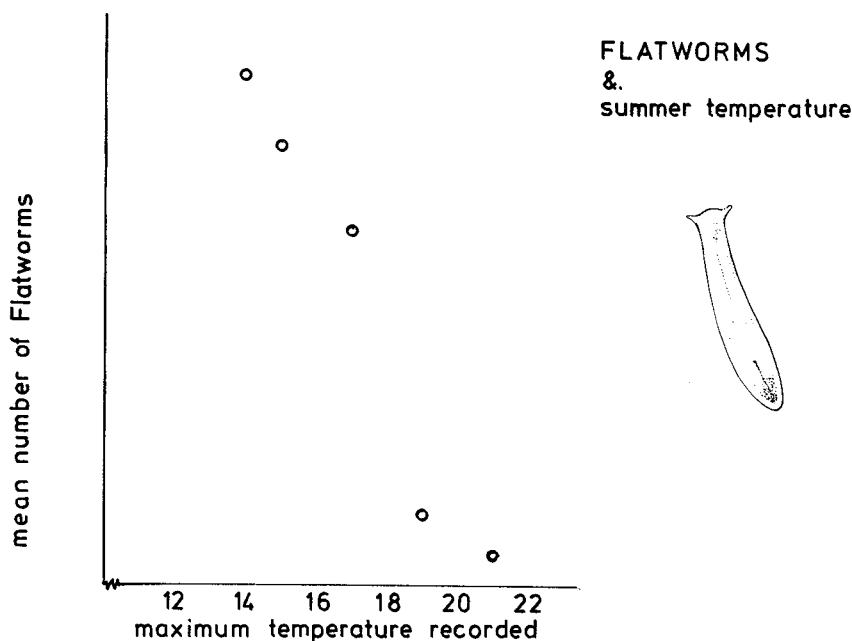


FIG. 6.

Overall mean flatworm (*Polycelis felina*) counts at the six stations, plotted against the maximum temperatures recorded. There are six points on this graph but the two at 21°C superimpose.

limit of indefinite survival for this species is 16–17°C. Water temperatures in Nutscale water reached 19–21°C during some summers (Table 5) and, in Fig. 5, it will be noted that very few flatworms were found at sites subject to these temperatures. However, correlation does not prove causation and, it is clear from Table 5 that anything which increases in abundance downstream *must* show a positive correlation with maximum temperature.

Nymphs of the stonefly *Dinocras cephalotes* are a major predator of *P. felina*. Wright (1975) noted an inverse relationship between abundance of flatworms and of *D. cephalotes* in Welsh streams. Unfortunately, the data under analysis do not discriminate between the different species of stonefly, but the large black nymphs of *D. cephalotes* always attracted attention from station 3 or 4 downwards.

The distribution of any species within its habitat is controlled by the availability of its food, the distribution of its predators and any limiting physico-chemical environmental factors. For these flatworms, all probably combine to confine the animals in the headwaters of the stream system.

Mayfly nymphs

Mayfly nymphs increased in abundance downstream (Figs 2 and 4) and occupied an increasing proportion of the total catch (Table 2). The stability of these animal's distribution patterns from season to season and from year to year is apparent from Appendix 3.

Their abundance showed an interesting negative relationship with that of the freshwater shrimp (Fig. 7) but this does not necessarily imply that the animals positively avoided each other; if one was commoner at stations 1–3 and the other at stations 4–6 a negative plot of this kind is almost inevitable. Nevertheless, Waters (1964)—quoted by Hynes (1970)—

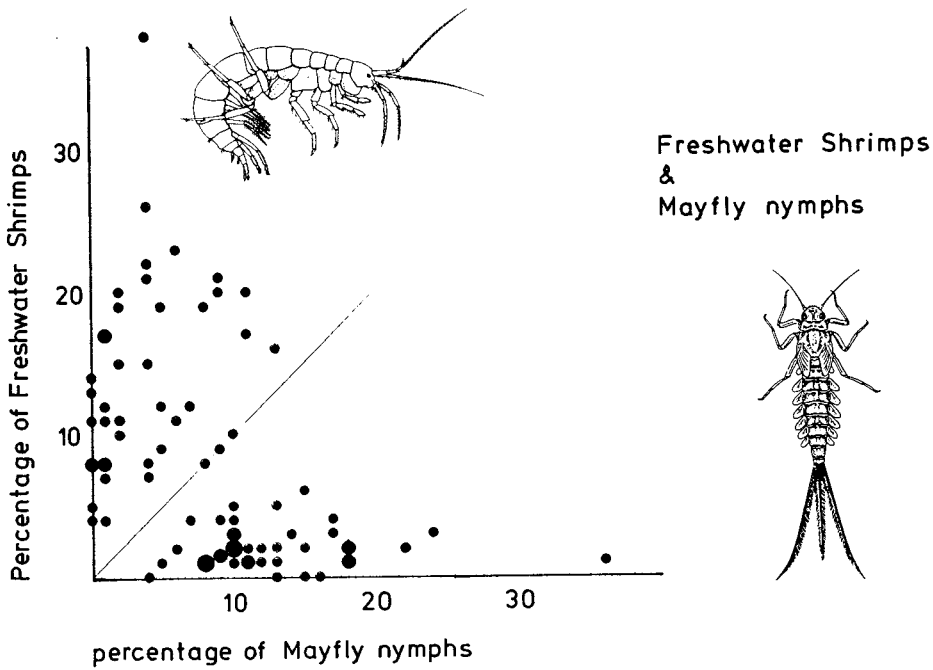


FIG. 7.

