A study of coexistence of gastropods in the River Hull system

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A STUDY OF COEXISTENCE OF GASTROPODS IN

THE RIVER HULL SYSTEM

being a Thesis submitted for the Degree of

Doctor of Philosophy

in the Open University

by

Robert Albert Sill Storey, B.Sc. (Hull)

September 1981
A study of co-existence of gastropods in
the River Hull system

Volume I
Contents

Volume 1

ABSTRACT vii
ACKNOWLEDGEMENTS ix
INTRODUCTION xi

CHAPTER 1

Methods and site descriptions

1.1 Description of the River Hull system 2

1.2 Detailed description of Hempholme Lock 5

1.3 The first level of abstraction: overall 7
distribution patterns
   a. Selection of sample sites 7
   b. Timing of samples 8
   c. Extraction methods 8
   d. Data analysis 9

1.4 The second level of abstraction: 12
   a single site, Hempholme Lock
       a. Sampling technique 12
       b. Frequency and timing of samples 14
       c. Data analysis 15

1.5 The third level of abstraction: 18
   microdistribution patterns within the
   rocks and weed beds
       a. The rocks 18
           i. Longitudinal zonation and stone aspect 18
           ii. Stone size selection 19
1.5  b. The weed beds
   i. Overall occurrence of snails in relation to plant cover
   ii. Estimation of plant surface areas
   iii. Microdispersion patterns within single plant species
   iv. Winter distribution patterns

1.6  Diet
   a. Nomenclature and identification of gut contents
   b. Assessment of snail diets
   c. Comparison with periphyton
      i. Epiphyton
      ii. Epilithon
   d. Data analysis

1.7  Radula and feeding tracks

1.8  Diurnal defaecation and locomotory patterns
   i. Faeces production (in the field)
   ii. Laboratory activity patterns

CHAPTER 2

Results and discussion at the first level of abstraction: the whole river system.

2.1  Longitudinal distribution patterns
2.2  Snails and plant cover
2.3  Discussion of results
CHAPTER 3
Results and discussion at the second level of abstraction: a single
site, Hempholme Lock, the tidal limit of the River Hull
3.1 Distribution on rocks and weeds
3.2 Life cycles: distribution in time
3.3 Discussion of results

CHAPTER 4
Results and discussion at the third level of abstraction
4.1 Microdistribution patterns on the rocks
   a. Longitudinal separation
   b. Stone aspect
   c. Stone size
   d. Between-stone dispersion pattern
4.2 Microdistribution patterns within the weed beds
   a. The estimation of plant surface areas
   b. Overall snail occurrence in relation to plant cover
   c. Distribution of the different snail species in relation to plant cover
   d. Seasonal distribution patterns
4.3 Discussion of results
   a. The rocks
   b. The weed beds

CHAPTER 5
Diets; results and discussion
5.1 Major species, considered separately; selectivity
5.2 Minor species
<table>
<thead>
<tr>
<th>Chapter 6</th>
<th>Radulae and feeding tracks: results and discussion</th>
<th>114</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.1</td>
<td>Structure in relation to individual radula prints</td>
<td></td>
</tr>
<tr>
<td>i.</td>
<td>Prosobranchs</td>
<td>115</td>
</tr>
<tr>
<td>ii.</td>
<td>Pulmonates</td>
<td>118</td>
</tr>
<tr>
<td>6.2</td>
<td>Relative radula size</td>
<td>122</td>
</tr>
<tr>
<td>6.3</td>
<td>Feeding tracks</td>
<td>124</td>
</tr>
<tr>
<td>6.4</td>
<td>Discussion of results</td>
<td>126</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Chapter 7</th>
<th>Diurnal activity: results and discussion</th>
<th>132</th>
</tr>
</thead>
<tbody>
<tr>
<td>7.1</td>
<td>Faeces production under field conditions</td>
<td>133</td>
</tr>
<tr>
<td>7.2</td>
<td>Diurnal activity patterns</td>
<td>134</td>
</tr>
<tr>
<td>7.3</td>
<td>Discussion of results</td>
<td>135</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Chapter 8</th>
<th>General discussion</th>
<th>137</th>
</tr>
</thead>
<tbody>
<tr>
<td>8.1</td>
<td>Spatial separation and diet</td>
<td>139</td>
</tr>
<tr>
<td>8.2</td>
<td>Radula, diet and substratum</td>
<td>142</td>
</tr>
<tr>
<td>8.3</td>
<td>Spatial distribution and feeding activity</td>
<td>145</td>
</tr>
<tr>
<td>8.4</td>
<td>Conclusions</td>
<td>146</td>
</tr>
</tbody>
</table>

