Studies in the community ecology of invertebrates in the springs, springbrooks and becks of the Eggleshope valley

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STUDIES IN THE COMMUNITY ECOLOGY OF INVERTEBRATES IN THE SPRINGS, SPRINGBROOKS AND BECKS OF THE EGGLESHOPE VALLEY

- by -

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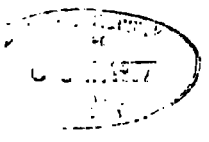
INTRODUCTION AND LITERATURE REVIEW

There are many types of freshwater habitat, such as lakes, rivers, canals, streams, ponds, dykes, pits and ephemeral puddles, but of all such habitats springs are amongst those that have been subject to the least scientific investigation. It is partly for this reason that this study has been made, and it is hoped that this will provide a firm foundation on which to base further research into this particular freshwater habitat type.

The area covered by rivers, streams and springbrooks is but one-thousandth of the total land surface; and yet all three are important and obvious features of any landscape. Despite this seemingly small area, it has been estimated that they carry about 3.0×10^4 km^3 of water to the seas each year, and this amounts to about 25 cm of precipitation spread over the entire land surface (Schmitz, 1961). In fact only about 2.8 per cent of the World's total water (1.337×10^6 km^3) occurs on the land, most of this is fixed as ice (2.24 per cent), of the rest, only 0.61 per cent occurs in the groundwater (Leopold et al., 1964). It is this water that supplies and gives rise to springs.

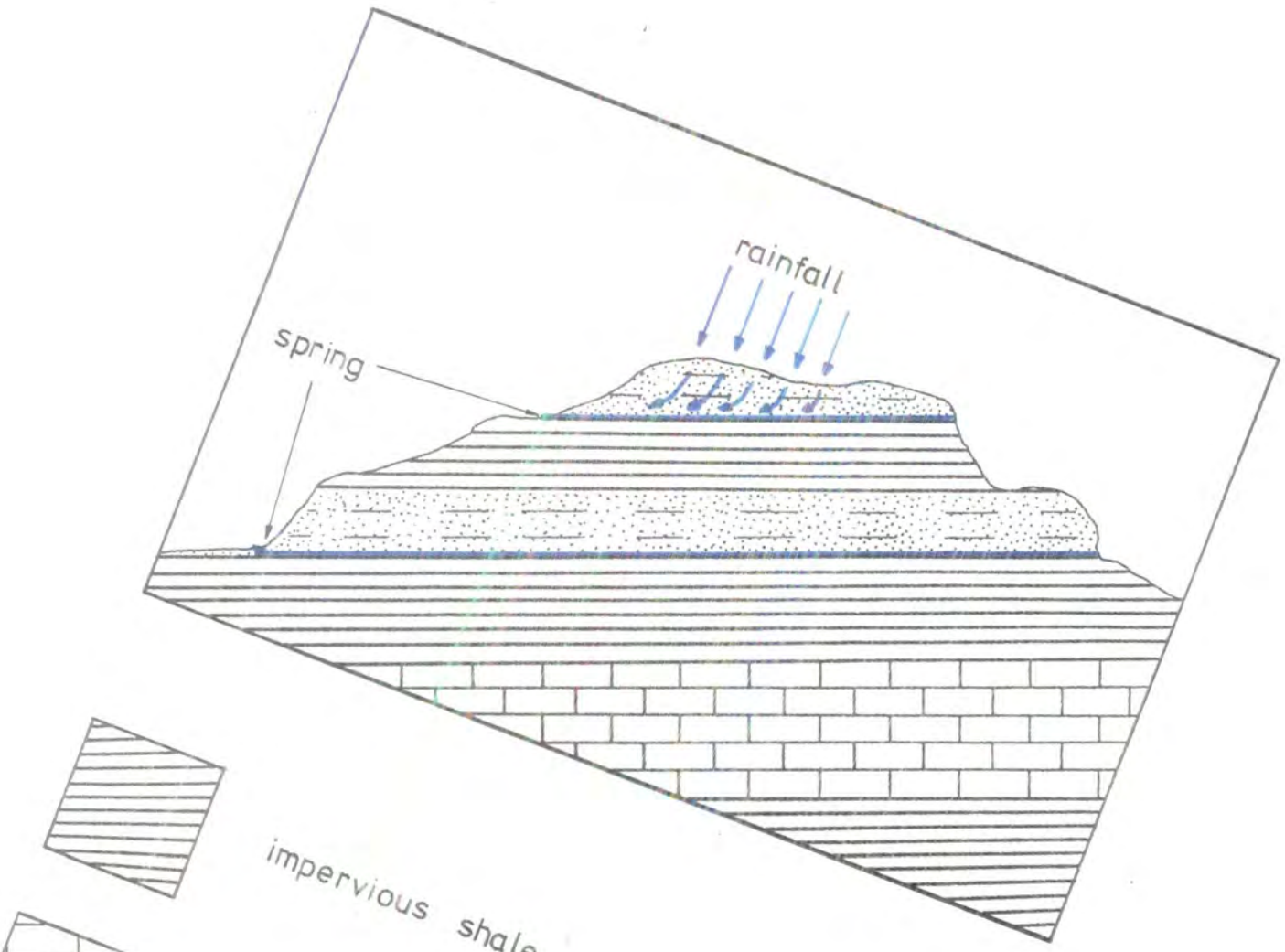
Not far below the surface of the earth, in most parts of Great Britain, porous soils and rocks are saturated with water that has infiltrated from the surface. The top of this zone of saturation is known as the water-table, the level of which tends to fluctuate according to seasonal recharge and infiltration, discharge by springs, and also extraction by man.



Where the water-table meets a topographical surface, as illustrated in Figure 1, there may be a spring, or even a line of springs. The line of springs that was used during much of this study is shown in plate 1. It is often thought that the individual springs in a line of springs will always be at the same height above sea level. This is not necessarily so, and the positions of the springs are determined by geological factors within the hill, such as the strike of the strata.

Springs and the springbrooks leading from them are not really part of the main drainage pattern, and clearly have quite well-marked biological and physical factors in their own right. Using Illies' (1964) terminology, springs and the springbrooks leading from them are termed the CRENON, and they differ from ordinary streams in many ways. They seem to maintain a very uniform temperature, which is often very close to the mean annual air temperature of the region. It is interesting to note that in volcanic areas the temperatures may be high enough to mean than in Brock's (1969) view, springs and springbrooks may be classed as extreme habitat types. They are sometimes de-oxygenated and many are iron depositing (such as the spring found at High Stoop - O.S. Sheet No. NZ 104408 - during the pre-study search for spring sites), and if they are neither they are often in contact with underground waters which harbour a fauna known as the 'phreatic' fauna.

Figure 1



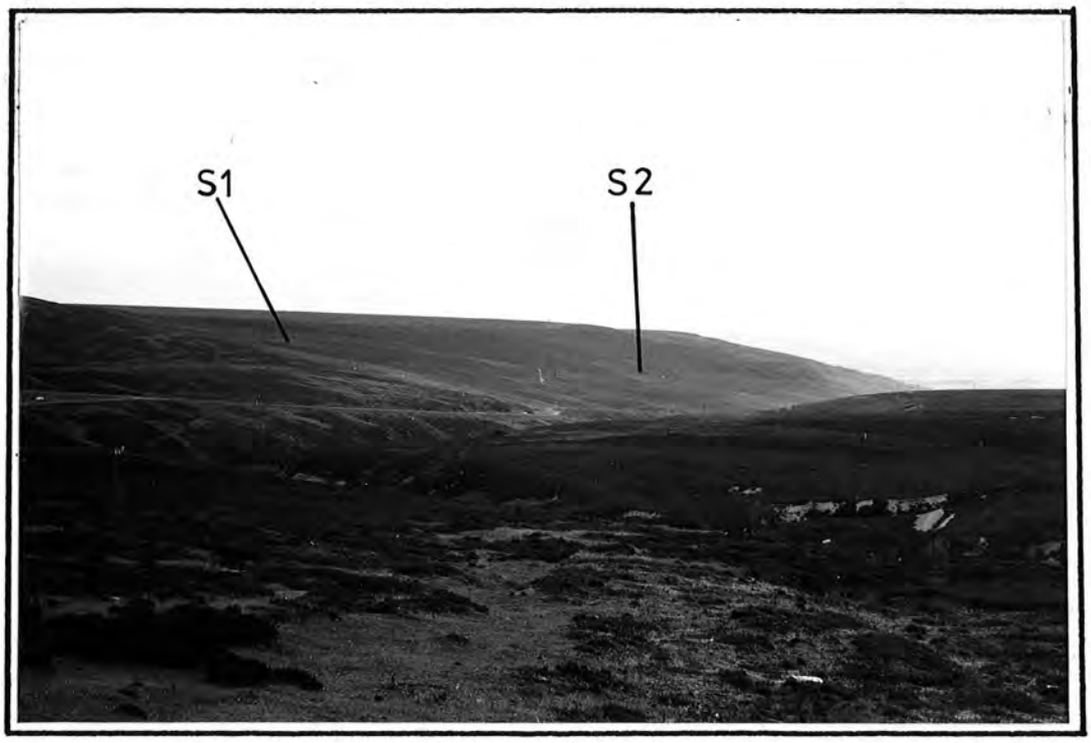
impervious shale.

limestone.

porous sandstone.

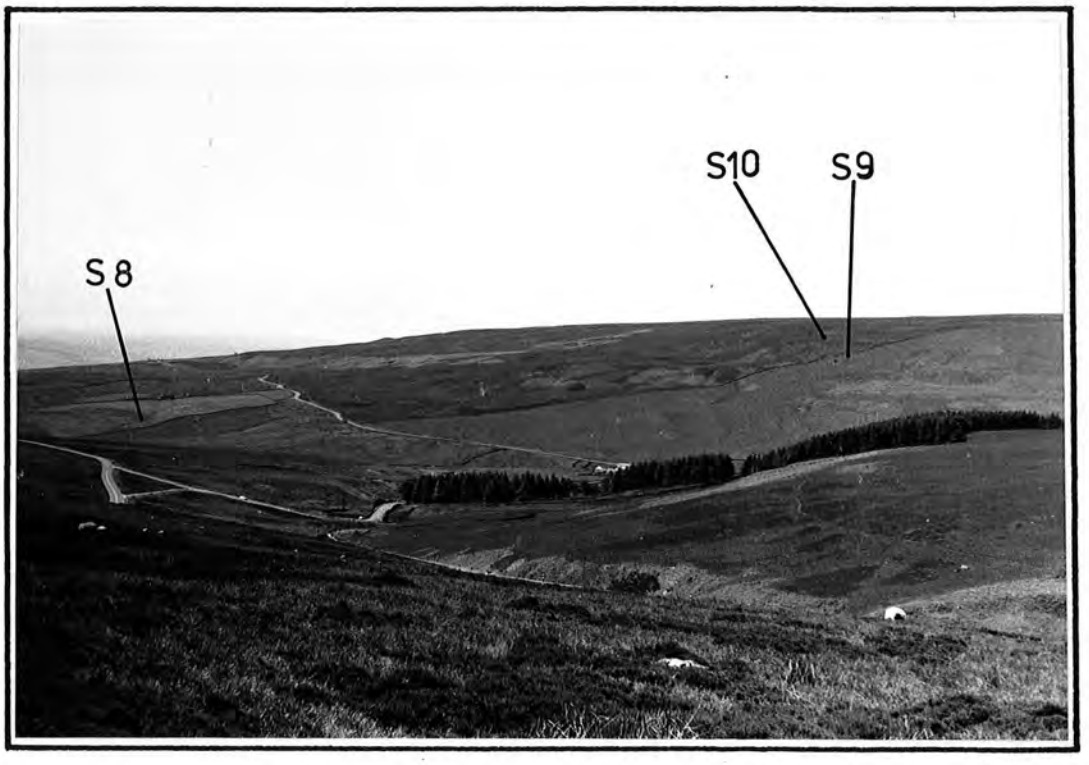
GENERALISED DIAGRAMMATIC REPRESENTATION OF A LONGITUDINAL SECTION OF THE STUDY AREA : showing relationships between water-table, springs and geological structure.

PLATE 1

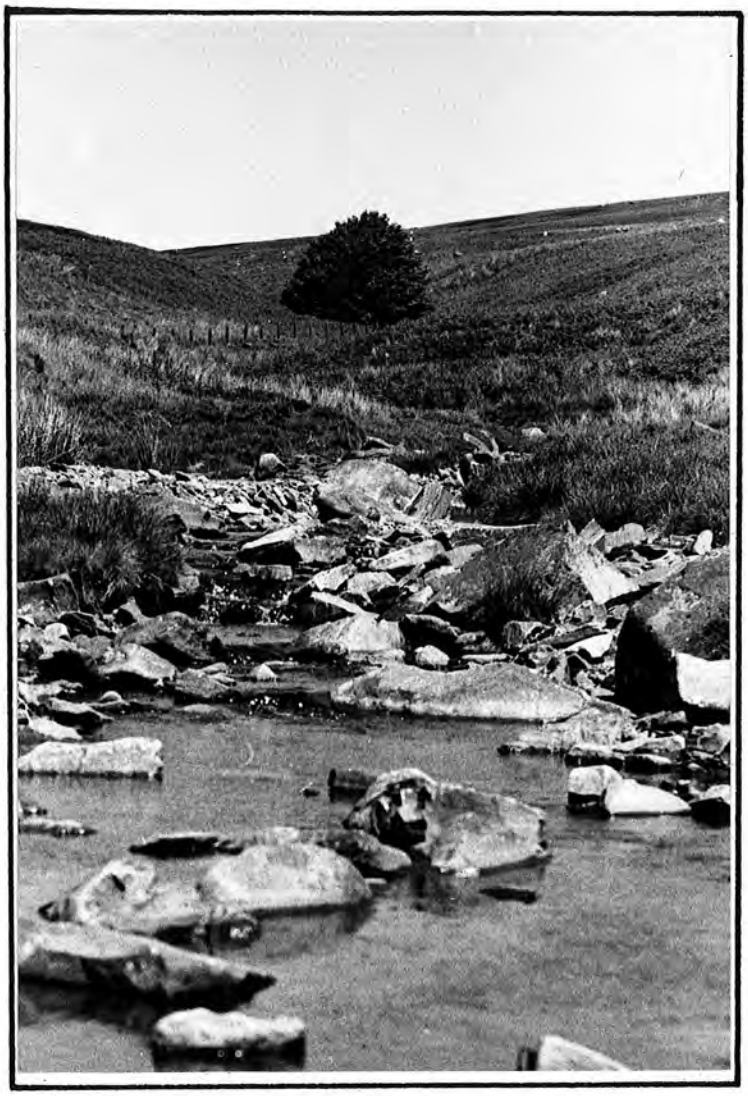


(a). View South down the Eggleshope valley from the 'California' mine area. Springs sites S1 and S2 are marked.

(b). View from West side of the Eggleshope valley, spring sites S6 and S7 are marked.



(c). View Eastwards across the Eggleshope valley from S1, springs S8, S9 and S10 can be seen in the distance on the East side of the valley.



(d). View Northwards of the Little Eggleshope Beck.

Springs discharge their water in a number of ways, for which suitable terms have been derived, and these were observed and noted by Bornhauser (1913). If the water flows directly into the channel of the springbrook it is termed RHEOCRENE, and if it first flows into a small basin or pond the term LIMNOCRENE is used. Often neither of these is the case and the spring flows out into a marshy area, it is then called HELOCRENE.

When no oxygen is found in the springwater at the source there are rarely any organisms visible, but despite this sulphur bacteria and cyanophyta have been found (Odum and Caldwell, 1955). Sloan (1956) found that some insects were able to enter water that contained very little dissolved oxygen, he found individuals of Callibaetis and Caenis in springbrooks in Florida where the oxygen content was as low as 2.5 $mg.l^{-1}$. It is of interest that he found that the number of species increased fairly quickly in a downstream direction. However, in 'normal' springs where the water surfaces with some dissolved oxygen many organisms occur right up to the source itself. In limnocrenes there may be equatic plants and species of animals that are more often found in ponds. It has been found that if this is the case the number of species is more restricted than in typical ponds, perhaps because of the relatively uniform temperature, also there are usually a few species more typical of lotic systems. It has been found that in rheocrenes the algal flora is similar to that of small streams (Whitford, 1965), and the dominant species tend to be Achnanthes, Melosira and

Fragilaria (Round, 1965). It seems that despite the very constant temperature regimes operating in springs a seasonal change of dominant species occurs. This may indicate that light is an important ecological factor (Teal, 1957).

Phreatic animals are often included in species found in and near the sources of springs, examples being Niphargus, Bathynella, white Phagocata, blind Asellus and Crangonyx (Thienemann, 1912; Carpenter, 1928; Beyer, 1932; Geijskes, 1935; Dahm, 1949; Dittmar, 1955; Matonickin and Pavletic, 1960; Minckley, 1961, 1963; and Montas et al., 1962). In certain springs such Phreatic animals may form an important section of the fauna, though their importance diminishes downstream they are often found in isolated sheltered pockets for some distance from the springhead.

Animals that are normally associated with waterlogged soils often form a substantial proportion of the fauna of some springs. Animals such as the lumbricid Eiseniella, the tipulid larva Pedicia and others are quite common, though they are normally linked with cool shaded places at the edges of streams (Thienemann, 1912; Demel, 1923; Kuhn, 1940).

The third major group of organisms are those that are truly aquatic and epigean, but are confined largely to springs and the cool springbrooks that flow from them. Animals in this category include the Triclads Crenobia alpina and Phagocata gracilis of Europe and North America respectively. Some Trichoptera such as Agapetus, Apatidea and Synagepetus are

found; as are some Plecoptera, in Europe the two species Leuctra nigra and Nemurella picteti are very common. Coleoptera are also represented by species such as Helodes spp. and Hydroporus ferrugineus; certain snails may also be restricted to this habitat, examples are the North American snails Paludestrina spp. and the European snails Bithynella spp. (Thienemann, 1912; Geijskes, 1935; Kuhn, 1940; Davidson and Wilding, 1943; Nielson, 1950; Noel, 1954; Dittmar, 1955; Matonickin and Pavletic, 1960; Chandler, 1966). The fauna of springs and springbrooks often includes many of the species that are common downstream as ordinary stream dwelling animals. Research has shown that this is often the case with amphipods and isopods which are commonly dominant species in hardwater springbrooks (Demel, 1923; Stella, 1956; Montas et al., 1962; Minckley, 1963).

The fauna of springs has many elements in common with other sorts of freshwater: e.g. Hydrophilid beetles may be found in the hygropetric zone of springs as well as at the margin of ponds or sheltered parts of lakes, and many animals are equally abundant in springbrooks and eurythermic streams. Still there are a great number of animals that are only found in springs. The cause may be that only in springs they find suitable habitats; emergent stones, moist leaves etc. are also found elsewhere, but in springs these habitats are characterised by their constancy: the leaves are always equally moist, and the stones are never totally submerged, nor does the ground beneath them dry out completely.

The hydroclimate of the springs differs considerably from that of other sorts of freshwater, and since the last Ice Age the macroclimate of Europe has been subject to considerable changes. Perhaps then, the distribution of crenobionts or spring inhabiting species can be explained in terms of 'historical zoogeography'. In the summer months the temperature of the springs is much lower than in other freshwaters. Hence, some of the early immigrants of the Late Glacial Period, now supplanted in the eurythermic streams have, as late glacial relects, found refuges in springs. An example would be the Trichopteran Apatidea muliebris MacLachlan, which is now only found in a few English springs and a few other springs in the North European lowlands. It is not found outside springs, and is absent from the fauna of the German mountains. It seems that the larvae of Apatidea muliebris cannot stand temperatures much higher than those prevailing in springs. Thus the Atlantic Period, in which the mean temperature of the year and hence the temperature of the springs were higher than now, was, no doubt an extremely critical period for Apatidea. This may explain why today it is only found in the largest of springs. One should bear in mind that the circumstance that a species is restricted to springs does not necessairly mean that the species in question has an absolute requirement for such low temperatures, it is possible the stenothermy may be a recent evolutionary development during postglacial time. It may be due to the species being unable to maintain its place in the competition with later immigrants in the eurythermic streams;

or that the balance of competition may be different in waters with different thermal regimes. In the Post Glacial Warm Period the temperature of Europe was notably higher than nowadays and Southern species would have moved North, and have now been supplanted in the Northern fauna. Some of these species probably had their distribution conditioned by a not too low winter-temperature. Some animals with this type of distribution might be expected to have found refuges in springs, owing to the comparatively high winter temperatures of these habitats, a good example is Odontocerum albicorne Scopoli, which is one of the commonest types of Caddis fly in Italy (Navas, 1930). For both types of relicts it seems to be of importance to the flying imagines that the localities of the refuges have a situation sheltered from winds in order to ensure the non-dispersion of adults. Perhaps one reason for the lack in the spring streams of many of the animals common in the eurythermal streams, is that they are probably not able to complete their development in the low summer-temperatures (Nielson, 1950). Because so many crenobionts are relicts, the faunas of springs in relatively recently glaciated areas tend to be less rich than those springs which have been longer in existance (Engelhardt, 1957). In fact some species, such as, Gammarus bousfieldi and Asellus bivattatus have only been identified from the Doe Run springstream in Kentucky (Cole and Minckley, 1961), this suggests that they are relicts from long ago, which have either changed in their isolated habitat, or simply died out elsewhere.

It would be expected that the flora, and fauna, of springs with different types of water chemistry differ in terms of both numbers and species present. This has been found to be the case, Schwoerbel found such differences between soft-water and hard-water springs (Schwoerbel, 1959). The type of substrate may also be an important factor, and studies between the substrate type and bottom fauna communities, made in England, Germany and America, have indicated that the substrate type is a better characteristic to use as a basis for a system of biocoenoces than the 'stream-zone' system, despite the fact that variations do occur in the faunal composition on certain substrates in different localities. Thorup's (1963, 1966, 1970, 1973, 1974) work on some Danish springs has shown that the faunas associated with certain substrates are well defined and may be called communities. His studies show that the variations in the fauna associated to a certain substrate occur from place to place, both qualitatively and quantitatively. Variations dependent on ecological factors other than substrate type may occur within a specific locality. For this reason it seems unlikely that a system of biocoenoces and biotypes, based simply on substrate type, could be constructed. However, in studies on interspecific relationships, and those between species and environmental substrate type may be helpful in the delimitation of biotopes and biocoenoces (Thorup, 1966).

It is most interesting to note, that like the algae, the spring-dwelling insects, molluscs, and fish tend to show distinct seasonal periodicity, so that they breed and emerge

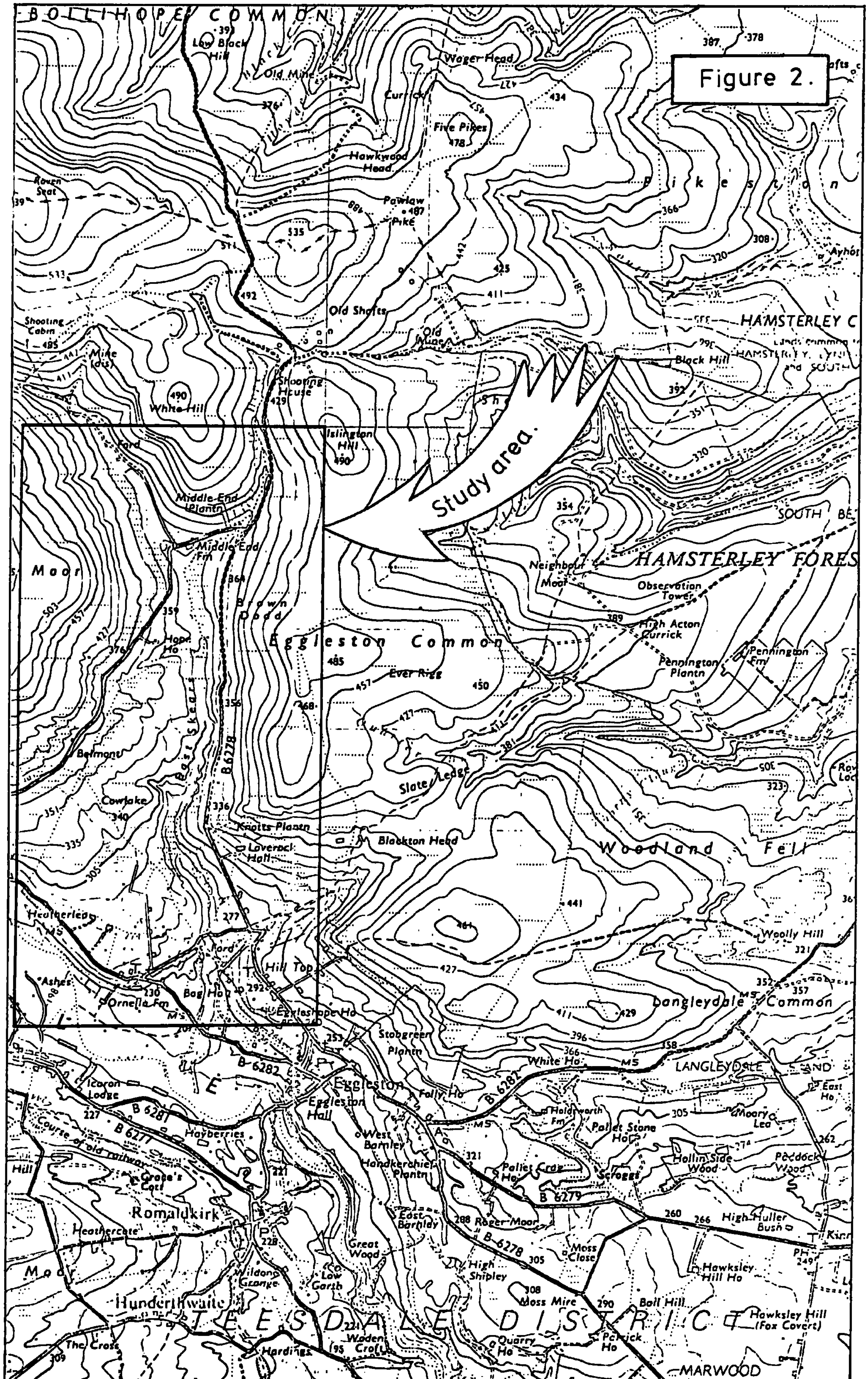
at the proper season for the species despite the uniformity of the thermal regime. Several researchers have concluded that day-length must be an all important controlling factor (Demel, 1923; Odum, 1957; Thorup, 1963, 1973). An interesting question that often arises, in the discussion of spring communities, is that concerning dispersal and colonisation. In a review (Maguire, 1963) the lack of knowledge in this field has been made clear, at least in terms of the passive dispersal of aquatic organisms, although it has been shown that micro-organisms travel fairly readily. However, for the larger invertebrates the problems of dispersal are immense, especially if they are true crenobionts. It is possible that there is very little movement of such species, and Thienemann has suggested that, when the flatworm Crenobia alpina appeared in some German springs after not being taken in sample catches for many years, it did so from a retreat in the very groundwaters that gave rise to the springs (Thienemann, 1949). Another very significant piece of correlatary information is that Hydroporus ferrugineus, a beetle of springs in all parts of Europe, is found in temporary 'winter-bournes', such as those in the chalk hills of south-east England, and has been found to be incapable of flight (Jackson, 1958).

Much of the work that has been carried out on springs has been research on quite large springs, the springs that Minckley (1963) and Odum (1957) have worked on were so large that boats and sub-aqua gear could be used. The work carried out by Thorup and Nielsen (Thorup, 1966, 1970, 1973, 1974; Nielsen,

1950) on Danish springs was also carried out on much larger springs than those used in this study, there the discharge was in the region of 100 $l.sec.^{-1}$, whereas in this study they range between values of about $0.1.min.^{-1}$ and 200 $l.min.^{-1}$. The low flow in springs used in this place of research was to present problems when sampling methods were to be decided upon.