The relationship between freshwater shrimps and mayfly nymphs, suggesting an avoidance distribution pattern.

studying recolonisation of artificially-cleared areas of stream bed, found mayfly (*Baetis vagaris*) numbers higher when freshwater shrimp (*Gammarus pseudolimnaeus*) numbers were low. This may indicate some kind of mutual interference between the taxa.

Mayfly nymphs are primarily herbivorous, scraping algae from the surface of stones on the stream bed. As the stream is appreciably wider in its lower reaches, much more light must reach the bed. It would be reasonable to suppose that there is, therefore, a greater growth of algae—provided the bed is not disturbed too often. The species concerned also consume a good deal of detritus (Hynes, 1970), and the availability of that material should also increase downstream. An increase in the abundance of mayfly nymphs downstream is hardly surprising.

Table 7. Mean percentage abundance of flatworms compared with mayfly nymphs

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
Flatworms	19	17	11	20	12	13	3	2	1	1	1	1
Mayfly nymphs	2	3	3	6	7	7	9	10	10	14	16	13
ranked:-												
Flatworms	20	19	17	13	12	11	3	2	1	1	1	1
Mayfly nymphs	6	2	3	7	7	3	9	10	10	13	14	16

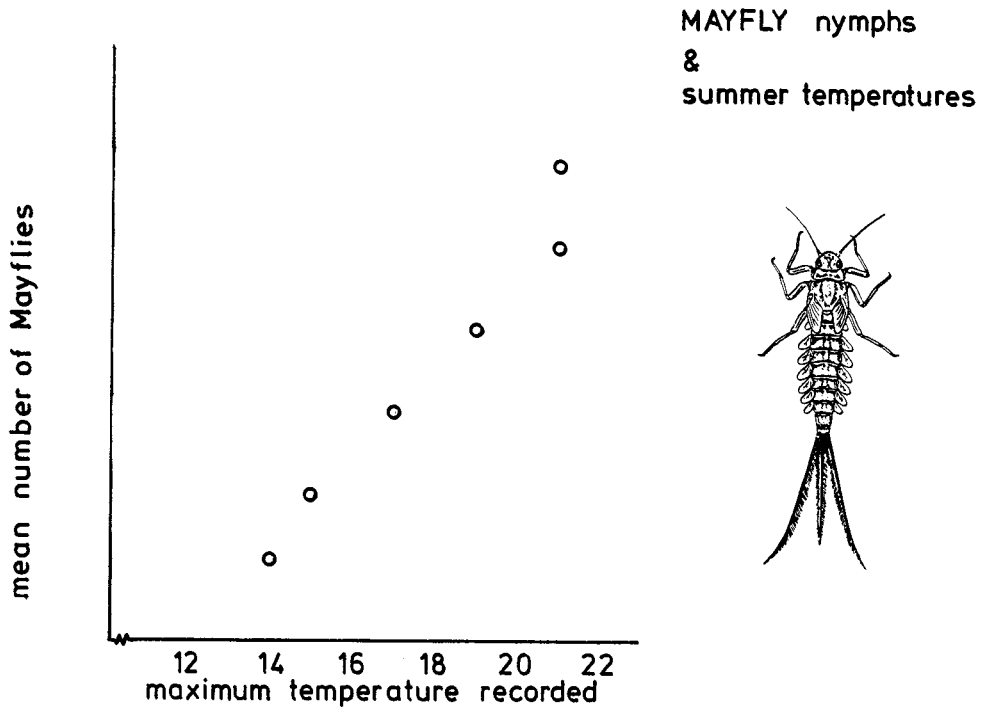


FIG. 8.

Overall mean mayfly nymph counts at the six stations, plotted against the maximum temperatures recorded.

Macan (1963) attributed the decline of Baetidae (swimming mayflies) in a lakeland stream to a rise in the *P. felina* population. These Exmoor data show a similar negative correlation with flatworm abundance (Table 7). Nonetheless, the positive correlation with distance downstream appears stronger than the negative one with flatworms. A third correlation is illustrated in (Fig. 8). Mayfly abundance appears positively linked to maximum recorded temperature. From the present data it is impossible to tell whether this is real or coincidental. Anything that increases in abundance downstream will show a positive correlation with maximum temperature.

On the occasions when flattened nymphs (family Ecdyonuridae) were counted separately from swimming ones (family Baetidae), it was generally found that they appeared in the catches from around station 4 downwards, except in autumn when the very newly-hatched nymphs were sometimes encountered in the headwaters. Flattened mayfly nymphs were either equally abundant in pools and riffles, or commoner in pools. Nymphs of swimming mayflies (Baetidae) were most often caught in riffles. Forty-six per cent of all mayflies were caught in pools.