REFERENCES

Volume 2

FIGURES

TABLES

PLATES

APPENDICES

PUBLICATIONS APPENDICES
A qualitative study conducted on the gastropod snails in the River Hull system provided evidence of spatial separation of some species. Computer analysis showed that the snails could be used to classify stretches of the river. Unifying environmental characteristics of each site were then used to identify discontinuities between snail groups. From this evidence, temporary drying-up and direct or indirect influence of flow appeared to affect snail occurrence. At the tidal limit, the wide species diversity was found to be a temporary phenomenon, for there appeared to be a 'rock' and 'weed' community which were seasonally displaced probably due directly to the flow over a weir. The 'rock' species were found to possess differences in microdistribution pattern since they were selective with regard to the size of stone, its aspect and its distance from the weir. The 'weed' species showed relatively little separation with regard to plant quality, but there was a seasonal distinction between the pulmonates and the prosobranchs. There was some evidence, during periods of spatial overlap, of resource partitioning in their diets also. The general observations that food in the gut reflected that which was available on the substratum suggested either a broad diet or possibly substratum selection.

There were differences both in radula structure and application which corresponded to substratum differences, and different diurnal activity patterns were also demonstrated.

Although it is possible that predation, competition with other invertebrates and other factors could have been instrumental in limiting population size, there is ample evidence from this study that sufficient differences existed along the niche dimensions of
space, nutrition and time, to have reduced the degree of overlap
between species to a level where competitive exclusion would not
occur, even with large population sizes.
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A study of coexistence of gastropods in the River Hull system

INTRODUCTION

A preliminary search for gastropods at a single site near the tidal limit of the River Hull revealed the presence of twelve different species. Such occurrence appears to conflict with the principle of competitive exclusion (Gause, 1934) which militates against the coexistence of species that are closely related. A study was therefore conducted, both extensively over the whole river system and intensively at one particular site with a view to finding out how the pattern of gastropod occurrence, revealed in this river system, meshed with existing theory governing the coexistence of related species.

The term 'coexistence' can be interpreted in more than one way. In its most precise usage it can be used to describe the harmonious utilisation of space by two organisms which have total freedom to occupy any part of that space and are therefore mutually tolerant of each other. In practice, 'coexistence' has been used simply to describe the occurrence together, i.e. the appearance in the same area of different organisms. This latter definition does not preclude the possibility of barriers existing within that area which limit the spread of the organisms, so that their ranges abut rather than overlap. It is this broader interpretation of the term that has been widely adopted in the literature (e.g. Levins and Culver, 1971; Horn and MacArthur, 1972; Slatkin, 1974; Shorrocks, Atkinson and Charlesworth, 1979), and it is this meaning therefore that the term 'coexistence' is meant to convey in the present study.

In view of the competitive exclusion principle, it is hardly
surprising that interest has been shown in the fact that closely-related species can, and frequently do, live together. In such circumstances, one would expect competition to be intense, and for selection to operate so as to increase ecological separation. The corollary of the Gause principle, that if two species coexist, there must be some ecological difference between them, has prompted the search for subtle, but important ecological differences between related species that occur together. Such coexisting groups may, for instance, exhibit different patterns of temporal or spatial activity or they may eat different foods. During the last ten years, more and more examples of this kind of coexistence have been described and the literature, replete with such examples, has been reviewed by Schoener (1974). The increasing volume of studies has led to a proportional increase in ecological lexicon and coexisting groups are variously referred to as congeners (Fenchel, 1975) syntrophia (Balogh, 1946), guilds (Root, 1973) and "communities" (Calow, 1973b). More and more aspects of organisms' activity have been explored and in terms of niche dimensions, the effect has been cumulative, resulting in the Hutchinson 'hyper volume niche' (Hutchinson, 1957) in which the entire set of optimal conditions under which the organism can live and reproduce, are embraced. Although conceptually powerful, the practical application of niche theory requires the isolation of a manageable number of niche dimensions that are considered to be of major importance. Of these, perhaps that of space is the most obvious.