From a preliminary literature search it seemed that little was known of the 'springhead' or 'springbrook' communities in this country. So it was decided that to look at community structure and diversity would be a good start to any longer term study of such systems, whilst at the same time other aspects of springheads and springbrooks could be considered. In order for this kind of a study to be made it was essential that quite a number of springs should be found within easy reach of the University.

A valley in which there were many springs was located to the north of Middleton-in-Teesdale; the B6278 road passes through it to Stanhope. The valley lies between Eggleston Common (to the east of the road) and Monks Moor (to the west of the road). Near Middle End Farm the valley divides and Eggleston Burn is formed by the confluence of Great Eggleshope Beck and Little Eggleshope Beck. Figure 2 shows the general area in which the study took place, and Figure 3 shows the study sites themselves. The spring heads are labelled S1 to S10, and the Beck is labelled B. There were other springs in the area, but these were found not to be suitable, mainly because of the exceptionally dry early Summer of 1976. For further details of the area O.S. (1:25,000 Series) Sheet No. NY 92 is essential.



BOLLIHOPE COMMON
Study area.
Low Black Hill
Old Mine
Wager Head
Currick
Five Pikes
Hawkwood Head
Raven Seat
Pawlaw Pike
Old Shafts
Old Mine
Shooting Cabin
Mine (dis)
Shooting House
White Hill
Islington Hill
HAMSTERLEY C
Black Hill
Pikeston
Middle End Plantn
Middle End Fm
Moor
Brown Dodd
Hope Ho
Eggleston Common
Ever Rigg
East Skears
B 6278
Belmont
Cowlake
Knotts Plantn
Laverock Hall
Blackton Head
Slate Ledge
Woodland Fell
Neighbour Moor
HAMSTERLEY FOREST
Observation Tower
High Acton Currick
Pennington Fm
Pennington Plantn
SOUTH
Heatherlea
Ashes
Ornella Fm
Bog Ho
Hill Top
Eggleshope Ho
Woolly Hill
Langleydale Common
Stobgreen Plantn
White Ho
LANGLEYDALE
B 6282
Eggleston
Eggleston Hall
Icaron Lodge
B 6281
B 6277
Hayberries
Course of old railway
Grove's Cott
Romaldkirk
Heathercote
Moor
Wildon Grange
Low Garth
Great Wood
West Barnley
Handkerchief Plantn
East Barnley
Roger Moor
Holdsworth Fm
Pallet Stone Ho
Pallet Crag Ho
Scroggs
Hollin Side Wood
Paddock Wood
Moory Lea
East Ho
B 6279
High Huller Bush
B 6278
High Shipley
Moss Close
Moss Mire
Hawksley Hill Ho
Boil Hill
Hawksley Hill (Fox Covert)
Hunderthwaite
TEESDALE DISTRICT
The Cross
Hardings
Woden Croft
Quarry Ho
Pelrick Ho
MARWOOD

Figure 2.

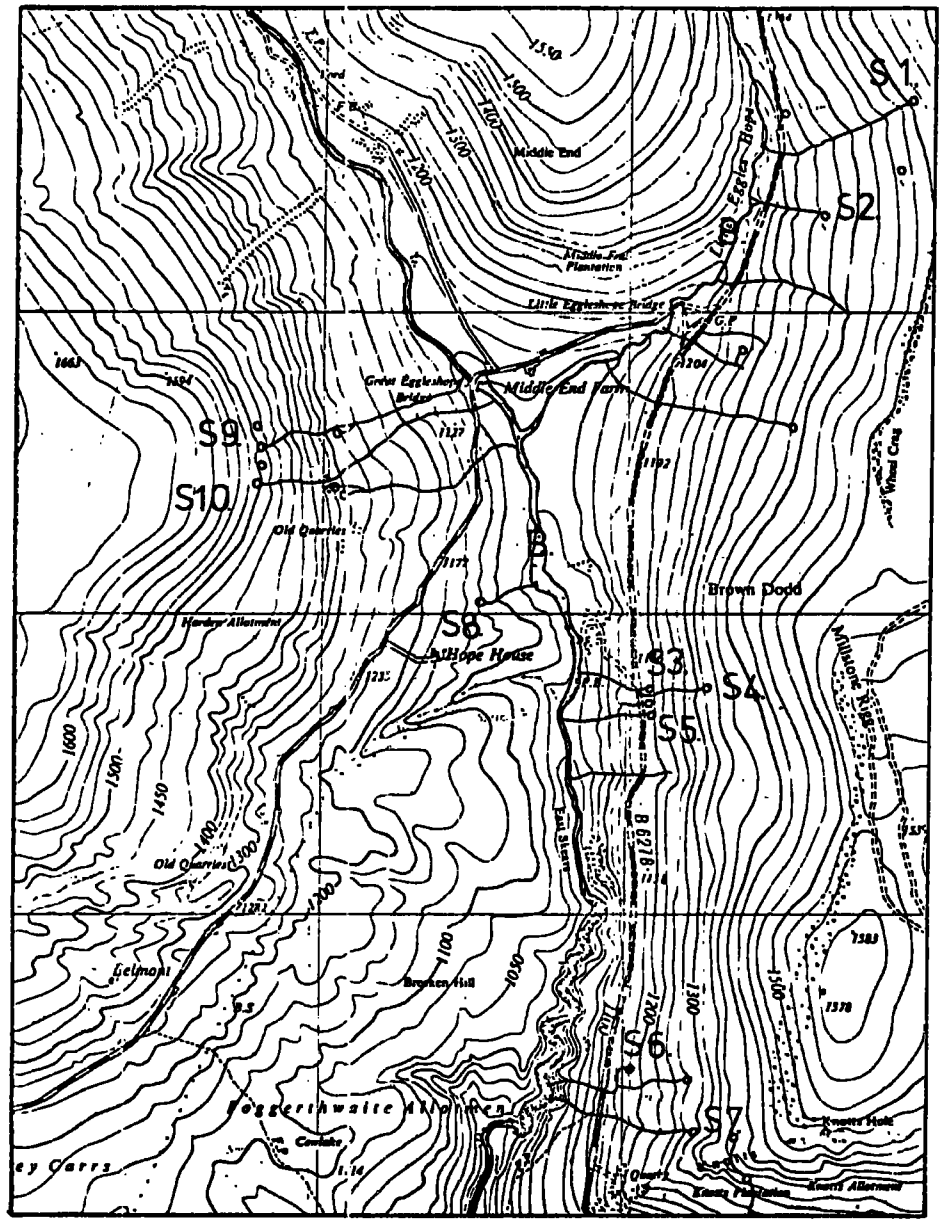


Figure 3

Map showing study area and sites.

The area of study is part of the Northern Pennine Orefield, and the mining of lead ores has for many generations been one of the principal occupations of the scanty population in the fell and dale country. Mining is still carried out in the area, but the mines nearest to the study site were no longer in production. The fells have broad, flat tops and their convex side slopes are sculptured into prominent features indicating the alternation of resistant and non-resistant beds in the gently dipping rock formations. In the bottoms of the broader valleys trains of rounded mounds of glacial drift are found, the higher slopes are usually free from drift; but the flat tops of the fells are covered with hill-peat, usually deeply eroded into 'haggs'. The population is restricted to the valleys, each having a district centre, such as Middleton-in-Teesdale. Geological occupations other than metalliferous mining include the quarrying of limestone (e.g. at Shake Holes, three miles to the north of the spring site on the Stanhope Road), sand and ganister, and in the past coal was mined on a small scale. These activities were though to be potentially important in terms of their effects on the water chemistry of the area. Agriculture is practised in the valleys, but at the spring site up in the fells sheep farming is dominant. Apparently, in the past the traditional Dales miner was a smallholder as well, and up to quite recent times work at the mines was restricted during the seasons of haymaking and harvest. A form of hydraulic mining known as 'hushing' was practised by the old miners, by which a torrent of water was allowed to rush over or along the course of a vein,

making in a course of years a great excavation or 'hush'. Deep prospecting trenches were cut in the same way. These activities have affected to patterns of drainage close to and around the mines, but as far as could be seen did not interfere at any of the spring sites that were used. In Teesdale the principal lead-mining area lay in the northern side-valleys of Hudeshope and Eggleshope, north of Middleton-in-Teesdale; the latter being the valley in which this study was carried out. It was in this valley that the London Lead Company, starting in 1752, worked an extensive complex of veins in the Upper Limestone group, the largest 'oreshoots' occuring in the sandstones high in the group. All the old mines were further up the valleys than the springs, and it was expected that they may have had significant effects on the flora and fauna of the Becks that flowed from them.

This dissertation describes the results of a study of the communities in certain springs, springbrooks, and the main beck (Little Eggleshope) of the Eggleshope Valley . An attempt has been made to identify the springhead community, if it does indeed exist, and to relate the communities studied, both qualitatively and quantitatively, to other physical and biotic factors. The physical factors included temperature, pH, oxygen levels, discharge, flow rate, and the heavy metal ions of lead and zinc, and also the amount of calcium present in the water. Biotic factors involved in the study were a measure of the available vegetable material, a survey of the major macrophytes present, and animal interspecific considerations

for each site. A species diversity analysis was carried out on the major sites, and stations down one of the springbrooks. An effort to examine the distribution of the invertebrates by 'frequency analysis' from springhead to beck was made, and it was designed to detect whether the distribution changed with time. The trophic structure of the springs was investigated, and Eltonian pyramids produced to illustrate for the spring with the highest standing crop. Much of the effort involved was directed into the development of suitable techniques and methods of analysis. These needed refinements which time did not allow, and the collection of more data from this most interesting freshwater habitat.

CHAPTER 1

METHODS

1.1 Community Study of Springheads and Egglestone Beck

After a detailed examination of the springheads in the Eggleshope Valley ten were chosen for further study. It was decided that an attempt should be made to investigate each qualitatively and, if possible, quantitatively. The definition of what was meant by the term 'springhead' was taken to be that part of the springbrook between the point of emergence of the underground waters, and a point 5 metres downstream.

The method of sampling and numbers of sub-samples to be taken was, as is always the case in benthic limnology, a problem. Because of the fragile nature of the springhead habitat, and its small size, the usual methods of deciding on the sample size and number were not rigidly adhered to for this part of the study. Eventually a sub-sample size of 400 cm^2 of springbrook bed was chosen, and a sub-sample number of five when using the net sampler. A bucket sub-sample of 227 cm^2 was taken when the vegetation was too dense, or the flow rate too low, for the net sampler to be used. Again five sub-samples were taken.

The net sampler was designed by the author, and was based on the pattern of the Surber Sampler (Surber, 1937), but on a reduced scale suitable for use in small springbrooks. It is

shown in Plate 2 and consisted of a standard F.B.A. net frame and net (apertures approx. 1.0 mm) with the typical Surber quadrat extension from the mouth of the net. The area of the quadrat (20 cm x 20 cm) was 400 cm^2. To its sides were attached two triangular plates of aluminium which were to direct the flow of water, and animals, into the net. To ensure a good seal between the stream bed and the sampler, plastic foam was attached to the bottom of the quadrat on its sides and rear.

The net sampler was used to sample the communities in all the springheads, except S7, S8 and S10 where low flow and dense vegetation prevented its use. The net sampler was also used to sample the beck community, where the high flow rate and greater depth were ideal for its use. In those habitats where the net sampler could not be used a 'bucket' sampler was used. It consisted of a plastic bucket with the base removed and the bottom rim sharpened; this was used in conjunction with a stiff plastic net of 12 cm diameter and holes with a diameter of approximately 1 mm. (This item was in fact a 'flour sieve' made by Addis.)

Samples were taken at 1 m intervals starting at 4.5 m downstream and working upstream towards the springhead. Net samples were taken in the following way, the net was placed firmly in position on the stream bed and settled into the substratum, any stones within the quadrat were picked up and scrubbed, in one direction with a stiff brush, so that any attached animals passed into the net. The substratum within

PLATE 2.

The net sampler : the rule in the foreground was 30cm. long.

PLATE 3.

The sampling apparatus beside Little Eggleshope Beck.

the quadrat was then well disturbed using the same brush for a period of 30 seconds, any vegetation remaining attached to the substratum after this time was dislodged and placed in the net. The net was then removed from the water and its contents placed in a screw topped plastic jar to which had been added 2 cm^3 of concentrated formaldehyde solution. Bucket samples were taken in a slightly different way, the samples were also taken working upstream, the bucket was placed firmly and quickly into position and rotated so that it rapidly cut its way through any plant material and soon reached a firm substratum. It was held in position, the vegetation was removed by hand and placed in a plastic jar held over the bucket. Next the plastic net was used to 'fish' within the bucket, any animals caught were placed in a white plastic tray, this process was continued until no further animals could be caught. The animals were then placed in the jar with the vegetation and 2 cm^3 of formaldehyde solution were added, the lid was then screwed tightly in place. If large stones were present within the bucket samples provision would have to be made for scrubbing, but this was not necessary in the present study.

The net sampler was used in the beck as above, but because of the larger habitat it was possible to take more sub-samples, the number was determined by plotting a species discovery curve. Twenty sub-samples were taken from the beck. These were returned to the laboratory in screw topped plastic jars treated with formaldehyde as before. Plate 3 shows the sampling apparatus beside Little Eggleshope Beck.

In the laboratory each sample was sieved (sieve aperture 0.25 mm) to remove silt and sorted in water in a white tray under strong light. All the macrofauna were removed. Flatworms were identified immediately while all other animals were preserved in 70% methanol for later identification.

1.2 Measurement of Physical Factors at the Springhead

1.2a Water Temperature

The temperature of the springhead water was taken at intervals throughout the study using a standard mercury in glass thermometer calibrated in 0.1 degrees centigrade, ten readings were taken at each site over the period of the study, May-August 1976. Maximum/Minimum mercury in glass Six's thermometers were used to determine the nature of the diurnal temperature range in the springheads, these readings each over 24 hours were taken three times in each springhead, at the start of the study, in the middle, and towards the end. The temperature profile from the source to end of the springhead zone was investigated by means of an electronic temperature probe placed on the surface of the substratum. It was found that it was not possible to read the mercury in glass thermometers accurately when used for this, and to ensure consistent results the probe was calibrated against the thermometer used during the rest of the study.

1.2b Slope/gradient

The slope over the first five metres was measured by means of ranging poles and a spirit level, so that a value for the height through which the water fell over this distance was obtained.

1.2c Flow rate

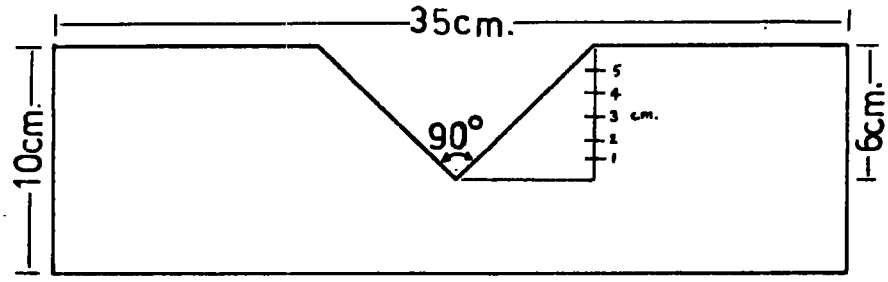
A measure of the flow rate was taken at each spring site using a Pitot tube. As there were certainly microhabitats within the springhead zone where the flow rate would have been zero, or even negative (upstream) only one value was taken, that was the highest that could be found in the zone. The extremes were taken to be between zero and the recorded maximum value.

1.2d Discharge/Flow Volume

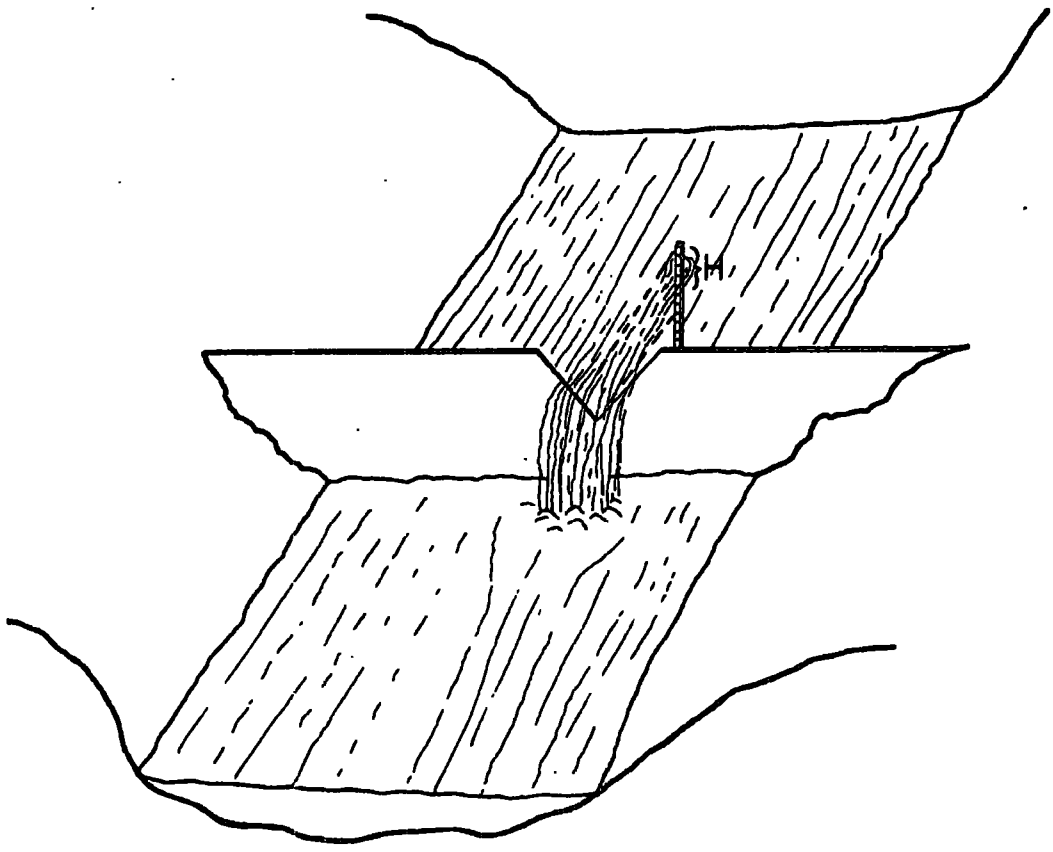
The discharge of each spring was measured twice, once at the beginning of the study (spring discharge) and once at the end of the study (summer discharge). The measurements were taken by means of a portable 'V-notch' weir made of flexible plastic. This was built into the springbrook temporarily so that all the water was forced to flow through the 'V'. The angle of the 'V' was 90^{o}, and to measure the discharge the 'head' (H) above the tip of the notch was measured at a distance about 3H upstream (Hynes, 1972). The discharge was calculated from the following formula:

Discharge = $0.925\ H^{2.47}$ $l.min.^{-1}$ When H is in centimetres. The use of the 'V-notch' weir is illustrated in Figure 4.

Figure 4.



(a) Diagram showing the dimensions of the 'V-notch' weir.



(b) Diagram showing how the 'V-notch' weir was used.

1.2e pH

Five readings of pH were taken at each springhead at 1 m intervals up to the source using a Pye Model 293 Field pH meter. Five readings were also taken in the beck.

1.2f Conductivity

Water samples were collected from each springhead, and the beck, in screw-topped polythene bottles and taken back to the laboratory. Within two hours of collection the conductivity of the water in each bottle was measured using an 'Electrolytic Conductivity Measuring Set - Model MC-1, Mark-V', made by Electronic Switchgear Ltd.

1.2g Oxygen levels in the water

Oxygen levels were taken in each spring five times at 1 m intervals up to the source, and five in the beck between the entry points of springbrooks S1 and S2. The measurements were made using a Field Oxygen Meter made by the 'Lakes Instrument Company' of Windermere.

1.2h Water Chemistry

Water samples were collected in small glass sample bottles that had been acid washed in 15% hydrochloric acid for 72 hours and then rinsed five times in flask distilled water. Two samples were collected from each springhead, and two from the beck. The levels of lead and zinc were determined by means of

Atomic Absorption Spectrophotometry using a 'UNICAM SP. 90', and the level of calcium in each sample was measured using an 'Eel Flame Photometer'.

1.2i The Classification of the Substrate

None of the common scales, such as the 'phi-scale', were really suitable for a classification of the springheads therefore a short description of the nature of the substrate was made in the field.

1.2j A Measure of the Vegetation/Detritus

All the vegetable material from each sub-sample in the faunal analysis was dried at 80^{o} centigrade to constant weight in the original sub-sample units and a value for each recorded.

1.2k Floral analysis

A list of the macrophytes in each springhead and the beck was made, also some indication of the abundance of the species was attempted.

1.3 Qualitative and Quantitative Sampling of Stations down Springbrook 1

Five sub-samples were taken using the net sampler, as in section 1.1 of the methods, at stations 100 m, 200 m, 300 m and 500 m down from the springhead. They were taken back to the laboratory and treated in the same way as the previous

samples. A temperature profile recorded for the springbrook during the sampling period using a 0.1^{o} centigrade mercury in glass thermometer. Short notes on each station were also made.

1.4 A Frequency Analysis of Springbrook 2 in the Spring and Summer of 1976

The essence of the method is that a series of samples are taken in a locality and the numbers of samples in which each species occur is noted and converted to a percentage. As with the botanical methods each sample covered a fixed area. The samples were taken as follows, at 2 m intervals from the point where the springbrook entered the beck to its source. A wire quadrat 20 cm x 20 cm was placed on the springbrook bed and the area within it was searched for animals, a hand sieve was held downstream and adjacent to the quadrat to catch any animals that were dislodged. During the sampling the collector moved against the current taking a sample every 2 m, being careful that new areas were not disturbed by taking the previous sample. The species found in each sample were noted. This process was originally developed by Raunkiaer (1934) a phytosociologist, he used it to characterise plant communities. Thorup (1970) was first to apply this method of analysis to the invertebrate fauna of a small springbrook. The main difference between the present study and his is that his sample was a 'fist' sized stone; the nature of the substrate in the springbrook of S2 prevented the use of his sampling technique.

The reliability of the method depends on the size and number of samples taken (Raunkiaer, 1934). In the present study it was found that ten 20 cm x 20 cm samples gave a consistent frequency value for the dominating species. A frequency analysis was carried out twice; in May on the 23rd and 24th 1976, and on July the 23rd 1976, one representing a Spring analysis, the other a Summer analysis. Other factors were recorded at each sample site, the temperature, the maximum flow rate, the nature of the substrate, whether it was in the shade or in the open, and what vegetation was growing nearby. Shade was due to both the growth of macrophytes and the depth to which the springbrook had cut into the substratum, only sites of obvious deep shade were recorded as shade sites.

1.5 An Investigation into the Effect of Slope/Gradient on Community Structure and Physical Factors within the Springbrook

This investigation was carried out in springbrook S6 because it provided an ideal situation for this type of study. The springbrook had been re-directed by man a number of years ago and in doing so two distinct and very uniform slopes had been produced, one about three times steeper than the other. The net sampler was used to extract twenty samples at one metre intervals working upstream along a 20 m stretch of each. Plate 5a shows the steep slope, and Plate 5b the gradual slope. The net sampler was used and samples treated as in the manner described in section 1.1 of Chapter 1. Specimens were sorted

PLATE 5.

(a). Shows the nature of the substrate on the gentle slope. (rule 30cm. long)

(b). Shows the nature of the substrate on the steep slope .

as previously, and plant material was dried to constant weight as before. Temperature readings were taken at each sample point, as were measures of pH, oxygen concentration and maximum flow rate. Photographs were taken to illustrate the different nature of the substrate on the two slopes.

1.6 Comparison of the Net and Bucket Samplers

A uniform stretch of the springbrook of S6 was used for this comparison, just below the shallow slope of the investigation outlined in section 1.5, downstream of a small road-bridge. Ten samples were taken with each sampler using the same techniques outlined above, the samples were taken working upstream using the samplers alternately at intervals of 1 m. The samples were treated and processed as before. The bucket sampler used in this part of the study had a working surface area of 312.5 cm^2, but was in other respects identical to that used throughout the rest of the study.

1.7 Transplant Experiment with the larvae of the Caddis, *Agapetus fuscipes* Curt.

Because it was noticed that certain species were present in some springbrooks and absent from others it was decided that a transplant should be carried out. The species *Agapetus fuscipes* was chosen because they were attached to stones which could be easily labelled and moved from one springbrook to another. Six stones covered with *A. fuscipes* were removed from springbrook S4 and the number of animals on each counted.

Three were placed in springbrook S1, where the species is not found, and three were placed as a control in springbrook S5, where the species is common. The labelled stones were temporarily lifted and examined at intervals. They were collected and transported to the laboratory on July 8th 1976 for detailed examination.

1.8 A study of the Sex Ratios of some Stone-Fly Species and of Gammarus pulex in the habitats in which they occur

This study was carried out on the organisms collected in the Community Study outlined in section 1.1. The Plecopterans, Nemurella picteti Klapalek, Nemoura erratica Classen, Capnia biffons Newman and Amphinemura sulcicollis Stephens; and the Crustacean Gammarus pulex Lin., were sexed. The numbers of each sex were recorded for each habitat. Figure 5 show the sexual diagnostic features used to distinguish between males and females of each of the above species.

1.9 A study of the Sizes of the Individuals in the Populations of some Stone-Fly Species and of Gammarus pulex in the habitats in which they occur

The animals measured in this study were the same animals and species that formed the basis of the previous study (section 1.8). All were measured in the same way. They were placed in a Petri dish and viewed under a binoccular magnifier,

Figure 5.

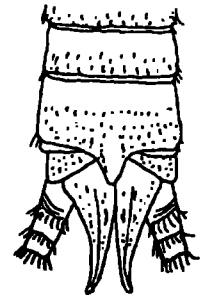
Sexual characteristics of the selected species :

(a)Amphinemura sulcicollis.

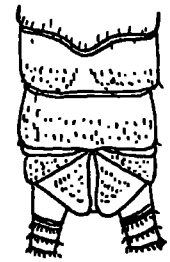
male.

female.

(b)Nemurella picteti.

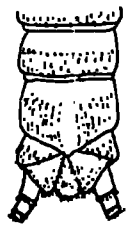


male.

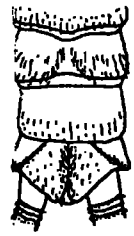


female.

(c)Nemoura erratica.



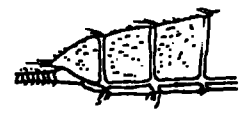
male.



female.

(d)Capnia bifrons.

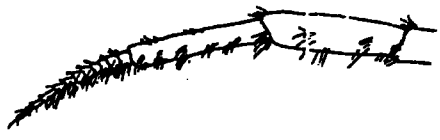
male.



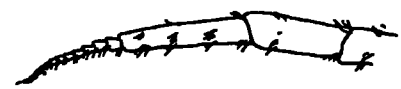
female.

Diagrams (a) to (c) show abdomen in ventral view, (d) shows abdomen in lateral view.

(e) Gammarus pulex.



male.



female.

Diagrams (e) show second antennae of both sexes.

below the dish was a piece of 1 mm ruled graph paper. Each organism was placed in a size class from 1 mm to 20 mm (i.e. 1, 1-1.9, 2-2.9, etc.). The distribution of the size classes for each species was recorded for each habitat.

1.10 An analysis of the Trophic Structure of the Communities in S10 and S4

The material collected in the initial community study (Chapter 1, section 1.1) was used in this analysis. New data needed was obtained by calculating the dry weight of each species, and by measuring the energy content of sub-samples of the species present. The dry weights of the individual species populations were obtained by drying the specimens to constant weight at 80° centigrade. The energy content of each species was measured using a Durham Miniature Bomb Calorimeter, the use of which is fully explained by Phillipson (1964). Three specimens of each species were 'bombed' and energy contents for each species calculated in K. Joules per gram.

CHAPTER 2

RESULTS AND ANALYSIS

2.1 Community study of the Springheads and Egglestone Beck

In this study the community considered is the invertebrate fauna of the various habitats, which for this section consisted of the ten springheads and the beck. They were analysed by the preparation of a number of dendrograms in which collections, in this case communities, can be related to each other at different levels of similarity. Dendrograms are more often used to represent genealogies or taxonomic affinities within a set of related species, and the techniques and limitations of drawing up dendrograms are discussed by Sokal and Sneath (1963). They are a relatively simple form of cluster analysis, and can be produced for many different indices.