Stonefly nymphs

From Fig. 4 (and Appendix 4), it is apparent that stonefly nymphs are much more often caught in riffles than in pools, but that there is little change in overall abundance downstream. The stability of these animal's distribution patterns from season to season and from year to year is apparent from Appendix 4. There are, however, changes in species

composition. The large black nymphs of *Dinocras cephalotes* first appear at station 3. This species is approaching the northern limit of its range in the British Isles and, according to Lillehammer (1987), requires a minimum temperature of about 12°C before the eggs can hatch. At this temperature the incubation time is between 70 and 80 days. The best survival rate for hatching is at 20°C, when they hatch in about 35 days. From Table 5 it is apparent that Embercombe Water is probably too cold for this species to reproduce successfully. This may be the reason preventing it, the major invertebrate predator of *Polycelis felina*, from occurring in significant numbers where the flatworm is most abundant.

The disproportionate number (65%) of stonefly nymphs caught in riffles is usually explained as a preference for water super-saturated with oxygen. Certainly nymphs of *D. cephalotes* rapidly commence jerky “pressups” when placed in still water, thereby producing current of water over their gills, situated in the “leg pits”.

Like many of the others presented here, the tables (Appendix 1:4) are chiefly remarkable for the stability of the patterns displayed. These figures are, of course, means of percentages and the raw data do show a wider fluctuation of numbers—thanks largely to the differing number of catchers on different occasions. Fluctuations in total number have thus been lost in the analysis, but the constancy of the proportional distribution pattern within the stream is highlighted.

Blackfly larvae

This is another group of animals for which the differences between pool and riffle are greater (84:16) than changes up and downstream (Figs 3 and 4). The stability of these animal's distribution patterns from season to season and from year to year is apparent from Appendix 5. British species are thought to favour velocities between 80 and 90 cm s⁻¹. Table 3 gives the maximum recorded velocities and (although there is no suggestion that these are the real maxima) it will be noted that none of the pool sections attained these levels. There was no dramatic change in the maximum velocity downstream, which probably accounts for the general evenness in the overall distribution (Fig. 2).

Most of the insects discussed in this paper have one generation each year. Flattened mayflies may spend two years as nymphs and the large black stonefly, *Dinocras cephalotes*, three, but blackflies go to the opposite extreme and some species may complete four generations within a year (Hynes, 1970). Considerable fluctuations in the number of larvae counted on different visits (sometimes only a few days apart) may be expected, according to whether eggs have hatched or larvae pupated.

Water beetles

Very little appears to have been written about the small dytiscid water beetles found in upland streams. All individuals we have examined closely appeared to belong to one species, provisionally identified from Friday (1988) as *Oreodytes sanmarkii*. Unlike the other insect groups considered here, it was the adult beetles that the students caught. Beetle larvae were only taken occasionally in this stream and the pupae are presumed to be terrestrial. *Oreodytes* is one of the genera mentioned by Hynes (1970) as having poor powers of flight, so that distribution within the stream is probably more a matter of swimming ability rather than of flying.

These little water beetles were more often (64:36) caught in pools than in riffles but, apart from the first station (where the pools are very small) they were generally distributed within the stream system (Fig. 2).

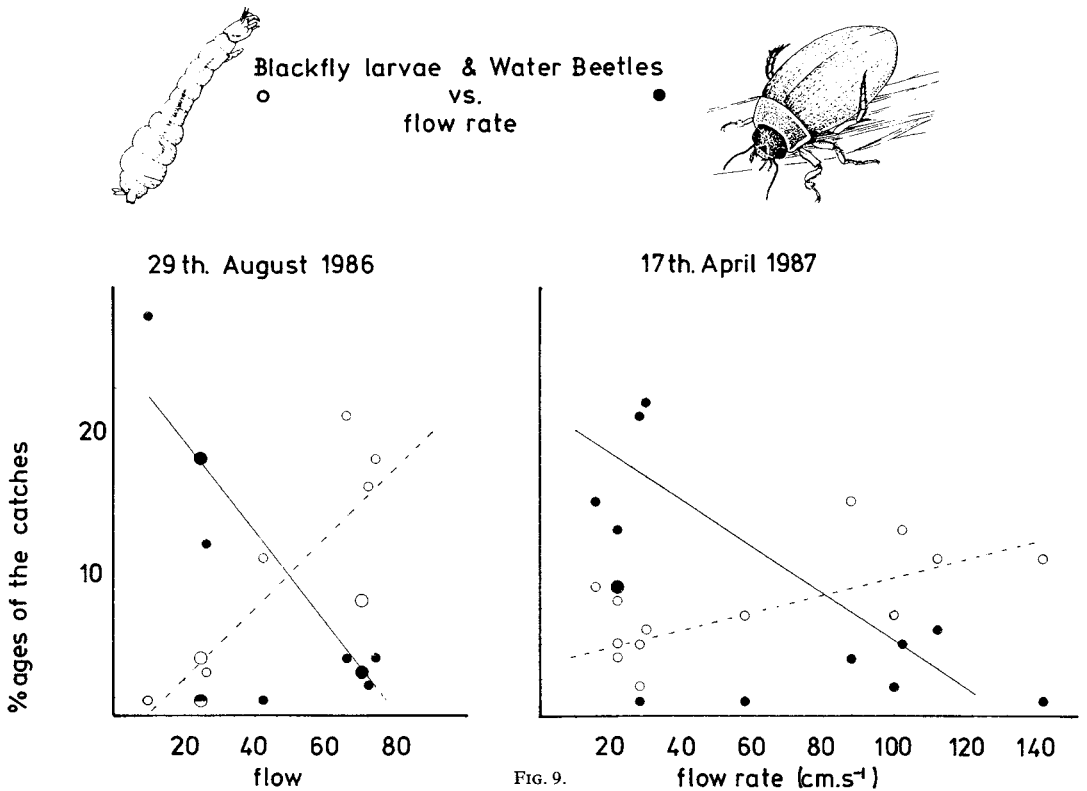


FIG. 9. The relationship between catches of blackfly larvae (open circles) and water beetles (closed circles) with the stream velocities measured on two different days.