Spatial overlap can be defined at various levels, depending upon the precision with which the observations are made. Thus the distribution of freshwater gastropods in a river system may begin with their overall occurrence in the system as a whole, their pattern of occurrence in different sections of the river, the breakdown of
the sections into different sub-habitats, and the final distinction of microhabitats within these sub-habitats. This study forms part of such an observational sequence. A consideration of the section-alisation of the whole River Hull system, the sub-habitats (rocks and weed beds) within a single section at Hempholme, and micro-dispersion patterns within the rocks and weed beds provide increasingly detailed observational levels and are referred to as the first, second and third abstraction levels respectively. The purpose of this part of the study was to resolve the degree to which spatial overlap occurred in the gastropods concerned and to isolate environmental factors that correlate with such separation.

Organisms may, of course, occupy similar spatial niches but avoid, or reduce the consequences of competition by not overlapping along some other vital niche dimension. A very obvious resource that could effect separation between related species that overlap in time and space is food, and a consideration of the diet, ingestion apparatus and feeding habits forms an integral part of the study.

The emphasis throughout this study is on observation of different natural patterns and where possible, the correlation of these with various environmental conditions. Such correlations do not constitute proofs in themselves, for proofs are very difficult to demonstrate in complex multivariable field situations. They do, however, provide useful clues and may be used as hypothesis-generating devices. Further corroboration of these explanations require an experimentally orientated approach, and although some laboratory experiments were performed, these in no way attempt to provide answers to, or explanations of, the patterns observed throughout this study.

The thesis is divided into two volumes: one contains the text and references. In order to avoid interruptions in the flow of the
text, figures, plates, tables and appendices relating to it are presented collectively in the second volume. Because of the diverse nature of the subject material, discussion has been included after the results of each chapter. Preliminary introductions to each section are contained within the methods (CHAPTER 1) and a discussion linking different chapters, a summary and general conclusions are contained in the final chapter.
CHAPTER 1

Methods
1.1 Description of the River Hull system

The River Hull has been the focus of attention for a number of biological studies. In addition to the early work on the algae of the Driffield Canal (Butcher, 1940) and the invertebrates of the Driffield Trout Stream (Whitehead, 1935) there are more recent descriptions of the aquatic macrophytes (Crackles, 1968) benthic invertebrates (Jones and Pearson, 1973, Pearson, 1974 and Litterick, 1973) and planktonic bacteria (Goulder et al. 1974). Of particular interest has been the recent survey of Higgins (1980) and it is largely from the latter that the information for the present description of the River Hull has been abstracted.

The River Hull arises from a series of springs at the edge of the chalk wolds near Driffield in the north of the River Hull Valley, (FIG.1). The wolds are chalk hills rising to a maximum height of 800 ft. with the springs emerging mainly below the 100 ft. contour. The wolds stretch in a crescent shape from Flamborough at the coast, inland to the north of Driffield and then south to Ferriby on the Humber estuary.

The area enclosed by the wolds to the north and west, the North Sea to the east, and the Humber estuary to the south is known as the Plain of Holderness and was formed by the last glaciation, when morainic material was deposited by glaciers and ice sheets from the Lake District, North Yorkshire and Scandinavia. The main materials deposited by the ice sheets were clay, sand and gravel. The River Hull Valley was formed as a glacial melt water channel and in its natural state much of the valley was flooded for several months of the year (Sheppard, 1957). The low lying areas of the valley were filled with swamps and carrs giving rise to alluvium and peat which, added to the range of deposits left by the retreating ice, resulted in a diversity of soil types over the whole area.
The main springs give rise to the Foston Beck and Driffield Trout Stream. These are fast-flowing, clear, hard waters and are well-known for trout fishing. At Emmotland, they unite to form the River Hull.