The method used to produce the dendrograms in this study was Mountford's, it was described by Davis (1963) in a study of soil invertebrates. Below is an example of how the dendograms were produced, it is much simplified:

1. Matrix Formation - similarity measures between each collection and all the other collections are organised into a matrix. These measures may be of the Sorensen type, % similarity, diversity, or evenness similarity.

	A	B	C	D
A	-	m	n	o
B		-	p	q
C			-	r
D				-

From this matrix the highest value is taken to form the first dichotomy. Let us suppose in this instance that p is the highest value.

The first dichotomy is B $\vee$ C at level p.

The matrix is then redrawn with BC as one collection. The similarity for BC and A is m+n divided by 2, in other words the average of A:C and A:D.

	A	BC	D
A	-	$\frac{m+n}{2}$	o
BC		-	$\frac{q+r}{2}$
D			-

The next stage is to take the highest value from this matrix; let us suppose that is o. The next dochotomy then is A $\vee$ D at the level o and this is yet unrelated to B $\vee$ C produced earlier.

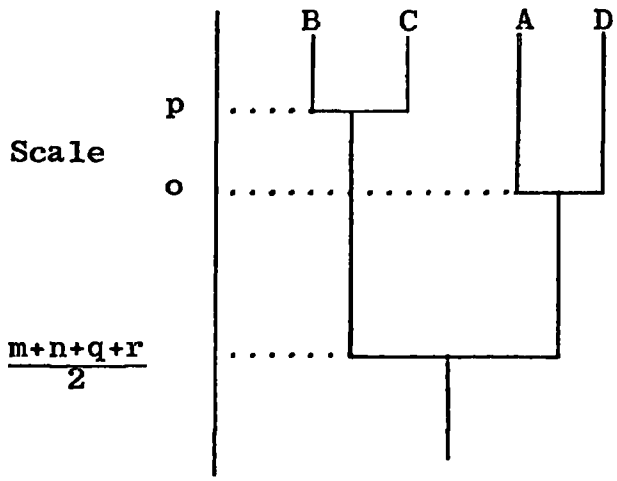
The matrix is now redrawn with AD as one collection.

$$\begin{array}{cc} & AD \quad BC \\ AD & - \quad \frac{m+n}{2} + \frac{q+r}{2} \\ BC & - \end{array} \quad \text{or} \quad AD:BC = \frac{m+n+q+r}{2}$$

Thus the final relationship is produced $AD \vee BC$ at a level $\frac{m+n+q+r}{2}$.

There only remains to decide whether A is closer to B or C, or D is closer to B or C. The dendrogram is drawn.

2. Dendrogram Formation -



From this it can be seen that there are two different groups BC and AD.

The first stage of the analysis was the preparation of 4 community matrices, one for each of the similarity values calculated, in which the similarity measures between each

collection and all other collections were organised into matrix form. Four such matrices were produced from the tabulated data for each site, this raw data may be found in the Appendix section A.1a. The first two measures of similarity were calculated with the aid of a computer; the programme was written by the author and is to be found in Appendix section A.1b. The first coefficient of community computed was Sorensen's Quotient (1948). This produced an index value which described the similarity in the species lists of each pair of habitats compared. Table 1 is the matrix of these values, the index was calculated from the following formula:

$$SQ = \frac{2j}{a+b}$$

j = no. of species common to both habitats

a = no. of species in one habitat

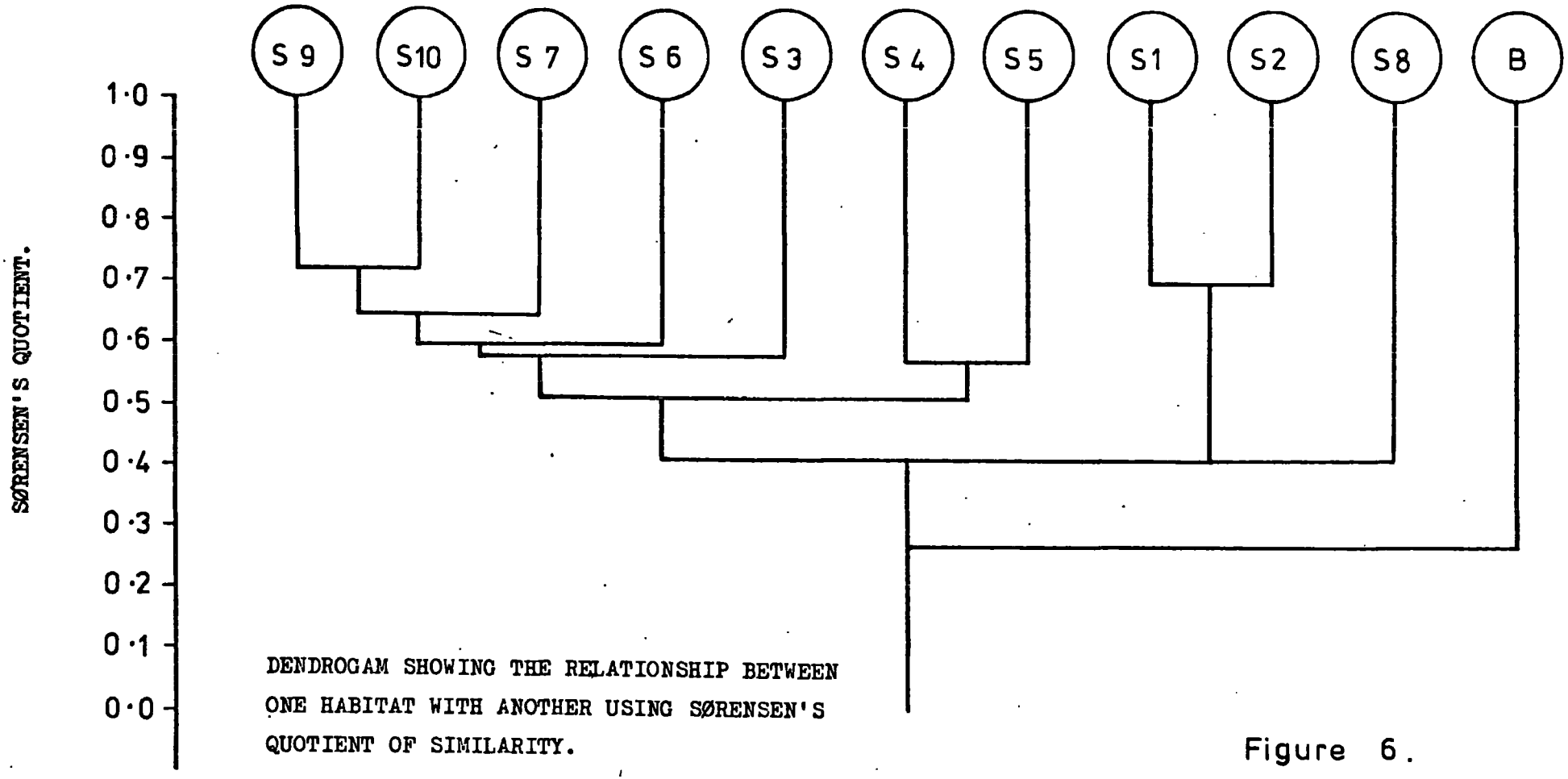
b = no. of species in the other habitat

The danger with this and all such indices, which rely on similarity in terms of species composition, is that they may over value the rare species relative to the dominant ones (Whittaker and Fairbanks, 1958). Figure 6 is the dendrogram that was drawn from these data, the first dichotomy occurred at an SQ. of 0.72 and linked S1 and S2, the second dichotomy was at an SQ. level of 0.70 and combined S9 and S10. These two groups which were most similar in terms of species composition were for springheads which were geographically very closely related, as well as fairly similar in terms of their physical and chemical

Table 1. Community Matrix for Sorensen's Quotient of Similarity

Habitats	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	B
S1		0.70	0.18	0.22	0.46	0.45	0.42	0.21	0.46	0.38	0.24
S2			0.38	0.36	0.60	0.69	0.50	0.25	0.53	0.53	0.28
S3				0.50	0.44	0.57	0.60	0.35	0.56	0.56	0.26
S4					0.57	0.50	0.62	0.47	0.36	0.57	0.22
S5						0.56	0.47	0.37	0.56	0.56	0.23
S6							0.60	0.41	0.63	0.56	0.45
S7								0.44	0.59	0.71	0.24
S8									0.42	0.53	0.32
S9										0.72	0.23
S10											0.17
B											

Sorensen's Quotient produces an index value describing the similarity in the species lists of two or a number of habitats



DENDROGAM SHOWING THE RELATIONSHIP BETWEEN ONE HABITAT WITH ANOTHER USING SØRENSEN'S QUOTIENT OF SIMILARITY.

Figure 6.

environmental factors. Considering the geographical relationship, it is interesting to note that S4 was linked most closely with S5, and although S3 belongs to another main cluster group it was also closely related in SQ. terms to the previous two springheads. Springheads S7, S6 and S3 joined the S9/S10 group at values above an SQ. of 0.5, and formed the largest cluster in terms of species similarity. Just below this level S4 and S5 also joined the group which tended to suggest that there was a core of species common to these springheads. The S1/2 group formed a dichotomy with the main cluster group (S9/10/7/6/3/4/5) at an SQ. of 0.41, as did S8. If we consider physical and chemical data, particularly the data on pH (Fig. 21) and conductivity (Fig. 22), some of the closeness of the relationship between S1 and S2 could be explained. Springhead S8 was not linked in species terms to any other springhead until all the springheads combined at the 0.41 SQ. level. This habitat was very different to the other springhead habitats, it was situated in a meadow whereas all the rest were on open moorland. Thus the flora associated with this spring was very different to that in the other springheads and consisted mainly of encroaching broad leaved grasses. Molluscs were also a feature of this habitat, and this may have been due to the high pH and high level of calcium in the water. Both previous factors may have been due to agricultural management or geochemical factors. All the springheads did form a major cluster group before the beck entered the analysis at an SQ. level of 0.27. This infers that the springhead

habitats were more similar to each other, in terms of species similarity, than the beck. Even the springhead which was the most 'abnormal' for the study area, S8, was more closely linked to the other springheads than the beck. This analysis does tend to indicate that there was a group of species that were common to all the springheads some of which are not found in the beck.

The second coefficient of similarity that was computed was that of Percentage Similarity. This is based on a comparison of the communities in terms of the numbers of individuals of the various species; as such, it places the emphasis on the dominant species (Raabe, 1952). It therefore compares the communities as the SQ. did but takes into account the relative abundances of the species. It was obtained by adding up the smaller of the two percentage composition figures (one for each community) of each species. For example:

SPECIES	HABITAT L.	HABITAT M.
A	50	15
B	20	0
C	15	50
D	10	10
E	5	5
F	0	20
	100%	100%

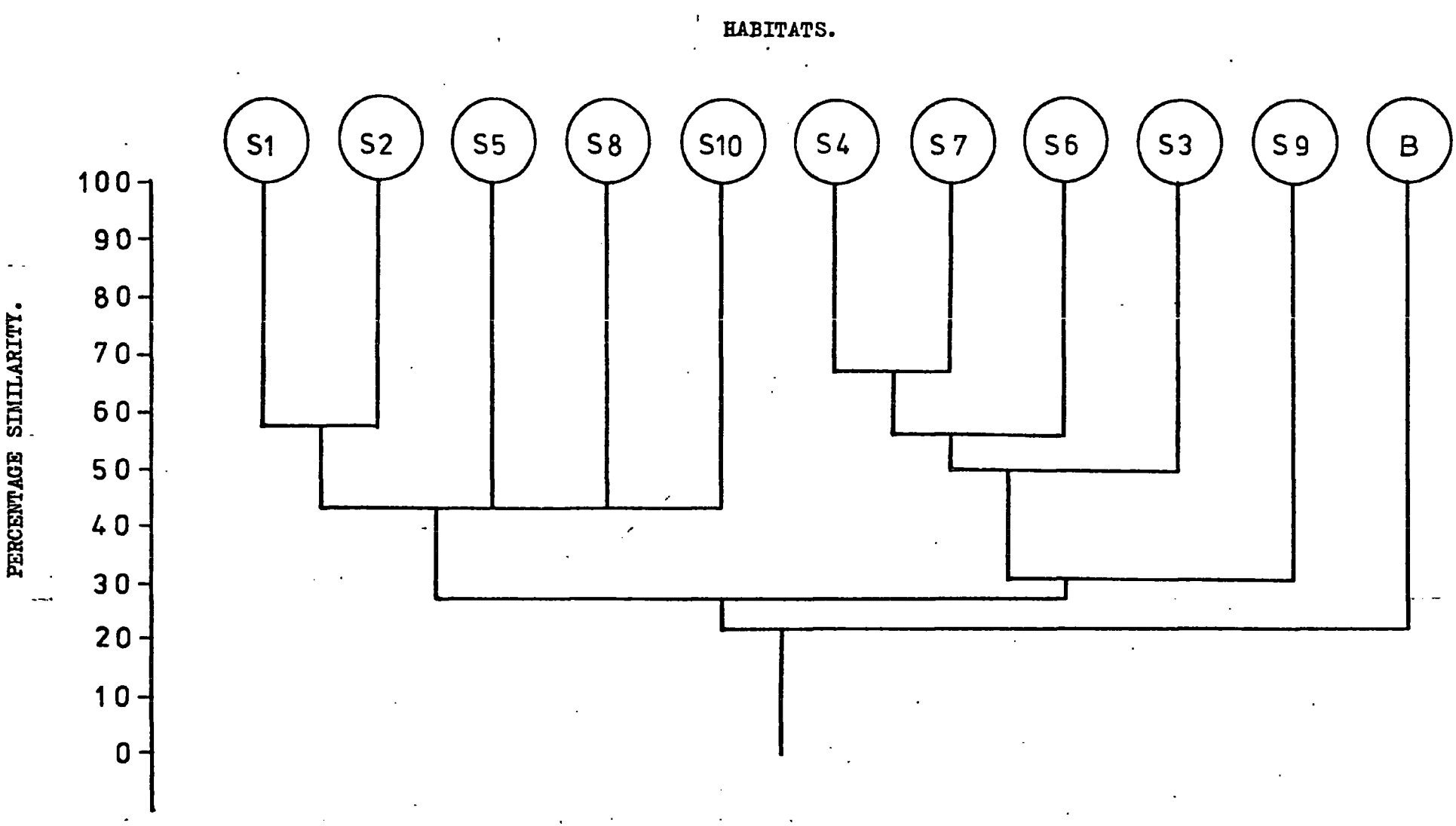
15 0 15 10 5 0 45% Similarity between habitats L and M.

The similarity values may be found in the form of a matrix (Table 2) which was used to produce a second dendrogram (Figure 7). The levels of similarity in this dendrogram were different to those in the first and so were the clusters produced, because this time the bias was in favour of the dominant species. The different clustering of the habitats may reflect the fact that different springheads were more suitable for the numerically dominant species. It is of use at this point to consider Figures 10(a), (b) and (c), which illustrate the percentage composition of the faunal groups at the 11 major study sites, these help to explain the new groupings. Springheads S1 and S2 were again very closely linked with a Percentage Similarity of 57%, this indicated that they were similar in both species composition and in the numbers of the various species. This is not surprising as they are perhaps the most similar habitats as Figures 12 to 20 show. In this dendogram (Fig. 7) there is not the same clustering which in Figure 6 tended to indicate that geography and altitude might be major factors affecting habitat similarity. Two main clusters are visible, S1/2/5/8/10 and S4/7/6/3, S9 seemingly rather different to the other springheads in terms of the Percentage Similarity, perhaps because it was dominated almost equally by three groups of organisms, Plecoptera, Diptera and Trichoptera. It did form a dichotomy with the rest of the springheads at a Percentage Similarity of 30.12% just before the dichotomy of all the springhead habitats with the beck at the 22.35% level.

Table 2. Community Matrix for Percentage Similarity

Habitats	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	B
S1		57	16	22	28	35	45	12	27	30	22
S2			20	24	29	31	56	11	27	56	23
S3				50	16	51	47	7	24	33	15
S4					43	53	67	33	35	25	33
S5						35	40	43	36	19	25
S6							59	23	34	19	54
S7								32	42	53	29
S8									28	12	23
S9										39	19
S10											7
B											

The Percentage Similarity compares two or more communities as before, but takes into account the relative abundance of the species as well



DENDROGRAM SHOWING THE RELATIONSHIP BETWEEN ONE HABITAT WITH ANOTHER USING THE PERCENTAGE SIMILARITY.

Figure 7.

This analysis, as did the previous one, tended to indicate that the springhead habitats were similar to each other in terms of Percentage Similarity at varying levels, but that they had more in common with each other, using this index, than with the beck. Perhaps in this case the presence of certain highly favourable microhabitats for certain faunal groups was a major factor in forming the pattern of cluster produced by the analysis.

Another distinct approach to community analysis is the use of rank correlation methods Kendall's Rank Correlation Coefficients were computed for each habitat with every other using a computer programme, adapted from the BMD programme BMDE3S, called NONPAR. The coefficients are to be found in Table 3, and the dendrogram produced from them is Figure 8. This analysis was used in addition to the two previous analyses because it was found to be possible to apply probability measures to the coefficients. The rank correlation coefficient, Tau, is defined by the formula:

$$\text{Tau } (\tau) = \frac{2S}{n(n-1)}$$

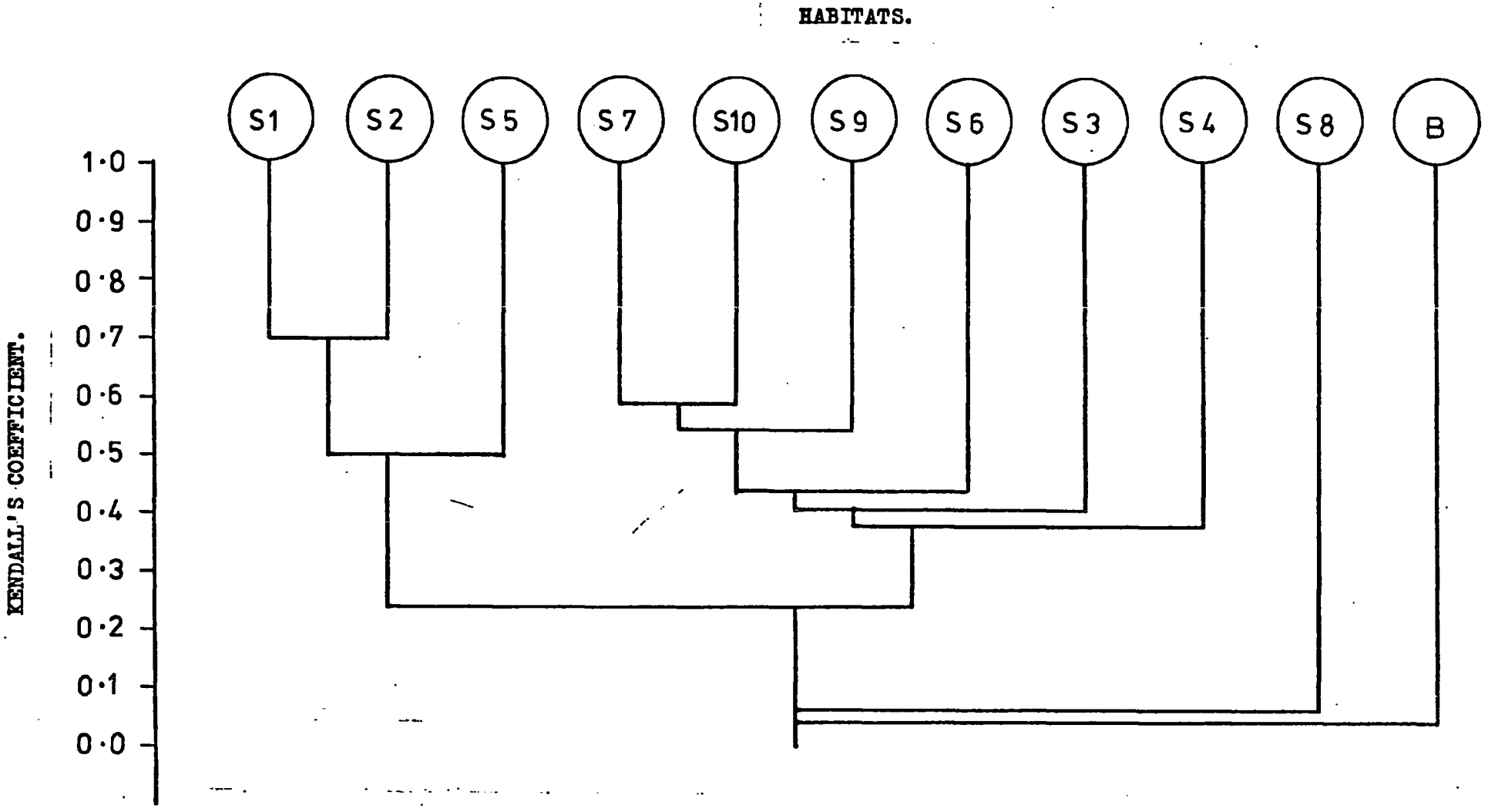
where S is the 'test statistic' and n is the number of pairs of observations. To test whether the correlation is significant, that is to test that the orderings of x and y were independent S was obtained using the formula above, the value below was then calculated using the formula:

$$\frac{S\sqrt{18}}{\sqrt{[n(n-1)(2n-5)]}}$$

Table 3. Community Matrix for Kendall's Rank Correlation Coefficients

Habitats	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	B
S1		0.7005	-0.0105	0.1029	0.4579	0.3159	0.3480	-0.0281	0.3600	0.2995	-0.0101
S2			0.1608	0.2377	0.5251	0.5543	0.3819	-0.0114	0.4057	0.3909	0.0192
S3				0.3653	0.1646	0.3955	0.4095	-0.0328	0.4704	0.3459	-0.0782
S4					0.4667	0.3954	0.5399	0.2166	0.2914	0.4217	0.0494
S5						0.3850	0.2572	-0.0364	0.3268	0.3048	-0.0939
S6							0.4260	0.0999	0.4762	0.3603	0.2067
S7								0.0750	0.5308	0.5745	-0.0638
S8									0.0876	0.2499	0.0451
S9										0.5596	-0.0983
S10											-0.1898
B											

Kendall's Rank Correlation Coefficients measures the association between two ranks of species, in terms of species and abundance



DENDROGRAM SHOWING THE RELATIONSHIP BETWEEN ON HABITAT WITH ANOTHER USING KENDALL'S RANK CORRELATION COEFFICIENTS.

Figure 8.

and the significance determined by treating this quantity as approximately a standardized normal deviate (5 per cent significance if it exceeded 1.960, 1 per cent if it exceeded 2.576 and 0.1 per cent if it exceeded 3.291). From Figure 8 it was observed that S1 and S2 were again very closely linked, when the above statistical procedure was carried out the correlation was found to have a significance of 0.1 per cent. In this dendrogram two main groups of springhead habitats emerged, S1/2/5 and S7/10/9/6/3/4. When the test statistic and the standardized normal deviate values were calculated it was found that the correlation for the extremes of the first group, S1-S5, had a significance of 0.1 per cent; the correlation for the extremes of the second group, S7-S4 also had a significance of 0.1 per cent. This indicated that the communities present were very similar within these two cluster groups. The correlation between S5 and S4, the two closest habitats from the main cluster groups was found to have a 0.1 per cent significance; this indicated that despite there being two main clusters at least the extremes of both were very similar. However, when the correlation between S8, the springhead habitat that did not enter either one of the major clusters, and S4 was tested the significance was found to be 5 per cent, still a significant correlation. It is very interesting to note that the correlation between S8 and B was not significant, neither was that between S1 and B, as would be expected from their obvious differences (see Figs. 12 to 20). This analysis, though it produced slightly different cluster groups to those previously

observed, did again tend to suggest that the springs were more similar to each other in terms of community than to the beck, and that some springs were very closely related to each other, whilst being less closely related to others. This indicated again the possibility of a core group, of what might be crenobiont species, forming the basis of the springhead community.

The final index used to analyse the community structure of the ten springhead habitats and the beck was the Shannon Index of Diversity (Shannon, C. E. and Weaver, W., 1963), H, which was calculated from the formula:

$$H = -\sum_{i=1}^{S} pi \log pi$$

Where: pi is the proportion of the total of the i^{th} species.

S is the number of species.

Diversity indices may be used comparatively or to measure similarity. One single parameter is produced describing the composition and structure of the community. Thus to compare the similarity between two or more communities in terms of their diversity one index must be taken from the other and then, to make a value which is bigger if the communities are more similar the absolute difference between them must be taken from 1. e.g.:

Similarity based on the diversity of two communities j and k $= 1 - \left|DI_j - DI_k\right|$

Vertical lines means the absolute difference, DI = diversity index.

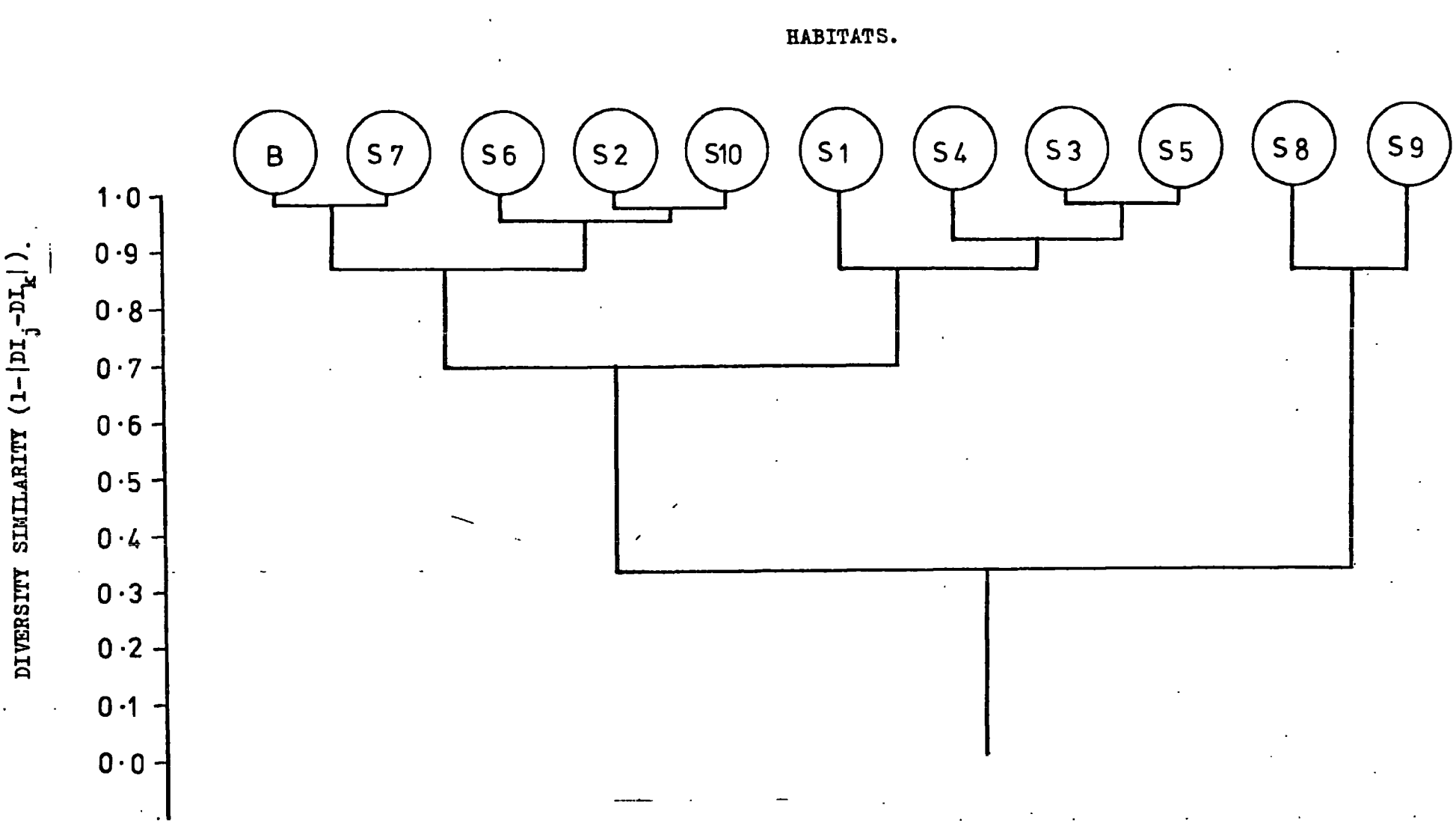
Table 4 is a matrix of diversity similarity for the 11 major study sites, and Figure 9 is the dendrogram that was produced from the data in it. From the dendrogram it appears that there are four clusters of closely related communities in terms of diversity similarity, B/S7, S6/2/10, S1/4/3/5 and S8/9. Considering the physical and chemical factors that were measured (Figs. 12 to 20) there seem to be few obvious reasons for the grouping, though the individual diversity indices do. Springheads S8 and S9 had the highest levels of diversity, 2.3284 and 2.4729 respectively. The S1/4/3/5 group had the lowest measures of diversity they are in the order above, 1.6376, 1.4562, 1.5568 and lastly 1.5275. The other two groups were intermediate with values ranging from the beck with 1.7916, to S10 with a value of 1.9484. From this analysis it can be seen there was a narrow range of diversity in the habitats investigated in the valley, and that some habitats had a great deal of similarity as measured by means of the Shannon Index of Diversity. The only obvious relationship between any of the habitat clusters produced in this analysis is the fact that the S3/4 and 5 group are springs that are closely linked in a number of ways, in particular altitude, close proximity to each other, pH and oxygen levels. Other measures of diversity may be found in the Appendix section 1c.