We have concluded that blackflies favour riffles and water beetles pools—but the designation of a particular stretch of stream as “pool” or “riffle” is subjective and, especially at station 1, somewhat arbitrary. Most scientists would feel happier working with “real” measurements of current velocity. On any given day, reasonably convincing plots may be obtained (e.g. Fig. 9) showing beetles more often caught in low velocities and blackfly larvae in higher ones. But it is also clear from that Figure that the relationship is far from constant. Attempts to derive an average relationship by combining all the available data are inevitably messy (blackfly Fig. 10). The plot of monthly mean catches against monthly extreme flows (Fig. 11a) is better, but five points “flying” above the rest of the scatter “spoil” the pattern. These dots represent data collected at times when the stream levels (and velocities) were particularly low. The water beetle (Fig. 11b) has no comparable “anomalous” points.

The simple plots of catches in pools versus riffles (Fig. 3) are much more clear-cut. The reason for this is not hard to see. Although blackfly larvae select sites on the basis of water velocities, and have been known to move into local shelter during spates (Zahar, 1951), they are comparatively sedentary animals. Stream velocities fluctuate all the time. Students counting the same individuals in the same place on different days are very likely to record different velocities, but will probably always note the site as being a riffle (or a pool). To survive, all stream animals must tolerate a considerable range of velocities, although certain species favour faster rates than others. For all there are limiting flows, above (and below) which life is not possible. For example, Phillipson (1956) found the

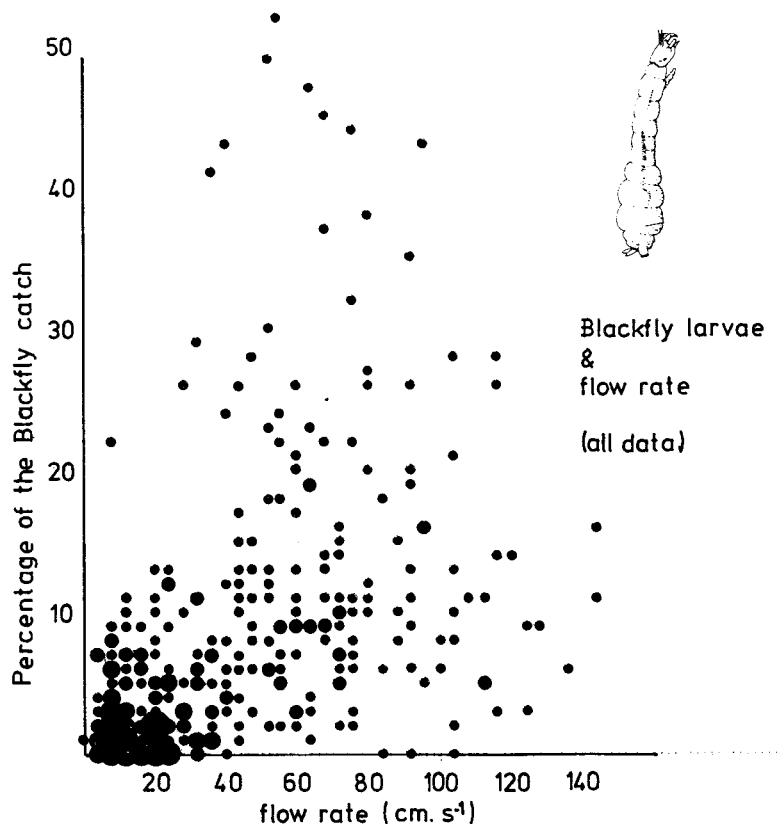


FIG. 10.

Raw data for catches of blackfly larvae plotted against measurements of stream velocity.

larvae of a common British blackfly *Simulium ornatum* within the range of 50 to 120 cm s^{-1} (mostly between 80 and 90 cm s^{-1}).

Only on exceptional days will the flow rates be critical. On all others, the measurements *per se* are of little (or no) significance. In any case, at best, they give only a general indication of the habitat occupied by the animals. Impellers do not measure water movement very close to the stones where the animals are actually living.

