A study of recolonisation and downstream drift in Sherburn Beck, County Durham

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A STUDY OF RECOLONISATION AND DOWNSTREAM DRIFT IN SHERBURN BECK, COUNTY DURHAM

- by -

HOWARD LEE

A dissertation in partial fulfilment of the requirements for the Degree of M.Sc. (Advanced Course in Ecology).

1975.

<u>CONTENTS</u>

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Lewis Davies for his helpful criticism of the first draft of this thesis and for his advice on stream sampling techniques. Thanks are also due to Mr. F. Venmore of Workshop Stores for help in the drift net construction and to Mr. Gillchrist, the farmer who allowed me to work on his land.

STUDY AREA

All work was done on Sherburn Beck, along a stretch of about ½ mile, between the villages of Shadforth and Sherburn, about 4 miles east of Durham City (Grid reference: NZ 24/34 335 414). This stream drains an agricultural area and its width varies from 0.5 - 1.25m. with a shallow stone gravel bottom over the ripple areas. (See Plate 1 and Map 1).

INTRODUCTION

The effect of stream current on the activity of stream invertebrates has been an important consideration since 1927 and not before but, a clear idea of this phenomenon in terms of drift has only been discussed in the past thirty years, and only extensively in the past fifteen years. Drift means the passive movement of bottom-living stream animals in the current and clear of the bottom. Percival and Whitehead (1927) were among the first people to consider the effect of current. They studied different types of stream bed and tried to correlate this and other physical factors with the abundance of stream-dwelling animals. Throughout this early paper they refer to all the common species studied in my thesis and conclude that, depending upon morphology, physiology and activity, these species are all affected by current speed and some are carried downstream. They do not, however, consider this movement as a significant factor in the distribution of stream invertebrates. Beak (1938) makes a simple classification of a water meadow carrier stream in terms of physical substrata which range from open stones to those covered in chalk or silt. He mentions that a decrease in numbers of Gammarus pulex in the autumn in such stretches resulted in an increase in numbers in macrophytic vegetation, which he thought was due to a "washing of the larger specimens .... into the shelter of the weeds", but he also did not mention drift. Moon (1940), in his study of the River Avon talks of a diurnal variation in animal movement with more activity at night, but he also does not talk of drift. Dendy (1944) made the first study of "stream organisms which occur in drift in streams not subject to floods", and concludes that the three streams he studied were, "constantly reducing their animal population by washing individuals away in the drift." This is explored more thoroughly by Müller (1954) who made a statement which has since often been quoted as the first which acknowledges the importance of drift. He says: "The travelling benthos (drift) was found during the whole period of the observations and we must regard it as a constant factor of running water ~~found~~." He is also the first to talk of repopulation mechanisms. The next important statement on drift comes from Japan. Tanaka (1960) opened an era of intensive drift research with his paper on diurnal changes in drift. For the first time the previous evidence was linked together and Tanaka concludes from his data that most species show an increase in their rate of drift at night. This important discovery has quickly been followed by a large number of papers during the 1960's. In Britain, Elliott (1965 a,b, 1967 a,b) has researched thoroughly on drift while in America, Waters (1961, 1962. 1964, 1965) has complemented this with a consideration of the relationship between drift and productivity, as has also Horton (1961) in this country. In his 1965 paper, Waters makes the first important references to excessive upstream production as a possible cause of drift, with little upstream movement. Hynes (1970) gives an excellent survey of this literature and discusses all aspects of drift.

This thesis describes results of a study of recolonisation of stones in a stream, the method being basically to remove (and keep for identification and counting) all macro-animals from marked stones and to repeat the process to get the recolonising forms at varying intervals (1-6 days) to study rate of recolonisation. A brief study was also made of the actual drift of these same bottom-dwelling stream animals to throw light on part of the mechanism responsible for recolonisation of any extensive unoccupied space. In the light of results obtained, further studies were made on recolonisation of stones by the

Ephemeropteran larva <u>Baetis rhodani</u> and the fresh-water shrimp <u>Gammarus pulex</u> and of the numbers of both species per unit area of stream bed in differing areas of the stream.

ALL-SPECIES RECOLONISATION EXPERIMENT (Map 1)
(first experiment)

Method

This was an experiment to study the rate of recolonisation of stones by all the macroscopic species present sampled over varying time intervals.

Twenty stones were selected in a length of stream of about 80 ft. (see plate 1). Ten stones were from an area of moderate current flow and 10 from a notably faster flowing area. Such faster flow areas were mainly in ripples where the width of the stream was narrow enough to provide a depth which would cover medium-sized stones (stones of about fist-size were selected for convenience of handling). The maximum length, breadth and width of each stone was recorded as well as characters such as stone surface (rough or smooth). Each stone was measured for speed of water flow over it with a Pitot tube (Beak, 1938) held near the stone surface in at least four positions. This gave a range of readings giving a general idea of flow speed in cm./sec. by the use of a calibration curve. The stone was then smartly lifted and all animals removed using a wash-bottle into a glass jar. Care was taken to avoid loss by holding the stone over the jar while the wash bottle was used, until every animal had been removed. A small area of its surface was dried with tissue and numbered with white cellulose "dope" paint. When the paint was dry the stone was replaced in as near its original position as possible. All animals removed were taken back to the laboratory, identified, and the numbers counted. All specimens were initially kept in a fridge and then preserved in 70% alcohol.

Other physical measurements which were taken during each sampling period were depth of water in centimetres on a well-fixed marker stone, and water temperature (°C) before and after the sample period, with the

THE SAMPLE AREA. MAP 1

SHERBURN BECK

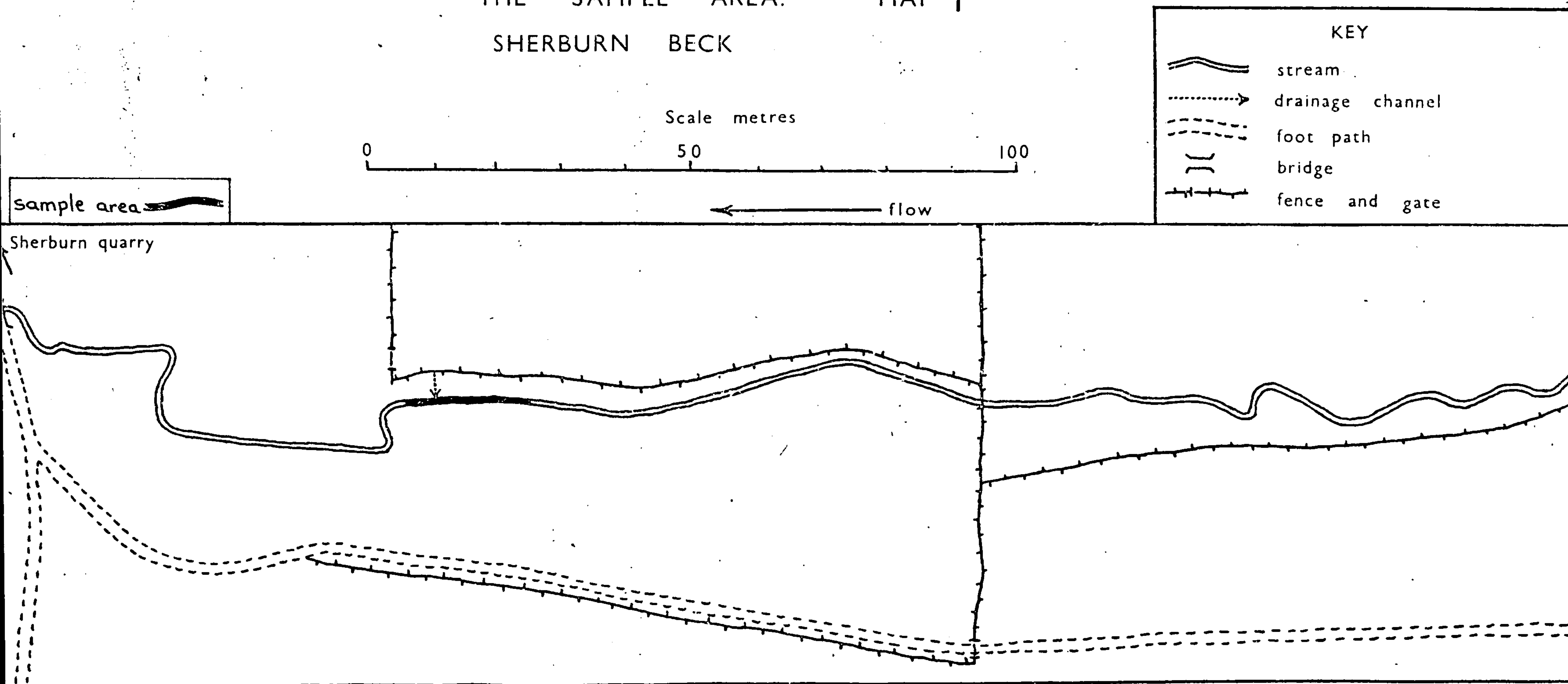


Plate 1. First stone recolonisation expt. The sample area.

time noted.

All 20 stones were then re-sampled as described above after varying periods of time ranging from 1-6 days. A sketch map of the sample area was made with the position of each stone noted and though some stones lost nearly all their paint, it was soon possible to recognise them visually.

The statistical procedure was as follows:

(1) Student's T-tests were used to test for any difference between mean values. When tests are referred to in the text, a Significant difference means that the value P was < 0.05 and a Non Significant difference means that the value P was > 0.05.

(2) In results tables all t-values which are not significant are omitted and only those that are significant are included.

Results

The average flow speeds over the 10 stones for the medium-flow regime and the 10 for the fast-flow regime have been plotted for each sample taken (graph 13). Flow depth (graph 13) and water temperature (graph 14) have also been plotted, and all results are on Table 12. To make the temperature readings comparable, only those taken near to 1200 hours are plotted on graph 14 so that any seasonal trend may be noticed. The temperature readings used are marked * on table 12. Depth readings, as they were all taken from the same stone which was firmly embedded, are comparable. The stone dimension measurement results (Table 13) indicate that there is a Statistically Significant difference between stone length measurements for medium and fast flow regimes but stone width and depth are not statistically different. There is unlikely, therefore, to be an overall Significant difference in stone surface area exposed to stream found as these measurements were maximum readings only and most stones were non-uniform in general shape.

When the actual results for fauna are considered (tables 1 to 8 and graphs 1 to 8), the most abundant species present are seen to be the Crustacean Gammarus pulex; the Gastropods Hydrobid jenkinsi and Limnaea truncatula; the Trichopteran Agapetus fuscipes; the Ephemeropteran Baetis rhodani; and larval Chironomidae. All of these have been plotted on graphs with Standard Errors for each mean.

As explained in Methods (page 6) half the stones were from a medium flow regime and half from a fast flow regime. Thus, for each species there are two sets of results. Each of the above 6 species will now be discussed separately. Each reading from medium and fast flow regimes was compared using T-tests, as were any variations within each regime with time that looked biologically meaningful. The Null Hypothesis here is that numbers of organisms are distributed equally between the two sampled flow regimes and that numbers of organisms present are not affected by the length of the sampling interval or by any other factors.

Gammarus pulex. (Table 1, Graph 1)

This crustacean shows almost no evidence of a correlation between sampling interval and number collected from stones. A "U" shaped plot for the histogram would be expected if this were so and this is clearly not the case here (Graph 1). Although the fast flow regime indicates a slight decrease and increase before and after the day sampling interval, this is not statistically significant. Therefore the Null Hypothesis is upheld. The only significant differences between medium and fast flow regimes are on 19.5.75. and on 26.5.75. These show that significantly larger numbers of Gammarus pulex were found recolonising stones in the medium flow areas in Sherburn beck. This is hardly surprising, for

TABLE 1

ALL-SPECIES RECOLONISATION EXPERIMENT, GAMMARUS PULEX

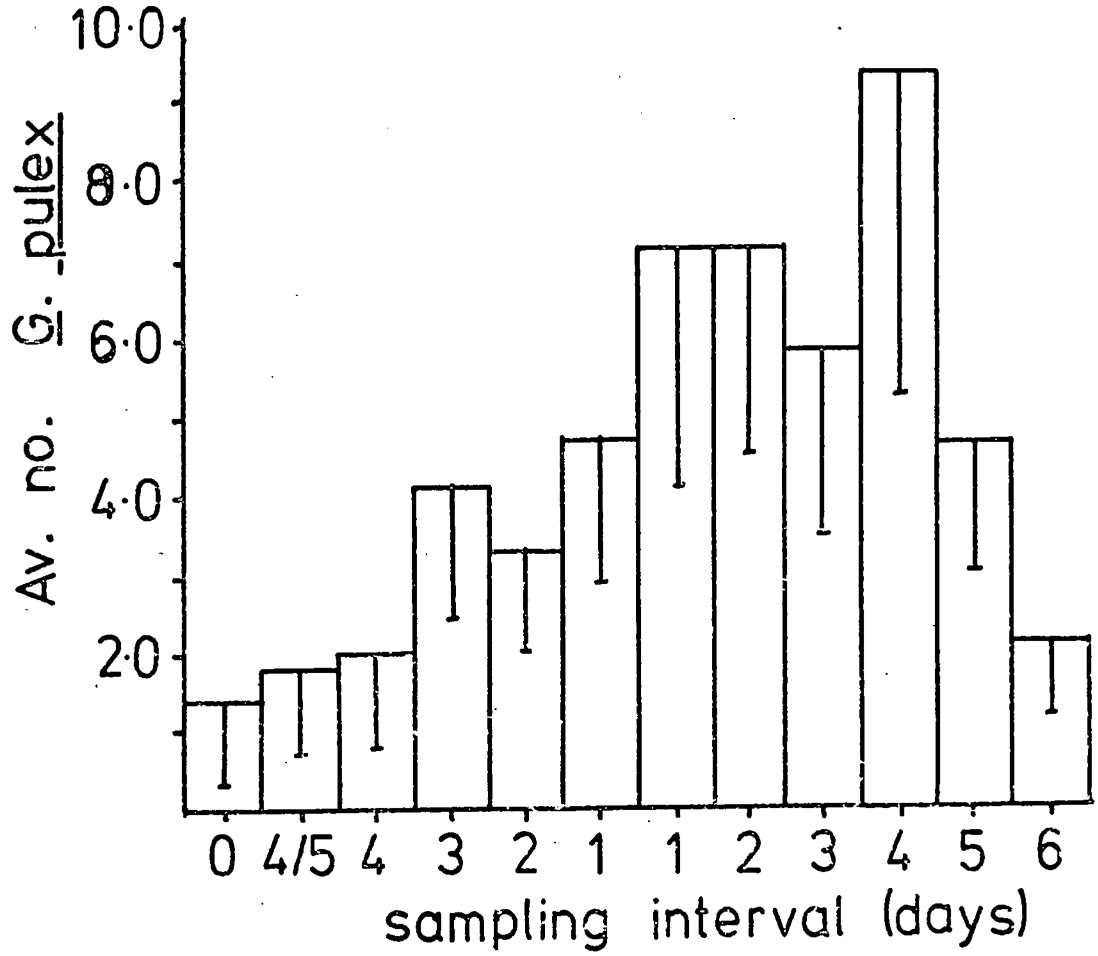
(first experiment)

		May											June
Date		2	6	10	13	15	16	17	19	22	26	31	6
Sampling intervals (days)		0	4 or 5	4	3	2	1	1	2	3	4	5	6
	Stone No.												
Medium Flow	1	1							2	1	16		
	2	10	2					1	2	1	6	disappeared	
	3	1			1	1	18		1	2	1		
	7		5	1	13	10	6	14	14	13	3	8	6
	8		1	9	6	6	5	22	23	19	24	13	4
	9			7	12	9	8	23	7	12		7	5
	10		9		1	1	3	11	stone disappeared				
	11	1				3				2	2		1
	12				6		5		3	2	32	7	1
	13			2	1	2	1		12			2	
Total		13	17	19	40	32	46	71	64	52	84	37	17
Average		1.3	1.7	1.9	4.0	3.2	4.6	7.1	7.1	5.8	9.3	4.6	2.1
S.E.		1.0	1.0	1.1	1.6	1.2	1.7	3.0	2.6	2.3	4.0	1.7	0.9
Fast Flow	4								2	1	2		4
	5					1	1			2		13	2
	6	5			1				1			5	
	14	4				1	1	1	3	1	9	5	
	15												2
	16		4	6							5	2	2
	17		2	2			1						
	18	1							1				
	19	1		3		11			2		4		1
	20	7		2		2					1	4	1
Total		18	6	13	1	15	3	1	9	4	21	29	12
Average		1.8	0.6	1.3	0.1	1.5	0.3	0.1	0.9	0.4	2.1	2.9	1.2
S.E.		0.8	0.4	0.6	0.1	1.1	0.2	0.1	0.4	0.2	1.0	1.3	0.4
t.									2.39		2.77		

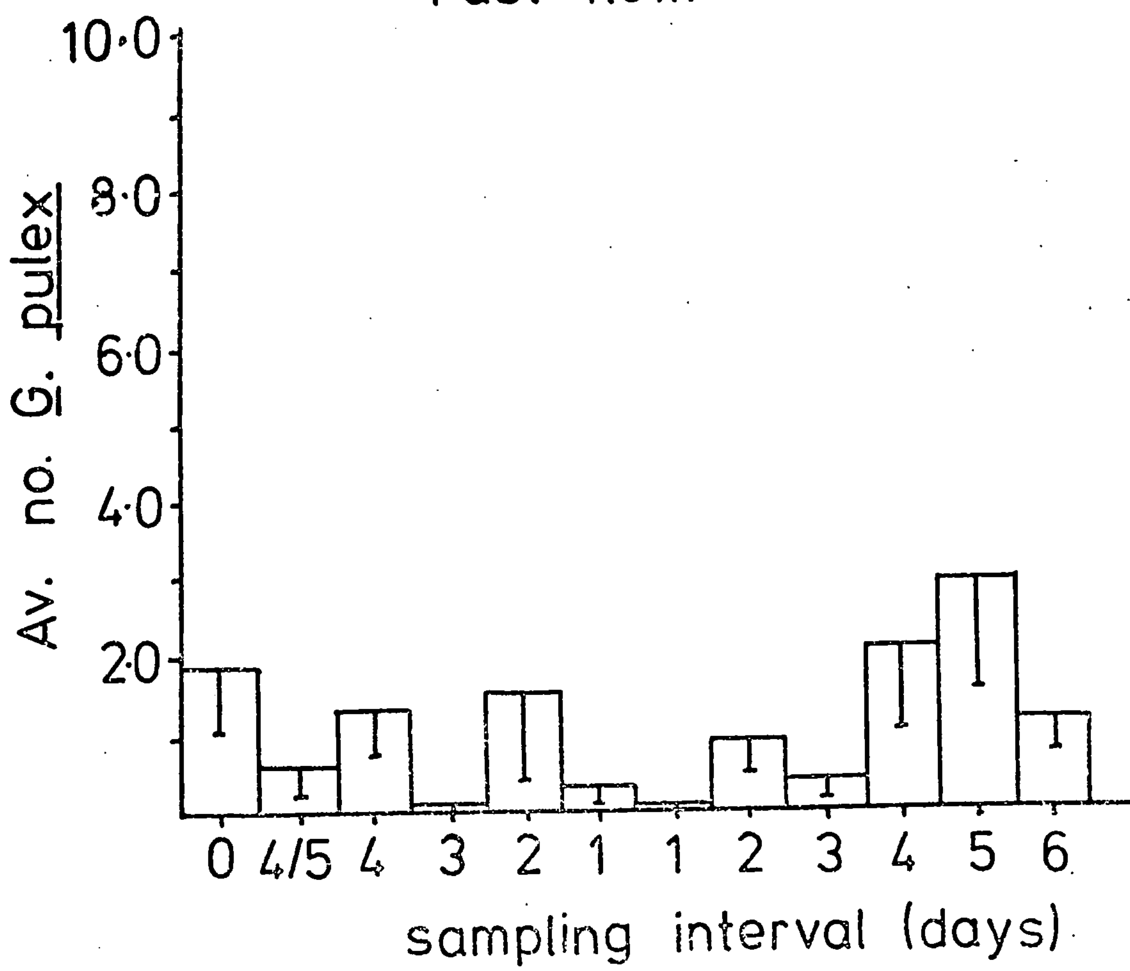
First stone recolonisation expt. RESULTS

Gammarus pulex. Graph 1

Medium flow.



Fast flow.



several reasons. G. pulex is very active in most streams and moves about on the stream bed by scuttling from rock to rock. It is, however, a poor swimmer (Hynes, 1954, 1970). This method of movement means that a swift current is liable to sweep them downstream as drift until they reach areas of slower flow where they can retreat from the current beneath stones. Consequently, an accumulation of G. pulex is likely in the medium flow areas, some of which will immediately colonise the experimental stones. Other colonisers can be expected from the resident population which can easily move onto the experimental stones from surrounding stones. The other important factor here is food supply. G. pulex is a scavenger and detritus feeder (Minckley, 1963) and will therefore tend to be found most in areas where such detritus accumulates, and it is only in the medium flow areas that larger amounts of detritus get a chance to settle. The constant clearing of the fauna off stones will obviously remove detritus from under and on stones so G. pulex individuals drifting in the water are unlikely to be attracted. However, detritus will almost certainly allow large populations to be supported in medium flow areas which will increase the chance of recolonisation from neighbouring stones.

The other interesting change here is within the populations inhabiting the medium-flow regime. A steady increase in numbers caught over the sample period can be noticed, irrespective of the sample period. This is statistically significant and after 26.5.75. shows a significant decrease. The steady increase in numbers caught in medium flow areas is probably due to the development of the next generation. During this period, increasing numbers of juvenile G. pulex individuals were collected. The decrease in numbers is more difficult to explain. The two alternatives seem to be some sort of change in the physical conditions or some change within the G. pulex population due to innate characteristics. The former alternative is unlikely, because all physical measurement and weather observations indicate constant conditions. The latter is therefore the more likely explanation. The most noticeable innate characteristic liable to affect the number of G.pulex individuals caught is the patchy distribution. If the original results are consulted (Table 1) it will be seen that the stones with the largest numbers of G.pulex within the medium flow regime were stone numbers 7, 8 and 9. These were in quite a small area of the stream bed and seemed to contain a pocket of high numbers of G.pulex. Such concentrations of numbers in detritus-rich areas are mentioned by Beak (1938) and Minckley (1963). It is from such pockets that the decrease in numbers after 26.5.75. is most marked and is probably due to removal of the food supply by continual disturbabce due to sampling or possibly because of exhaustion of the food supply by the large numbers of G.pulex individuals present.

The decrease in numbers for the medium flow regime around 22.5.75. was not significant.

Limnaea truncatula (Table 2, Graph 2)

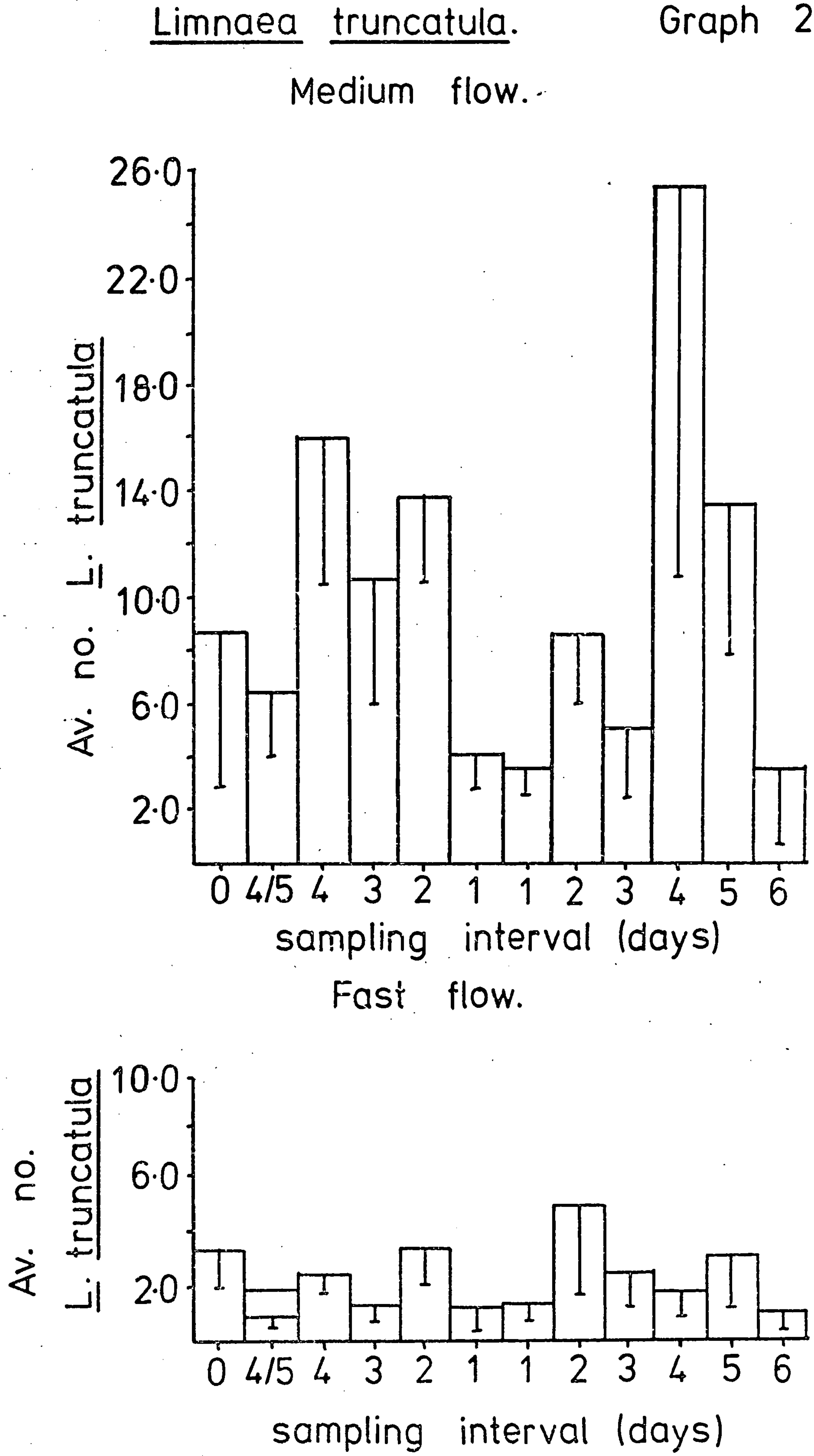
This species shows indications of a correlation between number caught and sampling interval, especially for the medium flow regime. There is a Significant decrease and increase before and after the one day sample intervals. The Null Hypothesis here can therefore be rejected. Rearranging the data, we can obtain averages of readings for each sampling time interval. These values (Table 11 and Graph 10) indicate that such a relationship may be true, but the variation is too large to give a reliable line. The original data shows, however, that the rate of recolonisation by Limnaea truncatula definitely decreases when sampling intervals are less than two days.

Within the medium flow regime there are noticeable increases on

TABLE 2

ALL-SPECIES RECOLONISATION EXPERIMENT, LIMNAEA TRUNCATULA (first experiment)

Date		2 May	6	10	13	15	16	17	19	22	26	31	June 6
Sampling intervals (days)		0	4 or 5	4	3	2	1	1	2	3	4	5	6
	Stone No.												
Medium Flow	1	1	4	7	14	10	4	3	9	2	9	1	3
	2				2						3	disappeared	
	3		1	3		4	3				16	2	2
	7	3	1	16		10	3	8	23	20	131	38	23
	8		1	12	6	10	1	6	4	14	53	18	
	9	2	3	16	1	15	10	4	8	8	15	39	
	10	2	13		4	10	1	2	stone disappeared				
	11		7	13	15	31	5	4	6	1		2	
	12	56	24	50	51	19	11	8	9		2	4	1
	13	23	10	43	14	29	3	2	18	1		4	
Total		87	64	160	107	138	41	37	77	46	229	108	29
Average		8.7	6.4	16.0	10.7	13.8	4.1	3.7	8.6	5.1	25.4	13.5	3.6
S.E.		5.7	2.4	5.5	4.9	3.2	1.2	0.9	2.6	2.5	14.3	5.8	2.8
Fast Flow	4			1						1			
	5		3	1	1				1	1	2		
	6	1	1			1			1			1	5
	14		1	6	1	10	2	3	1		5	3	
	15	5	1	8	3	3						7	
	16			4	1							2	
	17	3	1	3	6	9	4	3	28	3	3		
	18	10	1				1	1		3			
	19	11		1		7		4		6	5		5
	20	4		2	2	5	6	3	18	12	4	19	1
Total		34	8	26	14	35	13	14	50	26	19	32	11
Average		3.4	0.8	2.6	1.4	3.5	1.3	1.4	5.0	2.6	1.9	3.2	1.1
S.E.		1.3	0.3	0.9	0.6	1.3	0.7	0.5	3.1	1.2	0.7	1.9	0.7
t.			2.08	3.95	2.25	27.38	2.59	2.78	2.29		2.39	3.49	


Limnaea truncatula.
Medium flow.
Av. no. L. truncatula
26·0
22·0
18·0
14·0
10·0
6·0
2·0
0 4/5 4 3 2 1 1 2 3 4 5 6
sampling interval (days)
Fast flow.
Av. no. L. truncatula
10·0
6·0
2·0
0 4/5 4 3 2 1 1 2 3 4 5 6
sampling interval (days)

10.5.75. and 15.5.75. of numbers collected from the sample stones. The increase in numbers before 10.5.75. is Significant. Comparing these results with the physical measurement results (Graph 13) it is noticeable that there are corresponding increases in flow depth and speed during these periods. The other most noticeable variation within the medium flow regime is the sudden decrease and increase in numbers collected around 22.5.75. These changes were Significant. Comparing this with the physical measurement results (Graphs 13 and 14) the most noticeable changes at this time were slight decreases in flow depth and speed and water temperature. The increase in rate of recolonisation coincides with a slight increase in flow speed. It could well be that flow speed, therefore, is the most important factor affecting drift in L. truncatula, although rate of recolonisation cannot be directly related to drift for this species (see below). Most full-grown individuals can be expected to have a maximum current which they can withstand. A current faster than this would cause a sudden release of contact for many individuals and so contribute towards a rapid increase in the rate of recolonisation. The subsequent decrease in numbers after 26.5.75. is Significant and again seems to be related to a steady decrease in flow speed during this period. A slower flow speed would reduce the number of individuals drifting and therefore reduce, to a certain extent, the rate of recolonisation.