Just south of Driffield, the river widens and current decreases. The substratum is predominantly silty in this zone. From its source up to the Hull city boundary the river is flanked by land which is predominantly agricultural, but within the city limit is bordered by factories and industrial plants, up to its junction with the River Humber at Hull Corporation Pier.

In total the river flows for approximately 25 miles, the lower portions of the river being strongly tidal (FIG. 2). During the highest tides, salt water penetrates as far as Wawne but the hold back effect of the tide is evident as far as Hempholme Lock, the tidal limit. The river is also fed by several smaller tributaries, e.g. Aike Beck, Watton Beck and Skerne Beck, and by west flowing streams from the drift deposits of the Plain of Holderness (FIG. 3).

The marshland in the River Hull Valley was first drained by monks in the 12th century, but adequate drainage was not attained until the major drainage works of the 18th century. The river was embanked for the whole of its course and the levels to the east and west of the river were drained by the Holderness, and Beverley and Barmston drains respectively. The Beverley and Barmston drainage follows a parallel course to the river for most of its length, entering the river at Hull in the south and being pumped into the river at Wilfholme in the north. The Holderness drains mainly enter the Humber Estuary or the North Sea. Extensive drainage schemes in the valley have improved the grazing lands and enabled arable crops to be grown.

During the 18th and 19th centuries there were many improvements in the River Hull system, one of these being the building of canals in...
the valley. The main canal is the Driffield Canal. These waterways were used for commercial traffic and the boats carried such loads as coal and lime from Hull as far as Driffield in the north of the valley.

The expansion in navigation, settlement and agriculture has led to pollution of the river, especially below Beverley. Effluent from sewage works (FIG. 1) and pig farms are the main sources of pollution, but the river above Hempholme is still free of pollution and provides water suitable for drinking. Water is abstracted for trout farms near Wansford. Expansion in population has also led to a greater demand for water in Holderness and in 1959 the River Hull abstraction works at TopHill Low were opened. In the 20th century the use of rail and roads for commercial transport led to a decline in the use of the river for commercial vehicles and today it has a greater use for recreation. The upper reaches of the river are well known for their trout and most of the River Hull system is important for coarse fishing. Boating and yachting are increasing in popularity and this has led to some conflict with the fishermen and naturalists. This has resulted in proposals for the river system to be sectionalised for particular recreational uses. The river system is also used by naturalists; a wildfowl refuge being situated at TopHill Low and some areas of the valley have been designated as Sites of Special Scientific Interest (FIG. 1).

The various uses to which the river is subject necessitate the management practices of dredging and weed cutting which are undertaken during the summer months.
1.2 Detailed description of Hempholme Lock

The site of field observations and samples for the second level of abstraction was a short (50 m.) canalised section of the River Hull at Hempholme Lock, its tidal limit, (Nat. Grid. Ref. T.A./080498.) Upstream the site is delimited by a weir, and downstream by the end of the reinforced side walls (PLATES 1-3 and FIG.4). Within these reinforced walls and running parallel to them are the brick remains of the old lock. These are lower than the present walls and become exposed at low water levels (PLATE 4). Between the walls the substratum is composed of bricks, large stones and gravel, with occasional silt or sandy patches. During the period of study, the bricks supported a rich growth of *Fontinalis antipyretica* (Hedw.). Away from the immediate influence of the weir, silt accumulates in patches, providing anchorage for macrophytes. Dominant plants were *Potamogeton pectinatus* (L.), *P. lucens* (L.) *Ranunculus aquatilis* (L.), *Fontinalis antipyretica*, *Elodea canadensis*, (Michx) and *Cladophora* sp. In 1974 and 1975 the macrophytes were abundant from April until late October and provided up to 80% surface cover. In 1976, the substratum was entirely dominated by *Cladophora* which provided a carpet-like canopy over most of the surface. Although the vegetation did not die down completely during the winter, the increased flow scoured the rocks and resulted in catastrophic losses of macrophytes from the whole area.