In Figure 10(a-c) the percentage composition of the fauna in each of the habitats is shown in terms of the major taxonomic groups, from these diagrams the dominant group(s) in the 'Spring'

Table 4. Community Matrix for Shannon's Index of Species Diversity, using Diversity Similarity

Habitats	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	B
S1		0.7200	0.9192	0.8186	0.8899	0.6563	0.8219	0.3092	0.1647	0.6892	0.8460
S2			0.6392	0.5386	0.6099	0.9363	0.8981	0.5892	0.4447	0.9692	0.8740
S3				0.8994	0.9707	0.5755	0.7411	0.2284	0.0839	0.6084	0.7652
S4					0.9287	0.4749	0.6405	0.1278	0.0167	0.5078	0.6646
S5						0.5462	0.7118	0.1991	0.0546	0.5791	0.7359
S6							0.8344	0.6529	0.5084	0.9671	0.8733
S7								0.4873	0.3428	0.8673	0.9759
S8									0.8555	0.6200	0.5368
S9										0.4755	0.3187
S10											0.8432
B											

Diversity indices provide a single parameter describing the composition and structure of the community



DENDROGRAM SHOWING THE RELATIONSHIP BETWEEN ONE HABITAT WITH ANOTHER USING SHANNON'S INDEX OF SPECIES DIVERSITY.

Figure 9.

community may be identified. For groups whose adult stage is not aquatic there must be fairly dramatic changes in their importance values in the community, therefore if research was carried out a seasonal pattern of community would probably emerge. The percentages from which Figures 10 were produced are to be found in Table 5.

An estimate of the Niche Breadth of the eight species of stonefly has been made. This parameter gives an idea of the nature of the species - whether it is more specialised and limited or whether it is wide ranging. The prefixes 'steno' and 'eury' are used to describe the two extremes. For instance a eurythermal species would be one that is tolerant of a wide range of temperatures. The niche breadth of the stoneflies was calculated from the formula:

$$B_i = \frac{1}{\sum Pih^2}$$

Where: Bi is the niche breadth of the i^{th} species.
Pih is the frequency of the i^{th} species in the h^{th} habitat.

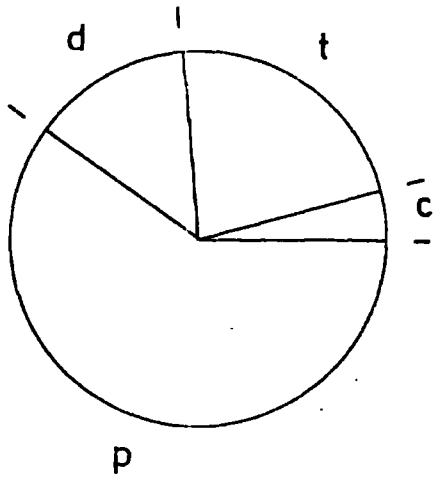
As the number of habitats in any study is variable, B_i is usually divided by the total number of habitats being examined, and in this work each value calculated using the above formula was divided by 11.

The frequency values for the stonefly species are shown in Table 6, and the calculated values for niche breadth in Table 7. The niche breadth measure condenses data related to

Table 5. Percentages of Major Faunal Groups

Faunal Group	Percentage of each group in each habitat										
	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	B
Plecoptera	60.06	66.26	17.34	17.64	9.10	21.67	42.88	0.53	36.61	44.33	42.29
Ephemeroptera	0	0	0	0	0	0	0	0	0	0	2.21
Diptera	13.60	13.85	3.72	28.41	70.20	17.48	29.17	37.60	24.64	8.65	18.23
Trichoptera	22.08	17.46	26.32	14.7	13.15	13.75	1.50	4.23	31.68	14.51	3.67
Coleoptera	4.23	1.20	3.72	0	1.53	25.86	0	25.26	0.70	0	28.48
Annelida	0	1.20	0.31	2.94	2.03	0.47	0.50	10.00	1.06	0.40	0
Mollusca	0	0	0	0	0	0	0	18.95	0	8.12	0
Tricladida	0	0	14.24	5.88	0	0	5.98	0.53	2.46	18.64	0
Crustacea	0	0	34.06	23.53	2.53	20.75	19.95	0.53	2.82	5.33	0
Other	0	0	0.31	5.88	1.52	0	0	2.65	0	0	5.12

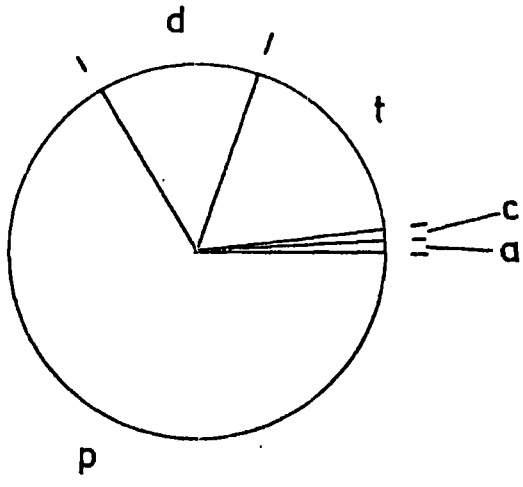
Figure 10(a).



Percentage composition of faunal groups in the 11 major study sites.
With levels of Calcium, Zinc and Lead in water samples.

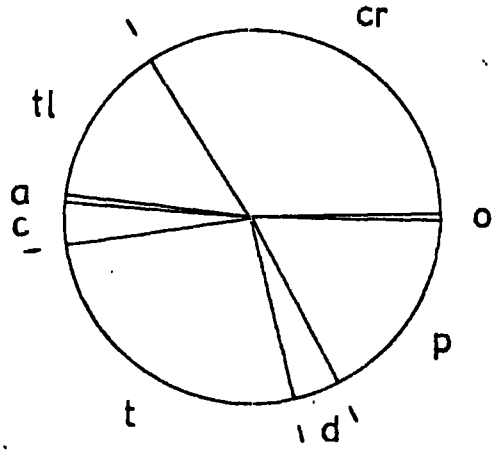
SPRING 1.

Ca=2.0 mg.l.$^{-1}$



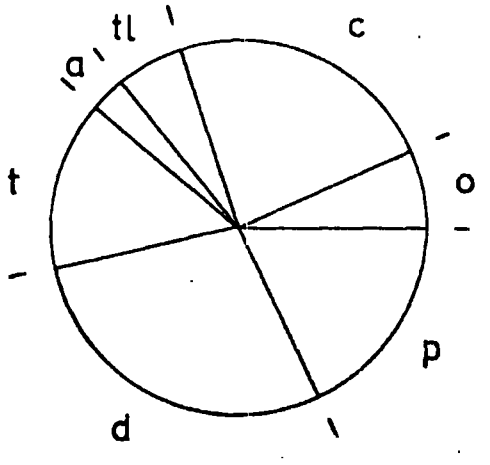
SPRING 2.

Ca=4.0 mg.l.$^{-1}$



SPRING 3.

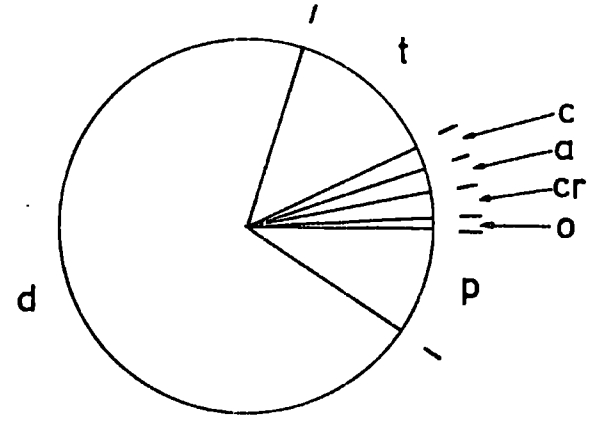
Ca=4.0 mg.l.$^{-1}$



SPRING 4.

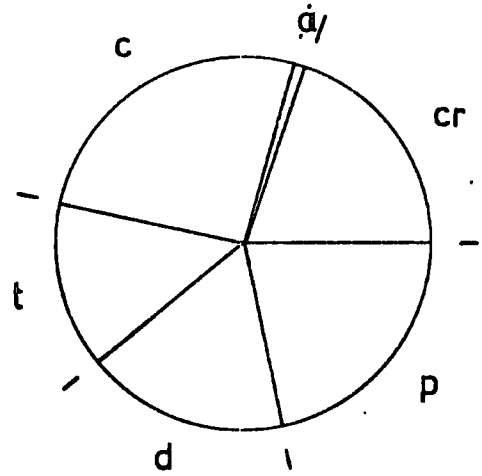
Ca=20.0 mg.l.$^{-1}$

Figure 10(b).



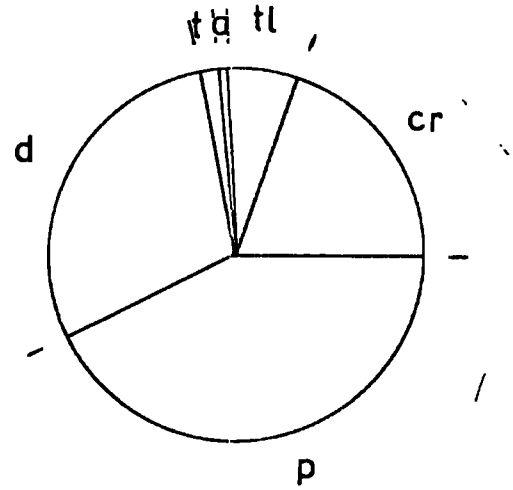
SPRING 5.

Ca=46.0 mg.l.$^{-1}$



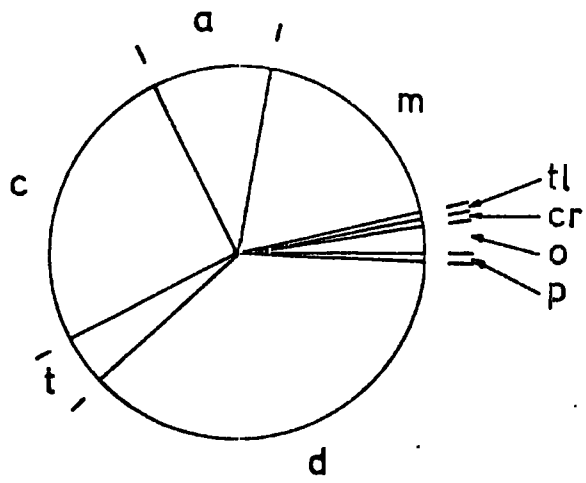
SPRING 6.

Ca=22.0 mg.l.$^{-1}$



SPRING 7.

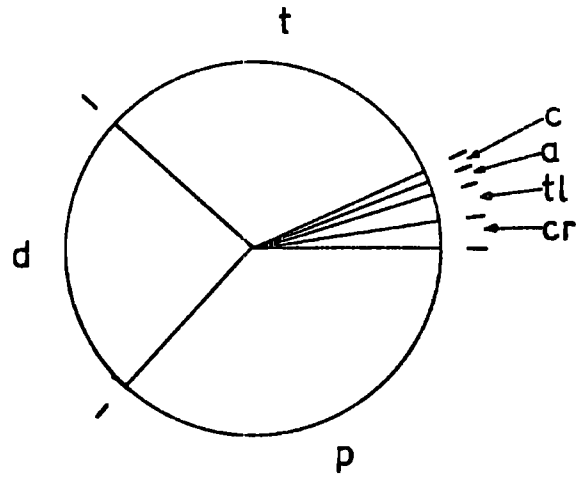
Ca=6.0 mg.l.$^{-1}$



SPRING 8.

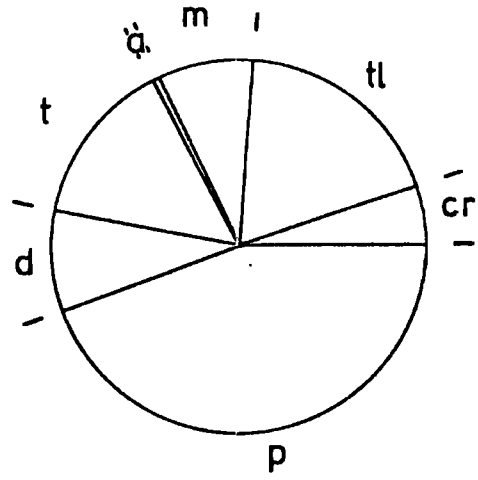
Ca=14.0 mg.l.$^{-1}$

Figure 10(c).



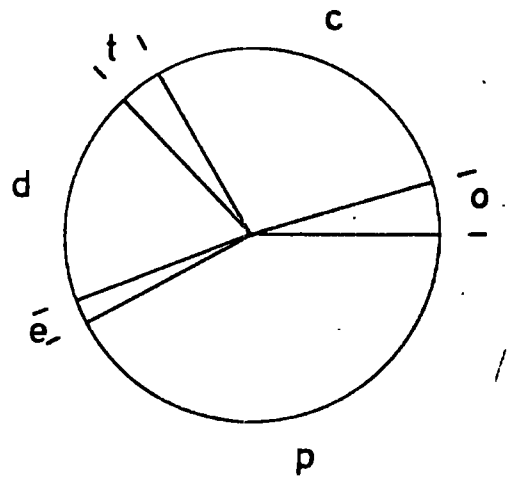
SPRING 9.

Ca-4.0 mg.l.$^{-1}$



SPRING 10.

Ca-2.0 mg.l.$^{-1}$



LITTLE EGGLESTONE BECK.

Ca-8.0 mg.l.$^{-1}$

Zn-0.15 mg.l.$^{-1}$

Pb-0.5 mg.l.$^{-1}$

Legend.

p = PLECOPTERA.

e = EPHEMEROPTERA.

d = DIPTERA.

t = TRICHOPTERA.

c = COLEOPTERA.

a = ANNELIDA.

m = MOLLUSCA.

tl = TRICLADIDA.

cr = CRUSTACEA.

o = OTHER.

Table 6. Stonefly Frequency Table

	Habitats / Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	B
7	Amphinemura Sulcicollis	0	0	0.1187	0	0	0.0475	0.0209	0	0.8070	0	0.0059
8	Brachyptera risa	0	0	0	0	0	0	0	0.5399	0	0	0.4601
9	Capnia bifrons	0	0.2465	0	0.0986	0.1479	0.1972	0.0868	0	0	0.0868	0.1361
10	Chloroperla torrentium	0	0	0	0	0	0.3333	0	0	0	0	0.6666
11	Leuctra inermis	0	0	0	0	0	0	1.0000	0	0	0	0
12	Leuctra nigra	0	0	0.1736	0	0	0	0.1528	0	0.5280	0.1528	0
13	Nemoura erratica	0.1872	0.0900	0.1584	0.144	0.0432	0.3024	0.3991	0	0.0180	0.1330	0.0135
14	Nemurella picteti	0.0188	0.0938	0	0	0.0035	0	0.2147	0	0.0293	0.6399	0

Table 7. Niche Breadth of Stonefly Species

Code No.	Stonefly Species	Niche Breadth
7	Amphinemura sulcicollis	0.14
8	Brachyptera risi	0.18
9	Capnia bifrons	0.55
10	Chloroperla torrentium	0.16
11	Leuctra inermis	0.09
12	Leuctra nigra	0.26
13	Nemoura erratica	0.27
14	Nemurella picteti	0.20

the numerical importance of a species in a number of habitats and is thus a measure of its success in invading a large range of habitats. Those species with a high niche breadth, such as Capnia bifrons Newman, are able to exist in a large range of habitats and would be termed eurytopes, whereas species such as Leuctra inermis Kempny have a small niche breadth and are stenotopes. Other species fell between these extremes.

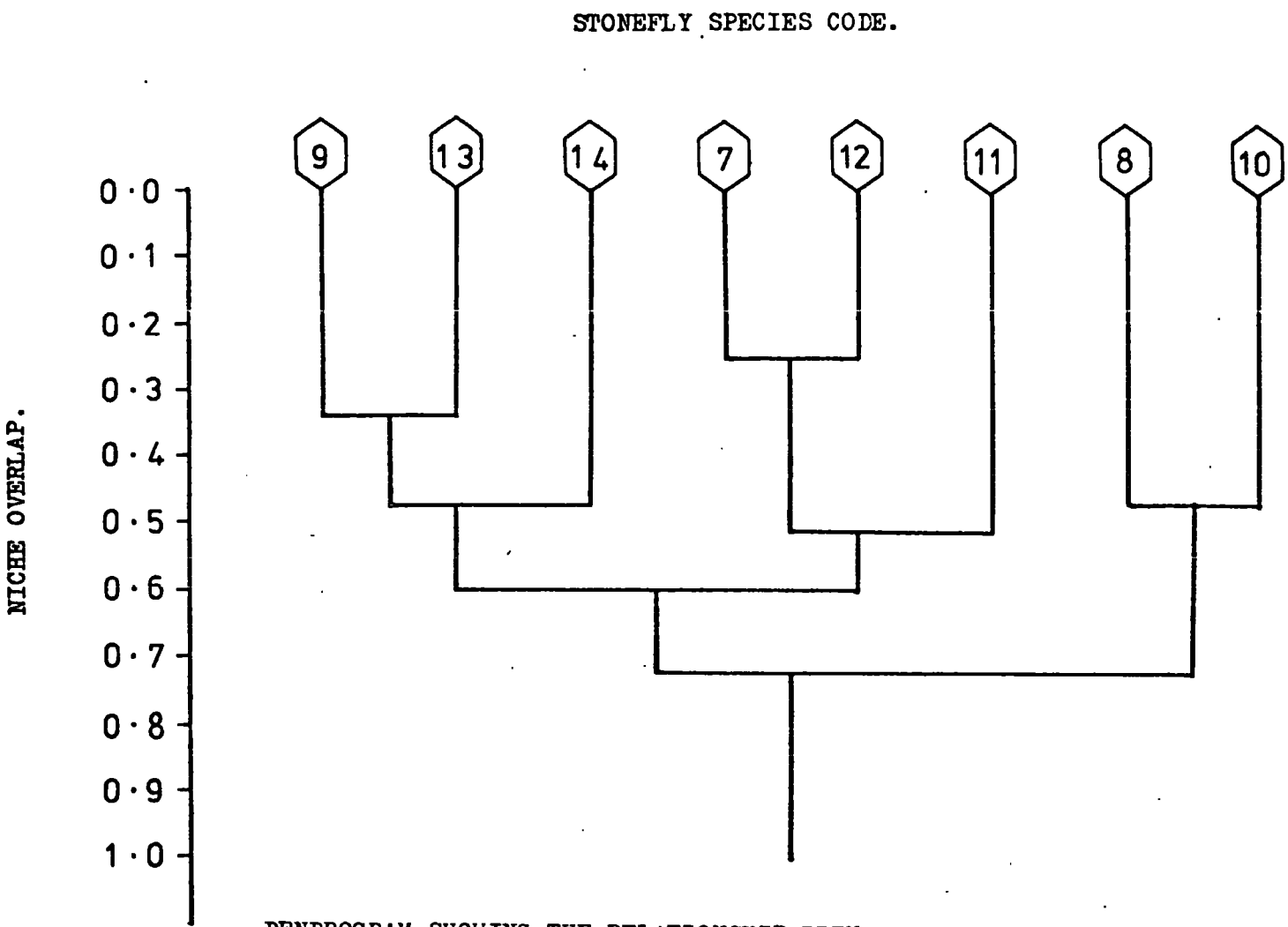
Niche Overlap between the stonefly species was considered next, this is a measure of the similarity between species in terms of their niche requirements. Not surprisingly, therefore, the dendrogram (Figure 11) indicates a similarity in the requirements of those species which lived in the greatest numbers in the same habitat. This statistic, D, gave an indication of the amount of joint use of a resource by two or more species. In practice the parameter D should be a measure of the distance between two species whose position has been plotted in a multidimensional coordinate frame whose coordinates were measures of aspects of the niche. Thus if the niche overlap is small the ecological distance between the two species being considered is also small and so there is considerable joint use of available resources. Niche overlap for the stoneflies was calculated by:

$$D_{ij} = \sqrt{\frac{\Sigma(Pih - Pjh)^2}{2}}$$

where: Pih was the frequency of the i^{th} species in habitat h and Pjh was the frequency of the j^{th} species in habitat h.

Table 8. Species Matrix for Plecoptera in Terms of Niche Overlap

Species Code	7	8	9	10	11	12	13	14
7		0.76	0.63	0.77	0.90	0.25	0.67	0.73
8			0.52	0.46	0.87	0.66	0.64	0.70
9				0.45	0.70	0.45	0.34	0.47
10					0.88	0.67	0.58	0.71
11						0.72	0.52	0.72
12							0.48	0.51
13								0.47
14								



DENDROGRAM SHOWING THE RELATIONSHIP BETWEEN STONEFLY SPECIES IN TERMS OF NICHE OVERLAP.

Figure 11.

In the niche overlap dendrogram three groups of stonefly appear, the species 9/13/14 group were perhaps the most cosmopolitan group, the species 7/12/11 group were also springhead dwellers, whereas the species 8/10 group were stoneflies that were most abundant in the beck. The species that had the highest niche breadths were species that linked the individual habitats in the similarity dendrograms.

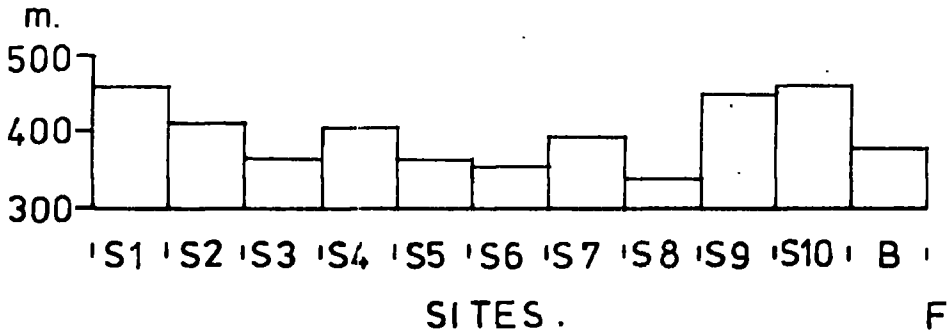
2.2 Measurement of Physical and Chemical Factors at the sites

Figures 12 to 20 summarise the parameters that were measured and should be studied in conjunction with other analyses. Results of the chemical analysis may be found in Figure 14.

2.2a A measure of the Vegetation/detritus

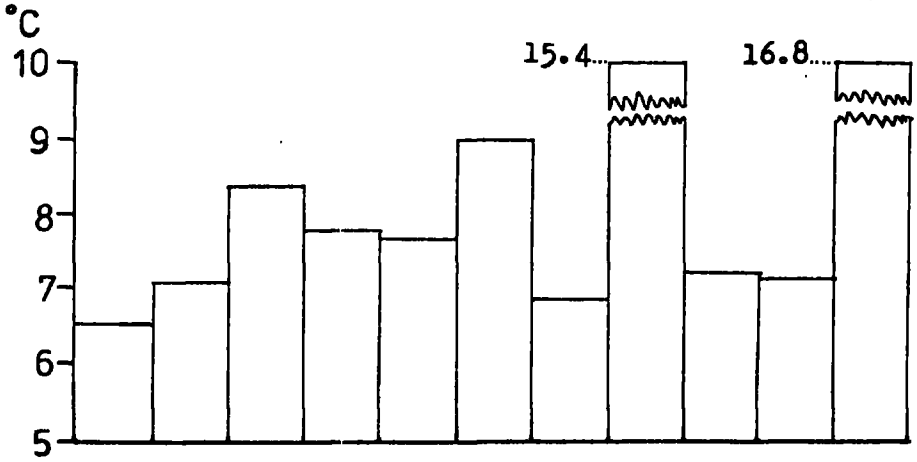
The results of this investigation are to be found in the Appendix section A.2j. When the amount of primary producer material was correlated with the numbers of herbivores and detritivores in each habitat a correlation coefficient of 0.7004 was obtained. This positive correlation had a probability of 0.02 with 10 degress of freedom, which means that the correlation between the variables was significant at the 2% level. Therefore an increased amount of vegetation/detritus was correlated with an increased number of herbivores and detritivores in the habitats studied.

Figure 12.



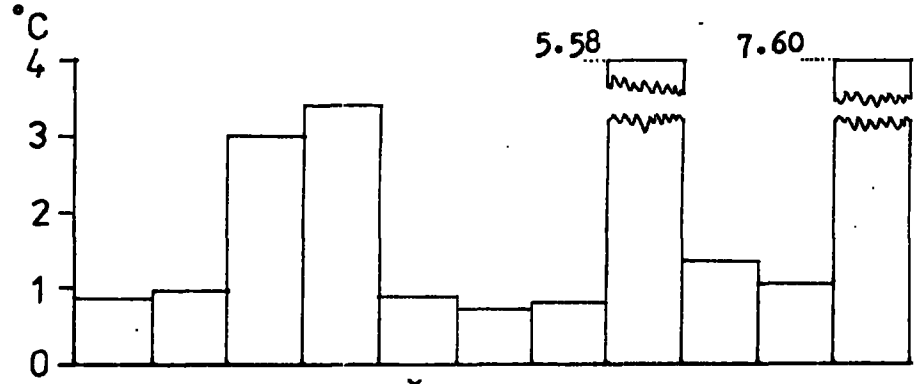
Altitude of springheads and beck below S1. in metres.

Figure 13.