T-tests between the two flow regimes show that nearly all values are Significantly different and that more individuals are taken from stones in medium flow areas. The Null Hypothesis can therefore be rejected. The higher numbers recolonising stones in the medium flow regime cannot be directly related to rate of drift, however. This is because of several subsequent experiments which suggest that there is a Significant proportion of Gastropod individuals (for Limnaea truncatula and *Hydrobia jenkinsi*) colonising stones by movement from neighbouring stones (Table 16 and Graph 16) and that even when neighbouring stones are not deliberately nearby as in the drift net studies using stones for comparison (Graphs 18, 19 and 20) there are far more individuals moving onto cleared stones than can be accounted for in the drift. Although, therefore, there is probably no direct relationship here between rate of recolonisation and drift, an indirect relationship seems quite definite. Large numbers of Gastopods can only recolonise stones in medium flow areas if there is a large population living there and it is quite likely to be so because of less drift from this area due to slower flow rates. This is supported by the physical measurement results as discussed above. The build up of numbers in medium flow areas is probably a gradual process taking at least 4 or 5 days. It seems to be irregular and could therefore take a lot longer, but nevertheless is quite distinct.

Hydrobia jenkinsi (Table 3, Graph 3)

The main interesting fluctuations which can be seen when Graph 3 is consulted occur before, during and after the shortest sampling period for the medium flow regime. A Significant decrease and increase during the one day sampling intervals indicates that this Gastropod species has a rather slow rate of recolonisation. However, the number recorded on the graph is subject to so much fluctuation that no steady relationship between sampling interval and number recorded exists. The average numbers for each sample period have been determined (Table 11) but were not plotted. The increase in numbers of individuals collected from stones increases for 10.5.75. and 15.5.75. for the medium flow regime. The increase before and decrease after 10.5.75. are both statistically Significant while the increase before 15.5.75. is

Table 3

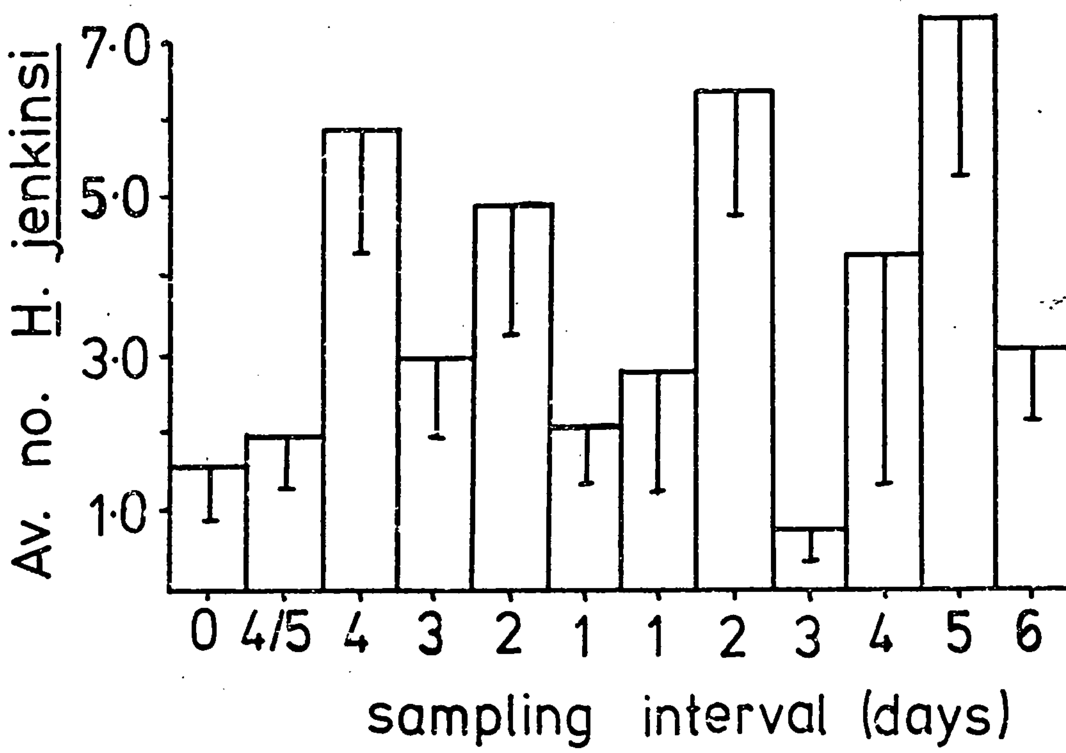
TABLE 3

ALL-SPECIES RECOLONISATION EXPERIMENT, HYDROBIA JENKINSI (first experiment)

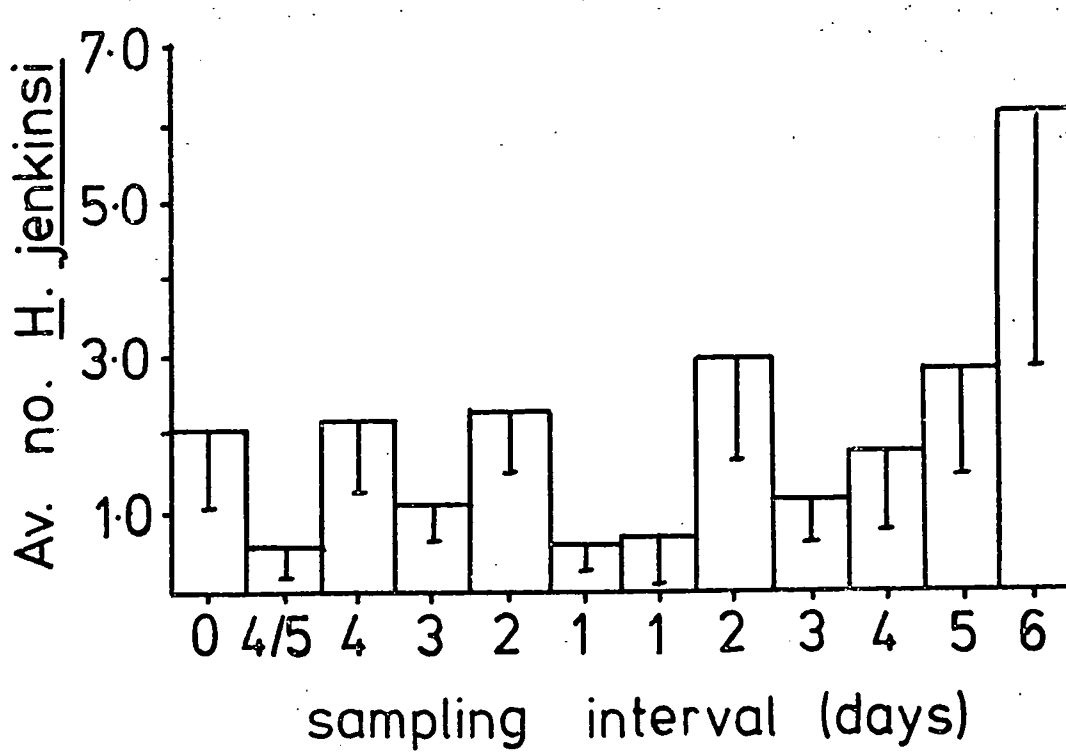
Date		May 2	6	10	13	15	16	17	19	22	26	31	June 6
Sampling intervals (days)		0	4 or 5	4	3	2	1	1	2	3	4	5	6
	Stone No.												
	1			6	6	5	1	1	7		5	8	7
	2		2		1		2	1	1	1		disappeared	
	3		1	2		2			2			2	1
Medium Flow	7	1		5			2	4	9	4	27	12	6
	8		1	2	1	1	2	1	2			8	
	9	1	5	6		1	1	1	2	1	4	16	5
	10		4	2	3	8			stone disappeared				
	11	6		8	5	14	2	5	10			2	3
	12	4	6	14	10	12	8	15	13	1	3	10	2
	13	4	1	14	4	6	3		12				1
Total		16	20	59	30	49	21	28	58	7	39	58	25
Average		1.6	2.0	5.9	3.0	4.9	2.1	2.8	6.4	0.8	4.3	7.3	3.1
S.E.		0.7	0.7	1.6	1.0	1.6	0.7	1.5	1.6	0.4	2.9	2.0	0.9
	4			1					2	3	10	5	
	5							1	5				2
	6	1	4	1	2	3	1		2		3		9
	14	9	1	8	2	4	2				3	3	2
Fast Flow	15			6	2	2						9	11
	16								1	1			
	17	2		3		4			9				1
	18									1			
	19	7	1	1	2	2				5			34
	20	2		2	3	8	3	6	11	2	2	12	3
Total		21	6	22	11	23	6	7	30	12	18	29	62
Average		2.1	0.6	2.2	1.1	2.3	0.6	0.7	3.0	1.2	1.8	2.9	6.2
S.E.		1.0	0.4	0.9	0.4	0.8	0.3	0.6	1.3	0.5	1.0	1.4	3.3
t.				3.34		2.32			3.38			3.68	

Hydrobia jenkinsi. Graph 3

Medium flow.



Fast flow.



Non Significant. The increase in numbers at 10.5.75. corresponds with an increase in flow depth and speed (see Graph 13), as for Limnaea truncatula. The decreases and increases in numbers caught from stones in both flow regimes towards the end of the sample period are also Significant for medium flow. Such a sudden decrease in rate of recolonisation (and partly, therefore, of drift) is difficult to relate to any physical factors. The most likely are flow depth and speed which were showing a steady decrease during this period. Earlier in the sampling around 6.5.75. rather small flow depth and speed figures also coincided with a slow rate of recolonisation. It seems likely, therefore, that Hydrobia jenkinsi is a species whose rate of recolonisation is affected by flow depth and speed. The decrease in numbers after 31.5.75. is also statistically Significant and may also be linked to flow speed which was decreasing at the time. It seems also that H. jenkinsi is a species which recolonises stones by short distance movement within a population rather than drift (see Limnaea truncatula results discussion where both species are considered together).

When differences between the two flow regimes are considered it is noticeable how similar the two graphs are. The most statistically Significant differences are between points on the two graphs which are still following the same basic pattern. These Significant results indicate that more individuals are caught from medium flow areas and the Null Hypothesis here can therefore be rejected. The experiment involving neighbouring stones considered Hydrobia jenkinsi and Limnaea truncatula together (since counting was done in the field and the species can only be separated in the laboratory) and recolonisation for H. jenkinsi is also mainly from neighbouring stones. The drift net results (Graphs 17 and 18) and stone comparison results (Graphs 19 and 20) also indicate that actual drift during 24 hours is a very small proportion of the total numbers moving to recolonise stones. Once again, however, an indirect relationship between number found in a flow regime and drift rate is probable, possibly over a long time period.

Agapetus fuscipes (Table 4, Graph 4)

The most noticeable fluctuation in numbers when Graph 4 is studied is that there is a definite and significant decrease and increase before and after the shorter sampling intervals (medium and fast flow). The Null Hypothesis can therefore be rejected. Furthermore, the fluctuation is not erratic but gradual. When averages are obtained for varying sampling intervals (Table 10) and plotted (Graph 10) an initial drop in numbers is seen as the resident population is reduced and then there is a steady increase in numbers until a maximum point after four days when the numbers decrease again. The decrease in numbers is almost certainly due to a life cycle change, as, during this period, the species was undergoing pupation. This decreases mobility because Agapetus fuscipes secures its stone case to the rock with silken thread before pupating and is therefore unable to continue to recolonise stones. When both flow regimes are separately plotted as log. numbers (Graph 12) an approximate straight line relationship is seen for part of the curve (i.e. 1 to about 4 days). This indicates that, during the early stages of recolonisation (1-4 days), A.fuscipes recolonises at approximately an exponential rate. Unfortunately, the levelling off of numbers which might be expected is not shown here due to life cycle developments (which caused a fall) but it seems fairly clear that full recolonisation would have been completed within a week.

The other noticeable change in numbers occurs at about 22.5.75. where a decrease and then an increase in numbers is seen. The decrease in numbers for the medium flow regime is Non Significant but the increase is Significant while both are Significant for the fast flow regime. As

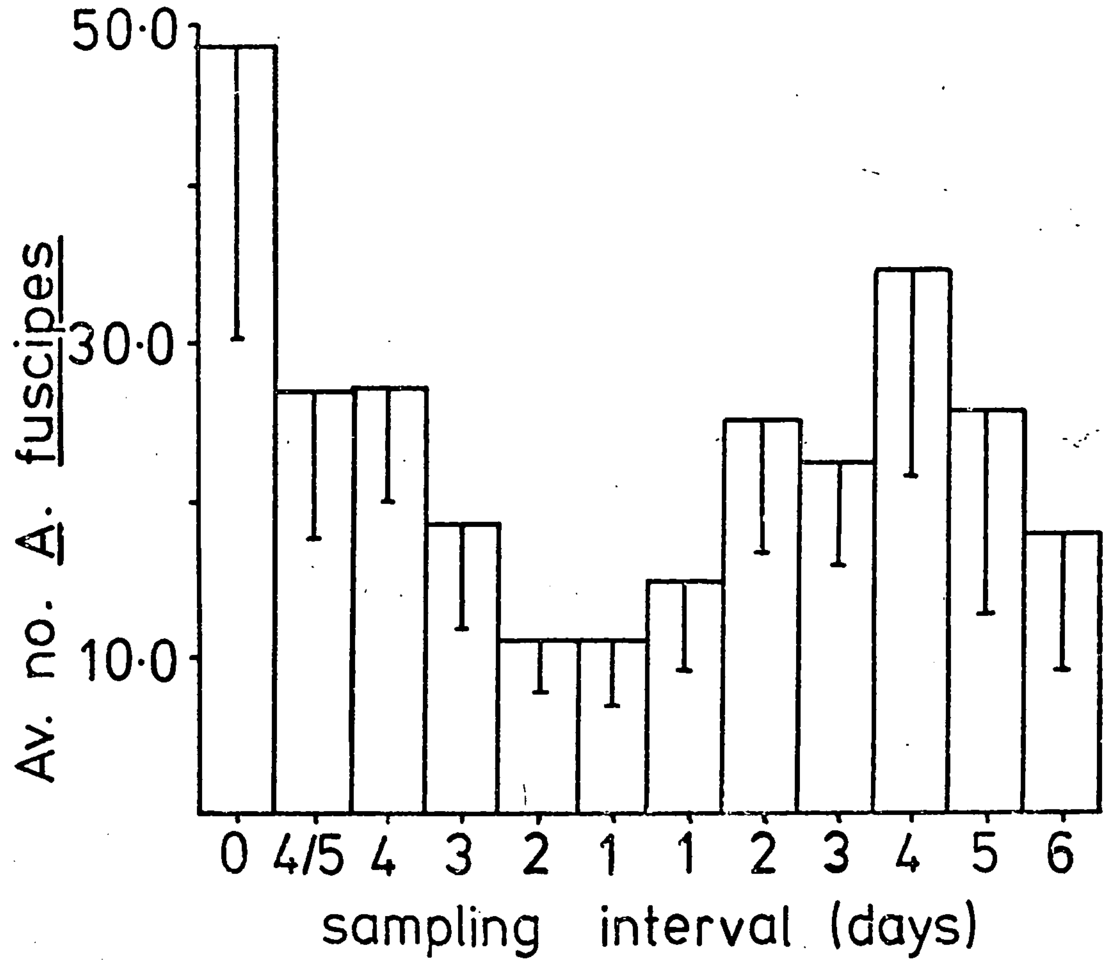
TABLE 4

ALL-SPECIES RECOLONISATION EXPERIMENT, AGAPETUS FUSCIPES (first experiment)

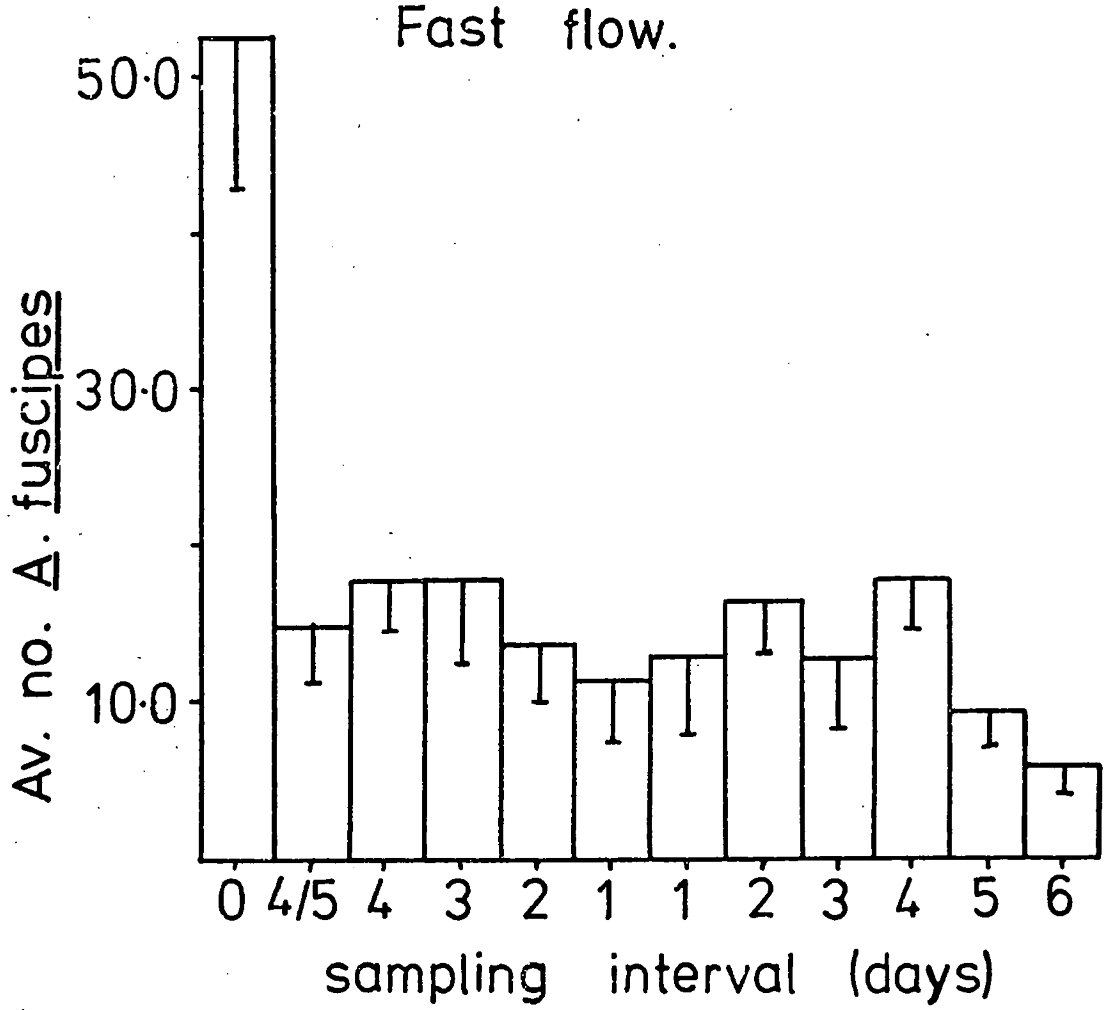
Date		May 2	6	10	13	15	16	17	19	22	26	31	June 6
Sampling intervals (days)		0	4 or 5	4	3	2	1	1	2	3	4	5	6
	Stone No.												
Medium Flow	1	11	6	8	8	4	8	8	19	20	24	15	3
	2	170	67	20	8	9	4	8	8	31	32	disappeared	
	3	39	7	15	14	4	3	3	11	5	3	3	3
	7	134	81	72	42	32	1	53	73	61	114	106	65
	8	46	21	45	34	17	7	7	19	15	67	26	26
	9	1	37	64	57	22	37	44	63	44	58	44	36
	10	28	34	18	8	9	5	4		stone	disappeared		
	11	32	9	9	7	3	3	6	13	8	3	2	5
	12	21		8	3	6	5	11	17	10	5	9	2
	13	5	5	10		3	6	3	2	5	3	1	3
Total		487	267	269	181	109	109	147	225	199	309	206	142
Average		48.7	26.7	26.9	18.1	10.9	10.9	14.7	25.0	22.1	34.3	25.8	17.8
SE.		18.0	6.9	7.7	6.1	3.1	3.9	5.7	8.4	6.5	12.9	12.6	8.1
Fast Flow	4	48	19	25	44	23	21	32	36	21	13	19	7
	5	6	2	6	4	5	3	11	10	6	1	3	4
	6	52	5	24	17	18	22	11	13	7	9	2	9
	14	60	15	29	21	19	37	44	20	11	25	15	14
	15	17	3	2	4	2			1	12	19	7	6
	16	22	14	18	11	6	2	6	6	1	10	2	3
	17	73	18	10	12	1	5	3	12	1	17	22	1
	18	75	27	21	9	7	1	1	24	11	31	7	5
	19	94	38	20	12	33	13	13	26	47	27	4	4
	20	79	8	24	44	22	10	6	14	10	24	11	3
Total		526	149	179	178	136	114	127	162	127	176	92	56
Average		52.6	14.9	17.9	17.8	13.6	11.4	12.7	16.2	12.7	17.6	9.2	5.6
S.E.		9.3	3.6	2.8	4.7	3.4	3.8	4.5	3.3	4.2	3.0	2.3	1.2
t.			4.92	4.74		2.03			4.21	[illegible].76	5.66	4.42	3.94

Agapetus fuscipes. Graph 4

Medium flow.



Fast flow.



for Hydrobia jenkinsi and Limnaea truncatula, such decreases and increases in numbers seem to coincide with similar changes in flow speed for medium and fast flow regimes (see Graph 13). When considering the biology of Agapetus fuscipes such a tendency is quite logical. An insect larva with a cumbersome stone case and six legs with which to cling to rocks is also likely to show a maximum current speed which it can resist, as for both Gastropod species. It seems that the decrease in current speed after 19.5.75. allowed larger numbers of individuals to resist the current and therefore reduced the rate of recolonisation, while the subsequent increase in current speed after 22.5.75. exceeded the maximum that could be resisted and caused a significant increase in the rate of drift and therefore of recolonisation. Individuals in fast flow areas would also be expected to show more sensitive reactions to current speed, as seems to be the case here.

Significant differences do exist between the numbers found in medium and fast flow areas but mainly for the larger sample intervals, and the Null Hypothesis here can be rejected. For one day intervals the numbers are not Significantly different. The difference in numbers as the sample interval increases is probably due to an initially faster rate of recolonisation in the medium flow areas. This is almost certainly due to the fact that more individuals are liable to get caught in the current in fast flow areas and drift downstream, and more are liable to accumulate in the medium flow areas. Recolonisation over 24 hours as shown by the drift results (Tables 20 and 21) indicates very little increase in numbers. The recolonisation curves shown here agree with this. There is quite a slow rate of recolonisation for the first 2 or 3 days which quickly increases due to the exponential nature of the curve. The near-neighbour stone results, (see later section on Agapetus fuscipes) do show that stones with cleared neighbouring stones are proven to have larger rates of recolonisation than those with neighbouring stones left uncleared. Recolonisation from neighbouring stones seems less important than drifting in the current.

Baetis rhodani (Tables 5,6, 7, Graphs 5,6,7)

This species was the one most intensively studied during the project. All the nymphs that were collected were measured for length in mm. (from tip of antennae to tip of anal cerci) and subdivided into 3 size categories; 0 to 5mm., 6 to 10 mm., and 11 to 15 mm., which covered the range of sizes encountered. Each category was analysed separately. The 1 to 5 mm. category (Graph 5) for fast flowing areas shows a decrease and then an increase before and after the shortest sampling intervals, but this is not statistically significant. There is an increase in numbers after 26.5.75. which is Significant. The medium flow regime shows smaller fluctuations in numbers and no increase after 26.5.75. The 6 to 10 mm. category fast flow regime (Graph 6) shows a decrease in numbers from 2.5.75. as the sampling interval decreases, which is Significant but as the sampling interval decreases still further there is very little decrease in numbers. This suggests that these larger nymphs have an initial rate of recolonisation which is rapid and consistent (occurring within 2 days). The decrease in numbers after 26.5.75. is Non Significant. The 11 to 15 mm. size category shows no statistically significant fluctuations in numbers. The recolonisation experiments for B.rhodani conducted towards the end of the project also support these results. Apart from the 11 to 15 mm. category which was Non Significant (Graph 22), the 1 to 5 mm. and 6 to 10 mm. categories both show Significant fluctuations with sampling interval (see discussion on page 84).

The three graphs from the all-species recolonisation samples indicate therefore, that some correlation does exist between the number collected and sampling time interval, but only for those individuals

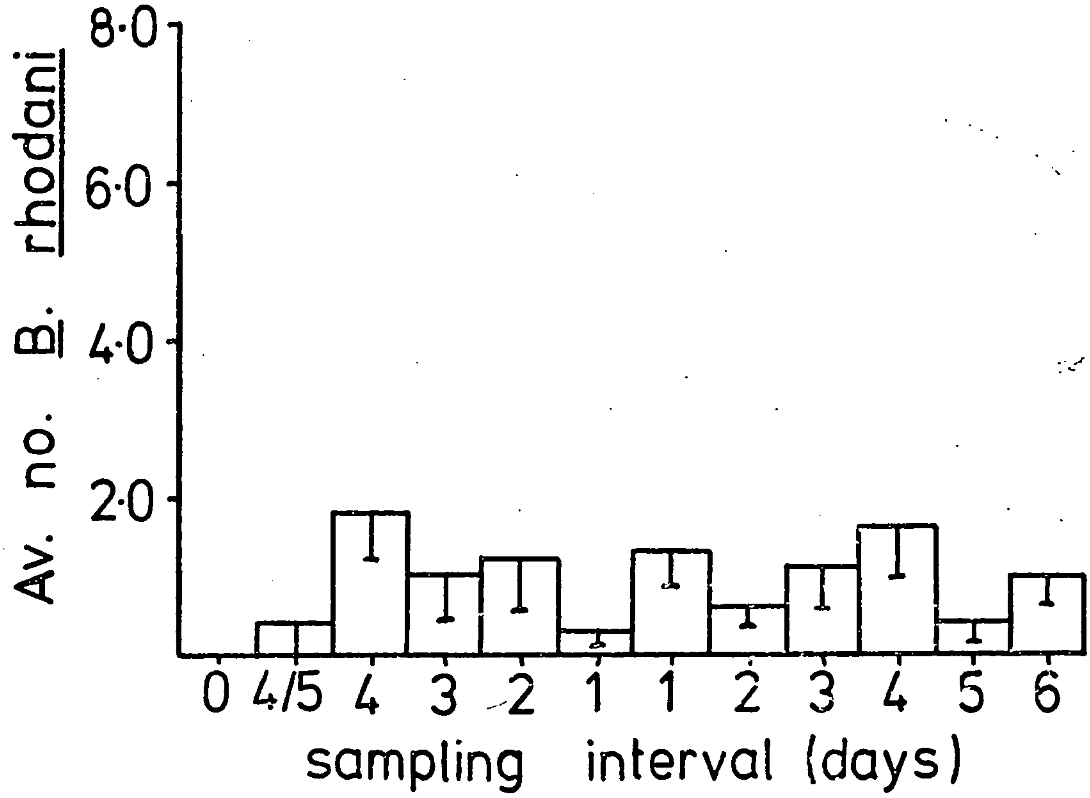
TABLE 5

ALL-SPECIES RECOLONISATION EXPERIMENT, BAETIS RHODANI (size category 1 - 5 mm.) (first experiment)

		May											June
Date		2	6	10	13	15	16	17	19	22	26	31	6
Sampling interval (days)		0	4 or 5	4	3	2	1	1	2	3	4	5	6
	Stone No.												
Medium Flow	1			6	4	1	1	1	1	5	3	1	
	2				2	1		2	1			disappeared	
	3			1				2		1			2
	7		1			1	1	2	1		4		
	8			4						1			
	9			1				1	1				1
	10			1		2			stone disappeared				
	11			3	1				1	1			1
	12			1		6		4		1		2	1
	13		3	1	3	1	1	1		1	2		3
Total			4	18	10	12	3	13	5	10	14	3	8
Average			0.4	1.8	1.0	1.2	0.3	1.3	0.6	1.1	1.6	0.4	1.0
S.E.			1.2	0.6	0.5	0.6	0.2	0.4	0.2	0.5	0.6	0.2	0.3
Fast Flow	4	1	1	1	7	1		6	4	3	4	15	12
	5	2			2	1	2		2		1	3	3
	6	1	1			2		2	2	5	1		2
	14	4				3		1	1				2
	15				6	1	2	1	4	4	6	8	2
	16	1	1					1		4	1	1	1
	17			1	2	4		1					4
	18	2	2	2	1	2	1		1	1	3	1	2
	19	1	2		2			1	2	2	1	7	15
	20	1	1						3		2	2	37
Total		13	8	4	20	14	5	13	19	19	19	37	80
Average		1.3	0.8	0.4	2.0	1.4	0.5	1.3	1.9	1.9	1.9	3.7	8.0
S.E.		0.4	0.3	0.2	0.8	0.5	0.3	0.6	0.5	0.7	0.6	1.6	3.7

Baetis rhodani (1→5 mm.) Graph 5

Medium flow.