Caddis larvae

The data relating to caddis larvae are the least satisfactory of all, and little of substance can be drawn from them. Undoubtedly there are several species present in the stream and, although attempts were made to separate larval counts into cased and caseless forms, it will be necessary to identify these insects more accurately in any future projects. Unfortunately, cased caddis larvae are notoriously difficult to identify (no attempt was made to discriminate between families—let alone species—in the collection of the data presented here). With caseless caddis, identification to family level is comparatively easy (Edington and Hildrew, 1981)—and is an obvious requirement for future monitoring. In the data

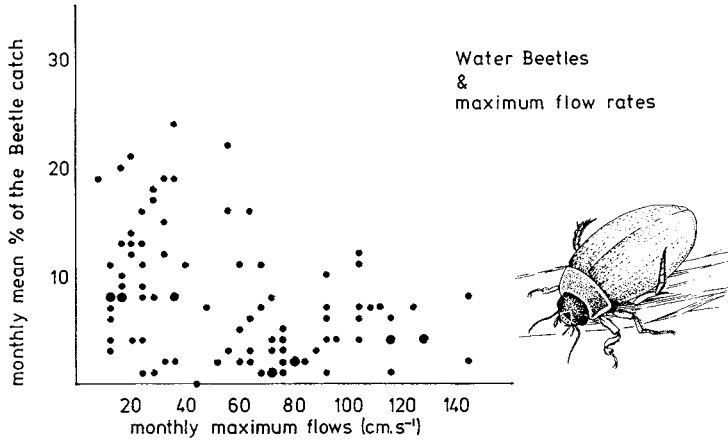
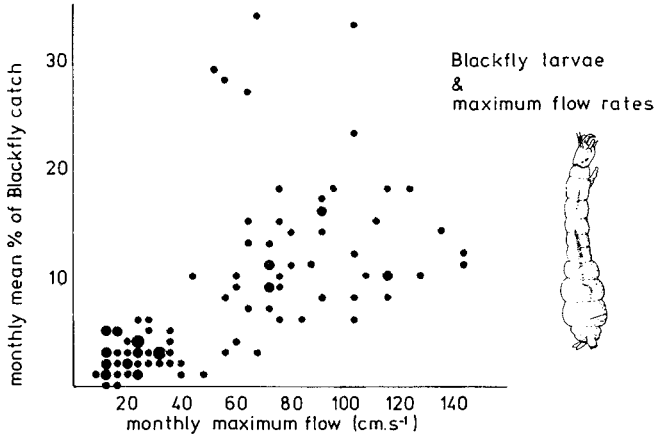


FIG. 11.

Monthly means of (a) blackfly larva counts and (b) water beetles, plotted against monthly maxima of the measured velocities.

contained in this paper, distribution patterns are inevitably confused and the overall pattern—such as it is—may merely reflect the differential abundance of certain species.

Cased Caddis larvae

The main advantage of the case is probably as ballast. An insect in a stony case—and almost all the caddis cases found in this stream are constructed of stones—is less likely to drift far downstream when dislodged. On the other hand, the resistance to water flow produced by the case must increase the likelihood of dislodgement in riffles. Perhaps this is one reason why cased caddis larvae are sometimes taken more often in pools (although the data average out to suggest no real preference for the one habitat over the other).

Cased caddis are eaten (case and all) by fish and, as suggested for freshwater shrimps, their greater frequency in Embercombe Water (where fish are rarely caught) may reflect a predator/prey relationship, although flatworms are also known to attack caddis larvae.

Many students fail to separate larval from pupal caddis cases. These data (Fig. 2, Appendix 5) probably include pupal cases of both cased and caseless caddis (the term “caseless” refers only to the larval stage) as well as the larvae they intended to study. This may have confused the overall distribution as some cased caddis are known to move into more rapidly flowing water before pupating (Hynes, 1970).

Caseless Caddis larvae

Almost all the caseless caddis we have found in this stream belong to the families Philopotamidae or Hydropsychidae. Both spin nets in which they trap drifting material. One would expect, therefore, to find them more frequently in riffles—and this is generally the case (Edington and Hildrew, 1981)—although some members of a third family, the Polycentropodidae, are more common in pools. However, the different species have particular ranges of current velocities within which their nets function.

As already mentioned, interpretation of these data is rendered almost impossible by our failure to distinguish the families in the field. Even so, it will be noted that whilst 68% of the overall catch was taken in riffles, the figures are 50% and 73% from the upper part of Embercombe Water (stations 1 and 2) and lower down, respectively. This suggests a change in species composition.

CONCLUSIONS

Despite the simplicity of the sampling techniques, this analysis has shown that:

1. Student data can give repeatable results that are sufficiently consistent to highlight major patterns of distribution.
2. The patterns so obtained are comparable to those that have been described from other streams and (in most cases) can be interpreted in the light of the known biology of the species involved.
3. There are inherently stable patterns of distribution shown by stream invertebrates that persist for decades, despite floods (as in May 1983) and droughts (as in 1975–76). This contrasts with the concept of the stream community being opportunists, forever recovering from (and exploiting) the latest catastrophe.
4. The data would have been much more useful had identification been taken further in some insect groups. For cased caddis and, to a lesser extent, stoneflies, this would have been difficult through the lack of a suitable key. But there was no excuse regarding caseless caddis. These larvae should be identified, at least down to family level, in future.

ACKNOWLEDGEMENTS

To say that this paper could not have been written without the assistance of many people is somewhat of an understatement. Without the information collected by more than 1600 students, and their accompanying staff, there would have been no data to analyse. I hope they will forgive me for not thanking them individually! The original drive to commence the study came with Malcolm Litterick (the first Assistant Warden at the Leonard Wills Field Centre) from Preston Montford Field Centre. Our initial ideas were smoothed and developed by succeeding "generations" of biology tutors on the Centre staff—Adrian Bayley, Paul Croft, Liz Cole, Mark Wilson, Jonathan Oldham, David Scales, Sally Hayns and Mark Bolland. My thanks to all and to the many visiting staff who by their pertinent comments and awkward questions caused us to think again on numerous occasions; John Barker deserves a special mention in this context. Finally, my thanks to Dr Steve Tilling for his editorial care and to anonymous referees for their suggestions. The errors of presentation and interpretation remain mine.