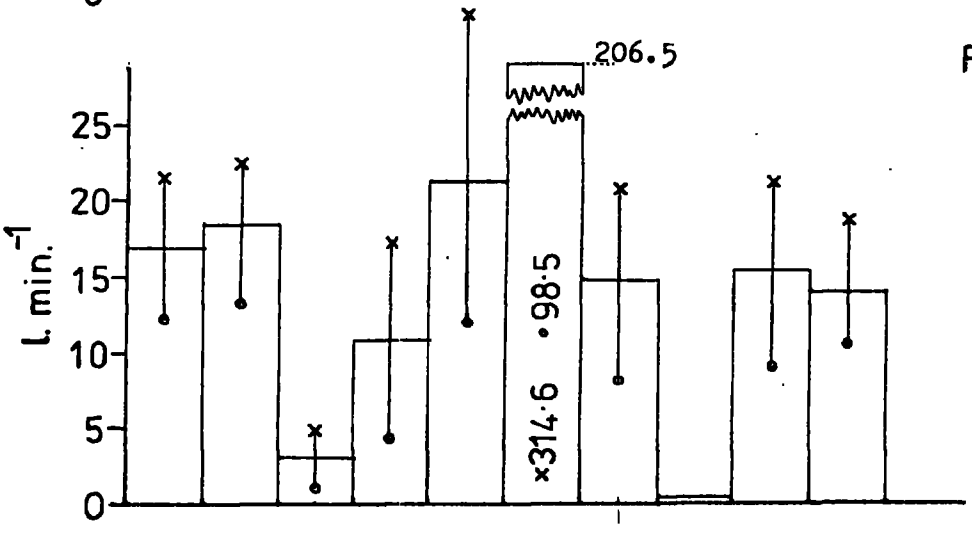
Mean temperature of springheads and beck on 10 visits during the study.

Figure 14.



Diurnal range in °C. The mean of three recordings with a Six's thermometer.

Figure 15.



Mean discharge in litres per minute. Spring and Summer values shown: 'x' and '•' respectively.

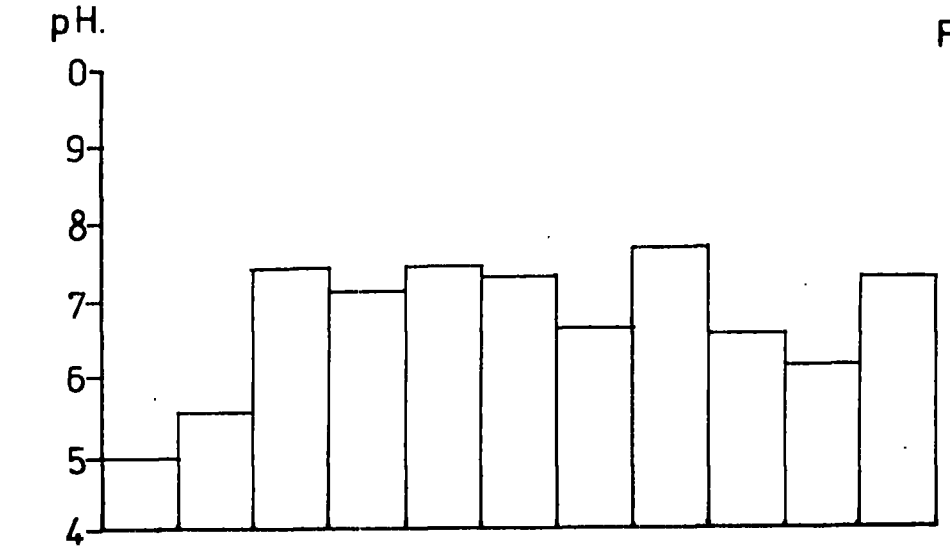


Figure 16.

Mean pH. in each springhead and the beck. Range too small to show on graph.

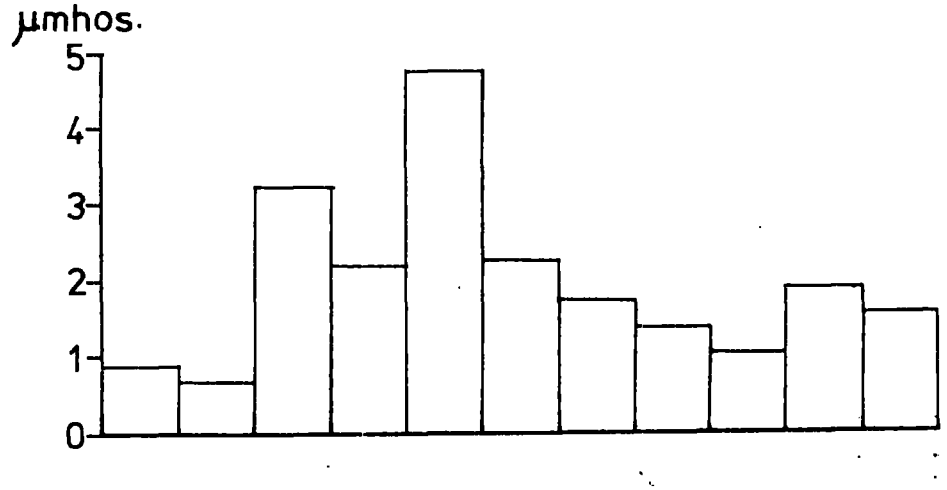


Figure 17.

Conductivity in micro mhos. in each springhead and the beck.

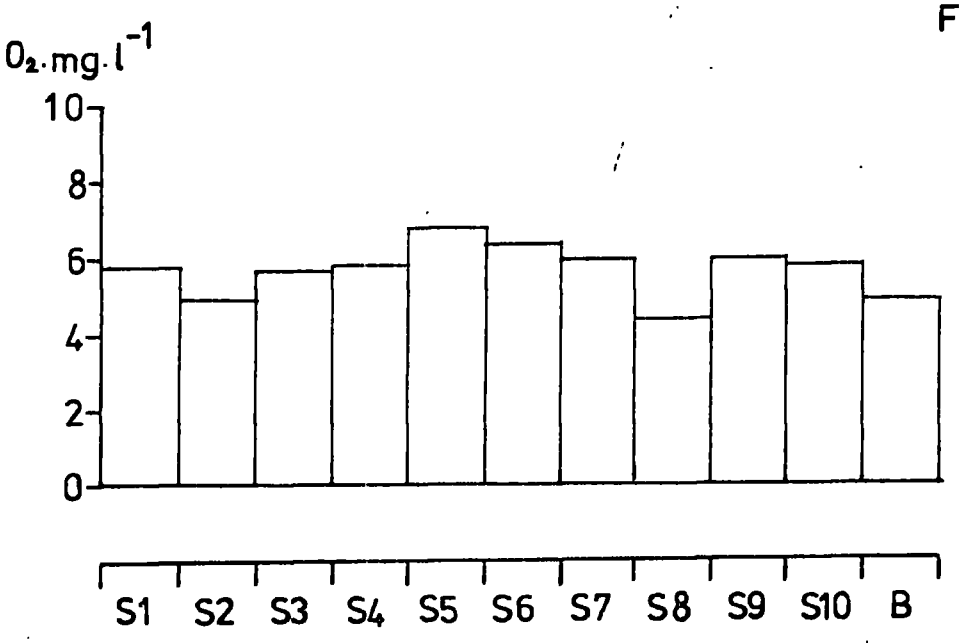


Figure 18.

Mean Oxygen concentration in mg. per litre. Range too small to show on graph.

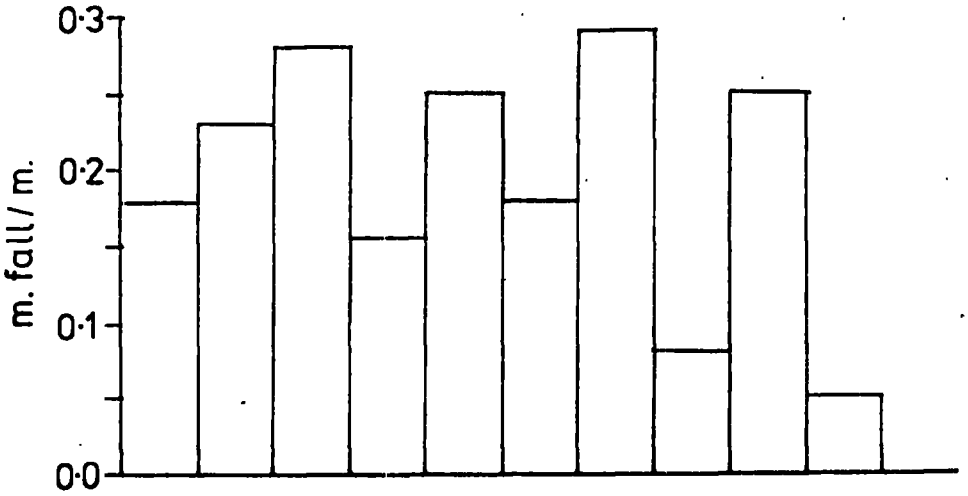


Figure 19.

Mean gradient in metres per metre over the first 5 metres : the springhead.

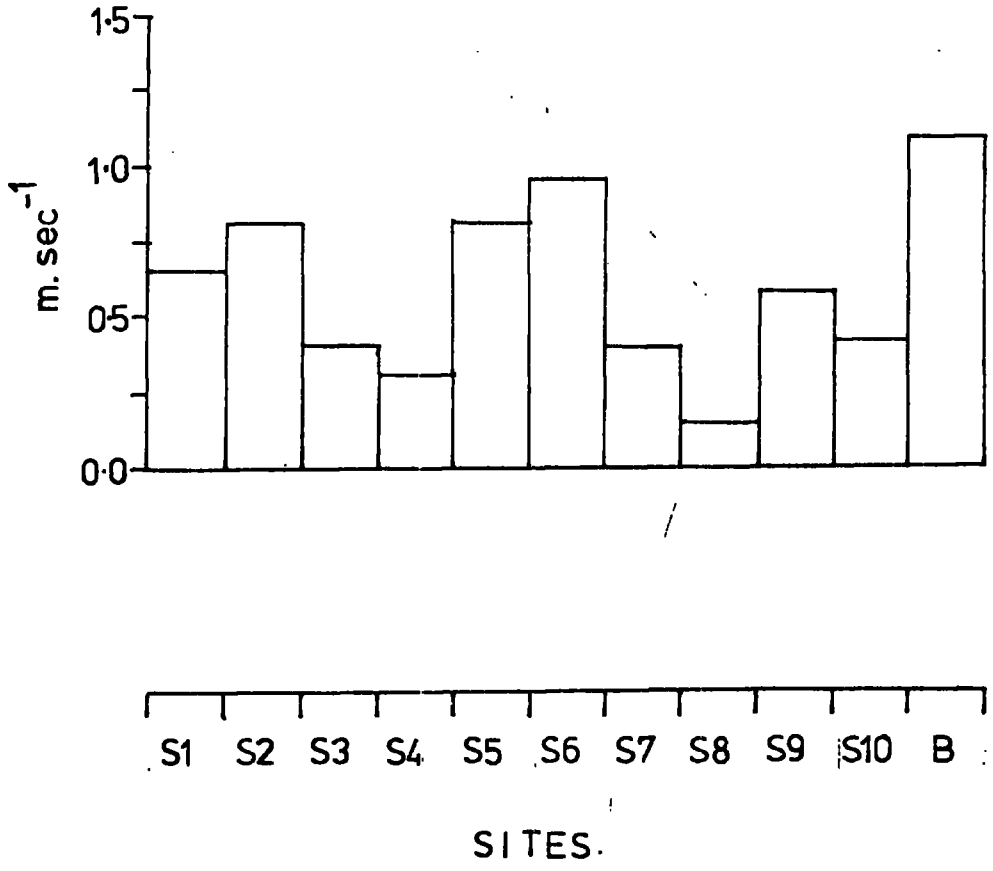


Figure 20.

Maximum flow rate detected at time of faunal sampling.

2.3 Qualitative and Quantitative sampling of Stations down the springbrook of S1

The data from which this analysis was derived can be found in the Appendix section A.3a, although histograms showing the log. of the numbers of organisms in the various species, or groups, form Figure 24 in this section of the study. The form of analysis used for this data was as in section 2.1 of this chapter. Firstly a community matrix and dendogram were drawn for Sorensen's Quotient to establish the relationships between the various stations and the springhead, defined as the 5 metres of springbrook, in terms of species similarity. These are illustrated in Figure 21. The dendrogram shows three groups, S1, the springhead itself, St1/St2, and St3/St4. The highest degree of species similarity occurred between St1 and St2 their dichotomy was at an SQ. (Sorensen's Quotient) level of 0.86, this was not unexpected as the sites were very similar in many respects, and of course they were nearer to each other than other sites, especially when direction of water flow is considered. Stations St3 and St4 were also closely related with an SQ. value of 0.75. All the stations formed a dichotomy at an SQ. level of 0.6, they were therefore all very similar in terms of the species present. It is interesting that the dichotomy with all the stations and the springhead was at quite a low level of similarity, this again tends to suggest that there was a core of species that were confined to the springhead habitat. The order in which the others cluster out suggests that a relationship exists between adjacent habitats, especially

(a)Community Matrix.

Habitats	Sl.	St.1	St.2	St.3	St.4
Sl.		0.27	0.35	0.63	0.70
St.1			0.86	0.50	0.40
St.2				0.56	0.45
St.3					0.75
St.4					

(b)Community Dendrogram.

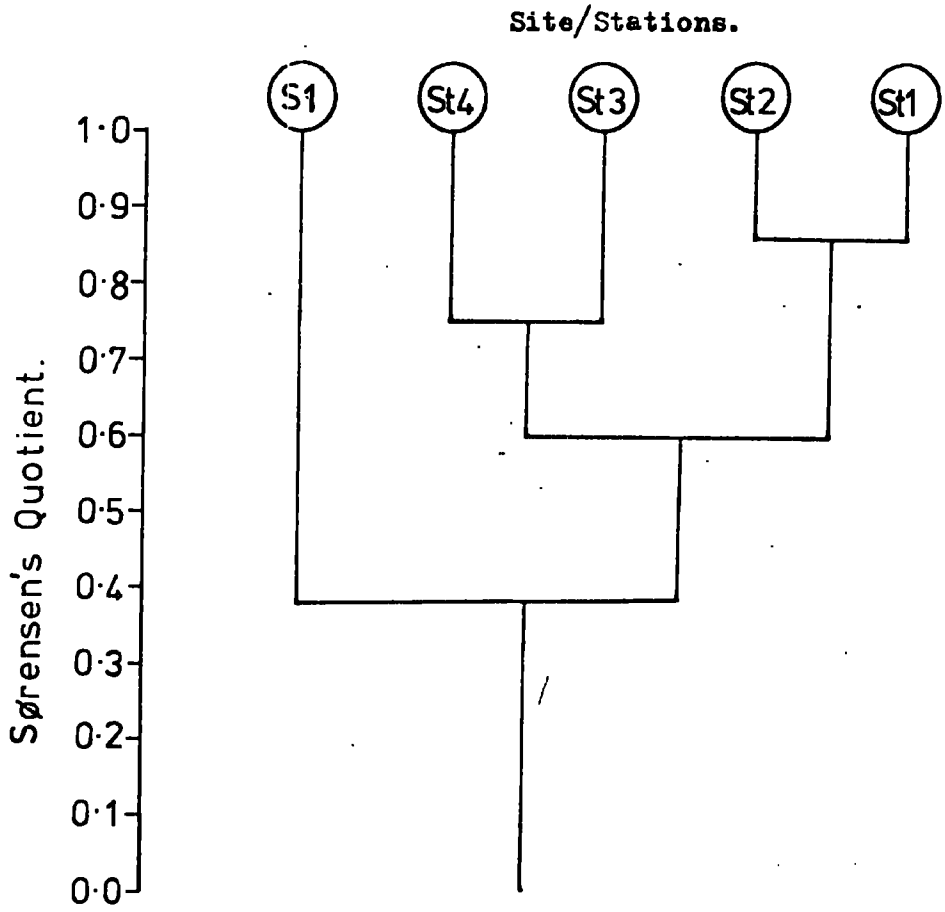


Figure 21. Community Matrix for Sorensen's Quotient of Similarity and Community Dendrogram showing the relationship between one habitat and another in the springhead and springbrook of Sl.

within the springbrook, but to a lesser extent between the springhead and its adjacent habitat. In fact in terms of SQ. the springhead was more closely related to other springheads than to stations on its own springbrook.

Secondly a matrix and a dendrogram were produced for Percentage Similarity (Figure 22) which show the similarity of the habitats in terms of the dominant species. The stations St3 and St4 were again found to be closely linked, but stations St1 and St2 were now found to be dissimilar. Station St2 was a site favoured by sheep for drinking, and because of this appeared to provide a habitat well suited to some species but not to others, Annelids and Chironomids probably account for the differences in the second stations position in Fig. 22b. The other habitats again appear to cluster out according to their closeness in the field, but again there was a considerable difference in similarity between the springhead and the stations along the springbrook.

Finally the Shannon Index of diversity was calculated for each station and the springhead (these indices and other indices of diversity calculated may be found in the Appendix section A.3b), these values were used to produce a matrix of diversity similarity and dendrogram Figures 23(a) and (b) respectively. Station St4 and S1 were found to have the highest degree of diversity similarity, the former had an 'H' value (Shannon Index) of 1.5935, whilst the latter had an 'H' value of 1.6376. These were the two habitats with the highest diversity index, they were also the most stable of the habitats at this spring

(a)Community Matrix.

Habitats	Sl.	St.1	St.2	St.3	St.4
Sl.		51	32	64	64
St.1			44	78	75
St.2				33	32
St.3					90
St.4					

(b)Community Dendrogram.

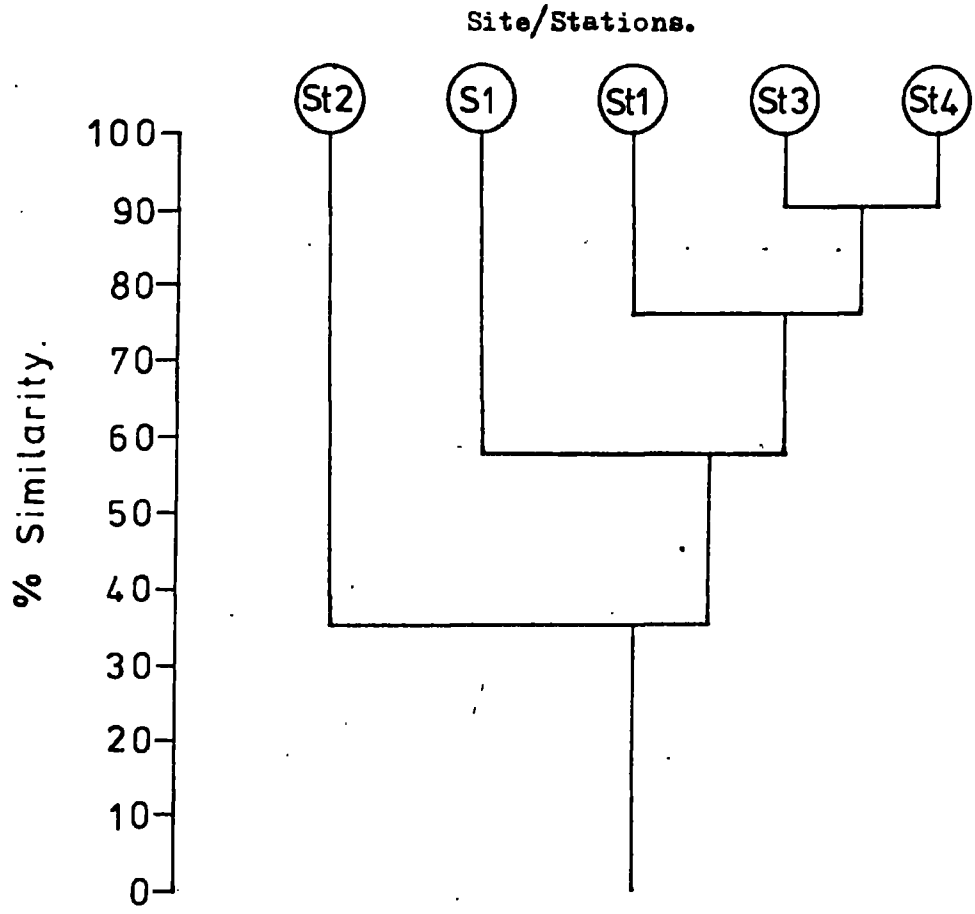


Figure 22. Community Matrix for Percentage Similarity and Community Dendrogram showing the relationship between one habitat and another in the springhead and springbrook of Sl.

(a)Community Matrix.

Habitats	Sl.	St.1	St.2	St.3	St.4
Sl.		0.53	0.91	0.68	0.93
St.1			0.43	0.84	0.60
St.2				0.59	0.84
St.3					0.75
St.4					

(b)Community Dendrogram.

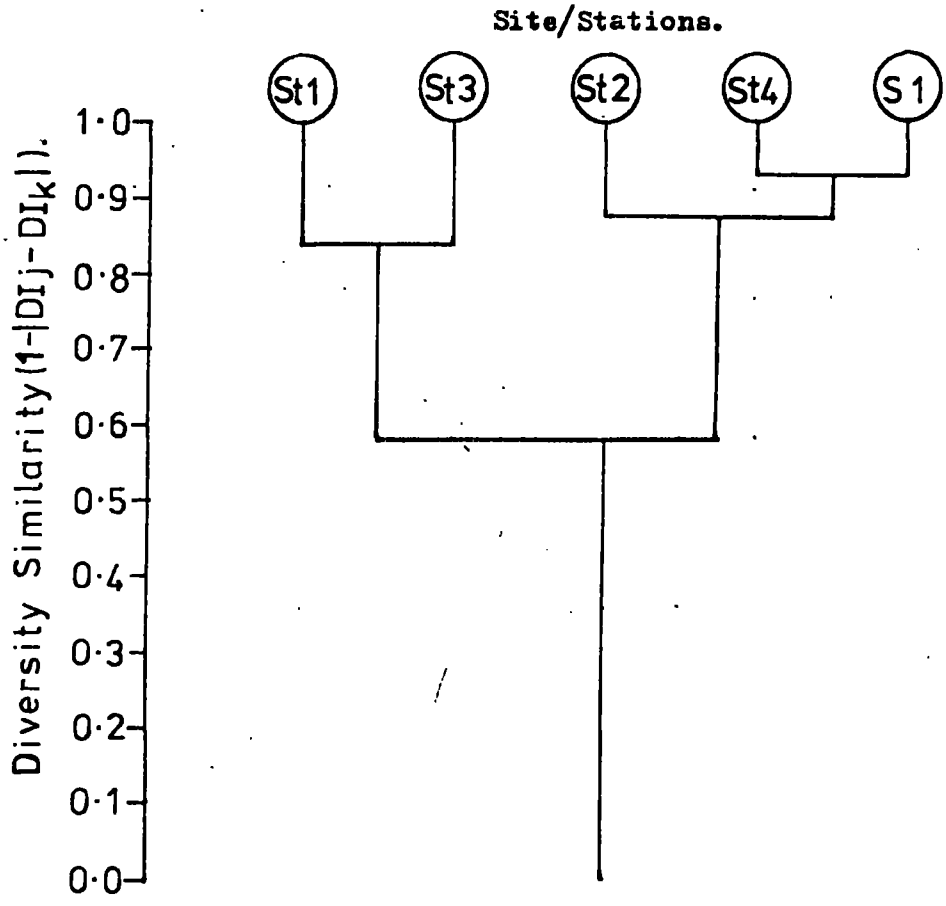


Figure 23. Community Matrix for Diversity Similarity and Community Dendrogram showing the relationship between one habitat and another in the springhead and springbrook of Sl.

Figures 24. Showing the log. of the number of each species per $m.^2$ at each site sampled in S1 and its springbrook.

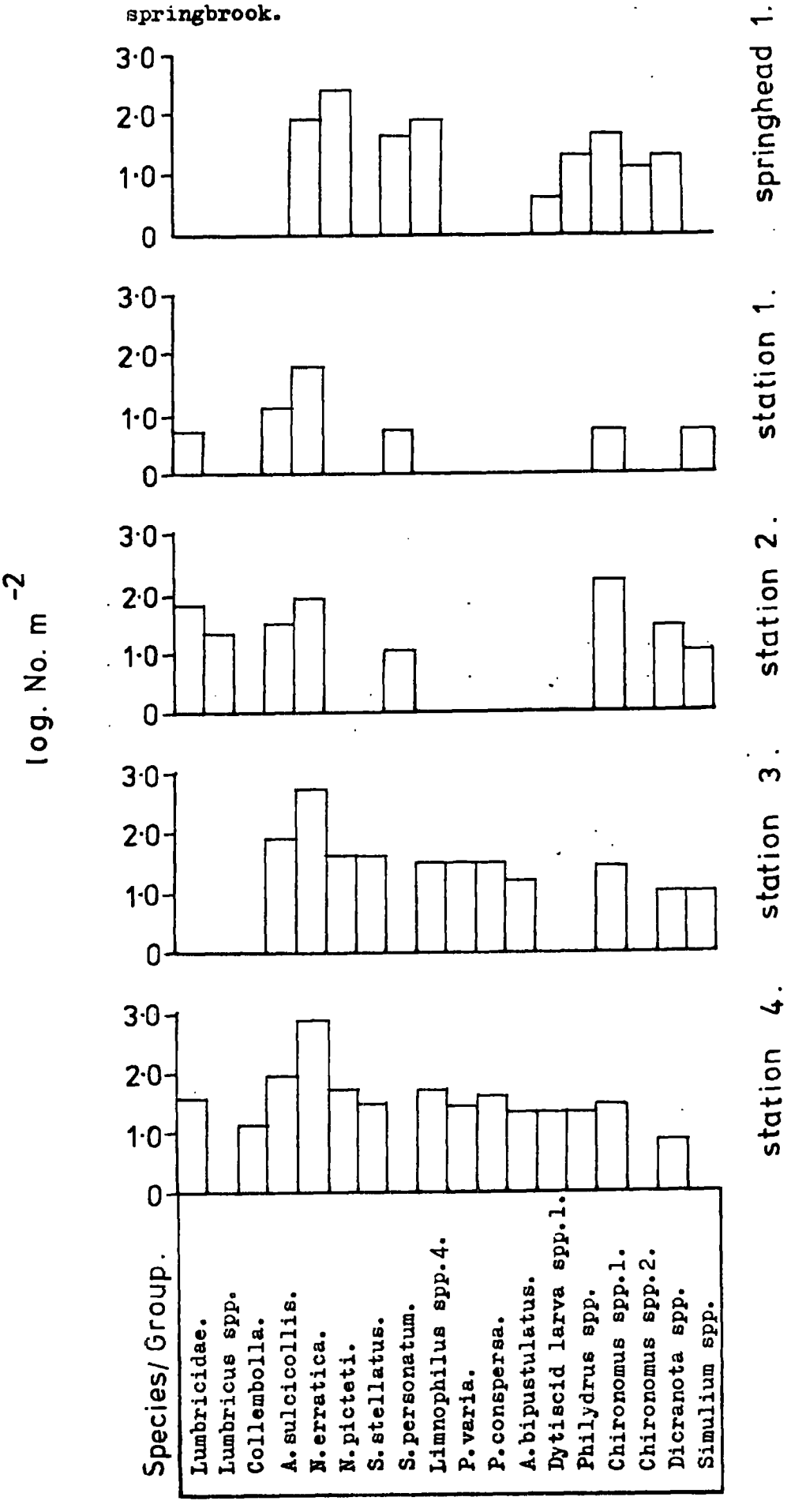
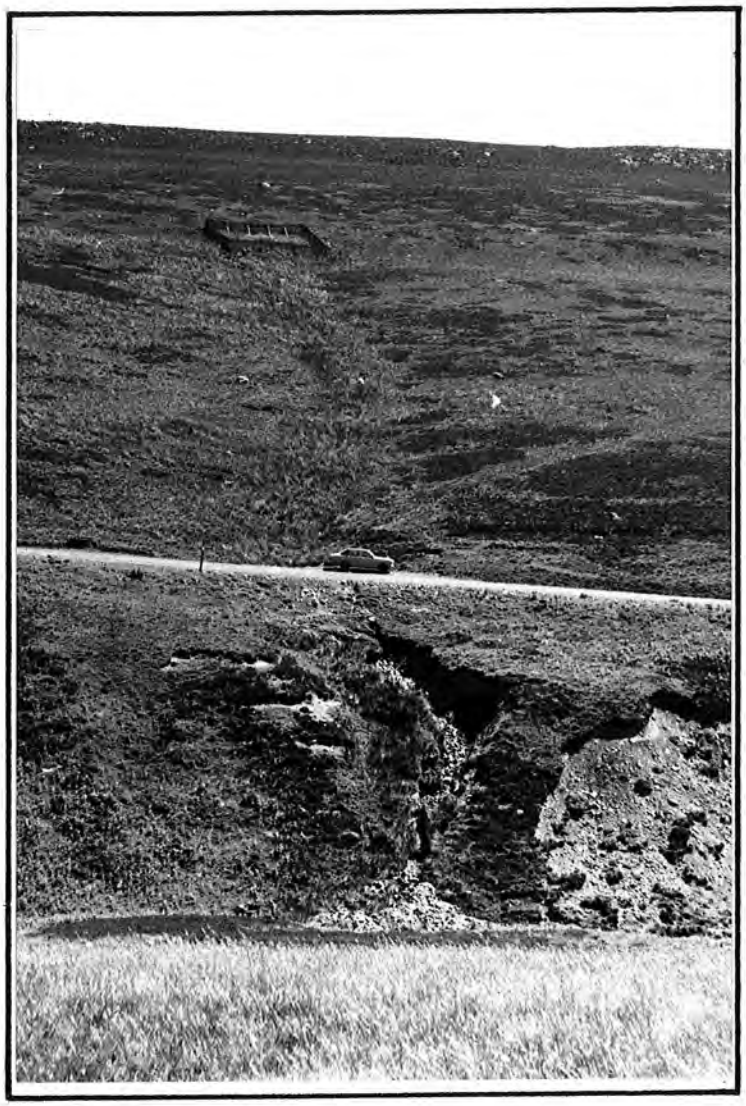


PLATE 4.