Fast flow.

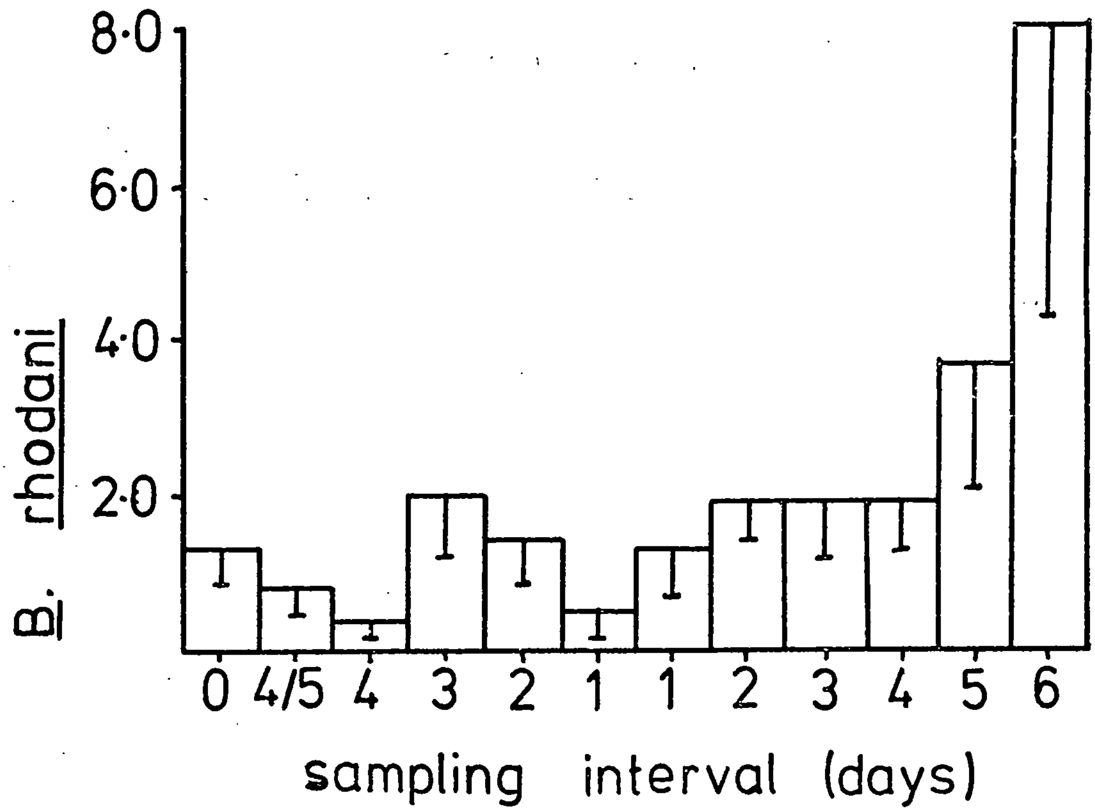


TABLE 6

ALL-SPECIES RECOLONISATION EXPERIMENT, BAETIS RHODANI (s6ze category 6 - 10 mm.)
(first experiment)

						May							June
Date		2	6	10	13	15	16	17	19	22	26	31	6
Sampling interval (days)		0	4 or 5	4	3	2	1	1	2	3	4	5	6
	Stone No.												
	1				1	1	1	2					
	2	1			1		1			1	2	disappeared	
	3	1							1				
	7		1					1		1	1		
Medium Flow	8										1		
	9			1			1	1	1	1			
	10			1		2			stone disappeared				
	11			1									
	12					2							1
	13		1			1			1				
Total		2	2	3	2	6	3	4	3	3	4		1
Average		0.2	0.2	0.3	0.2	0.6	0.3	0.4	0.3	0.3	0.4		0.1
S.E.		0.1	0.1	0.2	0.1	0.3	0.2	0.2	0.2	0.2	0.2		0.1
	4	9	8	1	2	1	1	2	4	3	1	1	1
	5	1	3	1	2	1	1		2		1		1
	6	8	4		2		4			5			
	14	9	4	9		2		3				1	
Fast Flow	15			1		1			2	4	1		
	16	1	4	2		1	1	1	2	5		1	1
	17	1		4	1	5	1				4	4	1
	18	4		4	3	1	2	1			1		
	19	5	3	8	3	3	4	3	2	2			
	20	4	3	2				2	1		3		
Total		42	29	32	13	15	14	12	13	19	11	7	4
Average		4.2	2.9	3.2	1.3	1.5	1.4	1.2	1.3	1.9	1.1	0.7	0.4
S.E.		1.2	0.8	1.0	0.4	0.5	0.5	0.4	0.5	0.7	0.5	0.4	0.2

<u>Baetis rhodani</u> (6→10 mm.) Graph 6

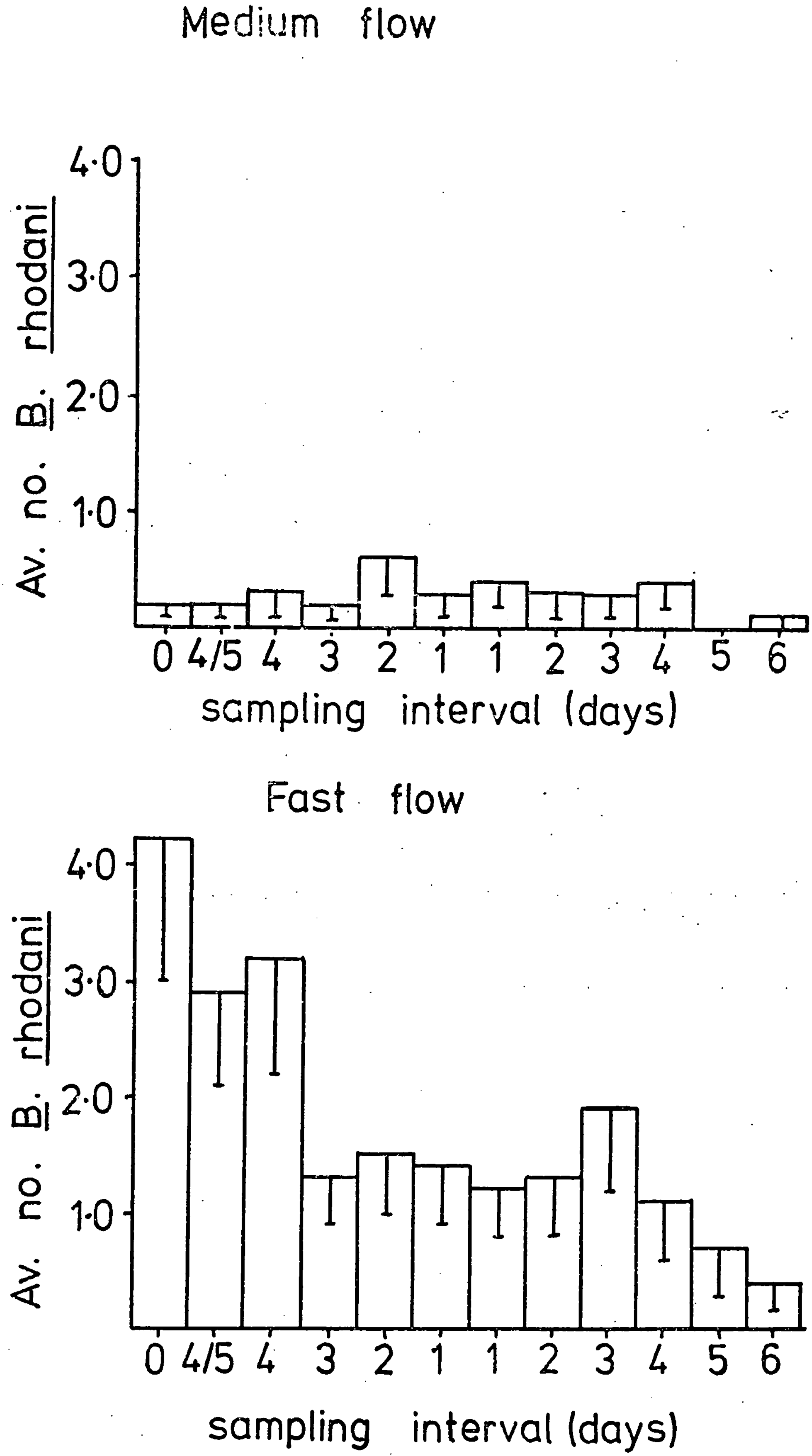


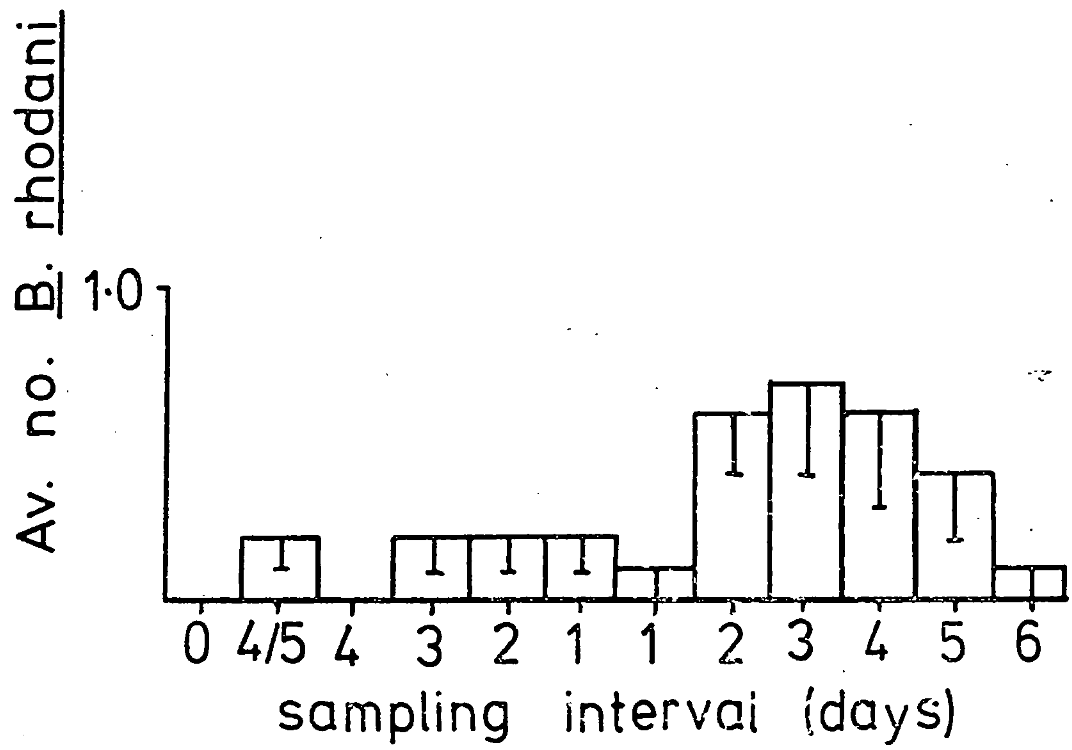
TABLE 7

ALL-SPECIES RECOLONISATION EXPERIMENT, BAETIS RHODANI (size category 11 - 15 mm.) (first experiment)

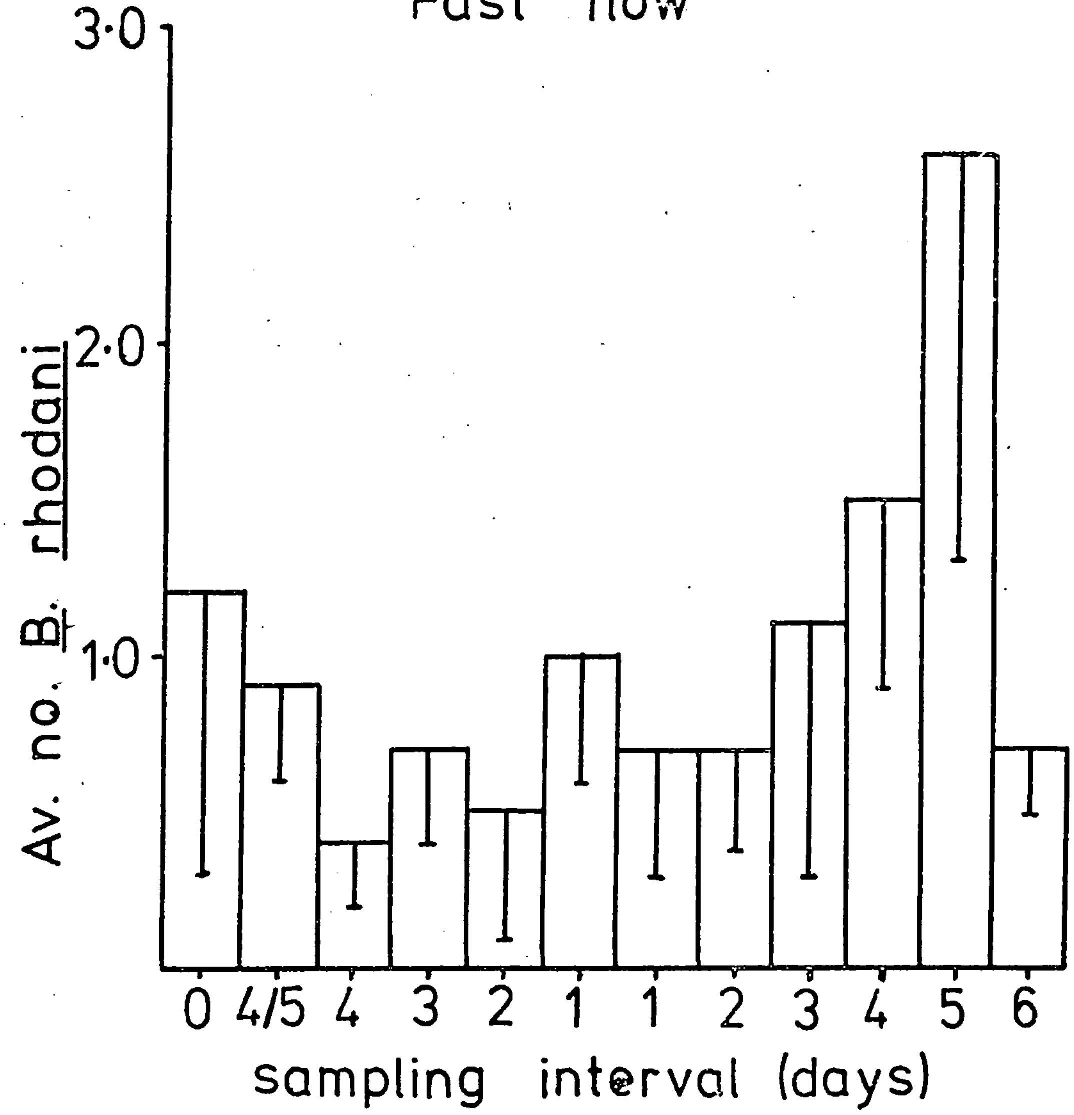
							May						June
Date		2	6	10	13	15	16	17	19	22	26	31	6
Sampling interval (days)		0	4 or 5	4	3	2	1	1	2	3	4	5	6
	Stone No.												
Medium Flow	1					1	1						
	2				2	1				2	2	disappeared	
	3								1	1			
	7		1				1		2	2	2		
	8								1		1		
	9							1	1				
	10								stone disappeared				
	11											1	
	12									1		2	
	13		1										1
Total			2		2	2	2	1	5	6	5	3	1
Average			0.2		0.2	0.2	0.2	0.1	0.6	0.7	0.6	0.4	0.1
S.E.			0.1		0.1	0.1	0.1	0.1	0.2	0.3	0.3	0.2	0.1
Fast Flow	4	8	2				3				6	5	1
	5											1	1
	6		2	1	1		2	3		1	1		1
	14												
	15												
	16		2		1	3		2	1	8	2	13	2
	17	4	1				2				1	1	
	18		2	1	3	2	1		1		2		1
	19				2		2	2	3	2	1	4	
	20			2					2		2	2	1
Total		12	9	4	7	5	10	7	7	11	15	26	7
Average		1.2	0.9	0.4	0.7	0.5	1.0	0.7	0.7	1.1	1.5	2.6	0.7
S.E.		0.9	0.3	0.2	0.3	0.4	0.4	0.4	0.3	0.8	0.6	1.3	0.2

Baetis rhodani (11→15 mm.) Graph 7

Medium flow



Fast flow



collected from fast flow areas. For these, therefore, the Null Hypothesis can be rejected. The graphs for average number collected for varying time intervals show, for all 3 size categories, an initially slow and then increasingly rapid rate of recolonisation (Graph 9). When the log. plots are studied (Graph 11), only 1 to 5 mm. and 6 to 10 mm. size categories appear meaningful. The 6 to 10 mm. category shows a straight line for part of the recolonisation, indicating an exponential rate of increase. However, instead of levelling off, the curve then decreases. In this situation the decrease is probably due to the emergence of adult insects in large numbers, many of whom are included in this category. The 11 to 15 mm. category when plotted as numbers and not log. numbers also shows this decrease, again due to emergence, while the 1 to 5 mm. size category shows a steady rate of increase with no decrease, due to the hatching and development of these early instar insects with no emergence because the full size had not yet been reached. All three categories therefore indicate a steady rise in the rate of recolonisation with time, with indications that full recolonisation would be attained in less than a week. As the T-test results show (Tables 5,6 and 7) there was no statistically significant difference between numbers collected from fast and medium flow regimes for all 3 nymphal sizes and the Null Hypothesis is therefore upheld. This means that although it appears quite likely that B. rhodani nymphs are mainly found in fast flowing water, as suggested by Waters (1965), the results here do not give proof. The B. rhodani recolonisation experiments (Graph 22) undertaken towards the end of the project were designed to study this aspect further. By the time they were conducted, a new generation of small nymphs in very large numbers was developing and the results were hoped to be more representative. They show the enormous numbers of nymphs to be obtained from fast flowing areas. The drift net stone comparison results (Graphs 19 and 20) are also relevant here. They were conducted during the same period and the numbers collected from the stone situated in the fast flow area are far in excess of those in the medium flow areas, although a Significance test is not possible because of the small sample size. To establish whether B. rhodani recolonises directly by drift or indirectly via movements between stones, the near-neighbour stone results and drift net and stone comparison results need to be consulted (see later sections). Here, the main results are briefly foreshadowed. The great majority of nymphs sampled here were in the 1 to 5 mm. size category only. The near-neighbour stone results (Graph 15) show that there was a Non Significant difference between numbers collected from stones with and without uncleared neighbouring stones for stone B. The drift net results (Graph 17) show that fairly small numbers of B. rhodani were in the drift but that these were of the same order of magnitude as the number of B. rhodani individuals recolonising a stone in a fast flowing area just downstream of the net (Graph 19), while a stone in a medium flow area just downstream of the net (Graph 20) showed fewer numbers recolonising.

These results collectively indicate that B. rhodani is found predominantly in fast flow areas, that it exhibits a recolonisation curve which can initially show an exponential rate of increase, that the larger nymphal sizes show more rapid recolonisation in the early stages and that nearly all individuals recolonising stones are carried along in the current as drift.

Chironomidae (Table 8, Graph 8)

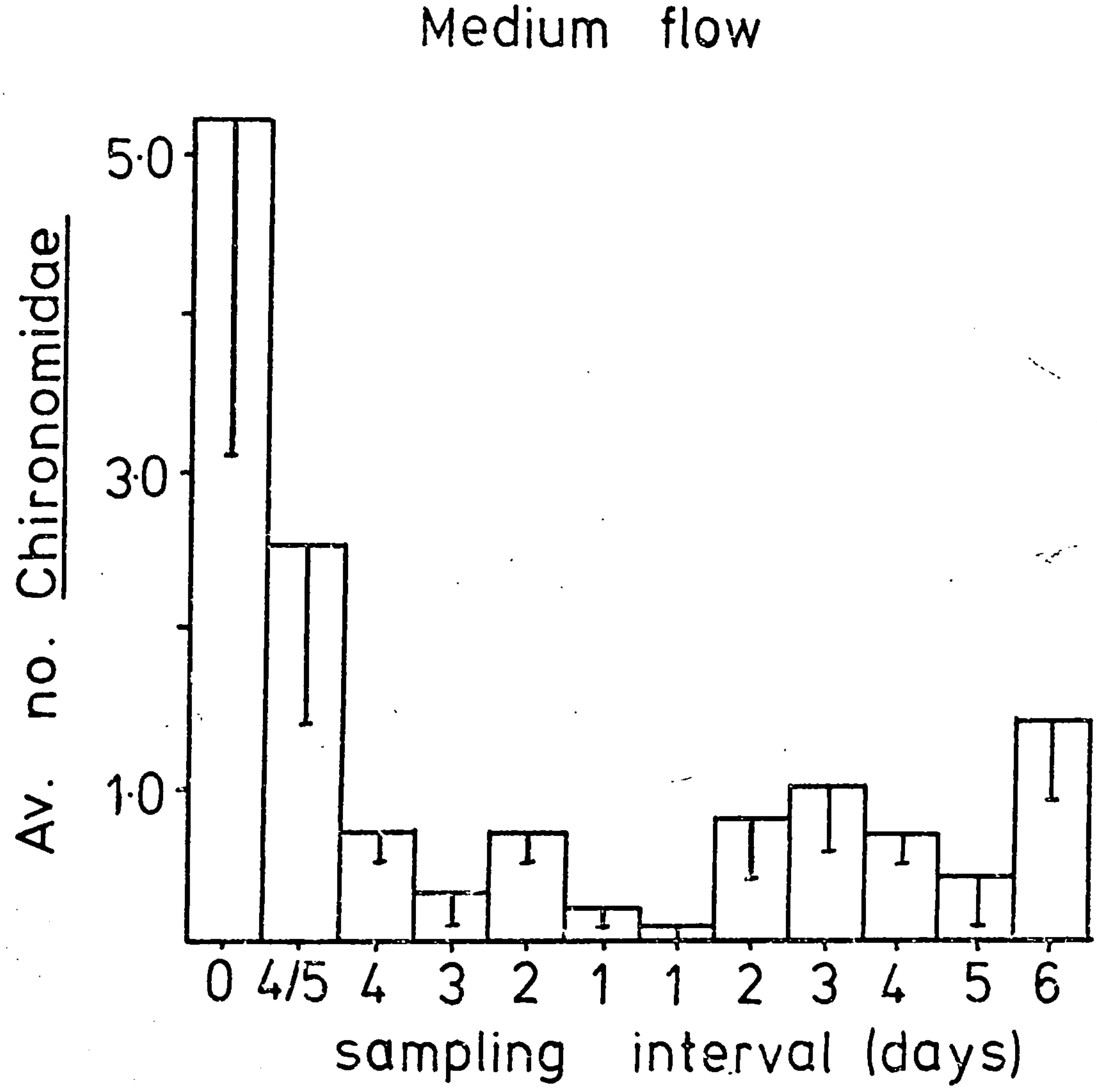
This animal was the least numerous of all those so far discussed but was nevertheless considered to show some interesting results. The all-species stone recolonisation results (Graph 8) shows that there is no relationship between number collected and sampling time interval.

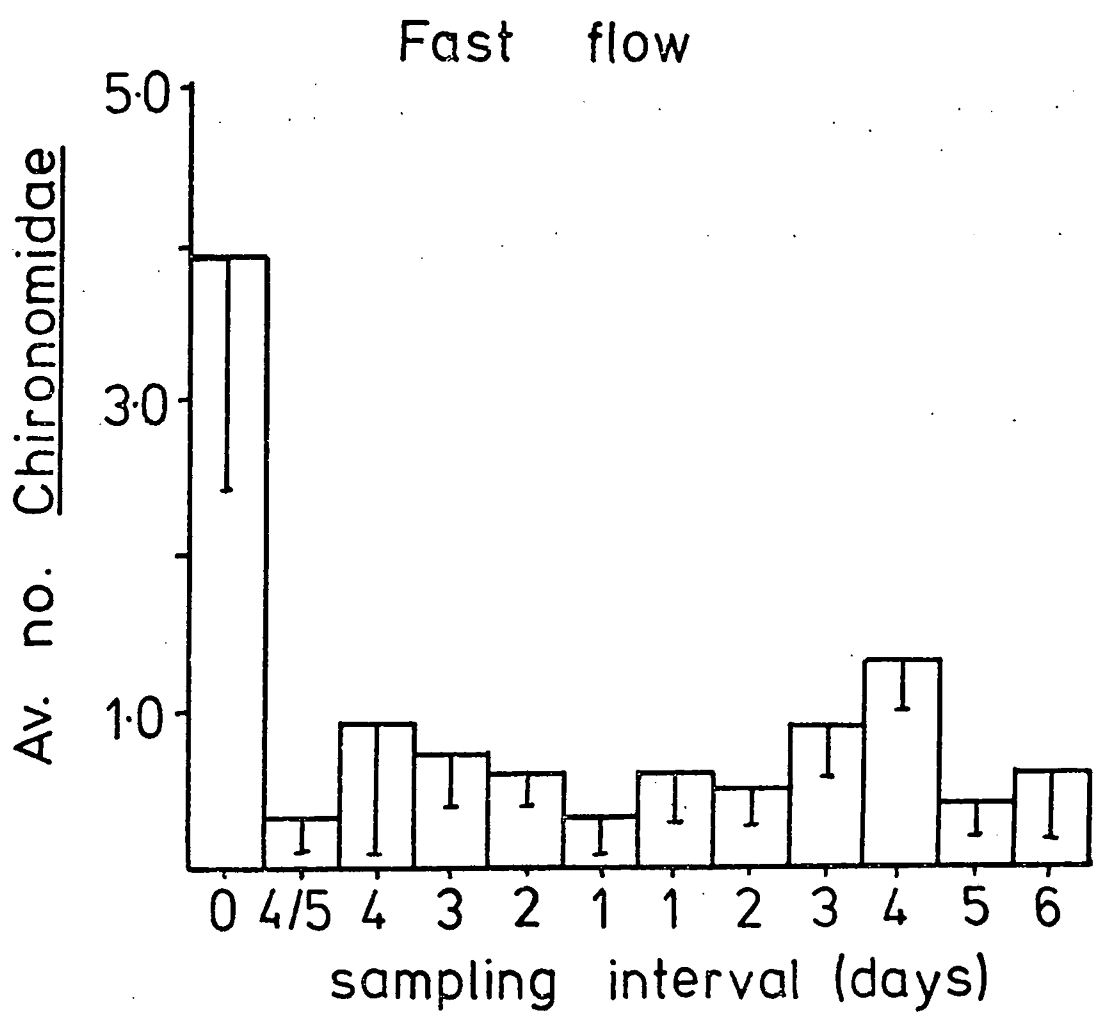
TABLE 8

ALL-SPECIES RECOLONISATION EXPERIMENT, CHIRONOMIDAE (first experiment)

		May											June
Date		2	6	10	13	15	16	17	19	22	26	31	6
Sampling interval (days)		0	4 or 5	4	3	2	1	1	2	3	4	5	6
	Stone No.												
Medium Flow	1	1		1		1			3	1	1	1	1
	2	21	2				1		2	1	1	disappeared	
	3	9	1	1	2	1							1
	7	3	2	2		1				1	2		2
	8	10	4								1	2	4
	9		6	1						1	1		2
	10					1			stone disappeared				
	11	4		1		2							
	12	4	10	1	1			1	1	4			
	13						1		1	1			1
Total		52	25	7	3	7	2	1	7	9	6	3	11
Average		5.2	2.5	0.7	0.3	0.7	0.2	0.1	0.8	1.0	0.7	0.4	1.4
S.E.		2.1	1.1	0.2	0.2	0.2	0.1	0.1	0.4	0.[illegible]	0.2	0.3	0.5
Fast Flow	4				3				1		1	1	
	5	1				2		2	1		1		
	6	3		8				1	2	3	1		
	14	1				1			1	1			1
	15		1	1						1	2	1	4
	16		1		2	1		1		2	1		
	17	3				1					1		
	18	9	1		1	1	1	2					
	19	12			1		1			1	3	1	
	20	10					1			1	3	1	1
Total		39	3	9	7	6	3	6	5	9	13	4	6
Average		3.9	0.9	0.9	0.7	0.6	0.3	0.6	0.5	0.9	1.3	0.4	0.6
S.E.		1.5	0.2	0.8	0.3	0.2	0.2	0.3	0.2	0.3	0.3	0.2	0.4

Chironomidae Graph 8





It also shows no Significant differences between numbers collected from fast and medium flow areas and the decrease in numbers for both flow regimes after 2.5.75. are Non Significant. This seems to indicate that the *Chironomidae* exhibit a very slow rate of recolonisation for stones. The drift net results (Graph 17) show that rather larger numbers are collected from the drift but that the comparison stones just downstream show almost no recolonisation over the 24 hours of sampling (Tables 20 and 21). The main point of interest therefore seems to be that the *Chironomidae* do drift in stream currents but that they do not recolonise stones in comparable numbers with those actually drifting. This may be because they are settling on other substrata such as silt and mud, for Macan (1960) mentions the *Chironomidae* as being extremely diverse in habitat.