The line drawings incorporated onto many of the figures were drawn by my wife, Marilyn, for Paul Croft's (1986) key and are reproduced here by permission of the artist.

We are grateful to the National Trust for permission to work in the stream.

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APPENDIX

Appendix 1a

Monthly mean percentage distribution of Freshwater Shrimps caught in pools (P) and riffles (R) at the six stations 1970-1987

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
February	13	4	17	14	17	11	16	0	6	0	1	1
March	10	8	12	7	22	19	6	5	2	2	3	3
April	10	9	9	8	26	22	2	3	1	2	3	3
May	7	11	5	11	22	39	1	2	1	0	1	1
June	15	11	10	9	19	20	4	3	4	1	2	2
July	21	14	8	6	22	21	2	1	1	1	2	0
August	15	13	9	7	21	22	2	6	0	2	1	2
September	11	16	8	10	21	22	2	4	1	2	2	2
October	8	18	12	12	13	22	2	3	1	2	1	1
Overall	12	14	11	13	17	21	2	4	1	1	1	2

Appendix 1b

Annual mean percentage distribution of Freshwater Shrimps caught in pools (P) and riffles (R) at the six stations

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
1970	15	3	12	5	8	19	12	4	5	6	6	4
1971	7	5	12	12	17	15	7	6	4	6	4	7
1972	10	10	12	8	24	19	4	3	3	3	3	1
1973	11	11	16	10	18	13	3	3	7	2	4	1
1974	17	3	10	9	21	19	2	2	9	3	4	2
(1970-74)	12	6	12	9	18	17	6	4	6	4	4	3
1975	3	6	3	3	2	6	2	3	29	11	30	3
1976	10	10	20	10	18	20	2	1	1	2	4	2
1977	21	13	7	4	17	9	1	0	11	8	1	4
1978	13	14	11	18	8	12	6	13	1	0	2	4
1979	23	30	1	3	22	9	4	0	4	0	1	4
(1975-79)	14	15	8	8	13	11	3	3	9	4	8	3
1980	13	9	4	4	26	33	1	3	1	2	3	0
1981	9	11	16	14	12	14	10	4	0	3	3	2
1982	13	7	7	7	34	24	4	0	2	0	1	0
1983	15	15	14	12	20	15	3	3	1	1	2	1
1984	23	22	8	8	12	22	1	2	0	0	1	1
(1980-84)	15	13	10	9	21	22	4	2	1	1	2	1
1985	8	14	8	10	25	29	0	3	0	1	0	0
1986	6	10	6	9	24	31	1	1	1	1	2	1
1987	14	19	10	11	19	20	2	3	1	0	1	1
1988	16	20	8	12	14	18	3	4	0	1	1	2
(1985-88)	11	16	8	10	21	25	1	3	1	1	1	1

Appendix 2a

Monthly mean percentage distribution of Flatworms caught in pools (P) and riffles (R) at the six stations 1970-1987

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
February	28	0	5	15	31	7	10	3	0	0	0	0
March	33	8	21	15	11	3	3	1	1	1	1	1
April	21	17	11	14	10	12	3	3	2	3	3	2
May	29	17	13	17	11	11	0	1	0	0	1	0
June	14	16	13	16	15	17	3	5	0	0	0	0
July	22	25	6	21	6	13	2	2	1	0	1	0
August	17	24	10	27	6	11	1	2	1	1	0	0
September	12	12	22	15	14	3	2	2	2	2	2	0
October	15	15	10	21	9	18	3	3	1	3	1	1
Overall	19	17	11	20	12	13	3	2	1	1	1	1

Appendix 2b

Annual mean percentage distribution of Flatworms caught in pools (P) and riffles (R) at the six stations 1970-1988

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
1970	15	3	12	5	8	19	12	4	5	6	6	4
1971	7	5	11	16	17	18	5	5	3	4	3	6
1972	14	12	18	23	17	11	2	1	0	0	0	0
1973	24	16	15	19	10	11	2	2	0	0	0	0
1974	27	20	11	13	12	9	1	1	1	0	2	0
(1970-74)	17	11	13	15	13	14	4	3	2	2	2	2
1975	11	25	11	17	10	20	2	2	1	0	1	0
1976	8	19	27	17	6	13	2	2	0	0	3	2
1977	12	9	26	9	19	14	5	5	2	0	0	0
1978	5	6	0	81	3	1	1	4	1	1	1	0
1979	21	14	17	29	5	11	1	0	0	0	1	1
(1975-79)	11	15	16	31	9	12	2	3	1	0	1	1
1980	9	30	11	30	5	11	0	2	0	0	0	0
1981	28	19	1	5	11	26	1	7	0	1	0	0
1982	7	13	41	7	9	16	6	2	0	1	0	0
1983	17	30	6	18	6	8	5	4	2	0	3	0
1984	19	15	12	23	9	17	1	1	0	1	1	0
(1980-84)	16	21	14	17	8	16	3	3	0	1	1	0
1985	23	18	2	17	12	14	1	1	2	4	0	1
1986	17	18	12	17	10	13	3	2	1	1	1	1
1987	24	21	9	18	10	12	2	4	0	1	0	0
1988	36	26	6	9	5	8	1	4	2	2	1	1
(1985-88)	25	21	7	15	9	12	2	3	1	2	1	1