A view of springhead 2 and its springbrook from the West side of the Eggleshope valley.

site and the largest. Station St2 was close to them in terms of diversity similarity, but St1 and St3 had 'H' values much lower at 1.1637 and 1.3200 respectively. In fact the actual range of diversity values was not great. The Shannon Index tends to favour the rare species, in the Appendix the Simpson Index is given for the same communities, this index is weighted in favour of the common species. The former was chosen for use in the analysis because in the springhead and springbrook it is perhaps rare species that delimit the various communities.

2.4 A Frequency Analysis of S2 and its Springbrook in the Spring and Summer of 1976. (Plate 4 shows site in Summer) Figures 31 and 32 show the results

Lumbricidae:

These were much more abundant in the Spring and were commonest in areas where the springbrook was weeded up and muddy. In the Summer they were still present in two of the areas but none were found in the springhead.

Amphinemura sulcicollis Stephens:

In the Spring the frequency of this species was high in the upper part of the springbrook and was not found below sample site 60, whereas in the Summer the situation was reversed, it was only present below sample site 60 and its frequency was much lower. Conditions of temperature were very different at this level, the amplitude of the range being much greater.

Capnia bifrons Newman:

This stonefly was common in both the lower and upper parts of the springbrook as well as being present at low frequencies over much of the rest. No specimens of this species were found in the Summer samples, this may have been due to the emergence period occurring between the two frequency analyses.

Chlorperla tripunctata Scopoli:

Was only found in the Spring samples and had a very restricted distribution. It was only found in the rough steep stoney part of the springbrook below the road. This was a very unstable area subject to rapid erosion which may explain its absence in the Summer samples, although its emergence time was between samplings.

Leuctra nigra Olivier:

This species was present in Spring and Summer, it was evenly distributed throughout the springbrook, except for the head region, in the early analysis, but was restricted to the mid regions of the springbrook at a similar frequency in the Summer analysis. The mid region included the majority of the shade habitat.

Nemoura erratica Claassen and Nemurella picteti Klapalek:

Both species had high frequencies in the Spring, the former being most evenly distributed and the latter being at its highest frequency in the springhead. In the Summer the former was absent from the lower part of the springbrook and at reduced frequency in the upper reaches. The latter species

was still present at high frequencies, but its distribution was restricted to the mid and head regions of the springbrook.

Velia caprai Tamanini:

This carnivore was much more frequent in the Summer sampling, its frequency was low in the harsh rocky habitat below the road and very high in the mid regions where open water favoured its way of life. Its frequency fell steadily towards the springhead where it was absent.

The Trichopteran Larvae Stenophylax stellatus Curt., Sericostoma personatum Spence, and Anabola nervosa Curt.:

Were all found at fairly low frequencies that changed little between the two samplings. Their distribution was irregular and they were almost always found in open areas where the substrate was of a stone/sand type.

Plectrocnemia conspersa Curt.:

In both analyses this larva did not appear until above sample site 50, it was therefore restricted to the upper part of the springbrook. The animals were larger in the Summer samples and appeared to be more abundant.

Dytiscid Larvae:

Of the two species recognised the first seemed to have highest frequency and the greatest abundance, it was fairly evenly distributed throughout the springbrook in both Spring and Summer. Species 2, which was less than half the size of the former, was more widely distributed in the Spring and was

present at low frequency up as far as sample site 80, but in the Summer its range did not appear to extend beyond sample site 40. It was still present where its frequency had been very high, but at a much reduced level.

Coleoptera adults, such as Agabus bipustulatus L, Hydrobius fuscipes L and Philydrus spp.

H. fuscipes was found at very low frequencies in the lower and upper reaches in the Summer, while A. bipustulatus was found only in the Spring, when it was most frequent in the lower third of the springbrook, but present at low frequency in the mid and upper regions. The Philydrus spp. beetle was very frequent in the samples between sites 50 and 80 in the Summer, whereas in the Spring it was found at a lower frequency over a much greater range.

Chironomid larvae:

Species 1 was cosmopolitan and was at a fairly high frequency throughout the springbrook at both times, whereas species 2 and 3 seem to have been restricted to the upper end of the springbrook, species 3 may well have been associated with sphagnum moss.

The dipterous larvae, Dicranota spp. and Pedicia rivosa Linn.:

Were both more frequent and widespread in distribution in the spring samples.

Simulium larvae and pupae:

Had a similar distribution in both Spring and Summer, but the frequency of the larvae in the Summer was much greater than in Spring, it is interesting that very high frequencies were not reached in springhead region.

Beetis rhodani Pictet:

This species was not found in the Spring samples, but was present throughout the lower part of the springbrook in the Summer and reached high frequencies in the samples from 30 to 45.

Odontocerum albicorne Scopoli:

This caddis species was only found in the Summer in the upper reaches of the springbrook and was present at low frequency in the springhead itself.

The temperature profiles show irregularities which were due to the inflow of other streams of water, for instance at sample point 85 in the Summer profile there was a substantial inflow at 7°C. As the samples were taken at 2 metre intervals, if the sample numbers are multiplied by 2, distances in metres may be obtained.

2.5 An investigation into the effect of Slope/Gradient on the communities of a steep and a gentle slope in the springbrook of S6

The tables of raw data for this investigation may be found in the Appendix section A.5. When the two communities were compared in terms of their species composition by the calculation

Figure 25. Frequency values of species along springbrook Sl., May 23rd. and May 24th. 1976.

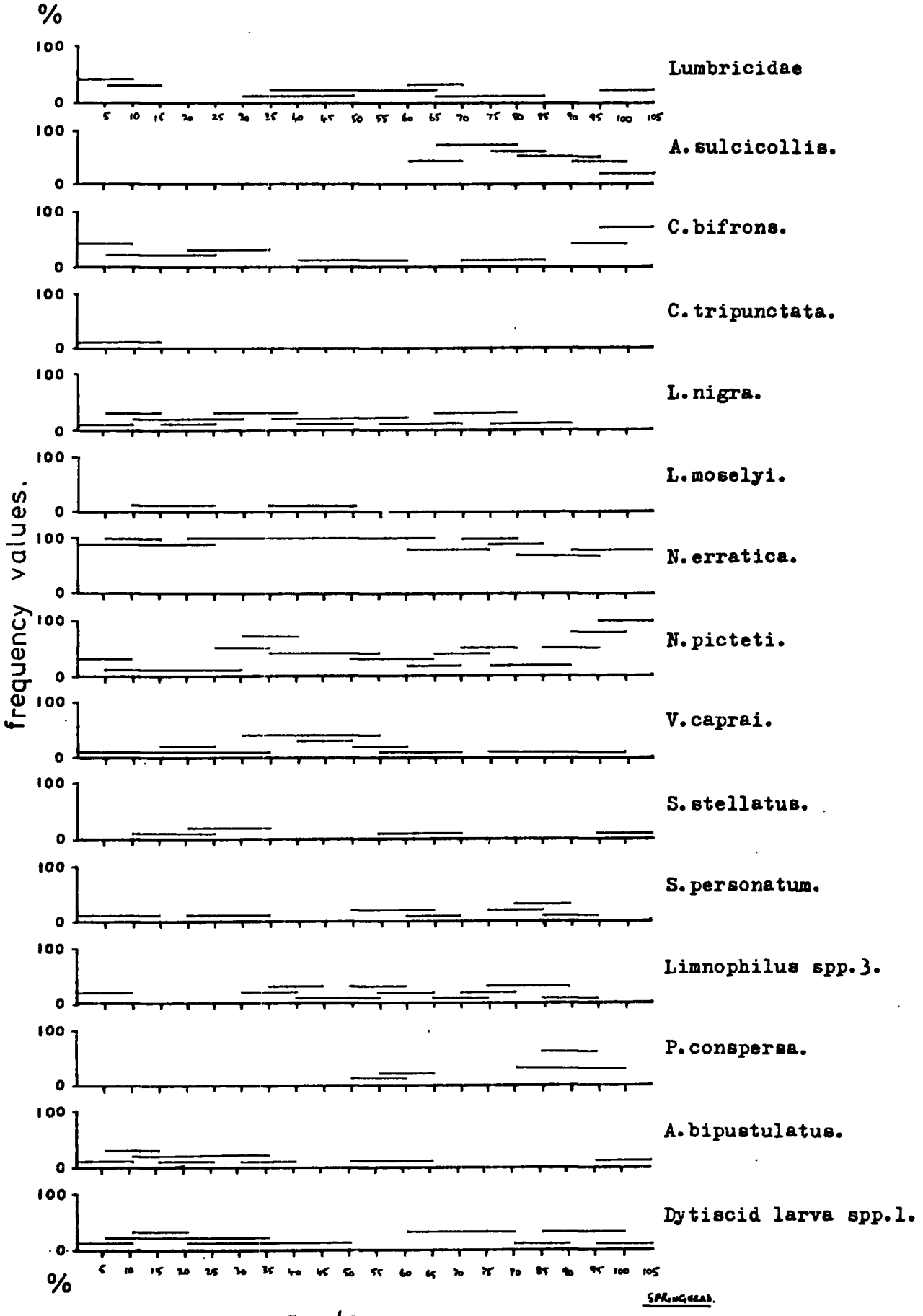


Figure 25. cont.

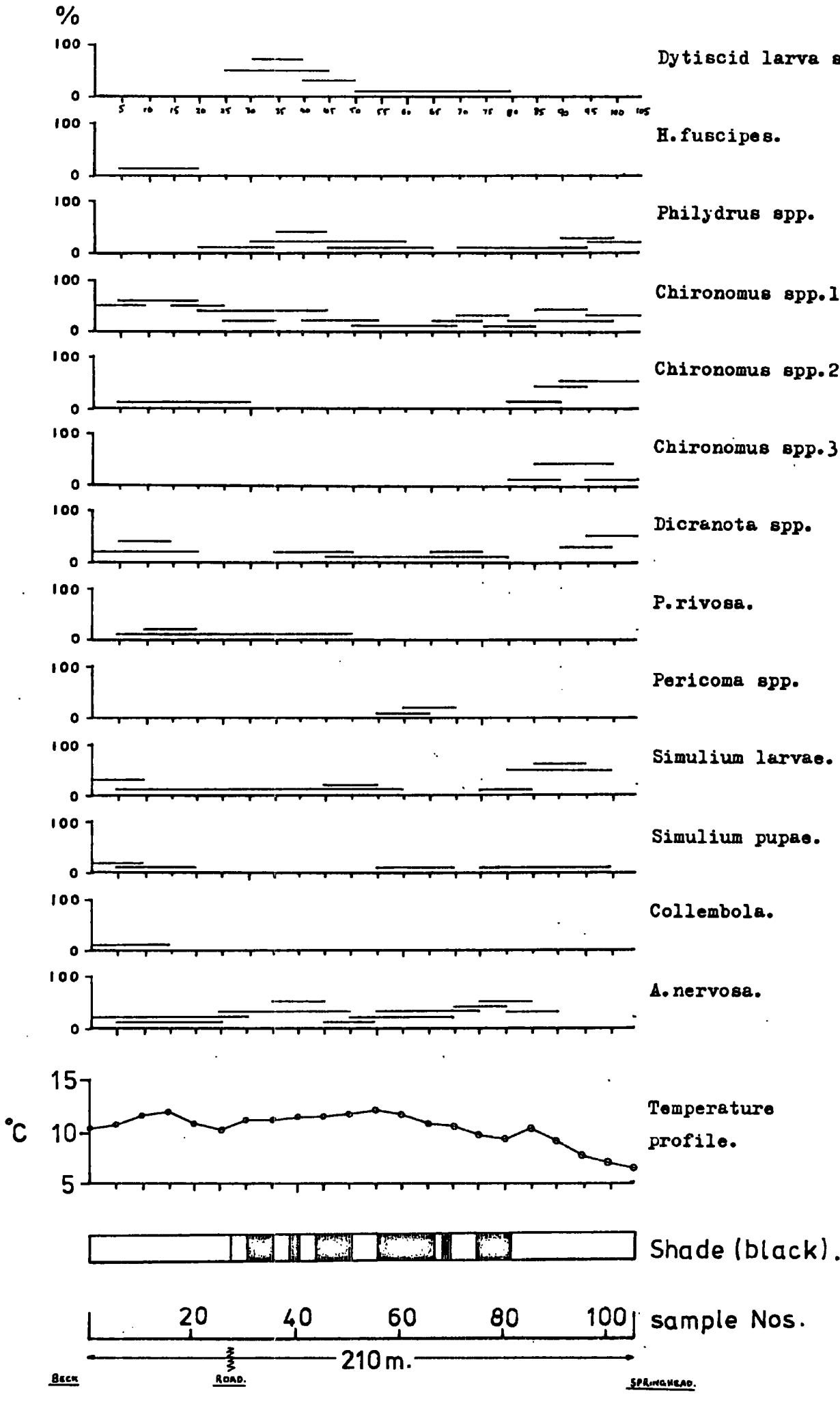


Figure 26. Frequency values of species along springbrook Sl., June 23rd. 1976.

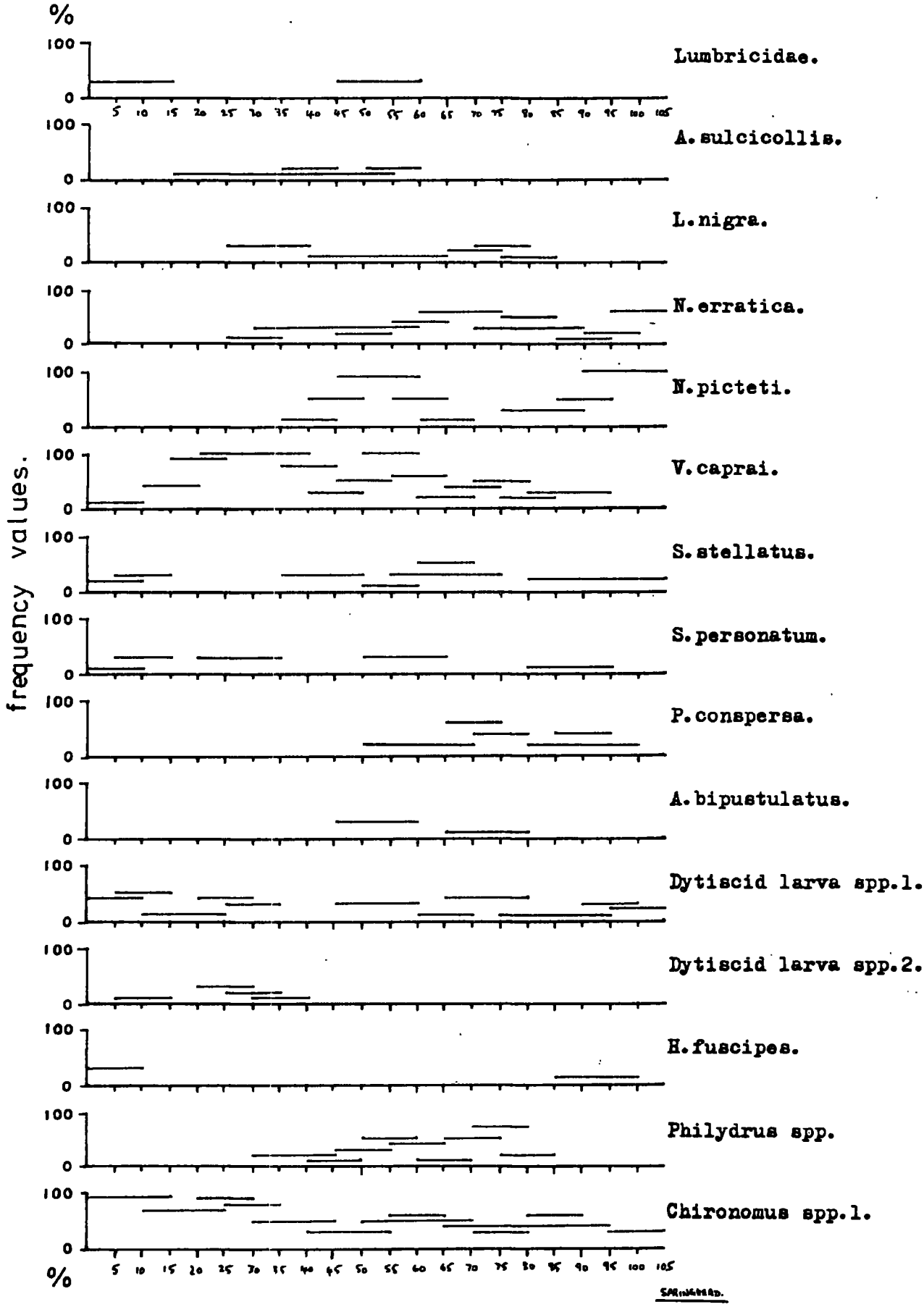
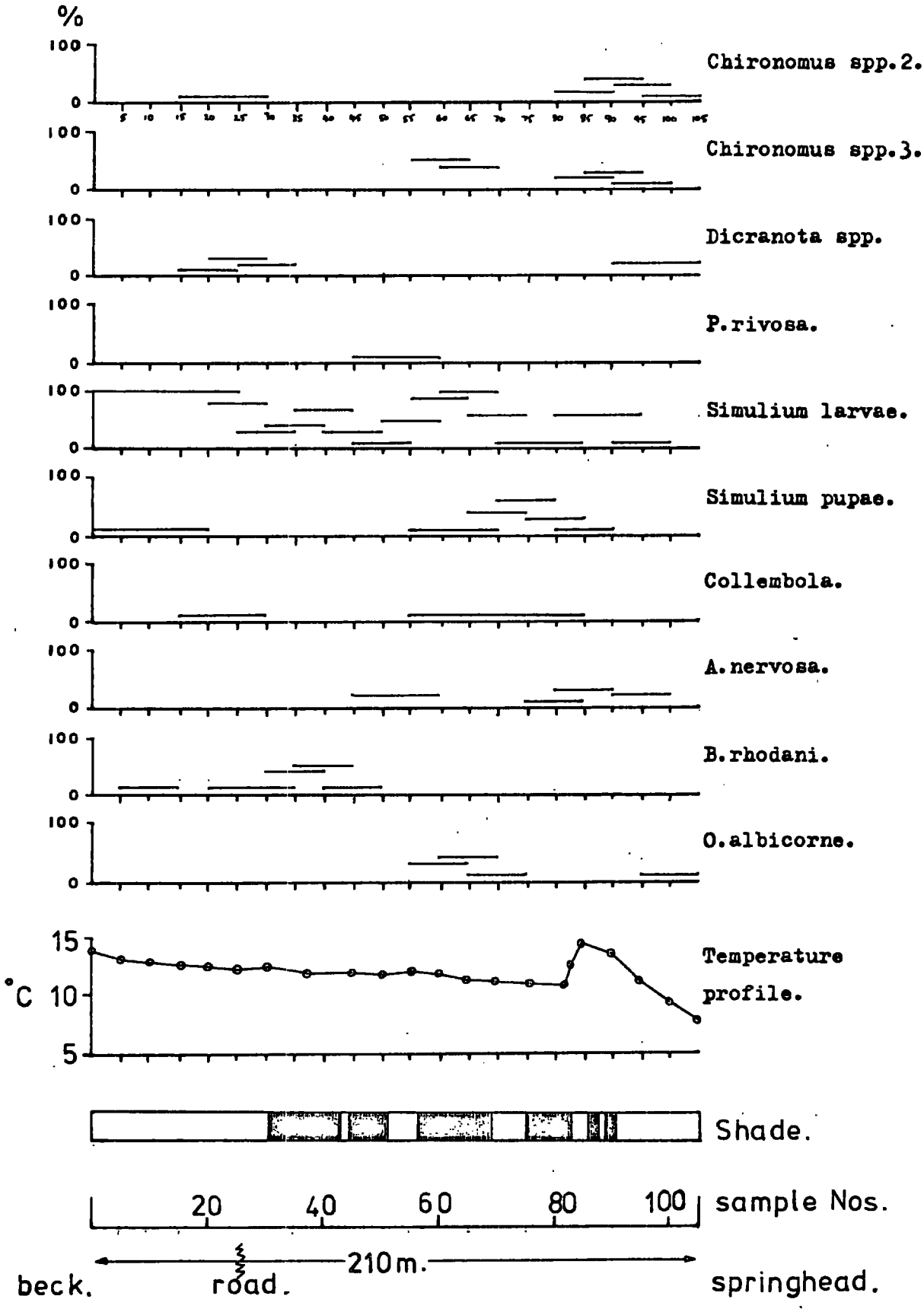


Figure 26.cont.

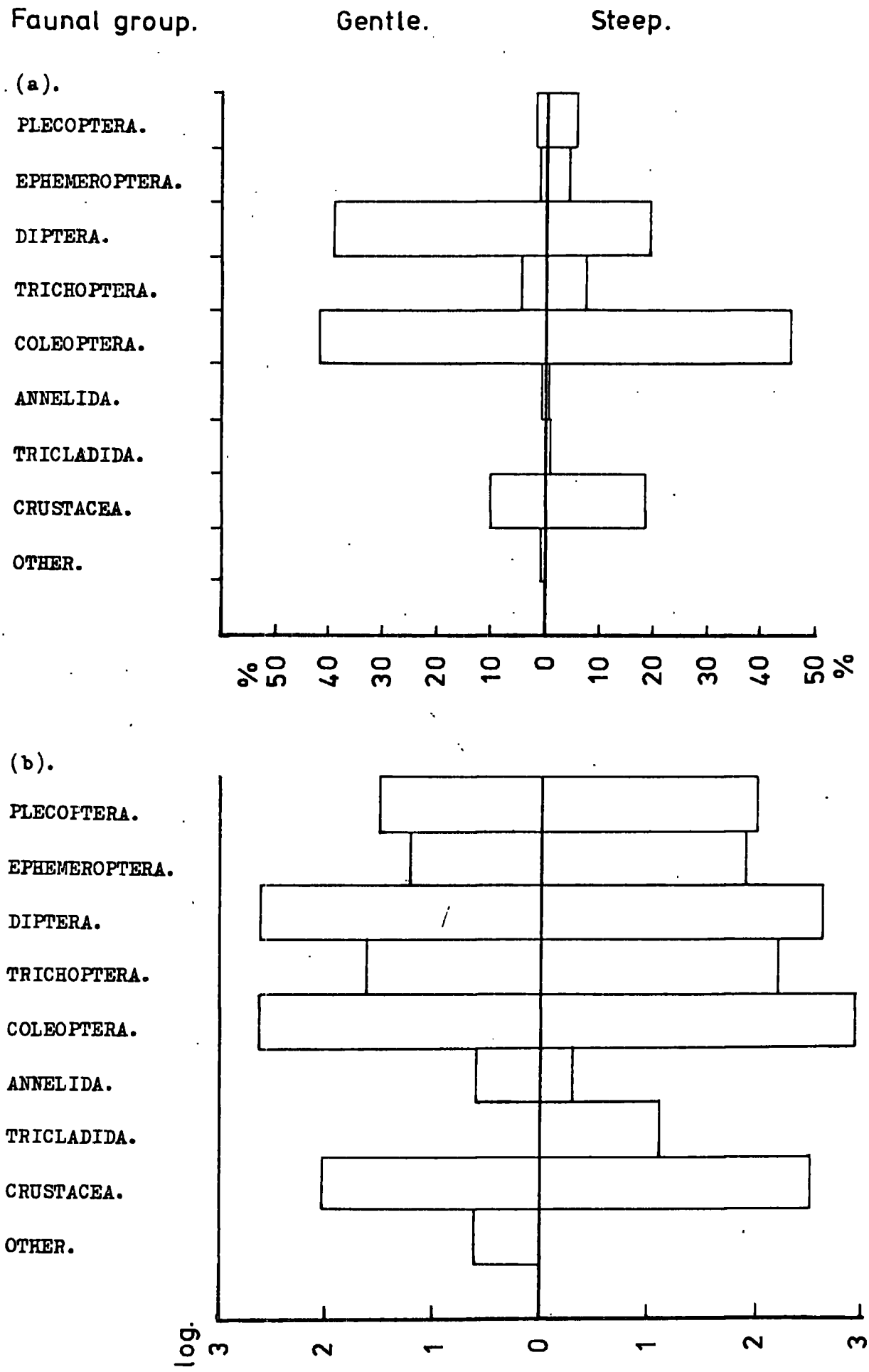


of Sorensen's Quotient, as in section 2.1 of chapter 2, an SQ. value of 0.74 was obtained, which meant that they were very similar, but by no means the same in terms of species. The Percentage Similarity was then calculated as before and a value of 74.6% similarity was obtained, again a difference of importance between the two communities. The computer was used to produce a Kendall Rank Correlation Coefficient for the two communities which had a value of 0.30. The calculated test statistic 'S' was 121.8 and when the 'standardised normal deviate' was calculated it was found to be 2.28, as this value exceeded 1.960 the Rank Correlation has a 5 per cent significance.

It seems that in terms of community structure the two slopes were very similar, in fact the major difference seemed to be the size of the communities, on the gentle slope the total number of organisms in the sample was 909, and in the sample from the steep slope the total number was more than twice that, 1878 animals. Figures 27(a) and 27(b) compare the percentage composition and the numbers of the major groups of organisms in each community, from these the underlying similarity of the two communities is quite clear. Certain species/groups were favoured slightly by one or the other, the Tricladida being an obvious example.

Plate 5 shows the different nature of the substrate on the two slopes. The temperature of the water on both slopes varied between 8.9°C and 8.4°C, and the flow maxima were similar on both also.

Figures 27. Comparison of the Communities of Different Slopes: (a)Percentage Composition, (b)Logarithm of number of organisms in the sample.



2.6 A comparison of the Net and Bucket samplers.

The data for this comparison of samplers may be found in the Appendix section A.6.

The computer was used to calculate a Kendall Rank Correlation Coefficient for the two communities, and a correlation coefficient of 0.68 was obtained. The test statistic 'S' was calculated to be 590.57, and when the 'standardised normal deviate' was calculated it was found to be 10.53. As its value exceeded 3.291 the correlation has a significance of 0.1 per cent. There was therefore very little difference in the two communities sampled by the two different methods, and as they were used to sample what was presumably one community, the efficiency of the two methods must have been very much the same when used under the same conditions. They were not normally used under the same conditions which was why two types of sampler were used. The results of this analysis do tend to suggest that results obtained with both should have been comparable. Slight differences in their catching efficiency of certain species is noticeable, for instance chironomid larvae.