TABLE 9

NUMBER OF ORGANISMS COLLECTED FOR AVERAGE SAMPLING INTERVALS - RESULTS

(first experiment) BAETIS RHODANI (category 1 - 5mm)

		Average sampling interval (days)							
		0	1.0	2.0	3.0	4.0	4.5	5.0	6.0
MEDIUM FLOW	Total	0	16	17	20	32	4	3	8
	Average	0.0	0.8	0.9	1.1	1.7	0.4	0.4	1.0
FAST FLOW	Total	13	18	33	39	23	8	37	80
	Average	1.3	0.9	1.7	2.1	1.2	0.8	4.6	10.0
	Log Average	0.11	-0.05	0.24	0.31	0.08	-0.10	0.67	1.00

BAETIS RHODANI (category 6 - 10 mm)

		Average sampling interval (days)							
		0	1.0	2.0	3.0	4.0	4.5	5.0	6.0
MEDIUM FLOW	Total	2	7	9	5	7	2	0	1
	Average	0.2	0.4	0.5	0.3	0.4	0.2	0.0	0.1
FAST FLOW	Total	42	26	28	32	43	29	7	4
	Average	4.2	1.3	1.5	1.7	2.3	2.9	0.9	0.5
	Log Average	0.62	0.11	0.17	0.23	0.35	0.46	-0.05	-0.30

BAETIS RHODANI (category 11 - 15 mm)

		Average sampling interval (days)							
		0	1.0	2.0	3.0	4.0	4.5	5.0	6.0
MEDIUM FLOW	Total	0	3	7	8	5	2	3	1
	Average	0.0	0.15	0.4	0.4	0.3	0.2	0.4	0.1
FAST FLOW	Total	12	17	12	18	19	9	26	7
	Average	1.2	0.9	0.6	1.0	1.0	0.9	3.3	0.9

Av. no. of organisms v sampling interval. Graph 9

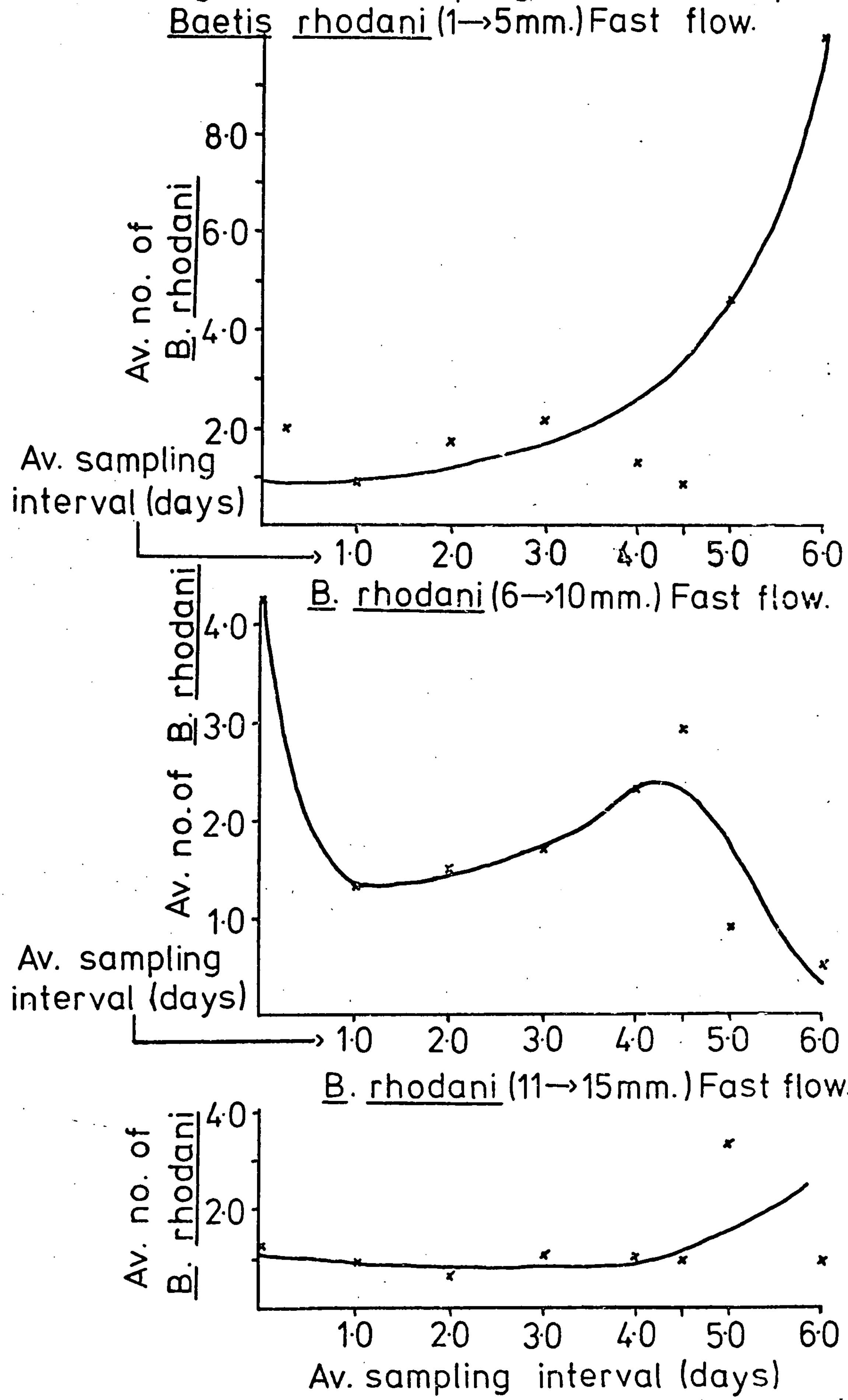


TABLE 10

NUMBER OF ORGANISMS COLLECTED FOR AVERAGE SAMPLING INTERVALS (first experiment)

CHIRONOMIDAE

		Average sampling interval (days)							
		0	1.0	2.0	3.0	4.0	4.5	5.0	6.0
MEDIUM FLOW	Total	52	3	14	12	13	25	3	11
	Average	5.2	0.2	0.7	0.6	0.7	2.5	0.4	1.4
FAST FLOW	Total	39	9	11	16	22	3	4	6
	Average	3.9	0.5	0.6	0.8	1.2	0.3	0.5	0.8

GAMMARUS PULEX

		Average sampling interval (days)							
		0	1.0	2.0	3.0	4.0	4.5	5.0	6.0
MEDIUM FLOW	Total	13	117	96	92	103	17	37	17
	Average	1.3	5.9	5.1	4.8	5.4	1.7	4.6	2.1
FAST FLOW	Total	18	4	24	5	34	6	29	12
	Average	1.8	0.2	1.3	0.3	1.8	0.6	3.6	1.5

AGAPETUS FUSCIPES

		Average sampling interval (days)							
		0	1.0	2.0	3.0	4.0	4.5	5.0	6.0
MEDIUM FLOW	Total	487	256	334	380	578	267	206	142
	Average	48.7	12.8	17.6	20.0	30.4	26.7	25.8	17.8
	Log Average	1.69	1.11	1.25	1.30	1.48	1.43	1.41	1.25
FAST FLOW	Total	526	241	298	305	355	149	92	56
	Average	52.6	12.1	15.7	16.1	18.7	14.9	11.5	7.0
	Log Average	1.72	1.08	1.20	1.21	1.27	1.17	1.06	0.85

TABLE 11

NUMBER OF ORGANISMS COLLECTED FOR AVERAGE SAMPLING INTERVALS (first experiment)

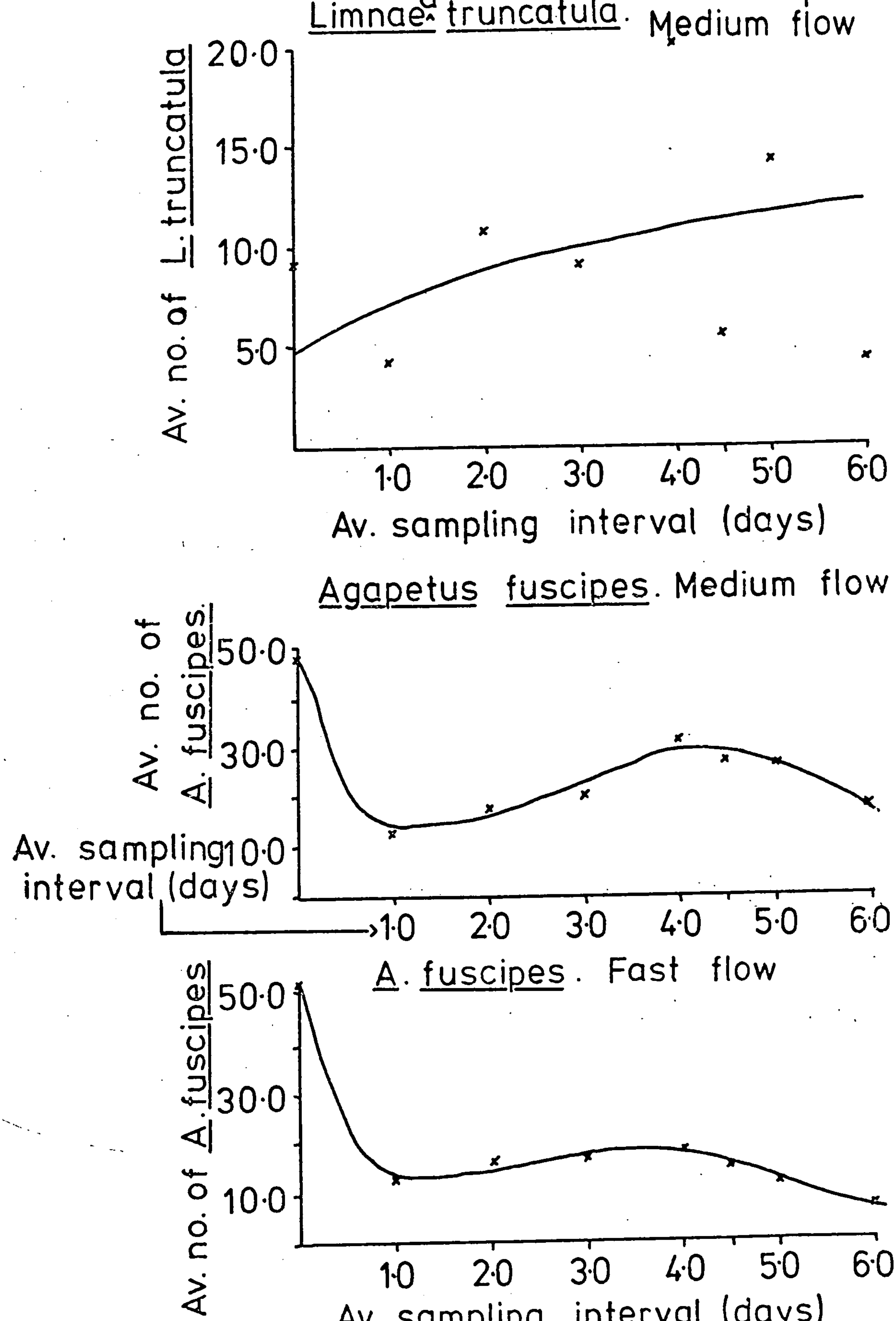
HYDROBIA JENKINSI

		Average sampling interval (days)							
		0	1.0	2.0	3.0	4.0	4.5	5.0	6.0
MEDIUM FLOW	Total	16	49	107	37	98	20	58	25
	Average	1.6	2.5	5.6	2.0	5.2	2.0	7.3	3.1
FAST FLOW	Total	21	13	53	23	40	6	29	62
	Average	2.1	0.7	2.8	1.2	2.1	0.6	3.6	7.8

LIMNAEA TRUNCATULA

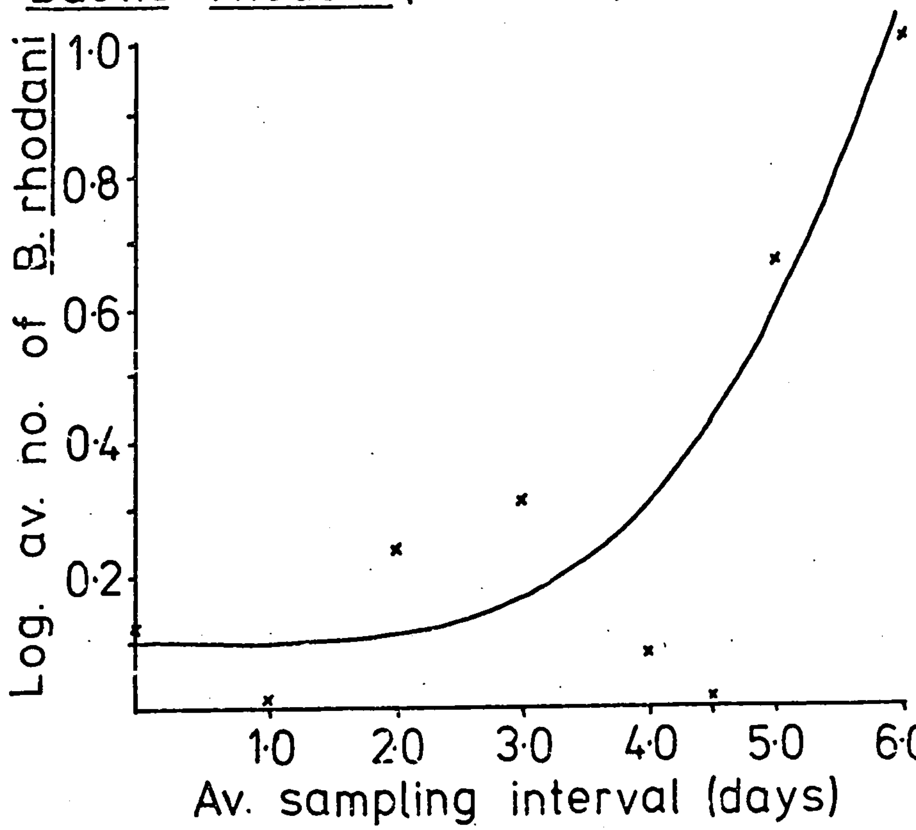
		Average sampling interval (days)							
		0	1.0	2.0	3.0	4.0	4.5	5.0	6.0
MEDIUM FLOW	Total	87	78	215	153	389	64	108	29
	Average	8.7	3.9	11.3	8.1	20.5	6.4	13.5	3.6
FAST FLOW	Total	34	27	85	40	45	8	32	11
	Average	3.4	1.4	4.5	2.1	2.4	0.8	4.0	1.4

Graph 10

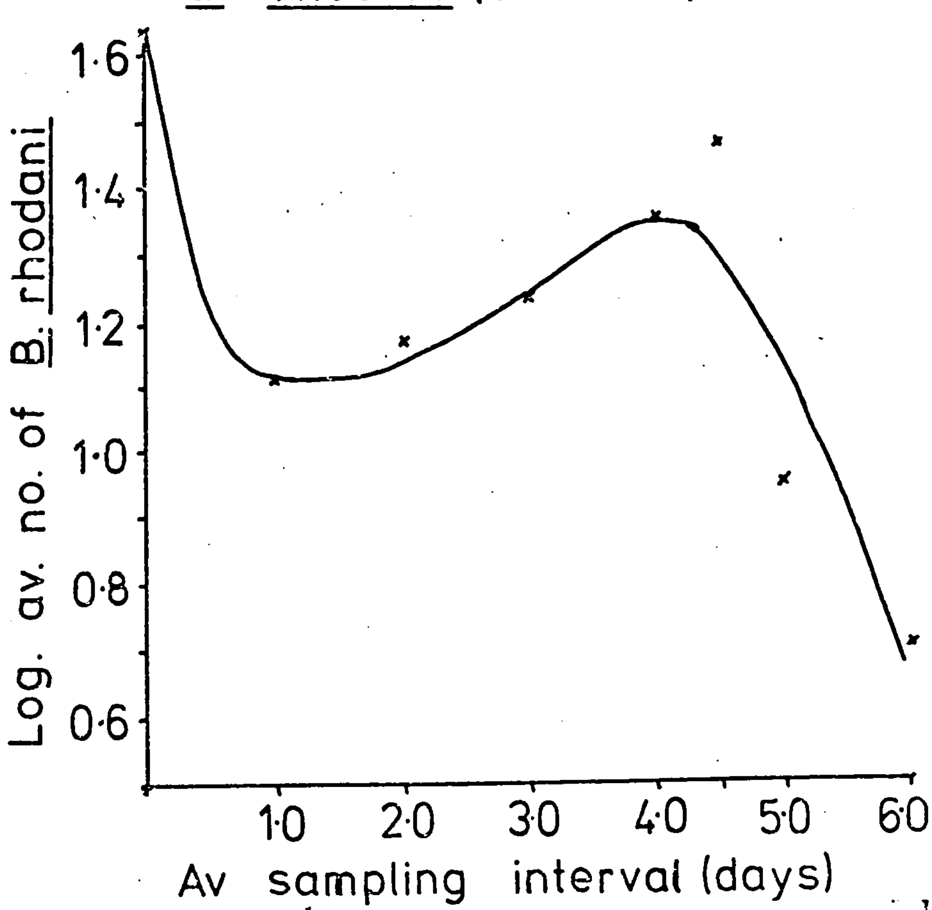

Limnaea truncatula. Medium flow
Av. no. of L. truncatula
20·0
15·0
10·0
5·0
1·0
2·0
3·0
4·0
5·0
6·0
Av. sampling interval (days)
Agapetus fuscipes. Medium flow
Av. no. of A. fuscipes.
50·0
30·0
10·0
Av. sampling interval (days)
1·0
2·0
3·0
4·0
5·0
6·0
A. fuscipes. Fast flow
Av. no. of A. fuscipes
50·0
30·0
10·0
1·0
2·0
3·0
4·0
5·0
6·0
Av. sampling interval (days)

Log. values of organisms. Graph 11

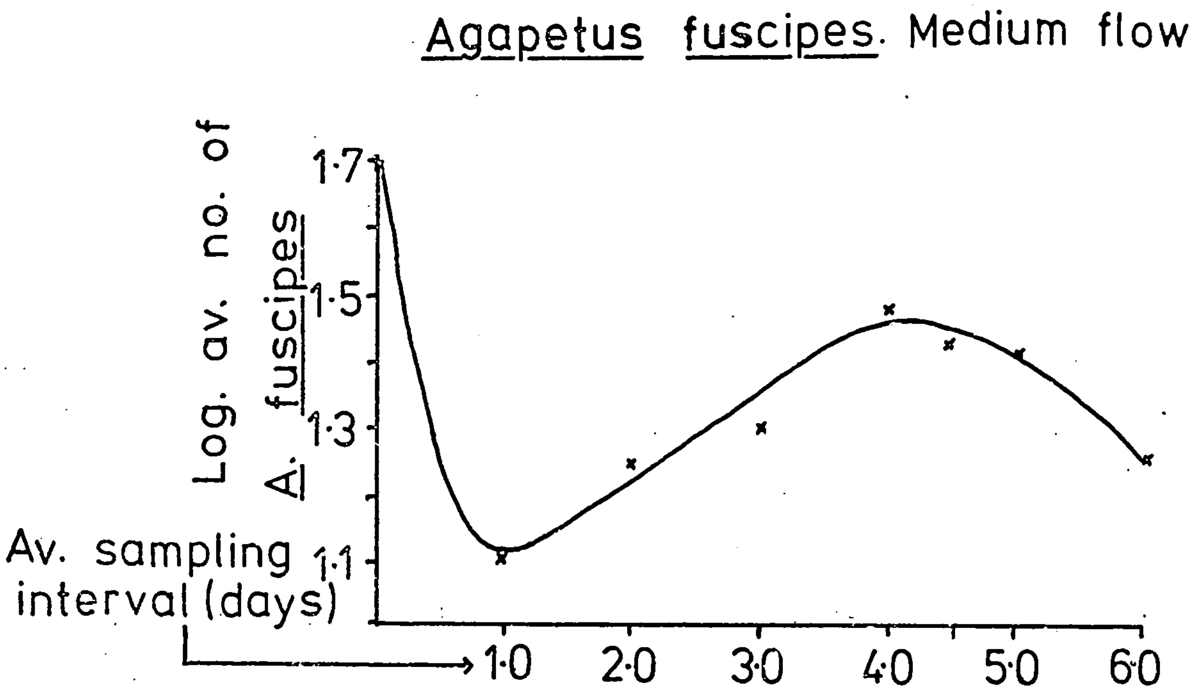
Baetis rhodani (1→5 mm.) Fast flow



B. rhodani (6→10 mm.) Fast flow



Log. values of organisms. Graph 12



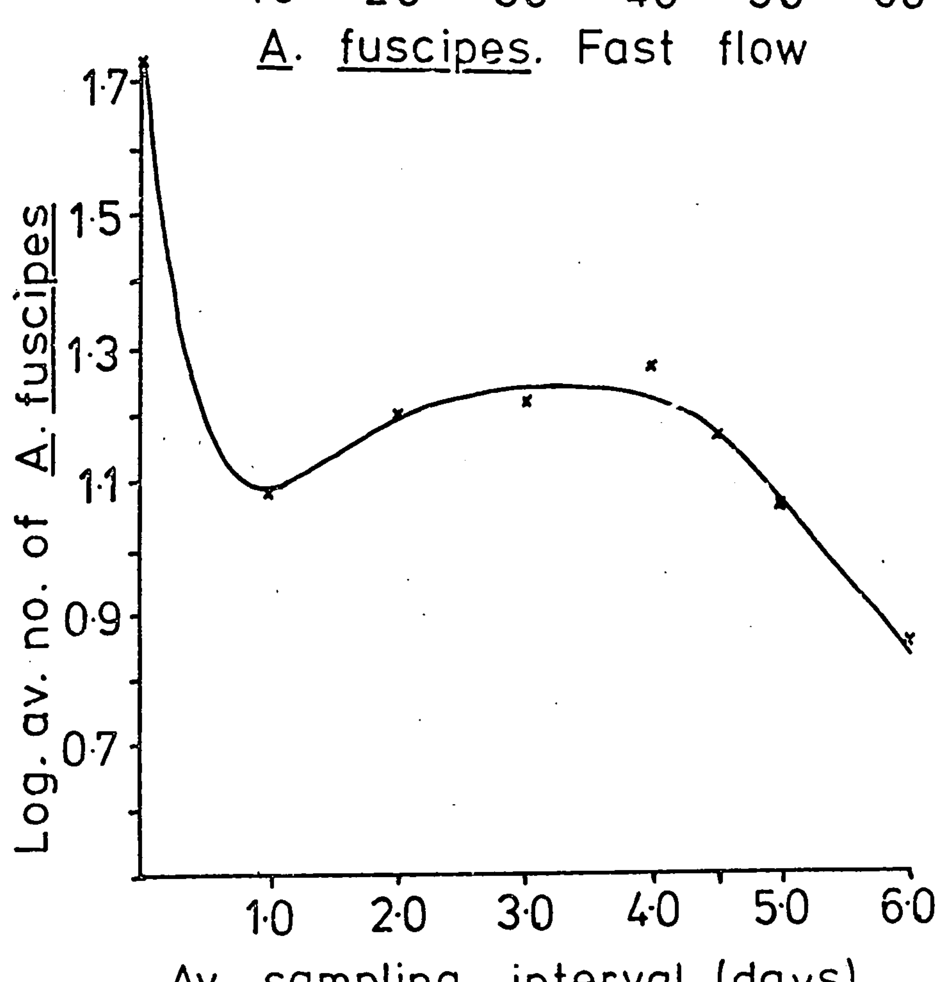


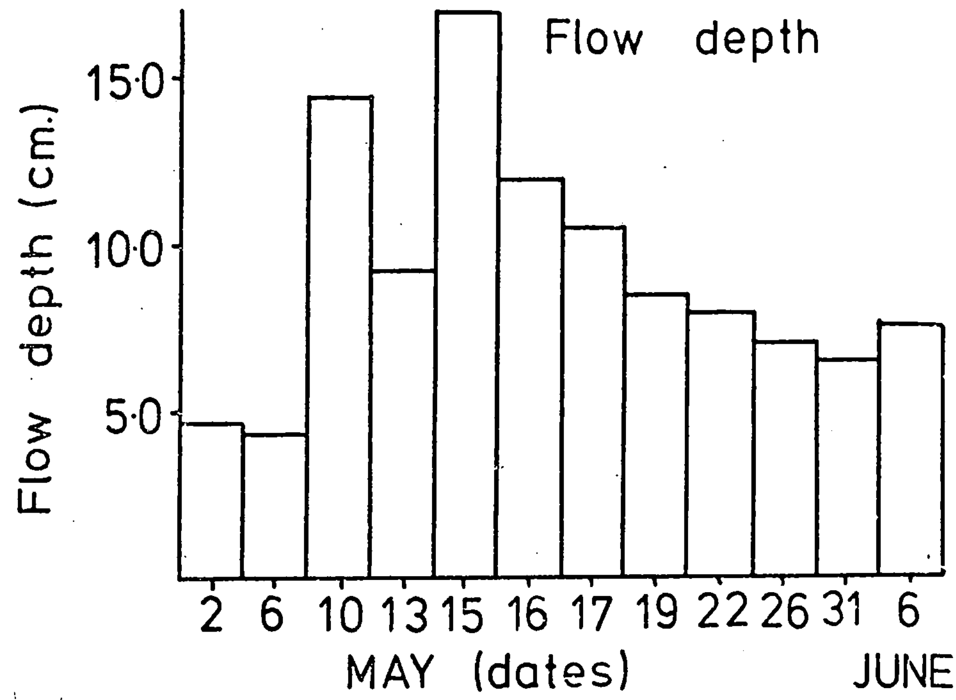
Table 12

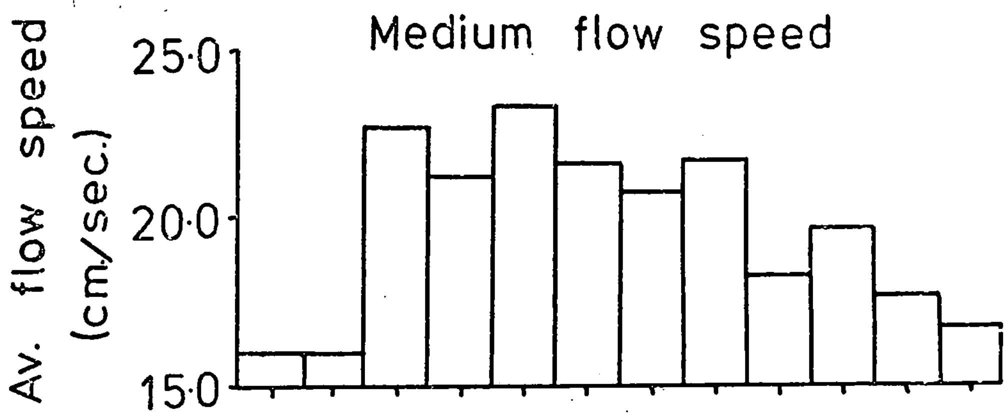
TABLE 12

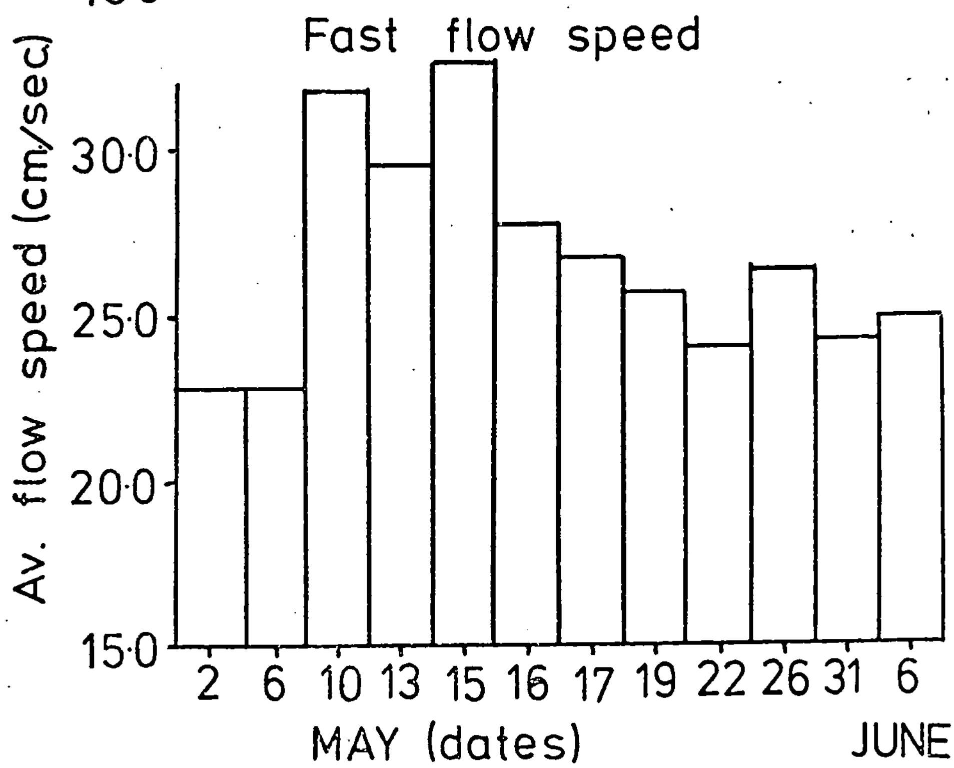
ALL SPECIES RECOLONISATION EXPERIMENT, PHYSICAL MEASUREMENT RESULTS (first experiment)