Appendix 3a

Monthly mean percentage distribution of Mayfly nymphs caught in pools (P) and riffles (R) at the six stations 1970-1987

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
February	0	0	1	0	11	1	13	4	15	13	36	5
March	0	0	1	1	6	2	10	13	15	18	17	17

Appendix 3a *Contd.*

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
April	2	1	1	1	4	4	10	10	12	22	10	24
May	4	7	0	6	4	4	8	10	11	15	11	18
June	4	5	5	9	9	11	7	10	9	12	9	10
July	5	7	4	8	12	8	8	11	9	11	8	10
August	2	2	4	8	4	9	6	13	8	18	10	16
September	0	1	2	10	5	8	9	14	8	11	18	13
October	1	2	5	7	6	12	8	12	9	16	9	14
Overall	2	3	3	6	7	7	9	10	10	14	16	13

Appendix 4a

Monthly mean percentage distribution of Stonefly nymphs caught in pools (P) and riffles (R) at the six stations 1970–1987

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
February	11	8	12	21	8	10	9	1	8	5	5	3
March	4	9	8	13	7	15	6	8	7	9	5	9
April	4	7	7	16	9	13	5	11	4	12	3	11
May	7	12	4	20	4	13	4	13	3	9	3	8
June	9	7	6	13	5	11	5	13	4	14	4	9
July	4	7	2	10	4	11	7	13	8	13	7	13
August	3	2	3	5	2	11	15	11	16	12	12	8
September	3	5	4	9	3	9	5	12	7	15	5	24
October	3	5	7	16	7	16	4	8	5	12	3	9
Overall	5	7	6	14	5	12	7	10	7	11	5	10

Appendix 4b

Annual mean percentage distribution of Stonefly nymphs caught in pools (P) and riffles (R) at the six stations

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
1970	6	6	6	11	6	12	9	12	7	9	6	10
1971	3	6	5	9	7	13	4	15	5	15	4	15
1972	8	9	8	14	7	11	5	5	6	9	6	12
1973	3	4	4	10	4	15	6	13	8	12	6	15
1974	3	6	6	14	6	12	5	9	7	10	4	18
(1970–74)	5	6	6	12	6	13	6	11	7	11	5	14
1975	4	6	6	15	8	11	5	10	7	12	5	11
1976	6	11	11	17	6	18	4	5	6	8	4	5
1977	7	8	8	13	7	13	6	5	9	11	4	8
1978	17	12	4	13	4	6	6	9	4	17	4	2
1979	20	16	4	4	3	5	5	8	6	16	3	10
(1975–79)	11	11	7	12	6	11	5	7	6	13	4	7
1980	7	9	9	10	4	13	6	9	6	8	11	8
1981	1	8	14	10	3	9	16	13	3	7	5	12
1982	3	8	16	6	15	10	8	4	11	1	9	9
1983	4	5	3	19	3	12	5	14	6	17	4	7
1984	3	10	5	22	5	14	3	12	4	10	3	8
(1980–84)	4	8	9	13	6	12	8	10	6	9	6	9
1985	5	6	9	19	9	13	3	7	3	17	2	8
1986	7	10	5	10	7	11	8	16	5	10	4	8
1987	5	11	5	16	9	14	7	11	5	7	3	8
1988	6	12	7	13	5	13	6	11	7	9	4	6
(1985–88)	6	10	6	15	8	13	6	11	5	11	3	7

Appendix 5a

Monthly mean percentage distribution of cased Caddis larvae caught in pools (P) and riffles (R) at the six stations 1970-1987

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
March	5	4	15	11	23	7	9	6	6	6	5	3
April	11	16	11	14	6	9	3	6	4	7	5	11
May	13	14	10	9	13	9	4	7	3	4	7	6
June	9	8	11	10	17	7	8	5	5	9	4	6
July	9	5	18	9	16	5	9	3	7	7	8	4
August	3	3	14	6	10	8	8	5	6	4	6	27
September	15	14	8	20	9	7	5	2	9	3	6	3
October	9	9	8	13	6	6	8	8	9	8	7	7
Overall	10	11	11	12	13	7	6	6	6	6	6	7

Proportion in pools = 51

Appendix 5b

Annual mean percentage distribution of cased Caddis larvae caught in pools (P) and riffles (R) at the six stations