2.7 Transplant Experiment with Agapetus fuscipes

The larvae on stones 1, 2, and 3, which had been placed in the springbrook of S1 where the species was not found, soon pupated. Many had emerged before the stones and animals were transported to the laboratory, where they were kept until the end of July in aerated springwater. The same sequence was

followed for the stones numbered 4, 5 and 6, the animals on these also pupated soon after transplantation to S5, and again many had emerged before removal to the laboratory. The same pattern of development was followed by larvae in the 'home' stream. The final results were:

Stone Number	No. larvae at start	No. emerged	No. pupae left
1	61	59	2
2	129	117	12
3	52	48	4
4	170	151	19
5	44	41	3
6	37	32	5

Table 11. Results of transplant experiment

Therefore, by the end of the experiment 92.6% of the animals that had been removed to the springbrook where the species was not found had emerged and flown away, whilst of the group moved to another springbrook where the species was found 89.3% had emerged and flown away. From this it seems that there is no significant difference in the rate of or chance of completing development in the two habitats.

2.8 A study of the sex ratios of selected species

The results of this investigation are shown in Table 9, there was a good deal of variation in ratios obtained which may be related to the very different population sizes. This will be discussed later.

Table 9. The Sex Ratios (♂:♀) of Selected Species at the Major Study Site where they occurred. (Ratio above, number of species present in brackets.)

	SITES									
Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10
N. picteti	1:1.7 (16)	1:5.2 (80)					1:1 (104)		1:0.9 (25)	1:1.8 (310)
N. erratica	1:1.4 (52)	1:1.4 (25)	1:1.4 (44)	1:3.0 (4)	1:3.0 (13)	1:1.4 (84)	1:1.5 (63)		1:0.7 (5)	1:1.6 (21)
L. bifrons				1:1.0 (2)						
A. sulcicollis			1:2.3 (10)			1:1.0 (4)			1:3.8 (68)	
G. pulex			1:2.0 (111)	1:1.6 (8)	1:4 (5)	1:1.7 (89)	1:2 (80)		1:0.6 (8)	1:1.7 (40)

Table 10. The Mean Body Lengths in cm (one Standard Deviation shown in brackets) for Selected Species in the habitats in which they occur.

Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10
N. picteti	7.00 (1.37)	5.43 (1.56)			6.0 (1.73)		6.08 (1.89)		6.00 (0.91)	5.09 (1.10)
N. erratica	6.17 (0.99)	5.25 (1.05)	4.44 (0.87)	4.25 (0.96)	5.62 (0.87)	6.44 (1.16)	5.14 (1.86)		5.6 (1.51)	4.14 (0.48)
L. bifrons		7.40 (0.55)		7.50 (0.71)	7.00 (0.0)	6.00 (0.0)	7.00 (0.0)			7.00 (0.0)
A. sulcicollis			4.2 (0.79)				6.00 (0.0)	4.00 (0.0)	5.16 (0.93)	
G. pulex			8.20 (5.63)	6.00 (0.71)	8.00 (2.55)	9.34 (2.04)	7.06 (5.81)		8.25 (2.43)	6.18 (2.05)

2.9 A study of the sizes of selected species

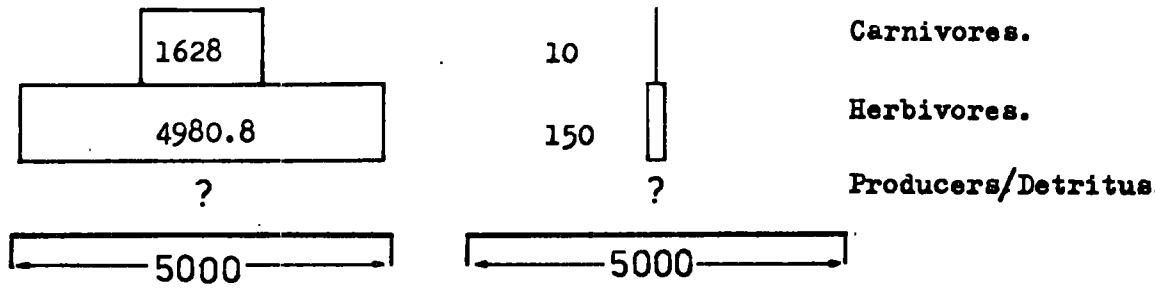
A summary of the results of this investigation are shown in Table 10, more data on size distribution within the populations may be found in Appendix section A.9. In this investigation varying samples, in terms of numbers of individuals, make detailed analysis difficult.

2.10 A preliminary analysis of the Trophic Structure of S10 and S4

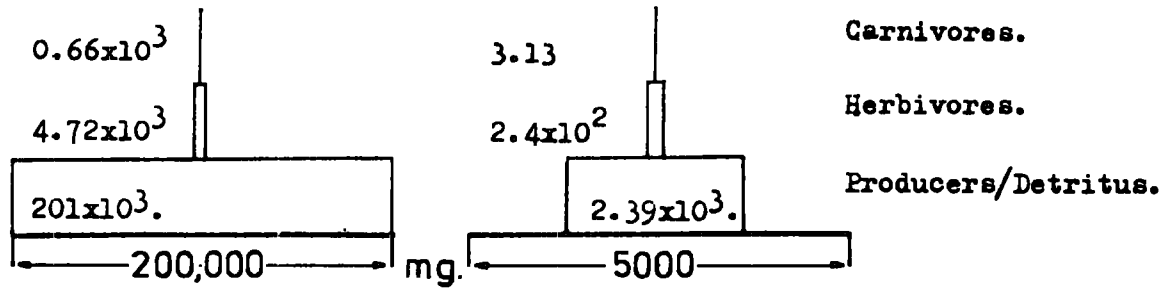
The Figures 28(a), (b) and (c) summarise the results of this analysis, data relating to this may be found in the Appendix section A.10.

Springhead 10 had the highest 'standing crop' of animals and springhead 4 the smallest. Because of this different scales were used when the various pyramids were drawn. Firstly, (a) shows pyramids of numbers for both habitats, only values for herbivores and carnivores could be included. In S10 the ratio of carnivores to herbivores was 1:3.06, whereas in S4 it was 1:15, a considerable difference. Both were however typical upright pyramids. In Figure 28(b) again the typical upright pyramids emerged, the ratio of herbivore biomass to producer/detritus biomass for S10 was 1:42.6, in S4 it was 1:10. The ratios for carnivore biomass to herbivore biomass in S10 and S4 were 1:7.15 and 1:76.8 respectively. In Figure 28(c) the energy pyramids gave a ratio of 1:46.3 for the herbivores to producers/detritus in S10, and 1:12.6 ratio for the same in S4. The ratio of

(a)Pyramids of Numbers per metre^2 of springhead.



(b)Pyramids of Biomass per metre^2 of springhead, units are mg.m.$^{-2}$.



(c)Pyramids of Energy per metre^2 of springhead, units are KJ.m.$^{-2}$.

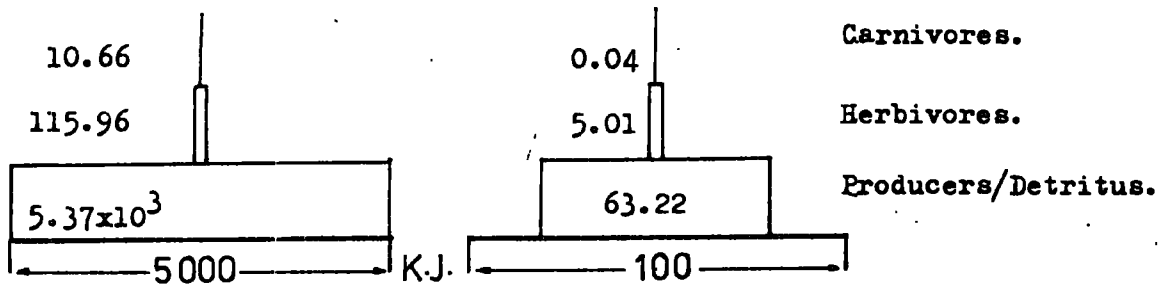


Figure 28. Pyramids of Numbers, Biomass and Energy per metre^2 of Springheads S10 (pyramids on left) and S4 (pyramids on right). The data represented above relates to'standing crop'measurements and illustrates the trophic relationships between levels in the Spring of 1976.

carnivore energy content to herbivore content in S10 was 1:10.8, and for S4 was 1:125.25. From this analysis it can be seen that it was not only the sizes of the populations in the two habitats that was different, but also biomass and energy. What is more important is that the ratios of one trophic level to another were very different in the two springheads investigated, these differences will be discussed later.

CHAPTER 3

DISCUSSION

The study of the community ecology of springs has been the subject of relatively few scientific studies. This is not that springs are uncommon, but appears mainly to be because of the sampling problems involved in this branch of limnology. How, in fact, does one know when one is confronted by a spring? The term spring is not easy to define. Nielsen (1950) suggested that a thermic criterion may be used. The ground water has a constant temperature, which lies near the mean annual temperature of the place; and the ideal spring is a spring in which the water wells out in such a great amount and on a so restricted area that its temperature is not materially influenced by the air temperature or insolation, neither in the summer nor in the winter. His limit was a maximum temperature of 12°C in the summer - if the water temperature rose above this the 'spring' was not a spring. If this definition is taken then S8 in the present work was not in fact a spring at all, though the rest were.

Having decided that the majority of the 'springs' studied were springs as studied by other researchers, what do they mean by the term 'spring fauna'. It is often used in two senses. Firstly to describe the fauna of hygropetric habitats which are peculiar to springs such as, part emerging stones, cushions of

water saturated mosses, helophytes in shallow spring areas, and moist leaves at the margin of forest springs, by some researchers. Secondly by others it is taken as partly comprising also the fauna in the springbrooks, which in fact does not differ from the fauna in other eurythermic streams. There can be little doubt that the 'spring fauna' that formed the basis of the present study belonged to the definition of the latter group. The work that has been carried out by other researchers has been mainly on much larger springs so there were no direct comparisons that could be made to the present study. When a habitat is as small as the ones that have been studied here it is doubtful whether there is a 'spring community' if we take the definition of a community to be 'a system of interacting, niche-differentiated species populations that tend to complement one another in the uses of the communities space, time, resources and possible kinds of interactions' (Whittaker, 1975). There is without doubt a substantial amount of zonal overlap and integration within the spring and springbrook communities of the Eggleshope Valley.

The analyses that were carried out on the data that was collected did show that there was a greater degree of species similarity (Sorensen's Quotient) and dominance similarity (Percentage Similarity) between the springheads, than between them and the beck (Little Eggleshope) or in fact stations down the springbrook of S1. One must bear in mind the fact that most of the species observed and identified in the present study were insects with terrestrial imagines, which means that

the structure of the springhead community would be a dynamic one showing a high degree of temporal variation; indeed, Thorup (1970) using his frequency analysis has shown this to be so for Danish springs and springbrooks both in terms of the phasic nature of insect life cycles, and the downstream migration of certain insect populations. The two frequency analyses carried out on the springhead and springbrook of S2 do on close examination show obvious trends of this sort such as seasonal change in numbers and position along the springbrook, despite the interval between them being a mere two months. The community analysis did indicate that there was a strong possibility that at the time of sampling there was a 'community' peculiar to the springheads, but that it consisted mainly of species common to eurythermic streams in other geographical areas. It is doubtful whether there were any true crenobionts (i.e. species confined strictly to springheads) in the community that was observed although the caddis Odontocerum albicorne has been described as such by other researchers (Nielsen, 1950).

When the samples communities were compared by use of Kendall's Rank Correlation Coefficient, which is a measure of the similarity or difference between assemblages of different numbers of individuals of the spectrum of species in each springhead, it was found that a significance level of 0.1 per cent could be attached to the springheads that formed the extremes of the two main cluster groups, which in fact excluded the 'non-spring' (by thermic definition) S8 and the

main Little Eggleshope beck. It is most interesting that the correlation between S8 and the extreme spring in the 'real' spring group had a significance of 5 per cent, and that there was no significant correlation between any of the springheads and the beck. Again this analysis provides good evidence that there was a springhead community in the Eggleshope Valley.

So far the only real difference discussed between springheads and other lotic waters in this study has been the difference in temperature. In fact there were many other variables worthy of consideration at the major sites, but unfortunately the short duration of this study did not allow the accumulation of sufficient data to make a full Multivariate Analysis feasible, and it is doubtfull whether a single piece of research analysed in such a way would be of any great value because of the dynamic nature of the springhead ecosystems in the valley. However, certain obvious differences may of importance, for instance the water analysis carried out revaled that the main beck was the only habitat polluted with Zinc (0.15 $mg.l.^{-1}$) and Lead (0.5 $mg.l.^{-1}$) which must have come from the once famed 'California' mine at the head of the valley.

Figures on the toxicity of lead and zinc vary tremendously in the literature especially for invertebrates, many of which seem to be very tolerant of heavy metal pollution. In his book Yapp (1972) gives examples of lead levels of 0.2-0.5 $mg.l.^{-1}$ excluding several insect groups such as caddis, and states that levels of 1.0 $mg.l.^{-1}$ are lethal to most animals. If the heavy

pollution was an important factor in determining the nature of the community, this was not reflected in the Species Diversity analysis that was carried out. The size and comparative complexity of the beck may have hidden any real comparison between it and unpolluted springheads and spring-brooks. A comparison with a beck of similar nature but unpolluted by heavy metals would make an interesting further study.

There was no great variation in the Shannon Diversity Indices calculated for the 11 major sites. This index is weighted in favour of the rare species. But the Simpson Index (D), which is weighted in favour of the common species and is more a measure of dominance, produced some interesting indices. These indices clearly reflected the presence of dominant species such as the N. picteti of S2, the Chironomid larvae of S5, and the stonefly larva A. sulcicollis and Chironomids together in S9. The dominance of certain groups, or species, at least numerically is clear from the 'Pie-Charts' showing the percentage composition of the springheads and beck. This may reflect the availability and quality of niches present within the habitats, it may be related to the different abilities of species to compete under a variety of conditions, or may, as did 'Fager's log' experiment, simply indicate which species have the most efficient means of dispersal and colonization (Fager, 1968).

Perhaps before a further consideration of some aspects of the niche concept it would be wise to quote Elton (1927):

> ...the 'niche' of an animal means its place in the biotic environment, its relations to food and enemies. The ecologist should cultivate the habit of looking at animals from this point of view as well as from ordinary standpoints of appearance, names, affinities and past history. When an ecologist says 'there goes a badger', he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said 'there goes the vicar'.

With this in mind we can extend the niche concept into the idea of 'hypervolume' within dimensions, each dimension representing a different variable property of the whole environment of the species; the properties should include the size of food, temperature variation, seasonality, shelter requisites and so on. Unfortunately the complexity of such concept in practical terms prevented such a study of the individuals in the communities of the Egglestone lotic habitats. However, niche breadth and niche overlap in simple terms were considered and have already been explained (pages 37&38).

Considered with the above discussion of the niche concept it can be seen that further investigations of niche breadth and overlap would be of considerable interest at different times of year, particularly for the Plecopteran populations. The positive correlation between the amount of primary producer material and the numbers of herbivores and detritivores (pages $A2_j$) may not have been entirely due to the plant material

representing a plentiful food resource. The presence of higher plants would also increase the habitats spatial heterogeneity and thus increase the number and quality of niches available. In any further study of these habitats the niche concept should play an important part.

When the stations down the springbrook of S1 were sampled one of the most important trends that was observed was that neighbouring stations were often alike in terms of species, which tends to suggest that there was, at least in the spring-brook of S1 some zonation. The diversity indices (see pages A1.c.) tended to suggest that diversity was greatest where the conditions were most stable. At these sites there appeared to be the highest degree of spatial heterogeneity. These conditions were fulfilled best at the springhead and at station St4. This meant that in turn it would seem that the diversity was linked to the nature of the substrate. Thorup (1966) goes into this in detail explaining how community and substrate type are linked in lotic systems. It was with the background of his 1966 research that Thorup started his study of the communities in springs. He chose them because it was possible in many cases to observe the animals in their microhabitats, which would indeed be a logical progression on from the present study. He did discover, as was found in this research, that some difficulties did arise through the use of springs for such studies; mainly because they are often small and it is difficult to take enough quantitative samples for analysis from small populations without destroying them.

Up to the present time there is no really efficient method for the quantitative sampling of the fauna from a stony bottom in running water. Although several methods for this purpose have been developed (Macan, 1958; Albrecht, 1959, 1961; Schwoebel, 1966) including the net and bucket samplers developed for use in this study, none of these really suited for use in small springbrooks. For this reason Thorup's (1970) frequency analysis technique was employed with only slight modification to investigate the distribution of invertebrates in the springbrook of S2. Large differences between the curves of frequency for various species are evident, and with very few exceptions no two curves are similar. Plectrocnemia conspersa, one of the carnivorous net-spinning caddis larvae of the springbrook was found mainly close to the banks or amongst vegetation. When a specimen was returned to the laboratory for observation it was found to prefer, and feed with voracity on chironomid larvae. It would only take these alive. It seems that other species have preferred foods also. Nemoura erratica has shown by other researchers to nibble dead leaves and higher plants, whilst Leuctra nigra brushes up detritus. As they were found together it is probable that the two species occupied different niches in the springbrook because of their different feeding methods. If the frequency values are ecologically meaningful in terms of the individual species in each locality, the fact that species co-exist must indicate that each species present places slightly different demands on the environment.

From the work that has been done it seems that the variation in frequency values throughout the springbrook were probably due to a number of ecological factors, these included, light conditions (shade or open), substrate type, the rate of water flow, and the availability of suitable food. A great deal more detailed study would be required to clarify the situation for each species, but their can be little doubt that frequency analysis may be extremely useful for the analysis of community structure, especially if it was closely linked to studies in the biology of species present.

In the investigation into the effect of different gradients on the nature of the springbrook community the Kendall's Rank Correlation between the steep slope and gentle slope fauna showed that there was no significant difference between the two communities. Further study would probably reveal the more subtle differences that must result from the effect of gradient on other factors such as, flow rate and the nature of the substrate. Transplant experiments may be of use in a further investigation of the effect of gradient, but ideally an artificial stream system would be required. The transplant experiment that was carried out tended to indicate that although a species was not found in a particular habitat (in this experiment the caddis Agapetus fuscipes) it could survive and complete its life-cycle when transplanted to it. In this study it seems probable that the nature of the substrate was mainly responsible for the absence of the species in certain springbrooks, the larvae of A. fuscipes has a requirement for large sand grains

and stones on which to attach the cases it makes from them, in some springbrooks both were absent. If further transplants were carried out it would be essential to quantify as many environmental variables as possible, and to ensure the setting up of adequate controls.

When the sex ratios of selected species were calculated it was obvious that there was a high degree of variation between sites, but that when the numbers of individuals examined at each site was taken into account, the site where many individuals had been examined produced similar ratios. For Nemurella picteti at all but one site there were more females than males in an overall ratio of about 1:1.5, this was the case for all species where a large enough sample had been taken, the females always outnumbering the males. It would have been interesting to study the change in this ratio with time as well as in the different springheads.

It was hoped that by measuring the sizes of the stonefly species and the gammarids some relationship between this and other variables at the major study sites might be established, however there were no significant correlations between mean size of individuals in a habitat and factors such as temperature. This may have been due to the relatively small differences in the variables between the habitats, adaption by the species themselves, or because many variables were interacting some to the advantage of, and some to the disadvantage of a species.

The analysis of the trophic structure of two of the springheads can only be considered as preliminary because it relates to only one instant in time, but it appears that in terms of

energy more is utilized, as opposed to 'wasted', by the macrofauna in S4. The energy ratios between trophic levels, 1:46 in SIO and 1:12 in S4, for the conversion of plant material to animal material suggest a greater ecological efficiency for the animals in S4. Whereas the situation is reversed for the exchange of energy between the next two trophic levels, the carnivore energy content to herbivore energy content ratios were 1:11 for SIO and 1:25 for S4. This implies the carnivore level was more efficient in SIO. This may have been due to the greater abundance of prey which would reduce amount of effort required by the predators to ensure being well fed, also it is possible that their food supply would have been more stable than for the predators in S4. These can only be hypotheses, much more detailed work would be required before such ideas could be either accepted or rejected. Detailed studies of complex ecosystems require many years of work, Odum (1957), aided by a team of researchers, studied the trophic structure and productivity of Silver Springs, Florida. It is difficult to compare the present study with his work at Silver Springs as it is many times the size of any of the springs in the Eggleshope Valley. Teal's (1957) approach to a study of community metabolism would be a model for further study. Though even a study of a relatively simple ecosystem, such as any of the Eggleshope springs, would involve a vast amount of work over a long period.

SUMMARY

1. Ten springheads and their springbrooks were sampled both quantitatively and qualitatively. The structure of the aquatic invertebrate communities in these and Little Eggleshope Beck were analysed for species similarity, dominance similarity and species diversity similarity in an attempt to determine whether a community of crenobionts was present in the springs of the Eggleshope Valley. Evidence suggested that this was so, but that the species were not true crenobionts. They were merely species well suited to life in upland streams, and equally well spring systems.

2. In an analysis of the fauna present at stations down a springbrook it was found that species similarity tended to be greatest between adjacent stations, and that diversity was greatest in the most stable, largest, spatially heterogeneous habitats.

3. The use of two samplers, a net sampler and a bucket sampler, is described and their efficiencies under the same conditions compared. These new samplers were found to give statistically similar data for most of the aquatic invertebrates in the springbrook in which they were compared.

4. A method for frequency analysis in small springbrooks is described, and its value in the study of such communities discussed. Results of frequency analyses carried out in the Spring and Summer are presented, and factors affecting

frequency values considered. Some evidence for the movement of populations during the interval between the analyses is shown.

5. The effect of gradient on the nature of the springbrook community was investigated. The results are shown and discussed for the gentle and steep slopes that were compared. Subtle differences were noticed in the community structure. The greatest difference was in the size of the communities, the gentle slope having approximately half the number of organisms on the steep slope, as indicated by the methods used and samples taken. The effect of gradient on physical factors is also considered.

6. Transplant experiments with Agapetus fuscipes indicated that its absence from a springbrook was not simply due to it being unable to survive there. A major factor was thought to be the availability of a suitable substrate.

7. The sex ratios of some stonefly species and Gammarus pulex are given for the sites in which they occurred, and are discussed.

8. The sizes of some stonefly species and G. pulex were measured and mean sizes with standard deviations are shown. These sizes were found not to correlate with the environmental parameters measured, this is discussed.

9. A preliminary investigation into the trophic structures of two of the Eggleshope springs was made and results are shown. The energy contents of the species present are tabulated. Trophic pyramids of numbers, biomass and energy are presented and discussed.

APPENDIX

RAW AND FURTHER DATA :

SECTIONS - A1a (i) to A1a (ii) Springheads and Beck Community Data.

- A1c Diversity indices for major sites.
- A2j Herbivore/Detritivore and Vegetation correlation data.
- A3a (i) to A3 (iv) Data from Stations down the Springbrook of S1.
- A5 Data from the effect of Slope Investigation.
- A6 (i) and A6 (ii) Bucket and Net Sampler comparison data.
- A10 Data for Trophic Level Investigations in Springheads S4 and S10.

SPECIES PRESENT.	NUMBER IN SUB SAMPLE.					TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
	S1.1	S1.2	S1.3	S1.4	S1.5			
N.picteti	1	1	0	2	12	16	3.2	80
N.erratica	1	4	15	12	20	52	10.4	260
S.personatum	0	6	0	1	2	9	1.8	45
A.nervosa	8	2	2	1	3	16	3.2	80
Philydrus spp.	3	1	0	0	0	4	0.8	20
Chironomid larvae spp.1.	3	3	1	0	2	9	1.8	45
Chironomid larvae spp.2.	0	0	1	0	2	3	0.6	12
Dicranota spp.	2	0	1	0	1	4	0.8	20
Dytiscus larvae spp.1.	0	0	0	1	0	1	0.2	4
TOTALS	18	17	20	17	42	114	22.8	566

Springhead community data for S1. TABLE 12.

A1a.(i).

SPECIES PRESENT.	NUMBER IN SUB SAMPLE.					TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M OF SPRINGBROOK BED.
	S2.1	S2.2	S2.3	S2.4	S2.5			
N.picteti	18	7	5	27	23	80	16.0	400
N.erratica	2	0	2	4	17	25	5.0	125
C.bifrons	1	1	3	0	0	5	1.0	25
Lumbricidae spp.	1	0	0	0	1	2	0.4	10
Chironomid larvae spp.1.	0	1	0	6	0	7	1.4	35
Chironomid larvae spp.1.	0	1	0	4	1	6	1.2	30
Dicranota spp.	0	6	0	0	3	9	1.8	45
Chironomid pupae	0	1	0	0	0	1	0.2	5
H.marginata	0	0	1	0	0	1	0.2	5
A.fuscipes	0	0	2	1	0	3	0.6	15
S.personatum	0	0	0	0	1	1	0.2	5
A.nervosa	0	0	1	0	24	25	5.0	125
Dytiscus larvae spp.1.	0	0	0	0	1	1	0.2	5
TOTALS	22	17	14	42	71	166	33.2	830

Springhead community data for S2.

TABLE 13.

A1a.(ii).

SPECIES PRESENT.	NUMBER IN SUB SAMPLE.					TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
	S3.1	S3.2	S3.3	S3.4	S3.5			
G.pulex	6	41	7	7	50	111	22.0	550
N.erratica	4	13	9	7	11	44	8.8	220
C.alpina	4	7	9	24	2	46	9.2	230
H.marginata	1	4	3	4	0	12	2.4	60
Thaumalea spp.	6	0	0	0	0	6	1.2	30
S.stellatus	4	2	0	5	5	16	3.2	80
A.fuscipes	6	15	18	15	1	55	11.0	275
Glossosoma spp.	3	1	1	2	0	7	1.4	35
A.sulcicollis	0	1	2	1	6	10	2.0	50
O.albicorne	0	3	0	3	0	6	1.2	30
L.nigra	0	2	0	0	0	2	0.4	10
Lumbricidae spp.	0	0	1	0	0	1	0.2	5
Acari spp.	0	0	0	0	1	1	0.2	5
Polycentropus spp.	0	0	0	1	0	1	0.2	5
TOTALS	35	89	55	70	75	325	65.0	1615

Springhead community data for S3.

TABLE 14.

A1a.(iii).

SPECIES PRESENT.	NUMBER IN SUB SAMPLE.					TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M OF SPRINGBROOK BED.
	S4.1	S4.2	S4.3	S4.4	S4.5			
G.pulex	2	3	2	1	0	8	1.6	40
N.erratica	0	0	1	2	1	4	0.8	20
C.bifrons	0	0	0	1	1	2	0.4	10
Chironomid larvae spp.1.	1	1	0	5	2	9	1.8	45
S.stellatus	1	2	0	0	0	3	0.6	15
Limnophilus spp.3.	0	0	0	1	1	2	0.4	10
Collembola	1	0	0	1	0	2	0.4	10
C.alpina	0	0	0	0	2	2	0.4	10
P.rivosa	0	0	0	1	0	1	0.2	5
Lumbricidae spp.	0	0	0	1	0	1	0.2	5
TOTALS	5	6	3	13	7	34	6.8	170

Springhead community data for S4. TABLE 15.

SPECIES PRESENT.	NUMBER IN SUB SAMPLE.					TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
	S5.1	S5.2	S5.3	S5.4	S5.5			
Chironomid larvae spp.1.	27	9	23	31	40	130	26.0	650
Chironomid pupae	1	2	1	1	0	5	1.0	25
S.personatum	2	1	3	0	0	6	1.2	30
Limnophilus spp.3.	1	0	0	1	1	3	0.6	15
A.nervosa	0	0	1	8	3	12	2.4	60
C.bifrons	1	0	0	1	1	3	0.6	15
A.fuscipes	1	1	0	1	0	3	0.6	15
G.pulex	0	1	0	3	1	5	1.0	25
S.stellatus	0	1	0	0	0	1	0.2	5
Collembola	0	1	1	0	1	3	0.6	15
Lumbricidae spp.	0	0	0	2	1	3	0.6	15
N.picteti	0	0	0	1	2	3	0.6	15
Elmidae spp.	0	0	0	0	1	1	0.2	5
P.conspersa	0	0	0	1	0	1	0.2	5
Aeolosoma spp.	0	0	0	0	1	1	0.2	5
N.erratica	1	0	0	8	4	13	2.6	60
Philydrus spp.	0	0	0	0	1	1	0.2	5
H.marginata	0	0	0	1	0	1	0.2	5
Pericoma spp.	0	0	3	0	1	4	0.8	20
TOTALS	34	16	29	62	58	199	38.9	990

Springhead community data for S5.