Date of Sample	2	6	10	13	May 15	16	17	19	22	26	31	June 6
Period since last sample (days)	0	4 or 5	4	3	2	1	1	2	3	4	5	6
Medium flow area Average flow (Pitot)	0.5	0.5	1.1	0.9	1.1	1.0	0.9	1.0	0.7	0.8	0.7	0.6
Medium flow area Average flow cm./sec.	16.0	16.0	22.8	21.2	23.2	21.6	20.8	21.8	18.2	19.8	17.8	16.8
Fast flow area Average flow (Pitot)	1.0	1.1	2.0	1.8	2.2	1.6	1.5	1.4	1.2	1.4	1.2	1.3
Fast flow area Average flow cm./sec.	22.6	22.8	31.8	29.4	32.6	27.8	26.8	25.6	24.0	26.2	24.2	25.0
time of 1st temperature reading	1400	1200	1245	1045	1100	1200	1030	1525	1030	1200	1515	1300
°C	11.5	9.0*	9.0*	10.0	7.5*	10.0*	9.0	8.0	8.0*	8.0*	10.0*	17.5*
time of 2nd temperature reading	1520	1300	1720	1300	1340	1400	1215	1705	1200	1400	1700	1430
°C	10.0	9.0	9.0	11.0*	8.5	11.0	11.0*	15.0	8.0*	9.0	10.0	18.5
time of 3rd temperature reading	1130										2000	
°C	9.0*										9.0	
Flow depth (cm)	4.7	4.3	14.5	9.3	17.0	12.0	10.5	8.5	8.0	7.0	6.5	7.5
Weather remarks				Damp ground	Rain	Sunny, dry	Sunny, windy	Sunny, dry	Cool, windy	Cool little rain		Rain

Physical measurements Graph 13







Physical measurements Graph 14

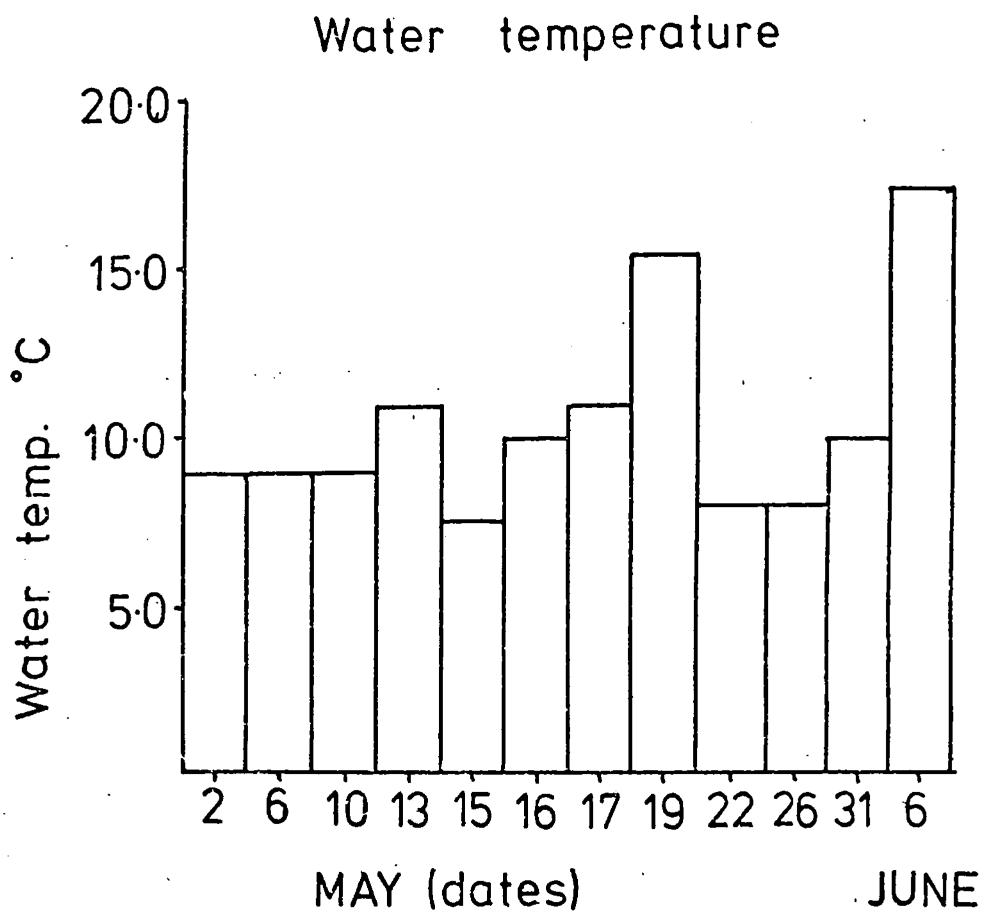


TABLE 13

ALL SPECIES RECOLONISATION EXPERIMENT
STONE DIMENSION MEASUREMENT RESULTS (first experiment)

Stone No.	Length cm.	Width cm.	Depth cm.
1	8.3	6.0	.3
2	9.5	5.7	4.3
3	7.3	5.2	2.0
7	12.8	7.5	7.0
8	8.2	4.8	4.0
9	12.5	6.4	5.2
10	7.2	7.2	5.0
11	10.5	7.2	4.8
12	14.5	11.5	6.7
13	7.5	7.0	4.2
SX	98.3	68.5	46.5
	9.8	6.9	4.7
S.E.	0.8	0.6	0.5
4	15.5	7.3	2.3
5	8.0	5.3	3.8
6	7.4	6.5	4.0
14	10.0	6.5	3.3
15	11.8	6.5	4.0
16	13.3	9.0	6.0
17	10.4	4.8	4.2
18	8.7	8.3	6.4
19	8.7	7.0	6.3
20	13.5	11.0	5.0
SX	107.3	72.2	45.3
	10.7	7.2	4.5
S.E.	0.9	0.6	0.4
t	2.4173		

Significant

NEAR-NEIGHBOUR STONE RECOLONISATION EXPERIMENT (Map 2)

Methods

Eight sets of three stones were set up for this experiment. Each stone had the number of *Agapetus fuscipes*, Gastropods and *Baetis rhodani* recorded (the most numerous species from the results of the previous experiment). 4 of the sets had all 3 stones cleared. The other 4 had the animals on the middle stone cleared, while the outer stones were counted and the animals left on as far as possible (a few fell of due to disturbance).

The purpose of this experiment was to try and see if there was a difference in the rate of recolonisation if the neighbouring stones were cleared or left uncleared.

After a period of time to allow appreciable recolonisation (2-3 days) the 8 sets of 3 stones were swopped over in terms of counting (those where previously all 3 stones were cleared now had only the middle stone cleared, and vice versa). All stones were left in the same position on the stream bed. When each set of three stones had been set up the speed of flow with a Pitot tube was recorded. A sketch map of each area was made and the stones were labelled A, B and C. Stone B was always the middle stone and all 8 B-stones were numbered with while cellulose paint from 1 to 8. Stones A and C were always kept in the same position in relation to flow, i.e. if flow on the map is north, then A, B and C are placed horizontally in alphabetical order.

Results

For any statistical analysis in this experiment, the Null Hypothesis is that there is no difference in numbers obtained from those sets of stones with just the centre stone cleared and those with all 3 cleared. A proper comparison to find if a "neighbour-stone effect" on recolonisation

THE SAMPLE AREA. MAP 2
SHERBURN BECK

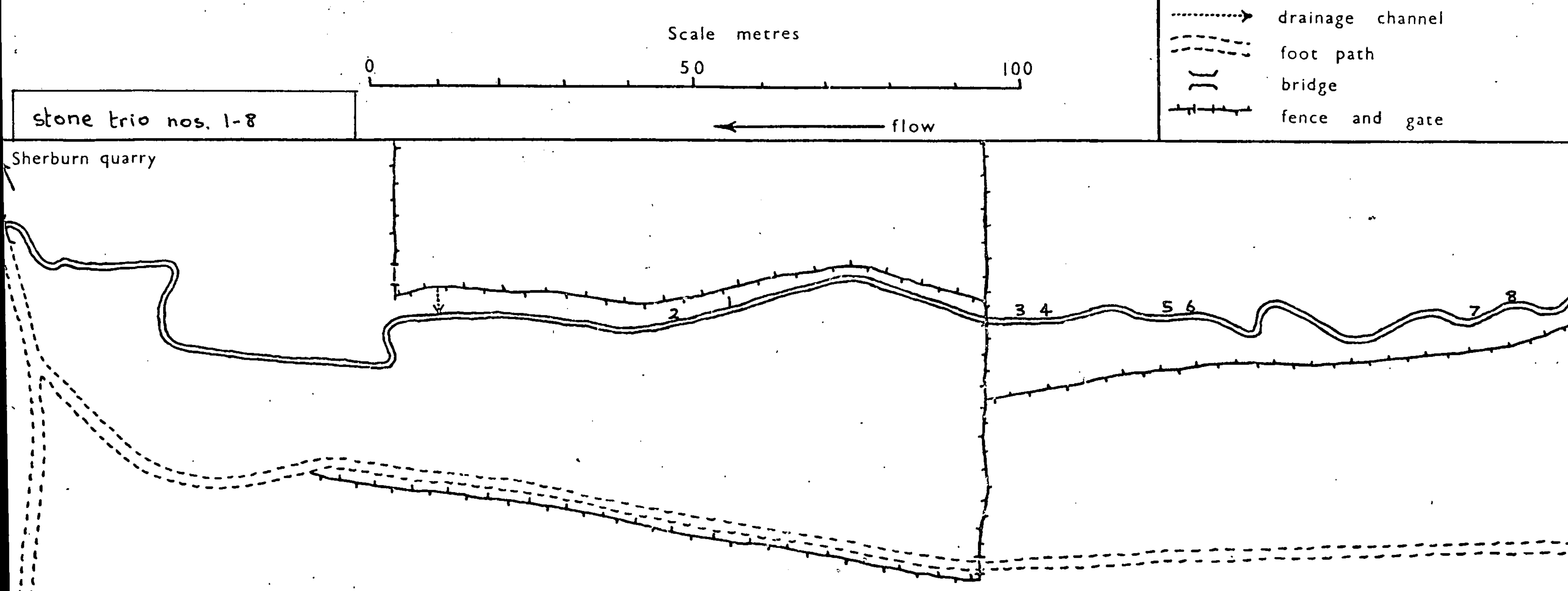


TABLE 14

NEAR-NEIGHBOUR STONE SAMPLING RESULTS

Sampled on 28.5.75.

Agapetus fuscipes
Stones A,B,C cleared

Stone Nos.	A	B	C
1	93	74	121
3	150	270	110
5	170	200	150
7	80	140	75
Total	493	684	456
Average	123.3	171.0	114.0
S.E.	21.8	41.9	15.5

Agapetus fuscipes
Stone B cleared only

Stone Nos.	A	B	C
2	250	222	210
4	260	160	130
6	220	180	210
8	180	160	170
Total	910	722	720
Average	227.5	180.5	180.0
S.E.	18.0	14.6	19.2

Sampled on 31.5.75.

Stones A,B,C cleared

Stone Nos.	A	B	C
2	260	18	160
4	170	19	150
6	110	12	150
8	110	66	110
Total	650	115	570
Average	162.5	28.8	142.5
S.E.	35.4	12.5	11.1

Stone B cleared only

Stone Nos.	A	B	C
1	13	4	15
3	3	6	4
5	24	31	37
7	14	35	60
Total	54	76	116
Average	13.5	19.0	29.0
S.E.	4.3	8.1	12.4

Sampled on 6.6.75.

Stones A,B,C cleared

Stone Nos.	A	B	C
1	18	14	17
3	18	38	32
5	38	36	42
7	34	32	36
Total	108	120	127
Average	27.0	30.0	31.8
S.E.	5.3	5.5	5.3

Stone B cleared only

Stone Nos.	A	B	C
2	7	27	28
4	6	10	35
6	25	21	40
8	42	41	46
Total	80	99	149
Average	20.0	24.8	37.3
S.E.	8.5	6.5	3.8

TABLE 15

NEAR-NEIGHBOUR STONE SAMPLING RESULTS

Baetis rhodani — *Baetis rhodani*

Sampled on 28.5.75.

Stones A,B,C cleared

Stone Nos.	A	B	C
1	10	5	5
3	2	1	2
5	8	4	7
7	11	2	5
Total	31	12	19
Average	7.8	3.0	4.8
S.E.	2.0	0.9	1.0

Stone B cleared only

Stone Nos.	A	B	C
2	3	3	2
4	2	3	0
6	0	2	0
8	0	0	0
Total	5	8	2
Average	1.3	2.0	0.5
S.E.	0.8	0.7	0.5

Sampled on 31.5.75.

Stones A,B,C cleared

Stone Nos.	A	B	C
2	4	14	5
4	1	4	4
6	0	3	6
8	2	3	3
Total	7	24	18
Average	1.8	6.0	4.5
S.E.	0.9	2.7	0.7

Stone B cleared only

Stone Nos.	A	B	C
1	5	5	13
3	1	4	0
5	10	19	0
7	5	3	4
Total	21	31	17
Average	5.3	7.8	4.3
S.E.	1.8	3.8	3.1

Sampled on 6.6.75.

Stones A,B,C cleared

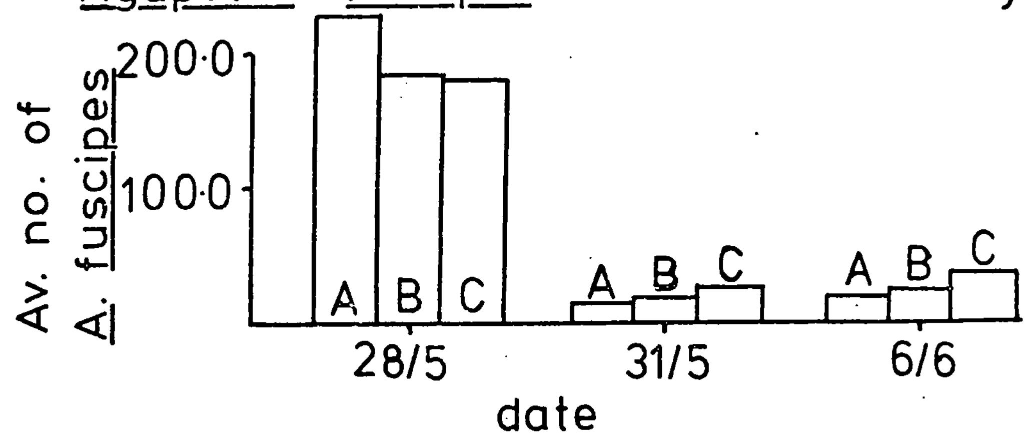
Stone Nos.	A	B	C
1	8	11	9
3	2	3	1
5	6	5	4
7	6	5	5
Total	22	24	19
Average	5.5	6.0	4.8
S.E.	1.3	1.7	1.7

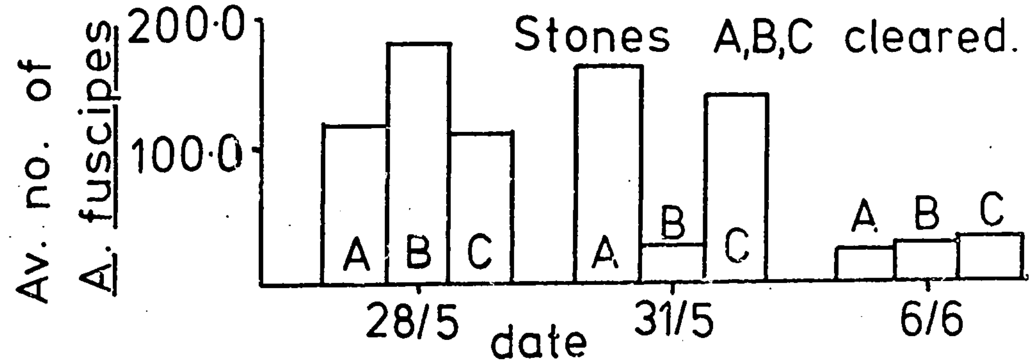
Stone B cleared only

Stone Nos.	A	B	C
2	5	8	5
4	0	3	3
6	1	6	2
8	0	0	0
Total	6	17	10
Average	1.5	4.3	2.5
S.E.	1.2	1.8	1.0

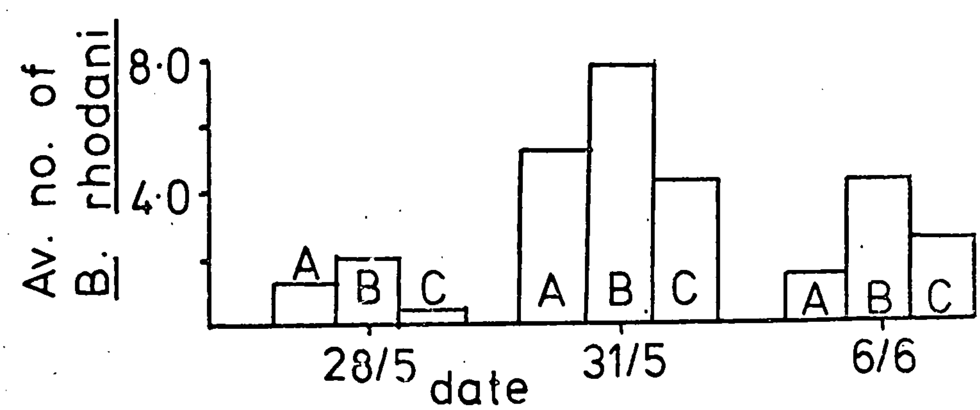
Near neighbour sampling. Graph 15

Agapetus fuscipes. B cleared only





Baetis rhodani. B cleared only.



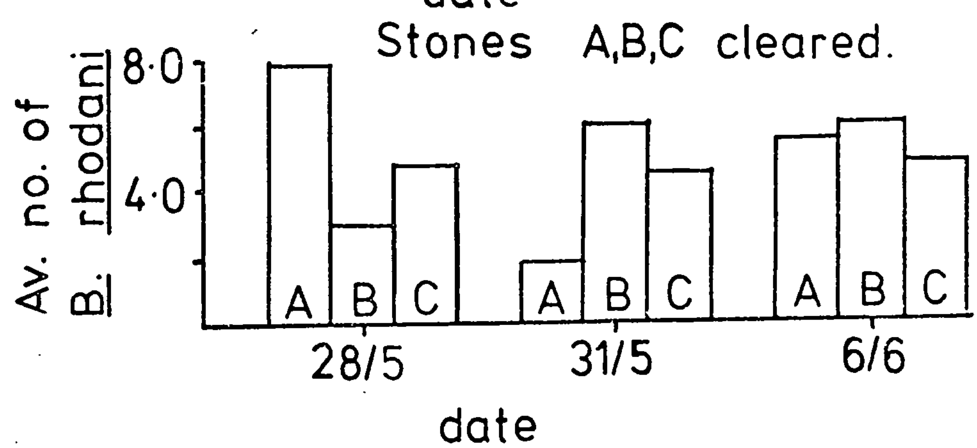


TABLE 16

NEAR-NEIGHBOUR STONE SAMPLING RESULTS

Mollusc species

Sampled on 28.5.75.

Stones A, B, C cleared

Stone Nos.	A	B	C
1	4	8	3
3	6	5	5
5	0	2	0
7	0	3	9
Total	10	18	17
Average	2.5	4.5	4.3
S.E.	1.5	1.3	1.9

Mollusc species

Stone B cleared only

Stone Nos.	A	B	C
2	2	2	3
4	35	4	0
6	1	2	15
8	5	8	6
Total	43	26	24
Average	10.8	6.5	6.0
S.E.	8.1	2.9	3.2

Sampled on 31.5.75.

Stones A, B, C cleared

Stone Nos.	A	B	C
2	10	3	4
4	25	46	26
6	50	20	12
8	3	3	16
Total	88	72	58
Average	22.0	18.0	14.5
S.E.	10.4	10.2	4.6

Stone B cleared only

Stone Nos.	A	B	C
1	7	0	13
3	8	22	5
5	0	0	0
7	8	3	1
Total	23	25	19
Average	5.8	6.3	4.8
S.E.	1.9	5.3	3.0

Sampled on 6.6.75.

Stones A, B, C cleared

Stone Nos.	A	B	C
1	4	0	9
3	8	20	11
5	3	2	0
7	14	4	2
Total	29	26	22
Average	7.3	6.5	5.5
S.E.	2.5	4.6	2.7

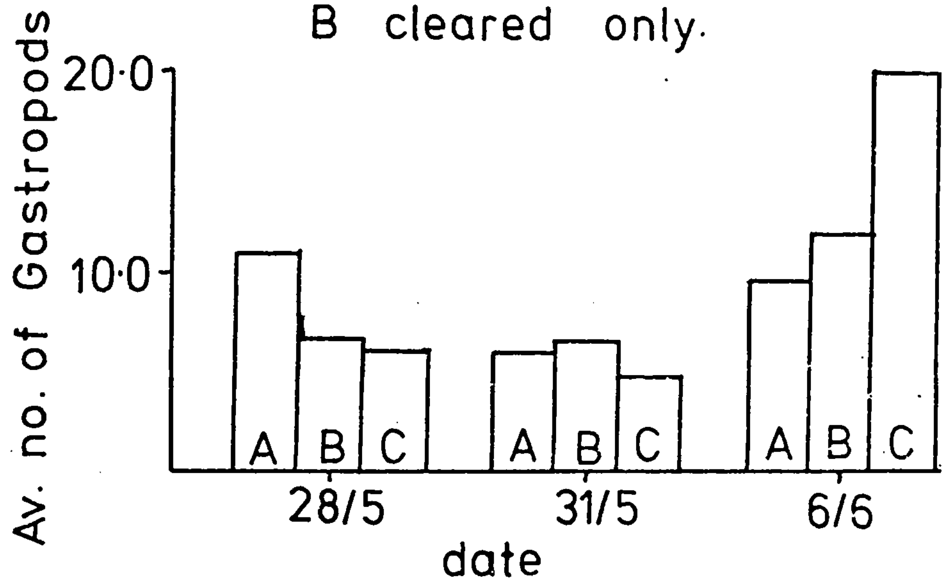
Stone B cleared only

Stone Nos.	A.	B	C
2	7	6	8
4	2	11	36
6	22	26	30
8	6	4	5
Total	37	47	79
Average	9.3	11.8	19.8
S.E.	4.4	5.0	7.8

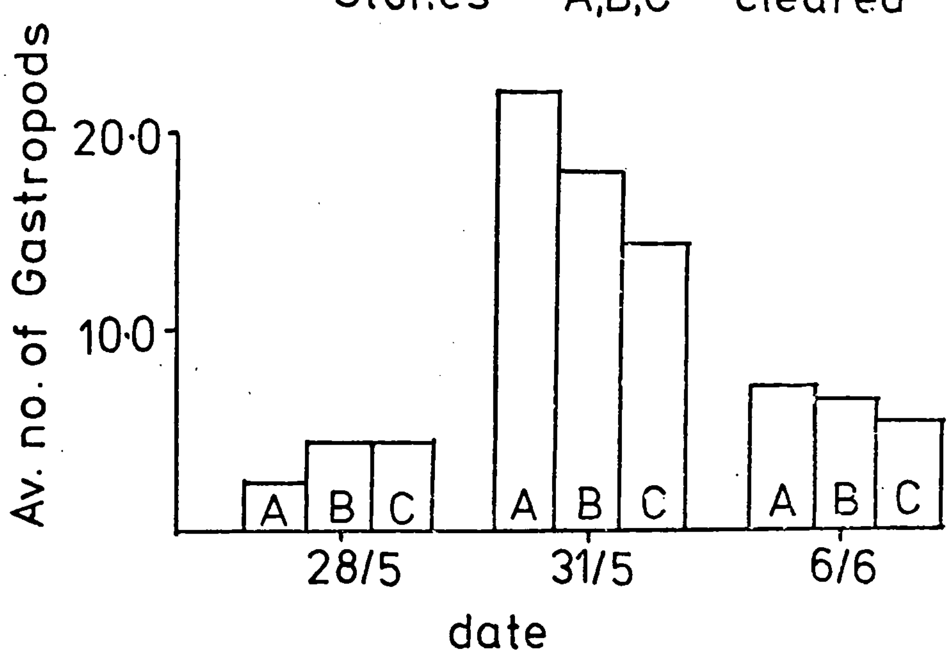
Near neighbour sampling Graph 16

Gastropod spp.

B cleared only.



Stones A,B,C cleared



rate existed was only possible for the 3rd sample, as samples 1 and 2 were still giving the initial high numbers for the resident populations before the sampling began.

The results are shown on Tables 14, 15 and 16 and the averages are plotted on Graphs 15 and 16. Stones A, B and C were compared for each of the three species examined; *Agapetus fuscipes*, *Baetis rhodani* and the Gastropod species, *Hydrobia jenkinsi* and *Limnaea truncatula*. T-tests were used for the statistical comparison. For each set of three stones, it is only the middle stone (stone B) which gives the most representative result, for it was cleared for each sample and had stones on both sides of it that were cleared or left untouched except for counting. Although T-test results are given for stones A, B and C, therefore, it is stone B which is the most important. *Agapetus fuscipes* gives a Significant result for stones A, B and C, but stone B is proven to have fewer numbers of individuals on it when the 2 outer stones are left untouched. Thus, stone B is more likely to have larger numbers recolonising it when its neighbours have also been cleared and therefore there is no "neighbour-effect" here. The Null Hypothesis is therefore upheld.

Baetis rhodani gives a result for stone B which is Non Significant again indicating that recolonisation here is mainly from drift and not from movement from neighbouring stones, which upholds the Null Hypothesis. The Gastropod species, however, do give a Significant result for stone C which rejects the Null Hypothesis. Stone B does not show a Significant result for the low degrees of freedom used here, and the fact that stone C does give a Significant result is not completely conclusive. Nevertheless, the stone comparison results in the drift net experiment results (Graphs 19 and 20) indicate that drift is not directly an important method of recolonisation, for the very large numbers being sampled from the stones at sunset should have also been expected in the drift, but were not. I would suggest here that the sample numbers used for the near-neighbour stone experiment are not large enough to give a Significant result and that further experiments in the future with 2 or 3 times the number of sets of 3 stone units used might give a more representative answer. For B. rhodani and A. fuscipes it can be concluded, therefore, that during the initial stages of recolonisation, the rate of recolonisation is directly proportional to the drift rate as discussed by Waters (1964). This probably corresponds to the straight line section for the log. plots for the all species stone recolonisation results (Graphs 11 and 12). Waters (1964) states that the quantity of organisms drifting over the denuded sampling areas is at all times ample to provide the source of organisms recolonising the areas. This period, on my graphs, when recolonisation is proceeding at a maximum rate is the period when a comparable idea of the drift rate can be obtained. As recolonisation proceeds further and approaches 100%, apart from life cycle effects, fewer of the drifting organisms will be acting as recolonisers. If this experiment were to be repeated throughout the year in any future study, a comparable idea of the drift rate over the year could be obtained.

SIMULIUM GRASS EXPERIMENT AND STONE COMPARISONS (Map 3)

Methods

This experiment was to study the rate of recolonisation by Simulium ornatum larvae on grass trailing in the water. It involved selecting 10 labelled grass stems with leaves trailing in the water. Stems were chosen in swift flowing areas where numbers of larvae were expected to be high. Each stem was marked with a piece of white cotton. Removal of S.ornatum larvae was done efficiently by running the thumb and forefinger from the base to the tip of each grass blade. The centre stones of the 8 sets of 3 stones (stones B) from the previous experiment were also sampled on the same dates to provide a comparison with the grass readings. As Map 3 shows, the labelled grass stems are within the stretch of stream containing those 8 sample stones so that some stones are upstream of the grass stems and some are downstream.

Results

The numbers taken soon indicated that the generation of S.ornatum larvae being studied was not numerous enough to give useable data. Consequently the experiment was discontinued. The stone comparison results however are given in Tables 17 and 18, since they provide an approximate comparison with the all species stone recolonisation results (fast flow regime, Tables 1 - 8), as stones are of similar sizes and are in the same current speeds. Hydrobia jenkinsi shows a considerable increase in numbers recolonising stones in the 2 weeks between the conclusion of the all-species stone recolonisation experiment and this experiment. This is probably due either to the increase and development of the Gastropod populations inhabiting this stretch of the beck, or to an influx of individuals from upstream due to drift. Limnaea truncatula, however, does not show a significant difference. Agapetus fuscipes

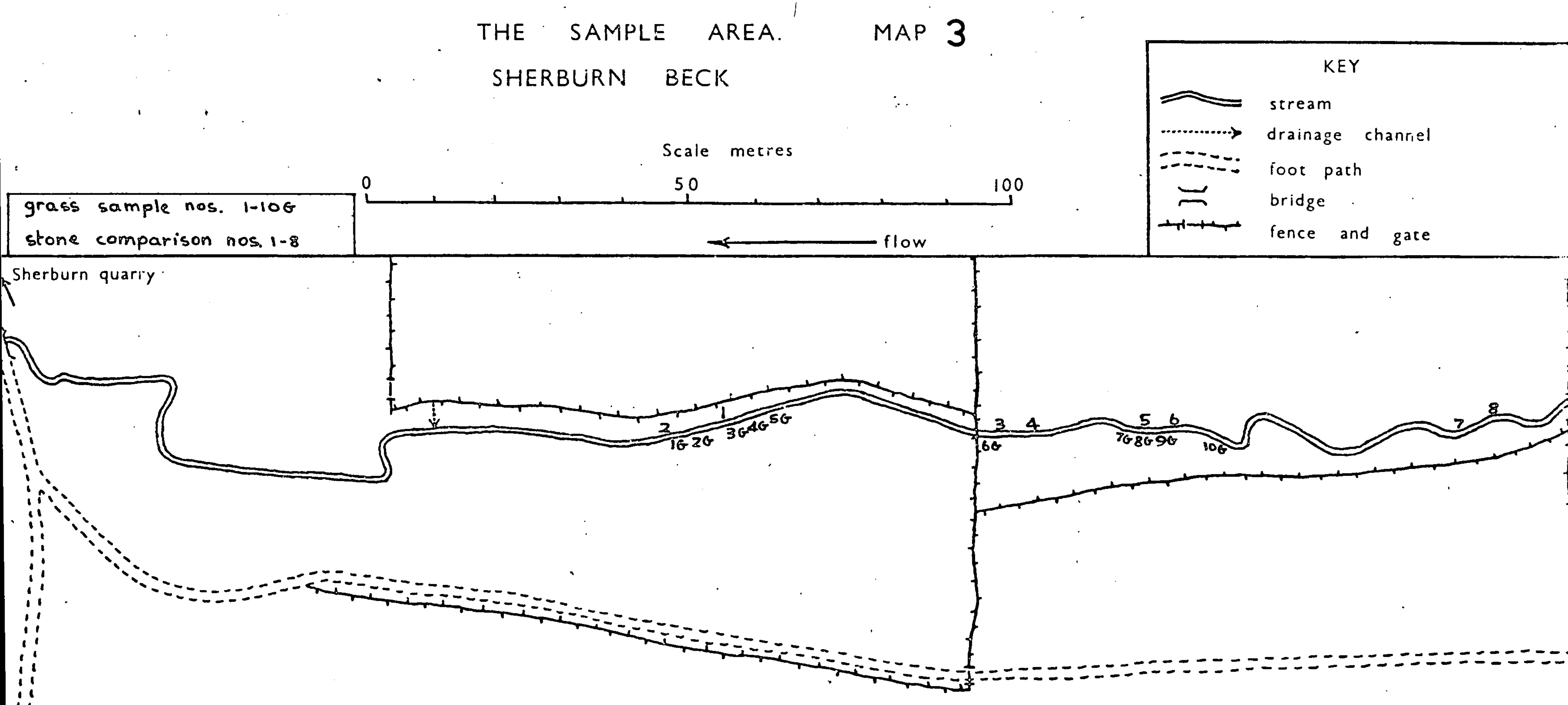

THE SAMPLE AREA. MAP 3
SHERBURN BECK
Scale metres
0
50
100
flow
grass sample nos. 1-10G
stone comparison nos. 1-8
KEY
stream
drainage channel
foot path
bridge
fence and gate
Sherburn quarry
1
2
3
4
5
6
7
8
1G 2G
3G 4G 5G
6G
7G 8G 9G
10G
59

TABLE 17

SIMULIUM RECOLONISATION STONE COMPARISON SAMPLE RESULTS

Sample taken on 13.6.75.