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
1970	3	5	14	11	1	8	3	8	4	22	3	19
1971	10	10	5	16	9	7	4	9	4	8	5	14
1972	10	7	22	5	7	3	17	0	10	3	13	3
1973	6	1	26	9	21	4	11	3	5	1	9	3
1974	4	4	13	14	17	5	7	4	8	9	9	6
(1970-74)	7	5	16	11	11	5	8	5	6	9	8	9
1975	3	4	15	10	26	11	4	4	3	7	5	8
1976	6	3	14	9	31	6	11	5	6	3	4	2
1977	6	11	17	9	12	6	6	7	10	8	4	4
1978	3	7	5	20	3	11	9	20	2	14	2	5
1979	20	5	7	10	13	2	6	1	12	16	4	5
(1975-79)	8	6	12	12	17	7	7	7	7	10	4	5
1980	2	5	6	8	4	1	4	5	7	5	8	46
1981	9	6	7	4	7	15	27	7	5	3	8	3
1982	12	9	10	6	9	4	16	2	11	6	8	6
1983	9	8	19	10	18	4	9	2	6	5	6	3
1984	11	11	9	10	10	9	5	9	7	9	6	6
(1980-84)	9	8	10	8	10	7	12	5	7	6	7	13
1985	18	19	9	17	8	8	3	4	2	2	4	6
1986	8	18	8	12	10	6	5	7	5	5	5	11
1987	13	10	13	10	10	6	4	8	7	9	5	5
1988	7	10	7	12	9	5	5	8	6	8	9	13
(1985-88)	12	14	9	13	9	6	4	7	5	6	6	9
Overall	8	8	12	11	12	6	8	6	6	8	6	9

Proportion in pools = 52.9%

Appendix 6a

Monthly mean percentage distribution of caseless Caddis larvae caught in pools (P) and riffles (R) at the six stations 1971–1987. Overall percentage in pools = 32%—but 46% at stations 1–3 (Embercombe Water)

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
March	14	5	7	2	7	11	5	9	7	14	7	14
April	8	4	8	9	11	11	4	7	5	11	9	10
May	9	4	6	4	7	8	6	13	5	16	3	18
June	9	11	6	12	4	12	5	9	3	7	7	16
July	14	16	5	15	7	7	4	6	2	9	3	11
August	7	5	2	2	2	29	4	16	2	9	0	23
September	8	14	6	6	6	4	2	10	2	18	10	16
October	9	8	9	10	4	15	4	5	8	13	6	11
Overall	10	8	6	8	6	12	4	9	4	12	6	15

Appendix 6b

Annual mean percentage distribution of caseless Caddis larvae caught in pools (P) and riffles (R) at the six stations

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
1971	9	12	9	5	9	21	9	5	9	0	9	5
1972	8	19	8	5	6	5	3	11	3	16	3	13
1973	9	10	1	6	1	16	1	12	3	15	4	19
1974	2	10	4	14	2	20	4	14	4	12	6	10
(1971–74)	7	13	6	8	5	16	4	11	5	11	6	12
1975	7	12	8	7	4	7	6	6	5	8	14	15
1976	12	5	2	12	5	19	5	7	5	8	9	12
1977	4	1	8	15	3	11	3	9	6	18	6	14
1978	0	7	20	7	7	7	27	7	0	20	0	0
1979	8	22	12	11	3	22	3	3	5	3	0	9
(1975–79)	6	9	10	10	4	13	9	6	4	11	6	10
1980	8	10	8	14	1	5	1	5	11	11	10	16
1981	7	3	2	15	3	5	9	27	1	13	4	11
1982	19	12	10	3	14	10	1	6	4	4	2	15
1983	16	15	7	14	8	8	6	6	6	7	3	6
1984	8	7	7	7	8	8	5	10	7	12	7	14
(1980–84)	12	9	7	11	7	7	4	11	6	9	5	12
1985	8	9	11	10	14	13	3	8	4	7	4	9
1986	15	14	5	12	6	5	3	8	1	14	3	14
1987	11	10	5	7	4	13	6	8	3	11	8	16
1988	9	16	7	11	4	11	3	9	5	11	4	11
(1985–88)	11	12	7	10	7	10	4	8	3	11	5	12

Appendix 7a

Monthly mean percentage distribution of Blackfly larvae (Simuliidae) caught in pools (P) and riffles (R) at the six stations

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
March	5	13	5	6	5	16	3	15	3	18	1	10
April	2	8	2	33	3	15	3	8	3	8	3	11
May	6	10	4	18	5	11	4	10	3	14	4	11
June	3	10	2	9	2	13	4	23	2	17	2	15
July	1	6	1	9	1	7	8	27	1	28	2	9
August	6	10	4	34	0	9	1	13	0	11	1	10
September	29	3	18	1	11	1	16	2	7	2	6	0
October	3	14	4	12	5	10	3	12	2	14	3	18
Overall	3	13	3	17	2	11	4	17	2	15	2	11

Overall percentage in riffles = 84, and pools = 16

Appendix 8a

Monthly mean percentage distribution of Water Beetles caught in pools (P) and riffles (R) at the six stations 1970-1987

	1		2		3		4		5		6	
	P	R	P	R	P	R	P	R	P	R	P	R
February	0	0	0	0	0	0	0	0	0	0	0	0
March	6	6	20	12	8	10	8	2	8	4	8	6
April	2	1	19	6	8	7	16	4	19	4	12	2
May	1	1	11	4	18	2	24	7	15	4	9	3
June	4	2	11	8	13	7	14	7	12	6	13	5
July	3	2	19	5	11	3	17	17	8	3	8	3
August	1	0	4	1	7	1	13	7	57	1	7	1
September	2	10	4	16	4	21	7	17	3	9	2	0
October	2	2	11	11	8	4	22	8	11	4	11	7
Overall	3	3	12	8	10	7	15	9	17	4	9	3

Overall proportion in pools = 64%