TABLE 16.

A1a.(v).

SPECIES PRESENT.	NUMBER IN SUB SAMPLE.					TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M OF SPRINGBROOK BED.
	S6.1	S6.2	S6.3	S6.4	S6.5			
A.fuscipes	17	0	10	15	1	43	8.6	215
H.maugei	8	3	5	30	63	109	21.8	545
G.pulex	44	14	12	15	4	89	17.8	445
N.erratica	16	5	5	34	24	84	16.8	420
Chironomid larvae spp.1.	3	2	16	4	9	34	6.8	170
Chironomid larvae spp.2.	4	6	4	10	13	37	7.4	185
Chironomid pupae	0	0	1	0	1	2	0.4	10
S.stellatus	0	0	3	0	0	3	0.6	15
S.personatum	1	0	6	0	6	13	2.6	65
Dytiscid larvae spp.1.	0	1	0	0	0	1	0.2	5
A.sulcicollis	0	2	0	1	1	4	0.8	20
Lumbricidae spp.	0	0	1	0	1	2	0.4	10
C.bifrons	0	0	1	1	2	4	0.8	20
Dicranota spp.	1	0	0	1	0	2	0.4	10
H.marginata	0	0	0	1	0	1	0.2	5
C.torrentium	0	0	0	0	1	1	0.2	5
TOTALS	94	33	64	112	126	429	85.8	2145

Springhead community data for S6.

TABLE 17.

SPECIES PRESENT.	NUMBER IN SUB SAMPLE.					TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M OF SPRINGBROOK BED.
	S7.1	S7.2	S7.3	S7.4	S7.5			
S.stellatus	1	1	0	0	2	4	0.8	35.2
S.personatum	0	0	0	1	0	1	0.2	8.8
Dicranota spp.	1	4	10	1	1	17	3.4	149.6
C.alpina	15	0	9	0	0	24	4.8	211.2
G.pulex	47	6	7	12	8	80	16.0	704.4
N.picteti	48	11	25	13	7	104	20.8	915.2
N.erratica	15	17	19	5	7	63	12.6	554.2
Chironomid larvae spp.1.	7	22	11	26	3	69	13.8	607.2
Chironomid larvae spp.2.	2	7	9	12	0	30	6.0	264.0
L.nigra	1	0	0	0	0	1	0.2	8.8
C.bifrons	1	0	0	0	0	1	0.2	8.8
L.inermis	2	0	0	0	0	2	0.4	17.6
G.aquaticus	0	1	0	0	0	1	0.2	8.8
O.albicorne	0	0	1	0	0	1	0.2	8.8
P.rivosa	0	0	0	1	0	1	0.2	8.8
Lumbricidae spp.	0	0	0	1	0	1	0.2	8.8
A.sulcicollis	0	0	0	0	1	1	0.2	8.8
TOTALS	140	69	92	71	29	401	80.2	3529.2

Springhead community data for S7. TABLE 18.

SPECIES PRESENT.	NUMBER IN SUB SAMPLE.					TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M OF SPRINGBROOK BED.
	S8.1	S8.2	S8.3	S8.4	S8.5			
Sphaeridae spp.	14	2	3	12	4	35	7.0	308.0
Chironomid larvae spp.1.	8	5	28	12	6	59	11.8	519.2
Chironomid larvae spp.2.	2	0	0	4	1	7	1.4	61.6
Lumbricidae spp.	2	4	1	2	10	19	3.8	167.2
V.caprai	1	1	0	0	1	3	0.6	26.4
G.pulex	1	0	0	0	0	1	0.2	8.8
C.alpina	1	0	0	0	0	1	0.2	8.8
Dicranota spp.	0	1	0	1	0	2	0.4	17.6
B.risi	0	1	0	0	0	1	0.2	8.8
Chironomid pupae	0	1	0	1	1	3	0.6	26.4
A.bipustulatus	0	3	2	5	2	12	2.4	105.6
Helophorus spp.	0	7	1	4	1	13	2.6	114.4
Oredytes spp.	0	3	1	3	2	9	1.8	79.2
H.riparia	0	1	0	1	0	2	0.4	17.6
Hydroporus larvae spp.	0	2	0	8	0	10	2.0	88.0
S.stellatus	0	0	0	0	1	1	0.2	8.8
S.personatum	0	0	0	1	0	1	0.2	8.8
A.nervosa	0	0	0	0	3	3	0.6	26.6
Limnophilus spp.5.	0	0	2	1	1	4	0.8	35.2
H.maugei	0	0	0	2	0	2	0.4	17.6
O.albicorne	0	0	0	0	1	1	0.2	8.8
Collembola	0	0	0	0	2	2	0.4	17.6
L.pereger	0	0	0	0	1	1	0.2	8.8
TOTALS	29	31	38	57	37	192	38.4	1672.0

Springhead community data for S8.

TABLE 19.

SPECIES PRESENT	NUMBER IN SUB SAMPLE					TOTAL IN SAMPLE	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
	S9.1	S9.2	S9.3	S9.4	S9.5			
Glossosoma spp.	2	1	1	1	0	5	1.0	25
A.fuscipes	8	7	2	0	0	17	3.4	85
S.stellatus	4	6	17	14	11	52	10.4	260
S.personatum	0	1	4	0	1	6	1.2	30
Limnophilus spp.4.	0	1	1	1	2	5	1.0	25
Limnophilus spp.5.	0	0	0	0	4	4	0.8	20
A.maugei	2	0	0	0	0	2	0.4	10
Chironomid larvae spp.1.	8	20	7	11	4	50	10.0	250
Chironomid larvae spp.2.	3	3	0	3	2	11	2.2	55
A.sulcicollis	14	31	3	16	4	68	13.6	340
N.picteti	2	2	0	0	21	25	5.0	125
C.alpina	0	5	0	2	0	7	1.4	35
Dicranota spp.	0	1	1	3	3	8	1.6	40
G.pulex	0	2	2	2	2	8	1.6	40
L.nigra	0	2	0	2	2	6	1.2	30
Pericoma spp.	0	0	1	0	0	1	0.2	5
Lumbricidae spp.	0	0	0	2	1	3	0.6	15
N.erratica	0	0	0	3	2	5	1.0	25
L.flavicornis	0	0	0	0	1	1	0.2	5
TOTALS	43	82	41	59	60	285	57.0	1425

Springhead community data for S9.

TABLE 20.

SPECIES PRESENT	NUMBER IN SUB SAMPLE. S10.1	S10.2	S10.3	S10.4	S10.5	TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
Sphaeridae spp.	12	18	12	18	1	61	12.2	536.8
Dicranota spp.	6	21	4	0	14	45	9.0	396.0
S.stellatus	0	1	6	30	0	37	7.4	325.6
S.personatum	13	17	8	5	2	45	9.0	396.0
Limnophilus spp.3.	0	0	2	1	0	3	0.6	26.4
Limnophilus spp.5.	0	0	2	4	0	6	1.2	52.8
L.flavicornis	0	0	1	0	0	1	0.2	8.8
C.alpina	51	26	21	10	32	140	28.0	1232.0
Lumbricidae spp.	2	0	0	1	0	3	0.6	26.4
Chironomid larvae spp.1.	0	3	8	3	0	14	2.8	123.2
Chironomid larvae spp.2.	1	0	0	1	4	6	1.2	52.8
N.picteti	41	87	128	17	37	310	62.0	2728.0
G.pulex	0	6	20	14	0	40	8.0	352.0
N.erratica	0	12	8	0	1	21	4.2	184.8
L.nigra	0	0	1	0	0	1	0.2	8.8
C.bifrons	0	0	1	0	0	1	0.2	8.8
L.hirtium	0	1	0	0	0	1	0.2	8.8
O.albicorne	0	0	4	0	1	5	1.0	44.0
A.fuscipes	0	0	11	0	0	11	2.2	96.8
TOTALS	126	192	237	104	92	751	150.2	6608.8

Springhead community data for S10.

TABLE 21.

A1a.(x).

Species present.	Sub-sample numbers.														
	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15
B.risi	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0
A.sulcicollis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N.erratica	6	0	1	2	0	0	0	0	0	0	0	0	0	0	0
Chironomid larvae spp.l.	2	1	0	2	0	0	1	0	5	1	2	0	0	0	0
L.hippopus	0	2	3	1	0	2	1	0	0	0	0	1	0	1	2
Hydroporus larvae spp.	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Helmis maugei	0	1	3	6	7	1	1	0	0	0	0	0	1	3	3
Hydraena riparia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
P.conspersa	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Velia caprai	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0
C.torrentium	0	0	1	1	1	0	1	2	0	0	0	0	1	0	0
Dytiscid larvae spp.l.	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Capnia bifrons	0	0	0	2	4	0	0	0	0	0	1	0	0	1	2
Hydracarina spp.	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Rhyacophila spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0
Simulium spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Baetis rhodani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
TOTALS	10	6	10	17	14	4	4	2	5	2	4	3	3	8	12

Community data for the Little Eggleshope Beck. (page one of two pages) TABLE 22.

Species present.	Sub-sample numbers.					Total in sample.	Mean no. per sample.	Est.no. per m of springbrook bed.
	B16	B17	B18	B19	B20			
B.risi	1	0	0	1	0	6	0.3	7.5
A.sulcicollis	0	0	1	0	0	2	0.1	2.5
N.erratica	0	1	4	0	1	15	0.75	18.75
Chironomid larvae spp.l.	3	1	1	2	0	22	1.1	27.5
L.hippopus	0	1	0	0	2	16	0.8	20.0
Hydroporus larvae spp.	0	0	1	0	0	3	0.15	3.75
H.maugei	0	0	0	5	1	32	1.6	40.0
H.riparia	0	0	0	0	0	1	0.05	1.25
P.conspersa	0	1	0	0	0	2	0.1	2.5
V.caprai	0	0	0	0	1	4	0.2	5.0
C.torrentium	0	0	1	0	0	8	0.4	10.0
Dytiscid larvae spp.l.	0	0	0	1	0	3	0.15	3.75
C.bifrons	0	0	0	0	1	11	0.55	13.75
Hydracarina spp.	0	1	0	0	0	3	0.15	3.75
Rhyacophila spp.	0	0	0	0	0	3	0.15	3.75
Simulium spp.	0	0	1	0	0	3	0.15	3.75
B.rhodani	0	0	0	0	0	3	0.15	3.75
TOTALS	4	5	9	9	6	137	6.85	171.25

Community data for the Little Eggleshope Beck. (page two of two pages) TABLE 23.

COMPUTER PROGRAM FOR SORENSEN'S QUOTIENT AND PERCENTAGE SIMILARITY.

```
      $COMPILE
      C SORENSENS COLLECTIONS SPECIES DATA
 1          REAL*8 SPEC  (50)
 2          INTEGER PER
 3          INTEGER PS(50)
 4          INTEGER HABIT   (50,20)
 5          INTEGER A,B,T
 6          READ(5,990)NSPEC,NHABIT
 7      990 FORMAT(2I5)
 8          WRITE(6,900)
 9      900 FORMAT('1')
10          DO 10 I=1,NSPEC
11          READ(5,980) SPEC (I),(HABIT(I,J), J=1,NHABIT)
12      980 FORMAT(A6,20I4)
13          WRITE(6,970) SPEC(I),(HABIT(I,J),J=1,NHABIT)
14      970 FORMAT(1X,A6,20I4)
15       10 CONTINUE
16          NHB=NHABIT-1
17          DO20 I=1,NHB
18          IP1=I+1
19          DO30 J=IP1,NHABIT
20          A=0
21          B=0
22          T=0
23          PER = 0
24          DO50 K=1,NSPEC
25          IF(HABIT(K,I).NE.0) A=A+1
26          IF(HABIT (K,J).NE.0) B=B+1
27          IF(HABIT(K,I).NE.0.AND.HABIT(K,J).NE.0) T=T+1
28          IF(HABIT(K,I).LE.HABIT(K,J))PER = PER + HABIT(K,I)
29          IF(HABIT(K,J).LT.HABIT(K,I))PER = PER + HABIT(K,J)
30       50 CONTINUE
31          Q=2.0*T/FLOAT(A+B)
32          WRITE(6,950) I,J,A,B,T,Q,PER
33      950 FORMAT('-',' SORENSENS QUOTIENT OF SIMILARITY',/
           1       ' FOR HABIT',I3,'  AND ',I3,1X/
           2     ' TOTAL FOR FIRST HABIT',I4,
           3     '       TOTAL FOR SECOND HABIT',I4,/
           4     ' TOTAL COMMON SPEC',I4,/,
           5    ' QUOTIENT =', F5.2,'     PERCENTAGE =',I4)
34       30 CONTINUE
35       20 CONTINUE
36          STOP
37          END

      $DATA
```

It will take up to 50 species and 20 habitats.

SPRING/SITE NUMBER.	SHANNON'S 'H'.	SHANNON'S 'E'.	SIMPSON'S 'D'.	SIMPSON'S (1-D).
S1	1.6376	0.7453	0.2665	0.7335
S2	1.9176	0.7476	0.4647	0.5353
S3	1.5568	0.5749	0.1874	0.8126
S4	1.4562	0.6324	0.1617	0.8382
S5	1.5275	0.4651	0.6683	0.3317
S6	1.9813	0.7146	0.1790	0.8210
S7	1.8157	0.6409	0.1725	0.8275
S8	2.3284	0.7426	0.1562	0.8438
S9	2.4729	0.8255	0.4896	0.5104
S10	1.9484	0.6617	0.2214	0.7779
BECK	1.7916	0.5981	0.1220	0.8780
Stations down S1.				
St1 (100m.)	1.1637	0.6494	0.4550	0.6494
St2 (200m.)	1.7300	0.8300	0.2300	0.7700
St3 (300m.)	1.3200	0.5700	0.4500	0.5500
St4 (500m.)	1.5663	0.5935	0.4196	0.5804

Diversity Indices for the major sites and stations down S1. TABLE 24.

SITES	Mean Veg. Material per sub-sample: in grams.	No. of Herbivores and Detritivores per square metre.
S1	2.78 (0.63)	526
S2	1.83 (0.44)	780
S3	0.24 (0.04)	1320
S4	2.39 (0.88)	160
S5	1.29 (0.33)	970
S6	1.04 (0.28)	2135
S7	15.48 (4.03)	3380
S8	4.72 (0.85)	1621
S9	2.87 (2.15)	1350
S10	8.04 (1.99)	4980
Beck	0.64 (0.36)	146

Standard errors are shown in brackets for veg. samples.

Slope of correlation = 229.49

Y intercept = 716.86

Correlation coefficient = 0.7004

Data used in correlation between the amount of vegetable material and the number of herbivores/ detritivores per square metre of springbrook bed.

TABLE 25.

SPECIES PRESENT.	NUMBER IN SUB SAMPLE. Springbrook no. 1. 1/1	2/1	3/1	4/1	5/1	TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
Nemoura erratica	1	0	3	5	4	13	2.6	65
Sericostoma personatum	1	0	0	0	0	1	0.2	5
Simulium spp.	0	1	0	0	0	1	0.2	5
Lumbricidae spp.	0	0	1	0	0	1	0.2	5
A.sulcicollis	0	0	0	3	0	3	0.6	15
Chironomid larvae spp.1.	0	0	0	0	1	1	0.2	5
TOTALS	2	1	4	8	5	20	4.0	100

Station St1. (100m.) community data.

TABLE 26.

A3a(1).

SPECIES PRESENT.	NUMBER IN SUB SAMPLE. Springbrook no. 1. 1/2	2/2	3/2	4/2	5/2	TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
Nemoura erratica	2	3	7	1	2	15	3.0	75
Sericostoma personatum	0	1	0	1	0	2	0.4	10
Simulium spp.	1	0	1	0	0	2	0.4	10
Lumbricidae spp.	4	3	2	1	2	12	2.4	60
Chironomid larvae spp.l.	5	9	2	10	4	30	6.0	150
A.sulcicollis	0	2	2	1	1	6	1.2	30
Dicranota spp.	2	1	0	1	1	5	1.0	25
Lumbricus spp.	1	0	2	1	0	4	0.8	20
TOTALS	15	19	16	16	10	76	15.2	320

Station St2. (200m.) community data.

TABLE 27.

A3a.(ii).

SPECIES PRESENT.	NUMBER IN SUB SAMPLE. Springbrook no. 1. 1/3	2/3	3/3	4/3	5/3	TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
Nemoura erratica	12	17	22	38	19	108	21.6	540
Stenophylax stellatus	1	0	5	2	0	8	1.6	40
Anabola nervosa	1	0	2	2	1	6	1.2	30
Simulium spp.	1	0	0	1	0	2	0.4	10
Chironomid larvae spp.l.	1	3	0	0	1	5	1.0	25
A.sulcicollis	3	2	6	1	3	15	3.0	75
Dicranota spp.	0	1	0	1	0	2	0.4	10
P.conspersa	1	2	0	2	1	6	1.2	30
Agabus bipustulatus	0	1	0	1	1	3	0.6	15
Nemurella picteti	1	2	4	0	1	8	1.6	40
TOTALS	21	28	39	48	27	163	32.6	815

Station St3. (300m.) community data.

TABLE 28.

A3a.(iii).

TABLE 29.	SPECIES PRESENT.	NUMBER IN SUB SAMPLE. Springbrook no. 1. 1/4	2/4	3/4	4/4	5/4	TOTAL IN SAMPLE.	MEAN NO. PER SAMPLE.	EST. NO. PER M^2 OF SPRINGBROOK BED.
Station St4.	Agabus bipustulatus	1	0	0	0	3	4	0.8	20.0
(500m.)	Philydrus spp.	1	1	1	0	1	4	0.8	20.0
Community data.	P.conspersa	1	0	0	4	2	7	1.4	35.0
	Dytiscid larvae spp.1.	2	0	1	0	1	4	0.8	20.0
	Nemoura erratica	15	21	6	29	68	139	27.8	695.0
	A.sulcicollis	4	6	0	0	4	14	2.8	70.0
	Stenophylax stellatus	0	2	3	0	1	6	1.2	30.0
	Anabola nervosa	0	0	3	2	4	9	1.8	45.0
	Limnophilus flavicornis	0	0	4	0	1	5	1.0	25.0
	Collembola	0	1	2	0	0	3	0.6	15.0
	Dicranota spp.	0	0	1	0	0	1	0.2	5.0
	Lumbricidae spp.	0	0	1	6	0	7	1.4	35.0
	Chironomid larvae spp.1.	0	0	0	1	4	5	1.0	25.0
	Nemurella picteti	1	0	0	6	3	10	2.0	50.0
	TOTALS	25	31	22	48	92	218	43.6	1090.0

SPECIES PRESENT.	NUMBER IN SAMPLE.		% OF SAMPLE.	
	Gentle.	Steep.	Gentle.	Steep.
Crenobia alpina (Dana).	0	13	0.00	0.69
Gordius aquaticus (Duj.).	0	2	0.00	0.11
Lumbricidae spp.	4	0	0.44	0.00
Gammarus pulex(L.).	92	330	10.12	17.57
Collembola spp.	3	1	0.33	0.01
Amphinemura sulcicollis (Stephens).	0	19	0.00	1.01
Capnia bifrons (Newman).	5	8	0.55	0.43
Chloroperla torrentium (Pictet).	0	12	0.00	0.64
Nemoura erratica (Classen).	11	66	1.21	3.51
Baetis rhodani (Pictet).	15	73	1.65	3.89
Velia caprai (Tamanini).	1	0	0.11	0.00
Agapetus fuscipes (Curtis).	2	97	0.22	5.17
Stenophylax stellatus (Curtis).	9	18	0.99	0.96
Sericostoma personatum (Spence).	4	20	0.44	1.06
Limnophilus spp.3.	1	0	0.11	0.00
Anabola nervosa (Curt).	5	8	0.55	0.43
Limnophilus spp.5.	5	4	0.55	0.21
Odontocerum albicorne (Scopoli).	1	1	0.11	0.05
Plectrocnemia conspersa (Curt).	7	0	0.77	0.00
Rhyacophila spp.	3	0	0.33	0.00
Helmis maugei (Bedel).	360	844	39.60	44.94
Helodes marginata	3	0	0.33	0.00
Oreodytes rivalis	16	0	1.75	0.00
Philydrus spp.	4	1	0.44	0.05
Chironomid larvae spp.	337	345	37.07	18.37
Dicranota spp.	11	14	1.21	0.75
Pedicia rivosa (Linn.).	2	1	0.22	0.05
Simulium spp.	7	1	0.77	0.05
Lepidostoma hirtium (Fab.).	1	0	0.11	0.00
TOTALS	909	1878	99.98	99.95

TABLE 30. Community data for the Gentle and Steep slopes of S6.

TABLE 31.

Community data for net catch in S6.

SPECIES PRESENT.	NET CATCH. C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	TOTAL CAUGHT.	% OF CATCH.
C.alpina	0	0	0	0	1	0	0	1	3	1	6	0.60
Gordius aquaticus	0	0	0	0	0	0	0	0	1	0	1	0.10
Lumbricidae spp.	0	0	0	0	0	0	0	0	0	0	0	0.00
Gammarus pulex	24	6	5	14	9	44	12	40	23	31	208	20.63
Collembola spp.	0	1	0	0	2	0	0	0	0	0	0	0.00
A.sulcicollis	1	0	0	1	3	1	2	0	0	0	8	0.79
Capnia bifrons	1	0	1	0	0	0	0	0	0	1	3	0.30
C.torrentium	1	0	1	1	3	0	1	0	0	0	7	0.69
Nemoura erratica	4	6	7	4	2	3	3	0	0	1	30	2.98
Baetis rhodani	6	0	0	9	13	3	0	5	6	3	45	4.46
Velia caprai	0	0	0	0	0	0	1	0	0	0	1	0.10
A.fuscipes	4	0	10	1	16	10	1	9	18	4	73	7.24
L.hirtium	0	0	0	0	0	0	0	0	0	0	0	0.00
S.stellatus	0	0	0	0	0	6	1	1	0	1	9	0.89
S.personatum	1	0	0	5	0	8	0	2	0	1	17	1.69
Limnophilus spp.3.	0	0	0	0	0	0	0	0	0	0	0	0.00
Anabola nervosa	1	0	0	0	3	0	0	0	1	0	5	0.50
Limnophilus spp.5.	0	0	0	1	0	0	1	1	0	0	3	0.30
O.albicorne	0	1	0	0	0	0	1	0	0	0	2	0.20
P.conspersa	0	0	0	0	0	0	0	0	0	0	0	0.00
Rhyacophila spp.	0	0	0	0	0	0	0	0	0	0	0	0.00
Helmis maugei	51	11	37	46	105	29	31	40	59	26	435	43.15
H.marginata	0	0	0	0	1	0	0	0	0	0	1	0.10
Oreodytes rivalis	0	0	0	0	0	0	0	0	0	0	0	0.00
Philydrus spp.	0	0	0	0	0	0	0	0	0	0	0	0.00
Chironomid larva spp.	0	19	8	12	35	13	7	8	18	17	137	13.59
Dicranota spp.	2	0	0	1	3	0	1	2	1	0	10	0.99
Pedicia rivosa	0	0	0	0	0	1	0	0	0	0	1	0.10
Simulium spp.	0	1	0	0	0	1	0	0	0	0	2	0.20
Tipula spp.	0	0	0	0	0	0	0	1	0	0	1	0.10
TOTALS	96	45	69	95	196	119	62	110	130	86	1008	100.90

TABLE 32. Community data for bucket catch in S6.

SPECIES PRESENT.	BUCKET CATCH. C11	C12	C13	C14	C15	C16	C17	C18	C19	C20	TOTAL CAUGHT.	% OF CATCH.
C.alpina	0	0	1	0	2	2	0	0	1	1	7	0.72
G.aquaticus	0	0	0	1	0	0	0	0	0	0	1	0.10
Lumbricidae spp.	1	0	0	0	0	1	0	0	0	0	2	0.21
G.pulex	11	15	9	15	8	31	20	30	22	40	201	20.66
Collembola spp.	0	0	0	0	0	0	0	0	0	0	0	0.00
A.sulcicollis	1	0	1	2	1	0	0	1	3	0	9	0.92
C.bifrons	1	1	0	0	0	0	0	0	1	1	4	0.41
C.torrentium	1	0	0	2	0	0	1	0	0	0	4	0.41
N.erratica	6	1	4	1	7	3	1	0	0	2	25	2.57
B.rhodani	2	5	5	4	3	3	3	4	8	3	40	4.11
V.caprai	0	0	0	0	0	0	0	0	0	0	0	0.00
A.fuscipes	0	2	2	0	0	41	11	4	4	2	66	6.78
L.hirtuim	0	0	0	0	0	0	0	0	0	0	0	0.00
S.stellatus	0	0	0	1	0	0	0	0	0	0	1	0.10
S.personatum	0	0	1	0	1	1	0	0	0	0	3	0.31
Limnophilus spp.3.	0	0	0	0	0	0	0	0	0	0	0	0.00
A.nervosa	0	1	1	0	0	0	0	0	0	0	2	0.21
Limnophilus spp.5.	0	0	0	0	0	1	0	0	0	0	1	0.10
O.albicorne	0	0	0	0	0	0	0	0	0	0	0	0.00
P.conspersa	0	0	0	0	0	0	0	0	0	0	0	0.00
Rhyacophila spp.	0	0	0	1	0	0	0	0	0	0	1	0.10
H.maugei	52	31	56	51	47	22	46	22	24	13	364	37.41
H.marginata	0	0	0	0	0	0	0	0	0	0	0	0.00
O.rivalis	0	0	0	0	0	0	0	0	0	0	0	0.00
Philydrus spp.	1	0	0	0	0	0	0	0	0	0	1	0.10
Chironomid larvae	17	19	34	39	18	28	29	22	8	14	228	23.43
Dicranota spp.	0	0	1	1	1	0	0	2	0	0	5	0.51
P.rivosa	1	0	0	0	0	0	0	0	0	0	1	0.10
Simulium spp.	2	1	0	0	1	0	1	2	0	0	7	0.72
Tipula spp.	0	0	0	0	0	0	0	0	0	0	0	0.00
TOTALS	96	76	115	118	89	133	112	87	71	76	973	100.00

SPECIES / GROUP.	Mean-J.mg^{-1}. energy content.	NUMBERS m^{-2}.		BIOMASS m^{-2}. in mg.		K.J.m^{-2}.	
		S4	S10	S4	S10	S4	S10
Sphaeridae spp.	9.04 (0.58)	0.0	536.8	0.00	538.14	0.00	4.86
Dieranota spp.	18.89 (1.03)	0.0	396.0	0.00	275.22	0.00	5.20
Limnophilidae spp.	28.54 (0.91)	25.0	959.2	32.91	1262.79	0.94	36.04
Crenobia alpina.	14.17 (1.25)	10.0	1232.0	3.13	385.00	0.04	5.46
Lumbricidae spp.	12.12 (0.57)	5.0	26.4	2.06	10.88	0.02	0.13
Chironomid larvae.	53.53 (2.11)	45.0	176.0	2.95	55.00	0.16	2.94
Plecoptera. (herbivorous)	35.27 (3.46)	30.0	2930.4	18.50	1772.89	0.65	62.53
Gammarus pulex.	8.68 (0.66)	40.0	352.0	123.70	1088.56	1.07	9.45
Pedicia rivosa	36.21 (3.16)	5.0	0.0	60.50	0.00	2.17	0.00
Primary producers	26.45 (5.34)	?	?	2.39×10^{3}.	201×10^{3}.	63.22	5.37×10^{3}

Standard errors in brackets.

A Summary of the Trophic Levels data for springheads S4 and S10. TABLE 33.

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