Species		Hydrobia jenkinsi	Limnaea truncatula	Agapetus fuscipes	Gammarus pulex	Chironomidae	Baetis rhodani nymph size categories 1-5mm.	6-10mm.	11-15mm.
Sample Stones	1	1	1	15	0	0	35	2	1
	2	2	9	21	2	3	11	8	9
	3	8	9	14	2	0	0	3	0
	4	17	64	19	6	0	5	2	0
	5	11	25	34	0	5	94	0	0
	6	62	408	14	1	0	72	1	0
	7	7	1	32	0	7	51	0	0
	8	32	20	34	0	11	0	1	0
Total		140	537	183	11	26	268	17	10
Average		17.5	67.1	22.9	1.4	3.3	33.5	2.1	1.3
S.E.		7.3	49.2	3.2	0.7	1.5	12.7	0.9	1.1

Extra species:

Limnephilidae:3, Simuliumornatum: 9, Hydropsychidae: 1,

Ecdyonuridae: 1, Amphinemura: 2

TABLE 18

SIMULIUM RECOLONISATION STONE COMPARISON SAMPLE RESULTS

Sample taken on 19.6.75.

Species		*Hydrobia jenkinsi*	*Limnaea truncatula*	*Agapetus fuscipes*	*Gammarus pulex*	Chironomidae	*Baetis rhodani* nymph size categories 1-5mm.	6-10mm.	11-15mm.
Sample Stones	1	2	0	5	0	0	112	1	3
	2	13	15	23	5	1	11	2	7
	3	12	17	11	3	1	0	0	0
	4	36	97	12	2	0	6	1	2
	5	2	0	7	0	0	224	1	2
	6	67	248	2	1	0	20	2	0
	7	16	18	17	2	0	112	1	1
	8	28	18	5	4	1	1	0	0
Total		176	413	82	27	3	486	8	15
Average		22.0	51.6	10.3	3.4	0.4	60.8	1.0	1.9
S.E.		7.7	30.1	2.5	1.5	0.2	28.8	0.3	0.8

Extra species:

Hydropsychidae: 2, Amphinemura: 2

shows a slight significant increase in numbers. This may well be due to the development of individuals at the tail-end of this generation coinciding with the appearance of newly hatched individuals at the beginning of the next. Baetis rhodani (1 to 5mm. nymph size category) shows a very large increase in numbers as the summer generation of nymphs emerges and begins to develop between the completion of the first experiment and this experiment. In the larger B.rhodani nymphs (6-10 and 11-15mm.) in Chironomid larvae and in G.pulex, changes in numbers between the two dates were not Significant. The only other interesting point was the discovery of the Ephemeropheran May-fly larva of the family Ecdyonuridae and the Plecopteran Amphinemura during this sampling.

TWENTY FOUR HOUR DRIFT NETTING AND STONE COMPARISON EXPERIMENT (Map 4)

Methods

A direct measurement of drift was made using drift nets constructed as follows:

A metal bar, 1.8cm. wide, 0.3cm. thick and 150cms. long was pointed at both ends and was forced into each bank to provide a horizontal support. In this bar were drilled 2 sets of two 4mm. diam. holes, 14cms. apart. Through these holes went 3mm. diam. copper wire, 91cms. long and extending into the stream bed and this gave the vertical support for the drift nets as shown in plates 3 and 4. The drift nets themselves were, essentially, nylon cones of 10 strands/cm. mesh (aperture approx. 0.5mm.) of 13cm. by 13cm. mouth dimensions on square wire frames, and with the narrow ends tightly sewn on to a 2.5cm. diam. tube (see plate 2). Each of the two completed nets was secured to the vertical wire by 2 copper brackets with a screw, allowing the nets to be moved up or down to the required position in the water (plates 3 and 4).

Hourly samples were taken from the two nets over 24 hours from 1200 hr. to 1200 hr. on 25 and 26.6.75. Hourly samples were also taken from 2 of the centre ~~or~~ "B" stones from the near-neighbour stone experiment (stones 7B and 8B), which were a short distance downstream of the net so that they could be sampled without disturbing drift caught by the net. At each hourly sample, speed of flow measurements with a Pitot tube were made at the entrance to the nets and the water temperature was recorded.

Results

These drift net results cannot be analysed statistically because there is only 1 reading for every hour for drift and from the 2 sample

THE SAMPLE AREA. MAP 4

SHERBURN BECK

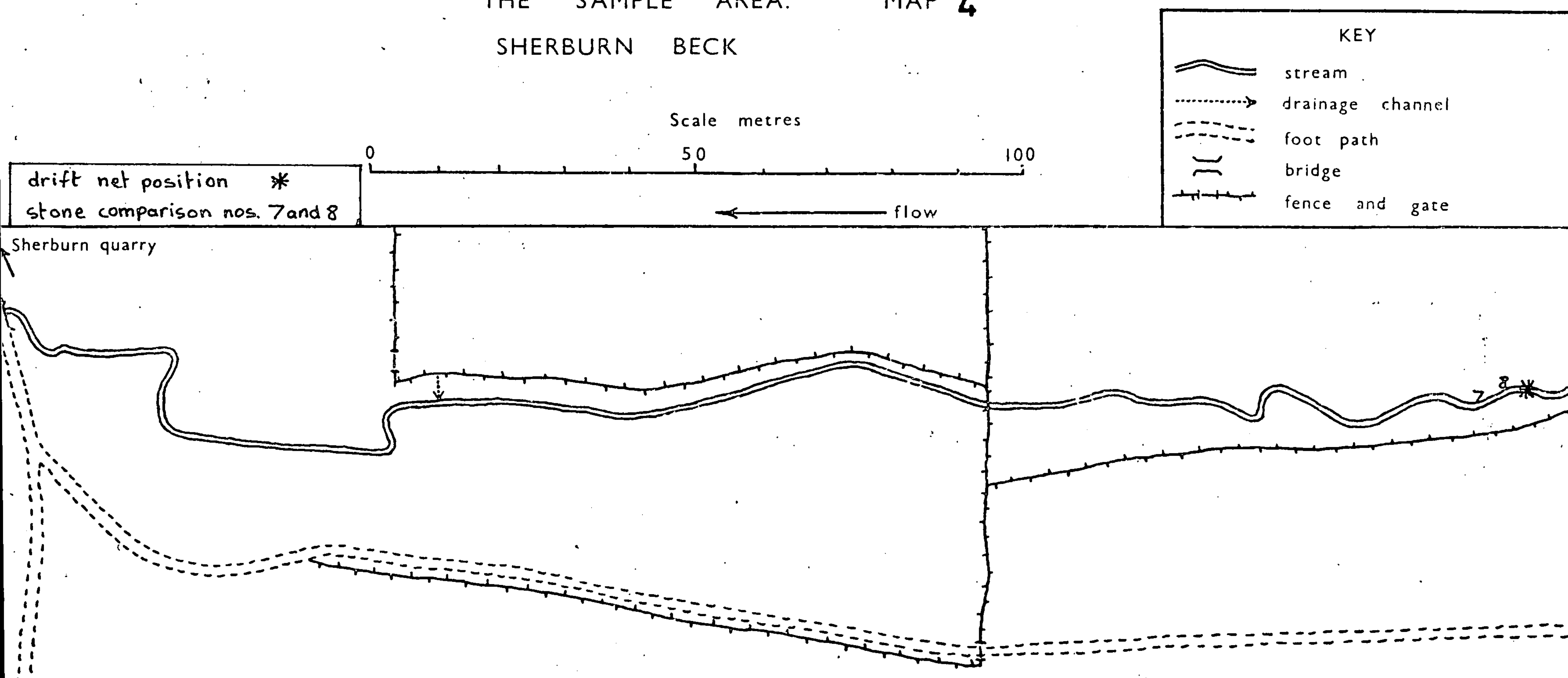


Plate 2. The drift net.

Plate 3. The drift nets in the raised position.

Plate 4. The drift nets lowered into the water.

stones. Attempts to repeat the experiment would not necessarily have made analysis possible because of the dynamic and changing nature of such small streams. Physical alterations in flow depth, speed and water temperature, and biological changes due to life cycle developments would have rendered a series of readings almost impossible to accumulate for average values.

From the combined surface area of the 2 nets used and a knowledge of the flow speed, which proved to be remarkably constant over 24 hours (Table 22), it was possible to determine the volume flow per hour which was being sampled. This was 16,190 l/hr. Because of the consistency of flow speed it was not considered necessary to alter figures for numbers of animals recorded, to number per hour per unit area of cross-section as mentioned by Elliott (1967). Instead, because all readings are comparable, they are left unaltered. The actual numbers recorded are shown in Tables 19, 20 and 21 and on Graphs 17, 18, 19 and 20. The 2 shown in tables and graphs was to mark disturbance in the beck by cattle. Physical measurement results are shown on Table 22 and on Graph 21. Stone 7 can be seen to show a consistently higher flow speed reading of 23.0cm/sec. while stone 8 has an average reading of 21.0 cm./sec. The water temperature readings show a diurnal fluctuation over the 24 hour study period with a maximum of 18.0°C at 16.00 - 17.00 hr. and a minimum of 11.0°C during the period 02.00 - 06.00 hrs. Since the beck is in a valley, when the sun reached the west, the water temperature began to drop as the stream was placed in partial shade. This began at about 18.00 hr. while it was still quite light. Similarly, as soon as dawn broke, at about 04.00 hrs. the temperature did not show a sudden increase but naturally exhibited delay and then a steady increase as the beck was less and less in shade. Another physical factor worth noting is the general weather, which, on 25.6.75. was clear, dry and sunny and on 26.6.75. was cloudy but still warm and dry. During the night there was a three-quarter moon and, as the night was clear, strong moonlight. The most numerous species caught from nets and stones were *Gammarus pulex*, *Baetis rhodani*, *Chironomidae*, *Hydrobia jenkinsi* and *Limnaea truncatula*, although not all were common for net and stone results.

If the drift net results are studied on Graphs 17 and 18, several species can be seen to show strong diurnal variations in numbers drifting. *G. pulex* is most marked in this respect. As soon as complete darkness prevailed, the number caught in the drift nets increased rapidly to reach a peak of 32 by 0200 hrs. which, as soon as dawn even began to break and when it was by no means fully light, decreased rapidly to reach a low point of 2 by 0500 hrs. Waters (1962) conducted similar studies on *Gammarus Limnaeus* in N. Americ.. and obtained similar results. As in *Gammarus pulex*, the increase and decrease in numbers is closely tuned to changes in light and not to temperature. Therefore, there seems to be little doubt here that drifting was related to light intensity changes. Moon-light does not seem to have caused any noticeable effect although this is one factor that would need more prolonged work to elucidate. Waters (1962) and Anderson (1966) consider it to depress nocturnal activity.

Baetis rhodani does not show such a clear diurnal variation. From 1200 hrs. until 1900 hrs. its numbers are very low. From then until the following morning at 0900 hrs. it shows 4 major increases and decreases in numbers at about 2100, 2300, 0400 and 0900 hrs. The middle 2 of these coincide with dusk and dawn but the other 2 fluctuations are just as large and cannot be fully explained. Water temperature decreases during the night might be postulated as contributing towards a stimulation of activity and therefore of drift in these insects, as the outer limits

TABLE 19

24 HOUR DRIFT NET SAMPLE RESULTS

Species / Time of Sampling	*Gammarus pulex*	*Baetis rhodani*	*Hydrobia jenkinsi*	*Limnaea truncatula*	*Agapetus fuscipes*	Chironomidae
*1200	2		1			13
13						9
14	1	1				1
15	4					1
*16	1	1	1			2
17	1					3
18	2			1		3
19	3		1			6
2000	1	3	1	4		1
21	6	7	2	2		1
22	2	1	2	6		1
23	6	5	3			1
2400	30	1	2			1
0100	29	3				
02	32	5				6
03	29	5				4
04	14	6				2
05	2	1				4
06	5	4				1
07	4	3				5
08	7	4	1			4
09	3	6				1
*1000	2	2				3
*1100	1	1				1

Extra species:

Limnephilidae: 3, Water beetle: 1

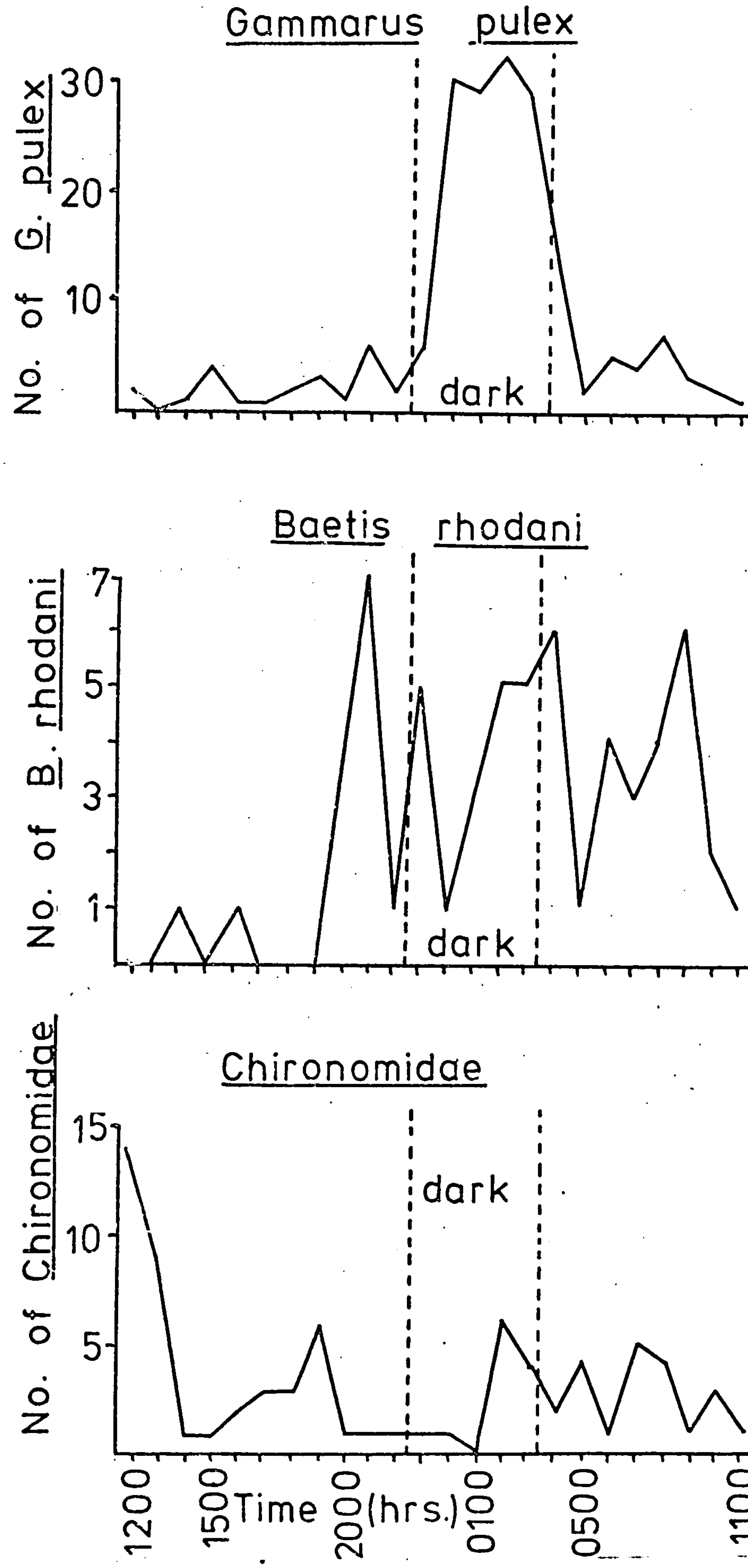
Simulium ornatum: 9, *Amphinemura*: 1

Elmidae (adult): 8, Acarina: 3

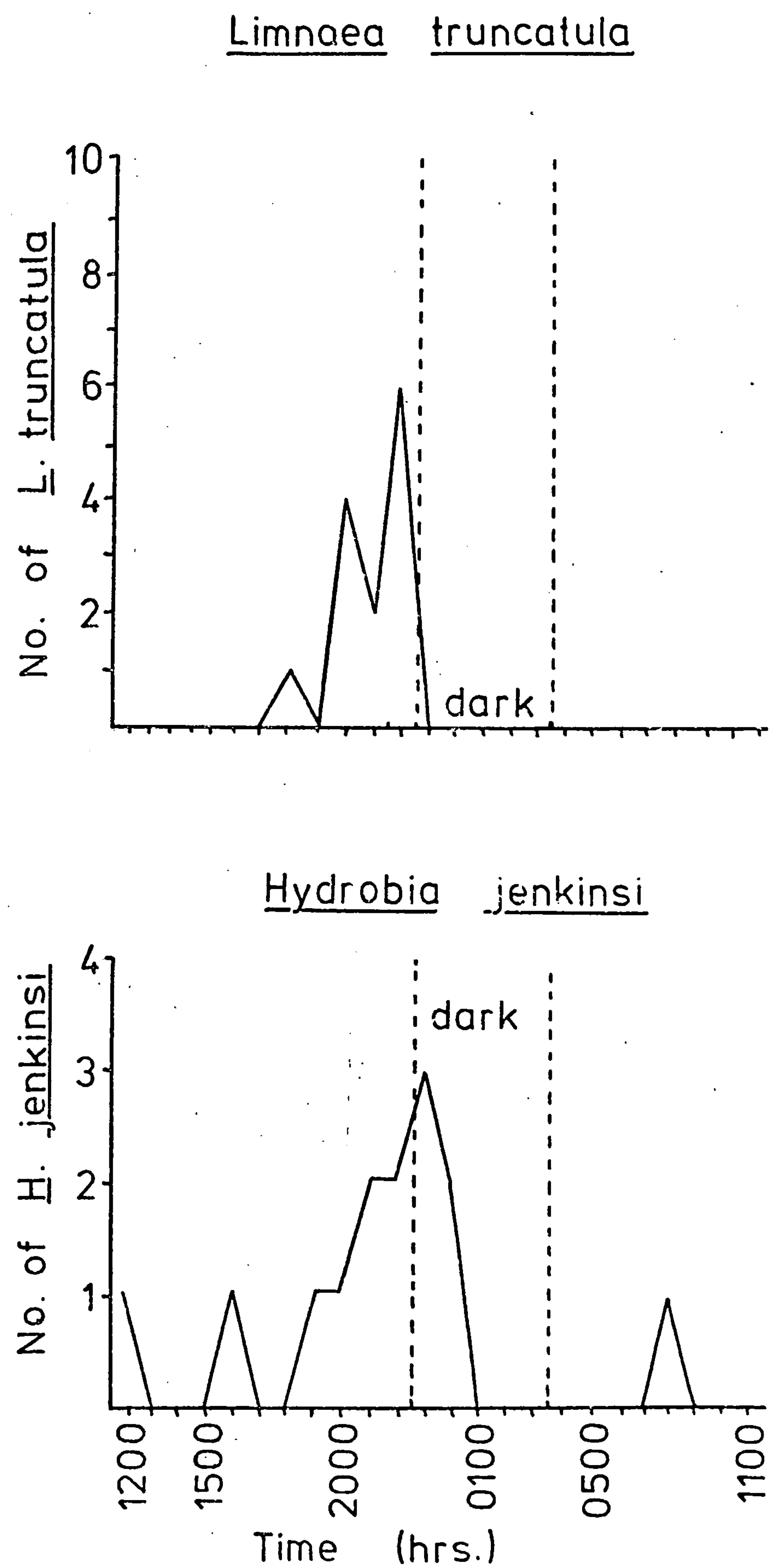
Stickleback (*Gasterosteus aculeatus*): 2

* = cattle disturbance upstream

24 hr drift net samples Graph 17



24 hr drift net samples Graph 18



of such activity seems to follow the temperature curve on Graph 21. A combination of water temperature and light affecting the activity of B. rhodani seems to be the most likely explanation. The Chironomidae do not seem to show any diurnal increase in drift. Apart from a drop in numbers due to the first sample, after 1200 hrs., all other fluctuations in numbers do not seem to be related to water temperature or light intensity. Nevertheless, the numbers in the drift here are greater than those collected from the 2 sample stones (Tables 20 and 21). Hydrobia jenkinsi and Limnaea truncatula both seem to show increased drifting as night approaches although the numbers involved for both species are rather small (Graph 18). H. jenkinsi seems particularly sensitive to the onset of dusk, where upon it increased its drift, but its numbers fell again soon after it became dark. L. truncatula also began to increase its drift at the same time but its numbers did not decrease until well into the night.

Stone 7, which was in a slightly faster stream flow, shows fairly high numbers of B. rhodani and of the 2 common Gastropod species (Graph 19). B. rhodani is shown in initially enormous numbers from the first sample taken at 1200 hrs. Thereafter its numbers became consistently low with little indication of an increase in drift due to water temperature or light intensity fluctuations. The 2 Gastropod species show something quite different. Both showed large increases in drift as dusk set, just before it became dark and both then showed a second but smaller peak in numbers during the night at 2400 hrs.

Stone 8, which was in a slower flowing area of water, only gives interesting results for the two Gastropod species. Although both species showed more apparently random fluctuations in numbers from 1200 to 1900 hrs. (see Graph 20) they also showed a definite increase in numbers caught as it became dark. Their numbers then decreased again

TABLE 20

24 HOUR STONE COMPARISON SAMPLE RESULTS

Stone 7 (Fast flow)

Species / Time of Sampling	*Gammarus pulex*	*Baetis rhodani*	*Hydrobia jenkinsi*	*Limnaea truncatula*	*Agapetus fuscipes*	*Chironomidae*
*1200	1	111	41	40	21	
13		10	2	3	1	1
14		17	3	6	1	
15		4	4	6		
*16		12		5		
17		1	36	87		
18		1	25	48		
19	1	4	73	197		
2000			63	287		
21	1		64	140	1	
22		1	35	76		
23		1	10	30		
2400	1	5	32	181		
0100		5	10	30		
02		6	2	23		
03	1	1	2	14		
04	1	4	5	12		
05			17	63		
06		3	4	21		
07		4	10	10		
08		3	1	6		2
09		2	2	8		
*1000		2	4	15		
*1100		3	2	1		

Extra species:

Simulium ornatum: 10, *Limnaea peregra*: 1,

Hydropsychidae: 2, *Acarina*: 3.

* = cattle disturbance upstream.

24 hr stone samples Graph 19

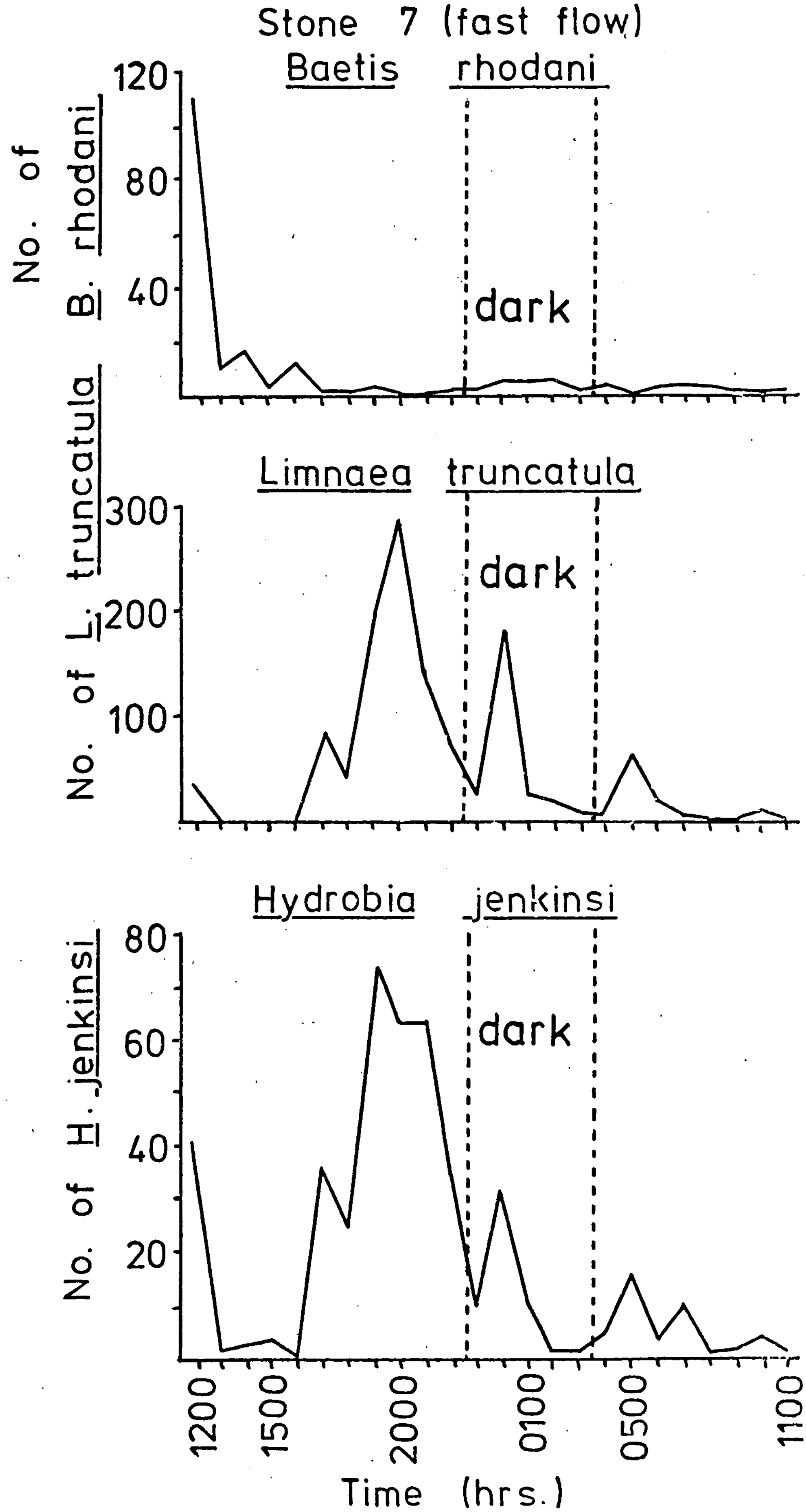


TABLE 21

24 HOUR STONE COMPARISON SAMPLE RESULTS

Stone 8 (Medium flow)

Species	Gammarus pulex	Baetis rhodani	Hydrobia jenkinsi	Limnaea truncatula	Agapetus fuscipes	Chironomidae
Time of Sampling						
*1200	1	2	28	23	1	
13			13	17		
14	1		5	21	2	
15			25	62	1	
*16	1		4	10		
17			12	34		
18			5	37		1
19	1		5	8		
2000			5	17		
21	2		4	13		
22	1		19	27	1	
23	2		10	34		
2400	4		1	73		
0100	1		1	10		
02			5	4		
03		2	2	3	1	
04			2	5		
05		1	3	7		
06			2	14		
07			4	20		
08			2	6		
09			1	3		
*1000		1		1		
*1100			2		1	

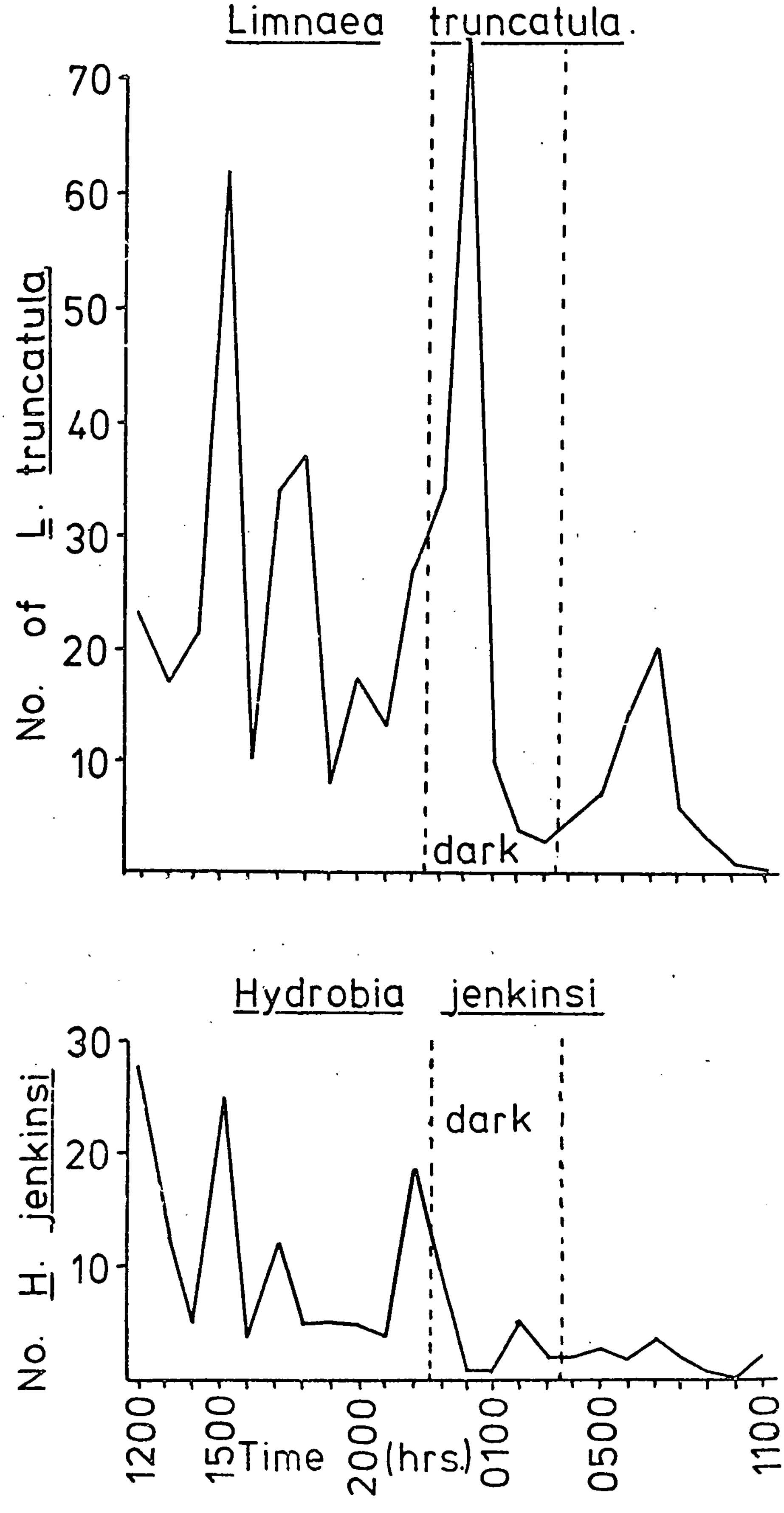
Extra species:

Glossiphonia complanata: 3, Acarina: 1.

* = cattle disturbance upstream

24 hr. stone samples. Graph 20

Stone 8 (medium flow).



by 0100 hrs.

Hydrobia jenkinsi and *Limnaea truncatula*, therefore, show a clear increase in drift as night approaches for the drift net results and both stone results. *G. pulex* only shows its night-time increase in activity for the drift net results and not for the stones. This suggests that at night it leaves its shelter and moves around on the stream bed in search of food. In so doing it is more likely to be swept up in the current and caught in the drift nets which were always carefully situated above the stream bed and not on it in order to catch only those individuals actually swept into the body of the current (Waters, 1962). *B. rhodani*, while showing small, but consistent numbers in drift and on a stone in the faster flowing area of the beck, does not appear to show a night-time increase in drift, and the *Chironomidae*, which were caught only in the drift nets in reasonable numbers also show no correlatable alteration in drift.

Overall, the several times that the stream was disturbed by cattle drinking water or grazing the stream bank vegetation, did not seem to affect results.

Table 22

TABLE 22

DRIFT NET AND STONE COMPARISON FLOW SPEED AND WATER TEMPERATURE RESULTS

	DRIFT NET			Stone 7	Stone 8	
Time of Sampling	Net top Pitot flow cm.	Net middle Pitot flow cm.	Net bottom Pitot flow cm.	Pitot flow cm.	Pitot flow cm.	Water temperature °C
1200	0.5 - 1.0	0.5 - 1.0	0.5 - 1.0	1.0	0.5 - 1.0	15.5
13	0.5 - 1.0	1.0	0.5 - 1.0	1.0	0.5 - 1.0	15.5
14	0.5 - 1.0	1.0	0.5 - 1.0	1.0	1.0	16.5
15	0.5 - 1.0	1.0	0.5 - 1.0	1.0 - 1.5	1.0	17.5
16	0.5 - 1.0	1.0	0.5 - 1.0	1.0 - 1.5	1.0	18.0
17	1.0	1.0	0.5 - 1.0	1.0	1.0	18.0
18	0.5 - 1.0	1.0	0.5 - 1.0	1.0	0.5	17.5
19	0.5 - 1.0	0.5 - 1.0	0.5 - 1.0	1.0	0.5	17.0
2000	0.5 - 1.0	0.5 - 1.0	0.5 - 1.0	1.0	1.0	15.5
21	0.5 - 1.0	1.0	0.5 - 1.0	1.0	1.0	15.0
22	0.5 - 1.0	1.0	0.5 - 1.0	1.0	1.0	14.0
23	0.5	0.5	0.5	1.0	1.0	13.0
2400	0.5	0.5	0.5	0.5 - 1.0	0.5	12.5
0100	0.5	0.5	0.5	0.5 - 1.0	0.5 - 1.0	12.0
02	0.5	0.5	0.5	1.0	1.0	11.0
03	0.5	0.5	0.5	1.0	1.0	11.0
04	0.5	0.5	0.5	1.0	1.0	11.0
05	0.5	0.5	0.5	1.0	1.0	11.0
06	0.5	0.5	0.5	1.0	1.0	11.0
07	0.5	0.5	0.5	1.0 - 1.5	1.0	11.5
08	0.5	0.5	0.5	1.0 - 1.5	1.0	12.0
09	0.5	0.5	0.5	1.0 - 1.5	1.0	12.0
1000	0.5	0.5	0.5	1.0 - 1.5	1.0	12.5
1100	0.5	0.5	0.5	1.0 - 1.5	1.0	13.0
Average flow cm./sec	17.0	17.0	17.0	23.0	21.0	

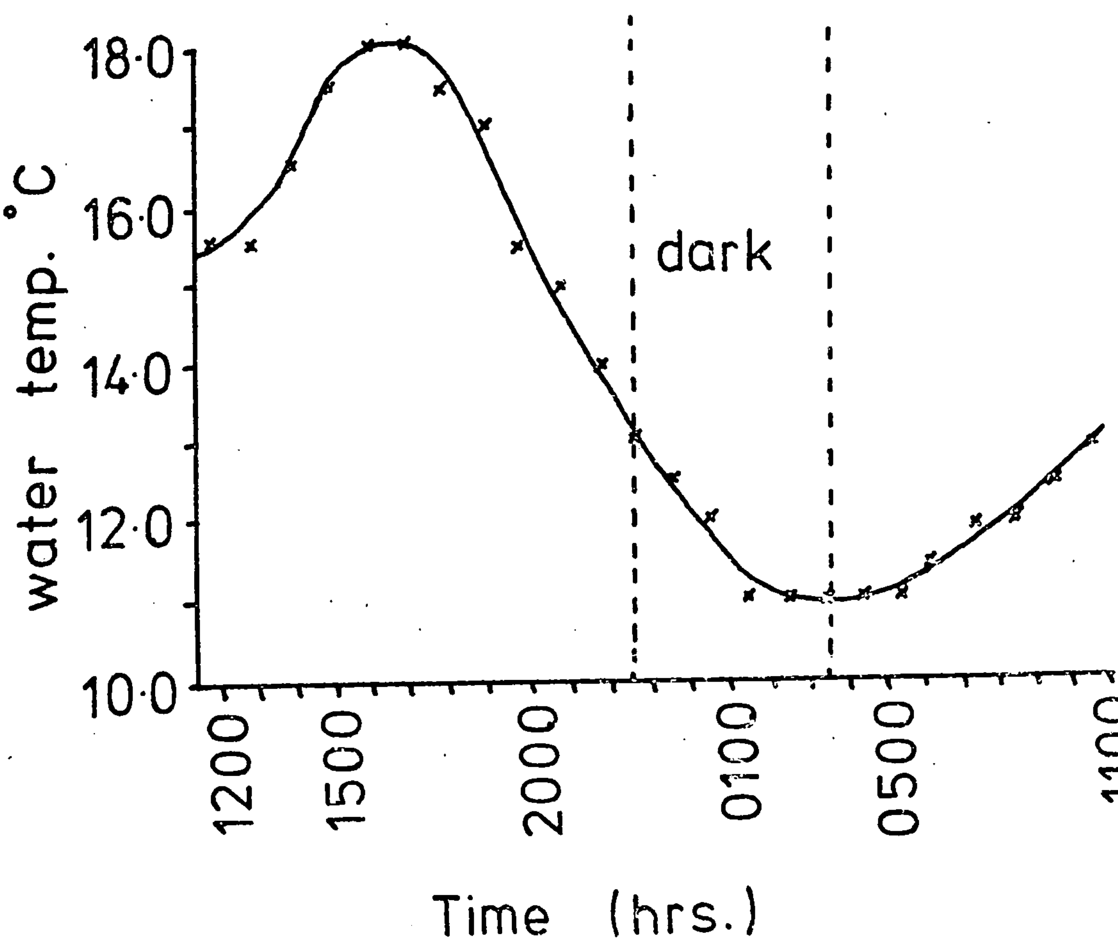
Drift Net Volume flow determination

Average flow speed = 17.0 cms./second

Total area of drift net exposed to current = 264 sq. cms.

Volume flow = 16,190 litres per hour

24 hr. water temperature readings. Graph 21



STREAM-BED SAMPLING EXPERIMENT FOR BAETIS RHODANI AND GAMMARUS PULEX (Map 5)

Methods

This experiment was an attempt to obtain an idea of the numbers of G.pulex and B.rhodani to be found in a certain area of stream bed over different substrata. A 12cms. by 12cms. metal frame was used and was dropped onto the stream bed in a random fashion. This was sampled 3 times for each sample area, giving a total sample area of $432cm^2$. The position of each sample area was mapped and the speed of flow with a Pitot tube was measured. Notes on the type of substratum were also made. The actual sample technique involved disturbing the substratum so that animals were washed into a large square net, with netting of 8 meshes/cm. which was held just downstream of the metal frame and fitted flush with the bed, to ensure that all animals disturbed were caught.

The animals caught in the net were transferred to glass jars and counting and measuring done in the laboratory.

Results

4 samples were taken from Sherburn beck. In view of the large numbers of G.pulex in drift during the night this experiment was an attempt to find out the actual numbers living on the stream bed. As the results show (Table 23), the numbers collected are quite variable. Furthermore, large numbers of G.pulex were collected only from a stream bed with fist-sized stones and some smaller stones ~~and~~ which was partially covered in detritus. A stream-bed with small pebbles showed lower numbers for the area sampled and totally mud covered substrata with no stones showed almost no G.pulex individuals at all. Further stream-bed sampling was therefore stopped as it became quite obvious that the number collected was related to substratum and it was not possible to obtain an average

THE SAMPLE AREA. MAP 5

SHERBURN BECK

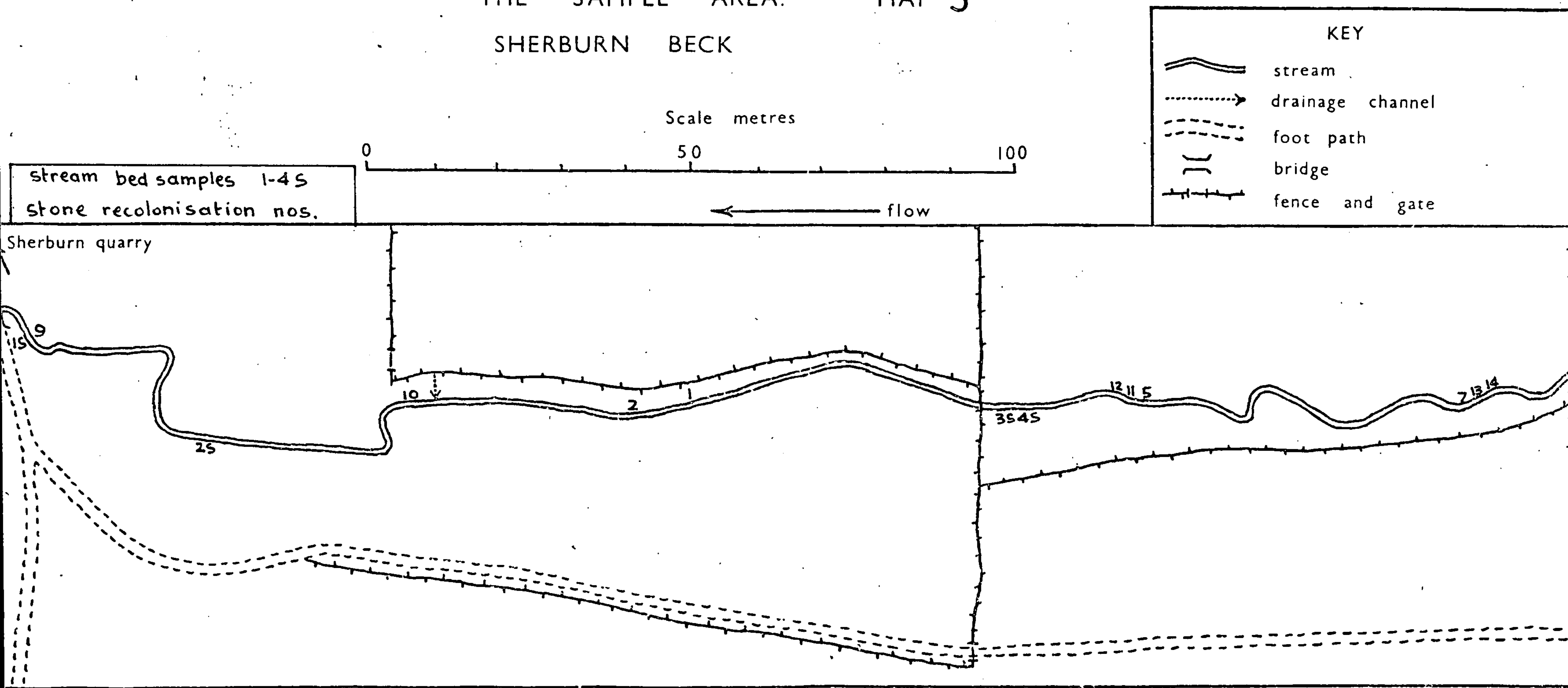


TABLE 23

NUMBERS OF BAETIS RHODANI AND GAMMARUS PULEX
IN A 432 SQ. CM. AREA OF STREAM BOTTOM

Sample Number	Baetis rhodani nymph size 1 - 5 mm.	nymph size 6 - 10 mm.	nymph size 11 - 15 mm.	Gammarus pulex
1	1	34	23	67
2	1	16	7	56
3	4	28	26	106
4	1	59	40	132

figure. While some areas were capable of supporting very large numbers of *G. pulex* individuals they were not typical. Such a large variation is mentioned by Waters (1961). The *Baetis rhodani* nymphs also collected, counted and measured, show a roughly parallel increase in numbers with those of *G. pulex*, being found most commonly on larger stones. This is most likely to be their most suitable habitat, for they can extract oxygen from the vortices of water which flow round such rocks and can also graze on the organic material present. The smaller nymphs are grossly under-represented because of the large mesh size of the net used for collection (8 strands/cm).

ADDITIONAL STONE RECOLONISATION EXPERIMENT FOR BAETIS RHODANI AND GAMMARUS PULEX (Map 5)

Methods

10 stones were set up, as for the all-species initial stone recolonisation experiments, but specifically here to study recolonisation by B. rhodani nymphs (which were very numerous at this time), and by G. pulex. The previous generation sampled in May were probably overwintering nymphs or an early summer generation, while this generation, their off-spring, could take full advantage of the favourable summer weather and hatched from numerous egg batches seen on stones.

Wherever possible, the stones from the near-neighbour experiment were used, but some were omitted, either because they had disappeared or because they did not have large enough numbers of B. rhodani (mainly in the slower flowing areas). 4 of the 8 "B" stones from the near-neighbour stone sets were used and another 6 stones set up and numbered from 8 upwards to avoid confusion with stones from the previous experiment. The 10 stones were sampled from 4-day to 1-day intervals.

Results

These results are shown on Graphs 22 and 23. As for the first recolonisation experiments, the Null Hypothesis here is that there is no relationship between numbers of individuals captured and duration of sampling interval. The 1 to 5 mm. category of nymphs show a Significant decrease in numbers when sampled at a one day interval. As the sampling interval increases the numbers recolonising the stones increased and after the 3-day interval Significantly decreased. Such a decrease seems to be related to a decrease in water temperature although further work would be needed to be sure. When the log. number is plotted (Graph 23) a straight line relationship for the initial recolonisation is given, indicating an exponential rate, but more points on this graph would give it more reliability. One especially interesting point is the sudden increase in flow speed to 26.2 cms./sec. during the 3-day sampling interval. This was caused by several days of heavy rain and the corresponding increase in numbers of small nymphs recolonising stones could well be because a lot more were being carried in the drift. The larger nymph sizes do not show a similar increase in numbers recolonising, probably because they could resist the current better than the smallest nymphs. The 6 to 10 mm. category of nymphs, which was much less numerous than the previous category, showed an initially Significant decrease in numbers and it was not until after the 3-day sample interval that a Significant increase in numbers was shown. Why there is such a delay in recolonisation is not altogether clear. It may be that some of these nymphs were fully grown and were emerging during the experiment thus altering the comparability of each sample reading. The 11 to 15 mm. size category showed Non Significant fluctuations in numbers as did G. pulex.

As some of the stones were identical and all were sampled in the same stretch of beck, these results provide an ideal opportunity to compare general changes in numbers colonising stones over the 3-weeks between the S. ornatum results (Tables 17 and 18) and those for B. rhodani and G. pulex. The 1 to 5 mm. and 6 to 10 mm. nymphal size categories both showed a Significant increase in numbers over this 3-week period, while the 11 to 15 mm. category did not. As the summer generation of nymphs continues to hatch and develop, such increases in numbers are quite expected. In contrast, the numbers of G. pulex did not show a Significant increase over this period, even though considerable numbers of juveniles were being seen. A corresponding mortality of adults as the juveniles develop, or a tendency for an under-represented proportion of the adults recolonising stones may have caused this.

TABLE 24

ADDITIONAL RECOLONISATION EXPERIMENTS WITH NUMBERS OF BAETIS RHODANI

Size category 1 - 5 mm.

Date (July)	8	12	15	17	18
Sampling interval (days)	0	4	3	2	1
Stone Nos. (see text) 9	28	89	176	50	35
10	111	135	125	89	110
1	230	187	239	144	133
2	45	45	134	121	98
5	282	164	287	222	270
11	184	164	256	300	251
12	80	6	71	1	4
7	116	135	138	40	18
13	85	24	8	25	19
14	71	80	86	271	118
Total	1232	1027	1520	1263	1056
Average	123.2	102.7	152.0	126.3	105.6
S.D.	82.8	63.4	88.3	106.1	94.1
S.E.	26.2	20.0	27.9	33.5	29.8
Log Average	2.09	2.01	2.18	2.10	2.03

Size category 6 - 10 mm.

Date (July)	8	12	15	17	18
Sampling interval (days)	0	4	3	2	1
Stone Nos. (see text) 9	54	69	66	23	29
10	25	45	25	26	26
1	11	22	2	6	8
2	37	36	25	30	68
5	6	18	1	24	10
11	5	5	4	19	5
12	31	1	7		8
7	27	8	6	3	5
13	24	5	1	6	5
14	14	10	4	12	3
Total	234	219	141	149	167
Average	23.4	21.9	14.1	14.9	16.7
S.D.	15.2	21.9	20.4	10.8	20.2
S.E.	4.8	6.9	6.5	3.4	6.4

TABLE 25

ADDITIONAL RECOLONISATION EXPERIMENTS WITH NUMBERS OF BAETIS RHODANI

Size category 11 - 15 mm.

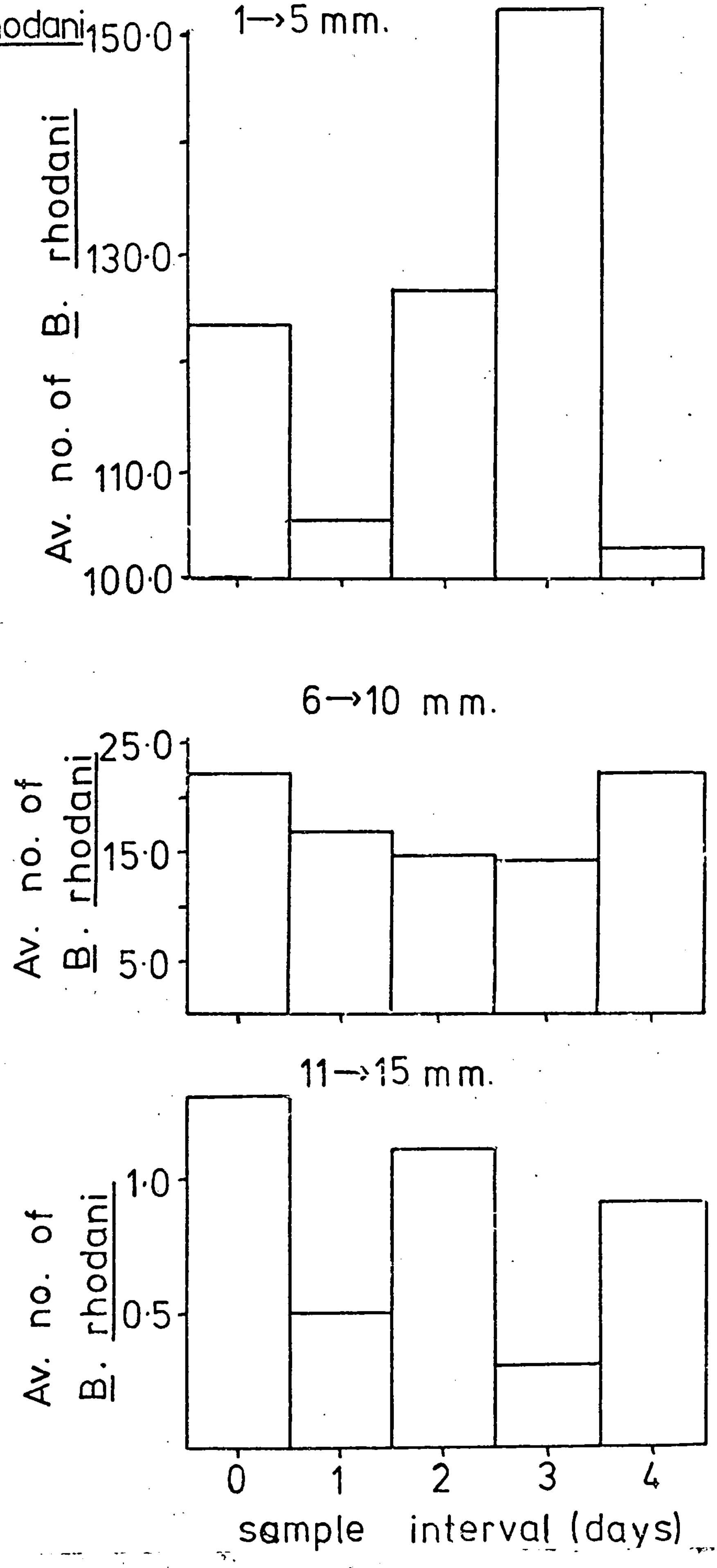
		8	12	15	17	18
Date (July)		8	12	15	17	18
Sampling interval (days)		0	4	3	2	1
Stone Nos. (see text)	9	5	8	1	2	2
	10	1				
	1					
	2	5			5	
	5	1		1	1	
	11				2	1
	12					
	7					1
	13	1		1		
	14		1		1	1
Total		13	9	3	11	5
Average		1.3	0.9	0.3	1.1	0.5
S.D.		2.0	2.5	0.5	1.6	0.7
S.E.		0.6	0.8	0.2	0.5	0.2

ADDITIONAL RECOLONISATION EXPERIMENTS WITH NUMBERS OF GAMMARUS PULEX

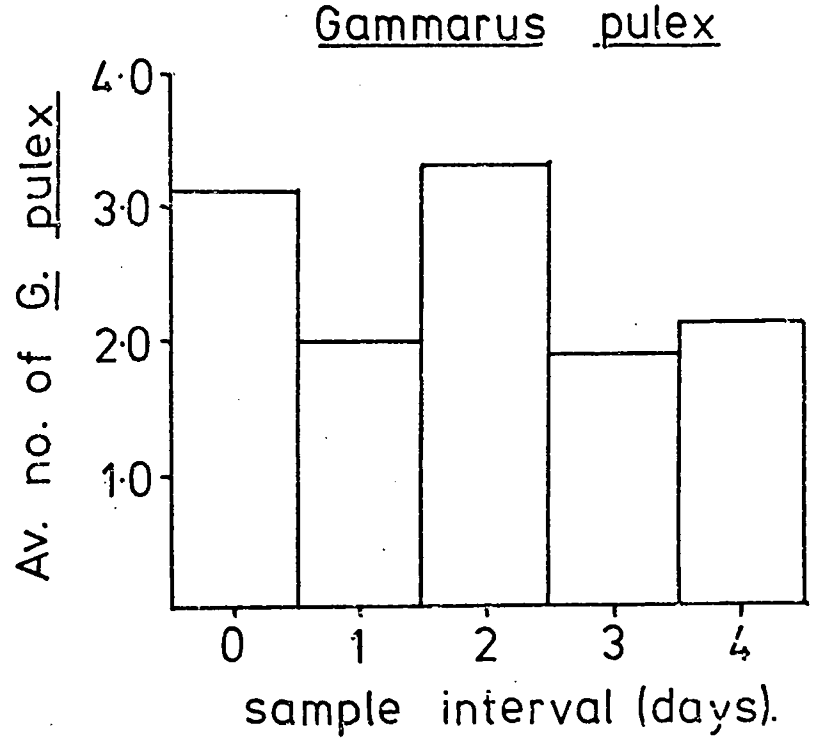
		8	12	15	17	18
Date (July)		8	12	15	17	18
Sampling interval (days)		0	4	3	2	1
Stone Nos. (see text)	9	10	2	2	9	
	10		1			
	1		2			
	2	1	1			2
	5		5			
	11	2	1	1		1
	12	3	4	1	13	15
	7	2		2	7	1
	13	5	5	9	4	1
	14	8		4		
Total		31	21	19	33	20
Average		3.1	2.1	1.9	3.3	2.0
S.D.		3.5	1.9	2.8	4.8	4.6
S.E.		1.1	0.6	0.9	1.5	1.5

Additional stone recolonisation. Graph 22

Baetis rhodani



Additional stone recolonisation. Graph 23



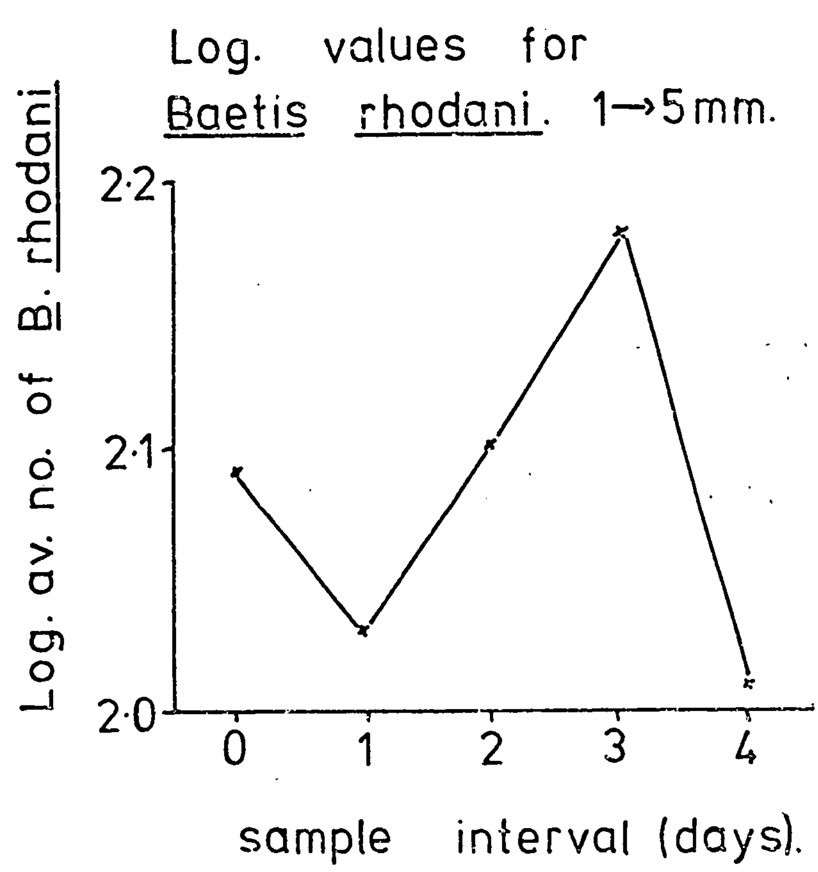


TABLE 26

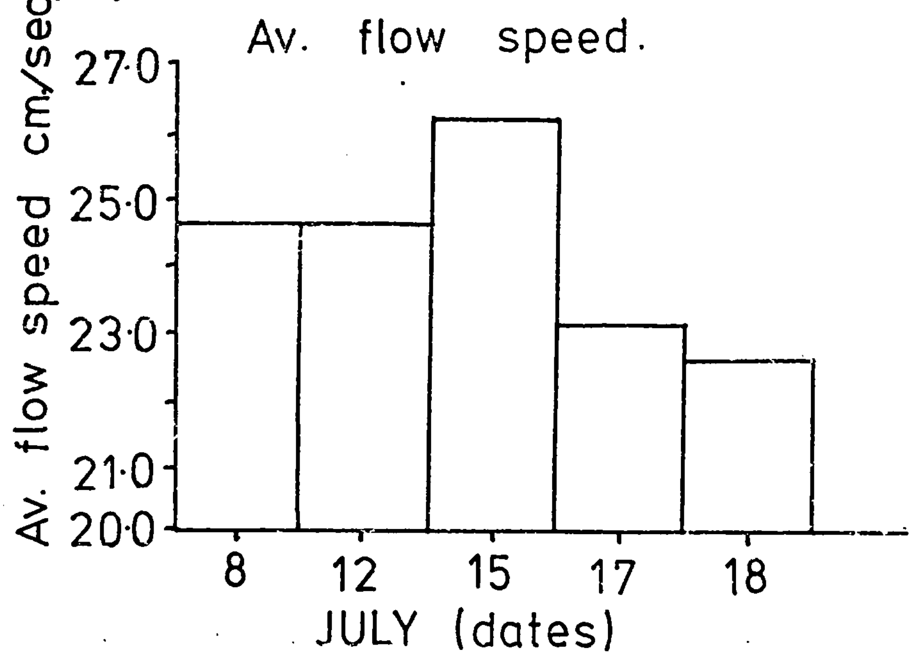
NEAR-NEIGHBOUR STONE EXPERIMENT, SIMULIUM EXPERIMENT AND BAETIS RECOLONISATION EXPERIMENT

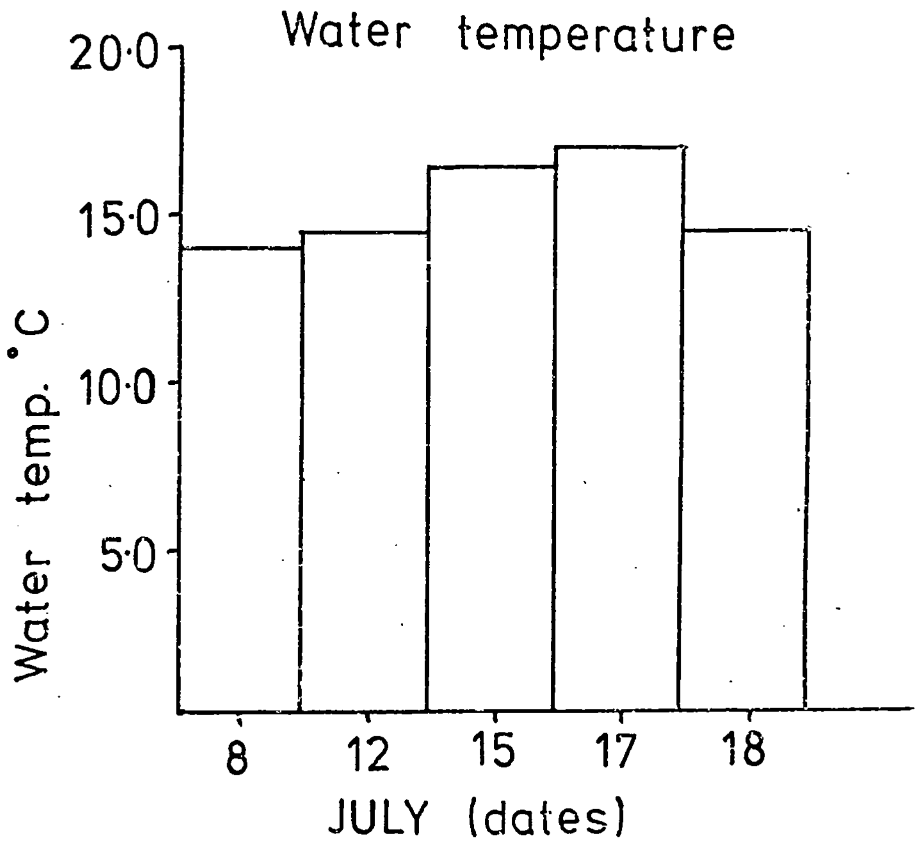
PHYSICAL MEASUREMENT RESULTS

	Near-neighbour stone experiment			Simulium recolonisation experiment on grass and stone				*Baetis* recolonisation experiment				
Date of Sample	28.5.75.	31.5.75.	6.6.75.	13.6.75.	19.6.75.	13.6.75.	19.6.75.	8.7.75.	12.7.75.	15.7.75.	17.7.75.	18.7.75.
Period since last sample (days)	0	3	6	0 Grass reading	6 Grass reading	0 Stone reading	6 Stone reading	0	4	3	2	1
Average flow speed (Pitot)	1.3	1.3	1.0	1.3	1.5	1.1	1.1	1.3	1.3	1.4	1.1	1.1
Average flow speed (cm./sec.)	24.0	25.2	22.4	24.6	27.4	22.8	24.2	24.6	24.6	26.2	23.2	22.6
Time of 1st temperature reading	1030	1515	1300	1300	1545			1430	1525	1545	1530	1600
°C	8.0	10.0	17.5	13.0	15.5			14.0*	14.5*	16.5*	17.0*	14.5*
Time of 2nd temperature reading	1600	2000	1430					2045	1700	1710	1705	1715
°C	9.0	9.0	18.5					12.5	14.0	14.5	15.0	14.0
Flow depth (cm.)		6.5	7.5	1.0	1.0					4.0	3.5	3.0
Weather remarks	Cool, dry.	Mild, dry.	Mild, wet.	Rain	Mild, windy.				Mild, wet.	Windy, wet.	Mild, wet.	Rain

Table 26

Additional stone recolonisation Graph 24
physical measurements.





A final consideration of the most extensively studied species, Baetis rhodani, is worthwhile. Some of the sample results over the whole period of the project have been used to see how numbers of this species varied during the late spring and early summer.

To make the results as comparable as possible, only numbers from fast flow areas and when full recolonisation was thought to have occurred, were used. The number of B. rhodani nymphs collected during the first of the 24-hr. drift net sampling period have been used. These results, are from one stone only and should therefore be treated with caution. All the other results are the average of at least 8 stones in similar stretches of the beck and from stones of a similar size. Results recorded during abnormal weather conditions have been avoided. Near-neighbour stone recolonisation results have not been included because nymphs were not categorised as to size and because these readings largely fall within the first stone recolonisation experiment sampling period. The readings (Table 27) considered are the beginning and end of the all-species stone sampling, the second of the 2 Simulium ornatum stone samples, stone 7 for the drift stone comparison results and the first B. rhodani recolonisation experiment sample (Tables 24 and 25). As already shown (see page 62) there was a Significant increase between 6.6.75. and 19.6.75. in numbers for the 1 to 5 mm. category of nymphs. The 6 to 10 mm. category does not show a Significant increase in numbers until nearly 3 weeks after the increase in numbers for smaller nymphs, while the 11 to 15 mm. category shows no Significant increases.

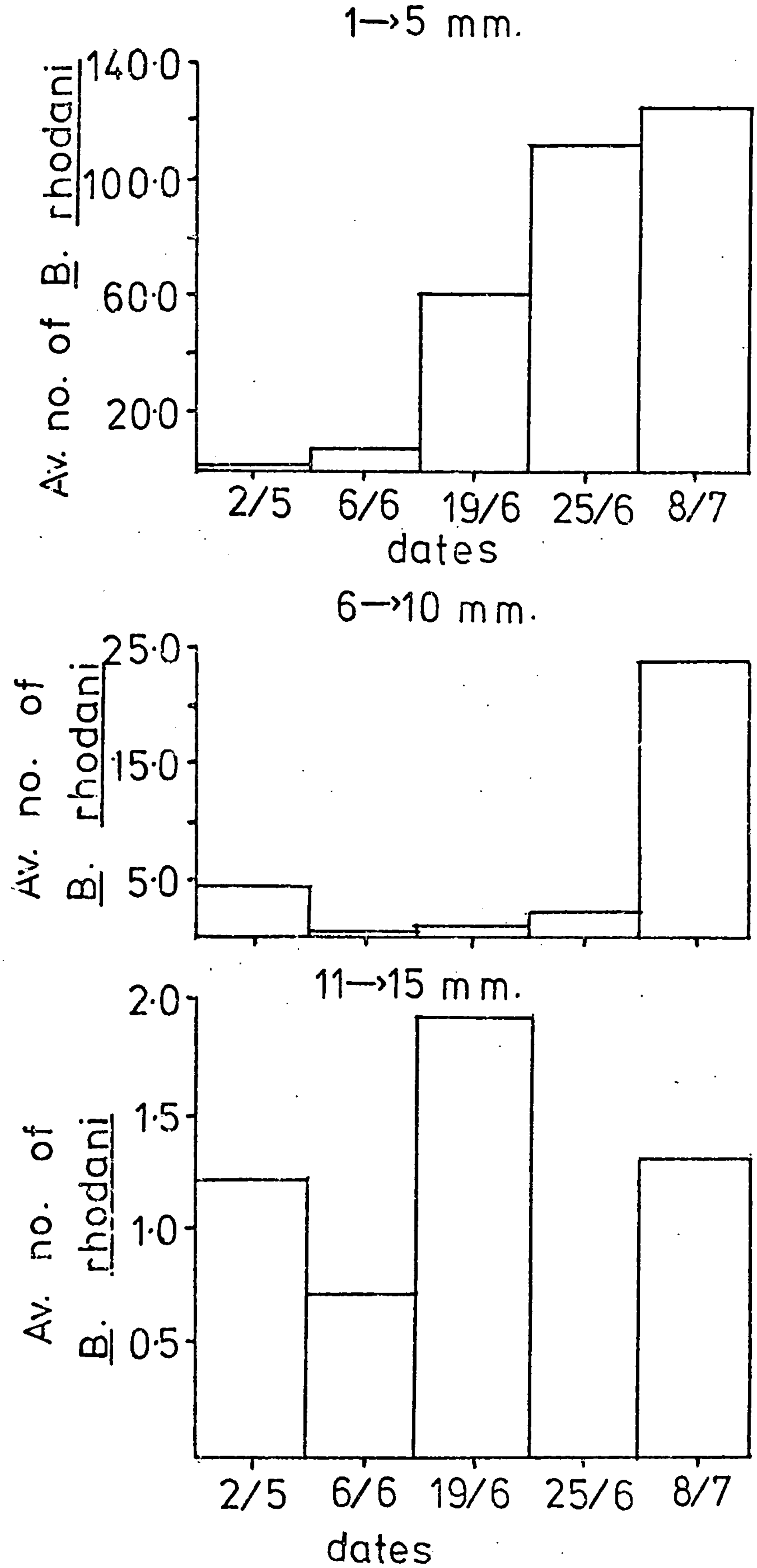
This clearly indicates the hatching and development of a summer generation of nymphs (Macan, 1957b; Elliott, 1967), which, by 8.7.75. are passing into the 6 to 10 mm. category as they grow. The lower numbers by this time are probably due to the considerable mortality that the smallest nymphs suffer (approximately 60 to 70% here) as they are eaten

TABLE 27

COMPARISON SAMPLE RESULTS FOR BAETIS RHODANI DURING THE TOTAL SAMPLE PERIOD

Experiment	1st recolonisation experiment. 2.5.75. fast flow regime			1st recolonisation experiment. 6.6.75. fast flow regime			*Simulium* recolonisation stone comparison 19.6.75.			24 hour stone comparison readings. Stone 7 25.6.75.			Additional recolonisation experiment with *B.rhodani*. 8.7.75.		
Nymphal size categories	size 1-5mm	size 6-10mm	size 11-15mm	size 1-5mm	size 6-10mm	size 11-15mm	size 1-5mm	size 6-10mm	size 11-15mm	size 1-5mm	size 6-10mm	size 11-15mm	size 1-5mm	size 6-10mm	size 11-15mm
Total or average	1.3	4.2	1.2	8.0	0.4	0.7	60.8	1.0	1.9	111	2	0	123.2	23.4	1.3
S.E.	0.4	1.2	0.9	3.7	0.2	0.2	28.8	0.3	0.8				26.2	4.8	0.6

Comparison results for Baetis rhodani from MAY to JULY. Graph 25



by sticklebacks (Gasterosteus aculeatus) and Trout (Salmo trutta) of which one young specimen was seen in the bec..

GENERAL DISCUSSION

The physical (environmental) and biological factors affecting drift will firstly be considered. The main physical factors which have been considered in this thesis and by other workers are light intensity, (including moonlight intensity), current depth, current speed, water temperature and nature of the stream bed.

Light intensity is stated as being one of the main factors affecting drift. Hynes (1970) notes that diurnal variation in drift is always related to light and dark periods. He also discusses work involving artificial illumination which indicates the same thing, and Muller (1963) notes that the "time signal" is given by the change from light to dark or vice versa. Other workers which mention that increased drifting occurs at night are Elliott (1965 a,b, 1967 a,b), Muller (1965), Tanaka (1960) and Waters (1962). My results also indicate that Gammarus pulex, Hydrobia jenkinsi and Limnaea truncatula increase their drift at night while the latter two species also increase their rate of recolonisation of stones during the same period (Graphs 18, 19 and 20). It seems quite certain, in the light of previous work, that the actual change from light to dark triggers off the increase in drift and vice versa at dawn. Periodicity or circadian rhythms do not appear to play a major role. Anderson (1966) explains nocturnal drifting by suggesting that it may have evolved as a protective or avoidance mechanism to escape attack by predators which hunt by sight.

Moonlight as a possible factor which may depress nocturnal activity in stream invertebrates is noted by Waters (1962) and Anderson (1966). Waters suggests that magnitude of drift may be, in part, a direct negative function of moonlight intensity. The drift net sampling that I undertook had a three-quarter moon in the sky and its pale light was falling on the stream just after midnight. Apart from a minor decrease in the number of G.pulex caught at this period (Graph 17) which cannot be statistically verified, no obvious effect was noticed from my sample results. Further readings on successive moonlit and un-moonlit nights would be necessary to make worthwhile conclusions.

Depth is mentioned by Percival and Whitehead (1927) who note that depth affects current speed. My stream physical measurement results largely agree with this (Graphs 13 and 14) in showing that current speed is a function of depth. There do appear to be complicating factors involved, however, (for my study stream in particular) such as stream width, and the nature of the stream bed, which may sometimes cause an increase in flow speed with depth instead of a decrease of flow speed with depth increase.

Current speed is mentioned by Dendy (1944), and Roos (1957), Minckley (1963) and Horton (1961) all refer to cases of increased drift after extra large discharges of water or spates. Percival and Whitehead (1927) make some early and accurate observations on changes in susceptibility of certain animals to currents which are not undergoing sudden spates. Agapetus spp. are said to be variable "in a way that can be correlated with the speed of the current", while a Baetis sp. is noted as being swept away by certain maximum current velocities. Other very rapid stretches of water are noted to be devoid of such organisms as Chironomidae while Limnaea peregra is noted as being found in lower water speeds. This is generalised by Elliott (1967a) who notes that "the drifting of Plecoptera and Ephemeroptera .... vary considerably .... with rate of flow". The whole concept of current effects on fresh-water fauna is excellently discussed by Jaag and Ambuhl (1964). They state that typical species of animals are not only affected by a current differently but that they also react quite differently. Specialists are mentioned for high current velocities such as species of Baetis, Simulium and Hydropsyche while some species such as Gammarus pulex are noted as finding their optimum at a relatively low velocity. The reaction of each species to the current it is living in is well exemplified by considering Baetis sp. and Simulium sp. which deliberately expose themselves to the current and are termed "lithophile fauna". They seem to seek a current to move in to, while others such as Ecdyonurus and Hydropsyche sp. which were found in Sherburn beck, behave more or less indifferently. A direct relationship between current speed and drift rate, however, is not usually possible to prove. As Jaag and Ambuhl go on to state, many types of stream bed substrata, particularly those with numerous stones, cause the formation of dead water pockets where there is some movement of the water but with its impact broken. This means that quite rapid currents over a stony bed will still allow the presence of a varied fauna which, although they cannot withstand direct contact with the current, can exist in sheltered areas. As my results show (see first stone recolonisation results discussion) G.pulex is indeed a poor swimmer and tends to accumulate in slower flowing areas. Furthermore its distribution can be patchy, very large numbers being found beneath the shelter of a single stone where they feed upon detritus. Limnaea truncatula and Hydrobia jenkinsi are also associated with slow flowing areas while Agapetus fuscipes seems to exhibit a tendency to drift in relation to current speeds, also accumulating in slow flowing areas. Baetis rhodani is shown to prefer fast flow areas while the Chironomidae are not shown to prefer either current, although Percival and Whitehead (1927) indicate that very rapid currents with fine deposits are practically devoid of them.

Water temperature is noted by Moon (1940) who states that the reactions of organisms to temperature will influence its movements, while Macan (1957) dismisses the importance of temperature as a means of classification for Ephemeroptera, preferring one using substratum. Waters (1962) suggests that temperature may affect the magnitude of nocturnal drift rate. Evidence in support of a general increase in drifting and of rate of recolonisation is given by my results (see first stone recolonisation results discussion). A decrease in numbers of L. truncatula can be tentatively related to a corresponding decrease in water temperature, while the drift net results (see results discussion) seem to suggest a nocturnal increase in Baetis rhodani activity with a decrease in temperature.

The nature of the stream bed is one of the more important factors affecting the distribution of stream animals. Not only does it affect the current speed, as discussed above, but it also provides differing plant substrata to which animals can cling to, hide within and feed from. The stream bed sampling results included in this thesis clearly indicate that G. pulex and B. rhodani are more commonly found on gravelly beds with larger stones and considerable amounts of detritus (see results discussion). Other workers such as Muller (1954), Macan (1957), Jaag and Ambuhl (1964), Percival and Whitehead (1927), Egglishaw and Morgan (1965), Minckley (1963) and Waters (1961) consider stream bed substratum as a factor affecting drift. Percival and Whitehead make the earliest thorough analysis here. They categorise substrata into loose stones, cemented stones, stones bearing Cladophora and other filamentous algae, among loose moss, and among thick moss. It is among the latter that they find the largest populations of animals although some species such as Baetis sp. are restricted to loose stones which are free of vegetation. From observations I have made myself in Sherburn beck, some species such as G. pulex can be found in very large numbers in clumps of rotting vegetation, while Minckley (1963) notes that this same species was common in leaf-packets in an American stream and Beak (1938) talks of a concentration of

Gammarids in macrophytic vegetation. Such animals are active enough to emerge into the current at times and, therefore, favourable substrata can be seen as liable to increase the number of organisms being caught up in the current which will increase the amount of drift. Muller (1954) notes that particular groups of animals such as the Hydracarina and Coleoptera (both represented in Sherburn beck) often form a relatively large portion of the benthos population but very seldom occur in the drift. He attributes this to their mode of life as they are usually found only among thick plant growth on stones and so largely avoid the mechanical influence of the current. Dendy (1944) also states that numerous benthos animals need not necessarily be abundant in drift samples. Such animals which are restricted to these habitats because of their methods of feeding, will definitely be under-represented in drift samples, but other animals such as Gammarids, which move around more between habitats and are capable of colonising leaf packets or rotting clumps of vegetation in large numbers will tend to increase their contribution to drift, so not all benthos organisms can be assumed to be under-represented in drift. Jaag and Ambuhl (1964) help to show here that it is not only the food that substrata offer which is important to animals, but also the physical shelter from current. Some organisms may actually rely on drift to supply them with food such as Simuliid larvae and are therefore forced to take up an exposed position in the current, while Ephemeropteran nymphs which rely on a steady oxygen supply from fast flowing water must do the same. It is organisms such as these which tend to furnish most drift material as well as poor swimming scavengers such as Gammarids. Because of the obvious connection between substratum and drift it is hardly surprising that it has been used by Percival and Whitehead as a means of stream classification, also noted by Macan (1957). Waters (1961) makes a further suggestion in that he proposes drift rate to reflect, in proper proportions, all productive components of the stream's bottom fauna by means of a sort of mixing process. If the degree of over or under representation for any species can be determined, then this method seems potentially useful for obtaining a quick, convenient and accurate idea of the faunal composition of a stream bed in the upstream vicinity of the drift net.

The Morphology, or physical shape and characteristics of the animal are liable to affect the force which the current can exert on them and also their ability to cling to certain substrata. Hynes (1960) mentions the fact that heavy creatures such as snails and caddis-worms with stony cases tend to be rare in drift. Waters (1962) notes that few Glossosoma larvae were found in drift nets with their cases and those he concludes to have crawled there. Larvae without their stone case were more common, indicating how the mode of life and "adopted" morphology of some Trichopteran larvae reduces their liability to drift. Waters also notes that light, unencased Simuliid larvae which live in fast currents, are liable to be dislodged by physical disturbance and so appear in drift. Percival and Whitehead (1927) suggest that L.peregra cannot resist fast currents because of the large surface exposed by the shell in proportion to the foothold. It is therefore more liable to be washed away (as drift) than Gastropod species with a smaller, flatter and more streamlined shell such as Ancylastrum fluviatile. Jaag and Ambuhl (1964), from experiments conducted on may-fly nymphs of the family Ecdyonuridae conclude that these can resist swift currents because of their flattened shape which places them within the boundary layer of the current flowing over the substratum and because of their well developed legs which can firmly grip the rocks. The results obtained from my work at Sherburn beck show quite clearly that the drift rate of Hydrobia jenkinsi and Limnaea truncatula is affected by the speed of current which seems to be due to their morphology (see page 101).

Agapetus fuscipes was caught in very low numbers in the 24-hr. drift netting, indicating that it is not liable to drift over such short time periods.

The physiology of stream animals is a closely related topic which has even more significance in determining how likely they are to be caught in the drift. The strength of some species seems to affect their susceptibility to drift. As Moon (1940) notes, the physiological state of the organism will influence its movements. Dendy (1944) in his observations on Gammarus spp. found that active individuals were more likely to drift than other species such as the Chironomidae larvae which inhabit sand cases. He found that most individuals collected from drift seemed "vigorous and in excellent state". It is well known that Gammarids are relatively feeble swimmers (Hynes, 1960). Nevertheless they are active in their movements about the stream bed and it is their internal physiology which causes them to be unable to resist very fast currents and so drift downstream. In other words a combination of innate muscular strength and activity in emerging into stream currents seems to be involved. Waters (1961) terms such animals as "free-ranging and relatively weak-swimmers". The Ephemeropteran B. rhodani can also be similarly described.

That drift is a normal and continuous phenomenon in fresh water streams has been well established by many workers. What has caused disagreement and controversy for a number of years is the method by which the numbers of drifting animals are replaced in stream head-waters. In logical terms, such areas can be expected to become denuded of animals, but in fact rarely do so. The first ideas on upstream repopulation mechanisms came from Muller (1954) who, from his studies on north Swedish streams proposed a "colonisation cycle". This idea explained possible reductions of upstream populations by suggesting that "there occurs a

migration of imagines upstream, which, following the direction of the stream, ensures a balance and a completion of the population."
Roos (1957) and Macan (1957) also proposed that upstream movements of egg-laying adults would repopulate upstream areas. Macan even suggested that aquatic nymphs may move upstream and Roos talks of mass movements of female adult insects containing mature eggs in an upstream direction, even against winds. By the early 1960's such ideas were being challenged by such people as Elliott and Waters. Minckley (1963) talks about Gammarid species, one group of animal that obviously cannot fly upstream to repopulate. He found that after spates, _Gammarus bousfieldi_ moved back upstream en masse. _Gammarus minus_, however, was described as exhibiting more subtle, short-term movements upstream and the author suggests that, alternatively, this species maintains its upstream populations by rapid reproduction. This last idea reflects a change of attitude in the ideas concerning repopulation and has been thoroughly explored by Waters and Elliott. Elliott (1967) talks of increased competition between Ephemeropteran nymphs for food and space, causing an increase in drift as more and more are pushed off stones. As early as 1961, Waters was stating that removal from upstream areas must be balanced by production rates much higher than may have been previously supposed. In his 1965 paper, he examines the complete question of repopulation. He criticises the colonisation cycle theory as inapplicable to non-flying stream species and made the main intention of his study one of determining whether drift net data could be interpreted as a measurement of permanent downstream displacement. This he established to be so for most stream animals and, furthermore, he showed that drifting organisms entered drift nets at all levels and not only at the stream bottom. His studies on _Gammarus_ spp. and _Baetis_ spp. indicated that although they were passively carried along by water currents, a certain amount of

activity was required for them to enter the drift with the regular diurnal periodicity (discussed earlier here). The precise nature of this activity, whether an active upward swimming or just an increased level of movement, he did not ascertain. He then divides drift into a number of categories; "behavioural drift" which is due, for example, to a behavioural response to changes in light intensity; "catastrophic drift" which is due to floods or other physical disturbances, and "constant drift" which relates to the occasional individuals of all species present that adventitiously lose their hold on the bottom and are caught in the current. This last group of animals will be found in low numbers without regard to any diurnal periodicity. He concludes that "behavioural drift" appears to occur as a form of density dependent removal under conditions of high rates of production.

I am inclined to agree with this more recent explanation for repopulation of upstream reaches, for it is well known by population ecologists that any species with abundant food and living space will exhibit an exponential rate of population increase until its increase in numbers is counter-balanced by some restricting factor. Upstream areas, therefore, will quickly become populated to a maximum level but, because of a constant reduction in population via drift, there is what might be termed a "safety valve" for intra specific competition so that species are able to continually maintain their numbers at a high level rather than suffer a population "crash" due to the adverse effect of restrictive environmental surroundings.

In Water's paper just discussed (1965) he notes that "the drift rate at any one point is some function of the area upstream serving as the source of drifted organisms, the population density on that area, and the relative rates of production and other forms of mortality". In his earlier 1961 paper he proposed that mean rate of drift would be in some constant relation to the mean production rate, assuming steady-state conditions. His data suggested that total standing crop cannot be used as an index of production rate because the ratio, standing crop : production rate, must be assumed constant and would not be so if there was varying relative quantities of organisms having different longevities.

Productivity studies on drift seem mostly to have stemmed from research performed on fish production in streams. As noted above, invertebrate drift is acknowledged as being one of the main food sources of fish and so invertebrate biomass increase has been studied as a means of boosting fish productivity for human consumption. Horton (1961) used drift netting to estimate the productivity of the stream he was studying while Warren et al (1964) tried the addition of sucrose to see if invertebrate biomass was increased. They showed that sucrose addition did indeed "increase the biomasses of virtually all the taxonomic groups". Furthermore they found that drifting in the enriched areas was less than in the unenriched areas which was probably due to reduced competition for plant food in the enriched sections.

The present work showed that drift does occur in certain organisms in this particular stream and that, in some cases, the initial rate of recolonisation of denuded portions of the habitat (i.e. stones) depends on the period of time involved. While some species seem to show a rate of recolonisation directly related to the drift rate, my results indicate that this is not so for all the animals studies especially the Gastropod species.

The studies on Sherburn beck thus showed that there were variations in drift, as opposed to any near-neighbour stone effect in terms of recolonisation, and in the actual rate of recolonisation, which varied between animal species. Preference for a particular flow regime also varied between species and all of this was affected by life cycle developments.

Gammarus pulex, *Hydrobia jenkinsi* and *Limnaea truncatula* showed an increase in drift as it became dark and the distribution of the former species was shown to depend on the type of stream bed substratum.

SUMMARY

In Sherburn beck, Co. Durham, drift sampling over a 24-hr. period completed with various stone recolonisation experiments showed that:

1. Some animals recolonised quickly (*Gammarus pulex*), others took about a week (*Baetis rhodani*, *Agapetus fuscipes*, *Limnaea truncatula*, *Hydrobia jenkinsi*) and some took considerably longer (*Chironomidae*).
2. The important of drift as a means of recolonisation varied from species to species. *Limnaea truncatula* and *Hydrobia jenkinsi* recolonised more by movement from neighbouring stones while *Baetis rhodani* and *Agapetus fuscipes* recolonised more from drift.
3. Some animals were found more in medium flow areas of stream (*Hydrobia jenkinsi*, *Limnaea truncatula*, *Gammarus pulex* and *Agapetus fuscipes*), others more in faster flowing areas (*Baetis rhodani*) and some showed no preference (*Chironomidae*).
4. In the early stages, drift dependent species such as *A. fuscipes* and *B. rhodani* showed a rate of recolonisation directly related to rate of drift.
5. Life cycle developments by some species (*A. fuscipes*, *G. pulex* and *B. rhodani*) tended to camouflage some of the above phenomena during the experimental period (early May to mid July).
6. A marked nocturnal increase in activity over the whole night was shown by *G. pulex* which decreased when dawn broke, while *H. jenkinsi* and *L. truncatula* showed an increase in the number drifting and, especially, in the number moving from neighbouring stones as it became dark but not during the whole night. *B. rhodani* indicated a dependence for activity on a combination of water temperature and light intensity.
7. The distribution of *G. pulex* and *B. rhodani* was shown to be dependent upon stream bed substratum.

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