The flow regime was determined by the hold-back effect of the tide, and amount of water flowing over the weir. Of the two, the tidal effect was the more regular, and altered rhythmically the water level between high and low tide by approximately 0.5m. By far the most drastic effects were those produced by heavy rainfall, during the winter months, when the volume of the water flowing over increased
and its rate of flow became rapid. At times of high flow and low
tide, there appeared a band of white water which extended downstream
3-4m. In times of very low flow the torrent of water normally casca-
ding over the weir was reduced to a trickle, scouring of the substratum
ceased, and silting occurred. The current speeds at a time between
these extremes is shown in FIG.5). The amount of water flowing over
the weir, together with measurements of temperature, colour, turbidity,
pH, dissolved oxygen and ammoniacal nitrogen are recorded every weekday
by the Yorkshire Water Authority. The relevant parts of these data
were abstracted and are presented in FIGS.6 and 27.

The water was alkaline, but pH values followed a cycle with
maxima in summer months and minima in winter.(FIG.6a). Pearson
(1974) reported that conductivity showed the opposite trend, with
maxima in winter, a finding that he attributed to ions washed out
of the soil by run off following heavy rain, since it coincided with
irregular, sudden increases in flow. The same probably applied to
ammoniacal N levels (FIG.6b ). Dissolved oxygen showed both seasonal
and diurnal fluctuations (FIG.6c and 7), but Pearson (1974) found far
less variation at this site than at any other of the 23 he monitored
on the river. Being below the weir, water not saturated prior to
entering became so as it crossed. Supersaturated water lost some of
its oxygen. Being generally turbulent and flowing, there was little
thermal or chemical stratification.
1.3 The first level of abstraction; overall distribution patterns

In a study involving species overlap in a river, detailed qualitative information concerning the occurrence in the river of all the different species is prerequisite. An initial sampling programme was, therefore, devised to provide such data from this varied river system.

(a) Selection of sites

Site areas were initially selected from a map, and within a 65 point scatter, all major sections of the river were represented. Thus the origins, upper, middle and lower reaches were all included in the sampling programme, although not in any systematic way. The precise site selection, although not pinpointed by co-ordinates from random numbers, were nevertheless chosen from the map in a haphazard way.

If any bias was introduced, it favoured ease of access to the area of river to be sampled. Having defined the sample sites from the map, they were visited and their exact location denoted by a site number and grid reference. When viewed, each sample site appeared to be representative of the pattern in that particular section of the river, but in two cases interruptions of the river produced what appeared to be different biotopes, in one case at different sides of a road and in the other, above and below a weir.

In these two cases both the original single sites were split into two, and each numbered, referenced and sampled independently. Of the 65 sites originally selected, five were undergoing weed-cutting operations during the sampling period and were devoid of weed and very turbid. These sites were not sampled and do not appear in the results. Location of the sites is shown in FIG. 8 and photographs of representative site types in PLATES 1 - 23. Grid references of sites are shown in APPENDIX 1.
(b) Timing of samples

Although the sites were visited on several occasions, at different times of year, the data presented at the first level of abstraction are those obtained during a single sampling period in August-September, 1979. Previous preliminary sampling had revealed that at this time of year, snail populations were large.

(c) Extraction methods

Because of the very varied nature of the substratum, a range of different extraction methods was employed. At each site a collection was made following roughly the path of a belt transect 2m. wide across the river. Whilst in most cases the water was shallow enough to permit sampling from the bank or by wading, in some cases, where the water was deeper, a boat was employed. In areas of silt, sand and gravel, the samples were removed with a sieve (mesh size 0.1cm.) or a net of similar dimensions and mesh size. Where rocks or submerged logs and debris were encountered, these were carefully removed, scrutinised for snails and then replaced. Plants were removed and searched for snails in the same way. Extraction took place, therefore, in situ, but on occasions when weed or snails provided identification problems, the specimens were placed in polythene tubes or bags and returned to the laboratory for examination. Ökland (1969) found that the number of snail species detected in a given habitat increases with the time spent in collecting, although the effect is less pronounced in streams and ditches than in large lakes. Because of the varied nature of the sites, and the plant growth they supported, no sampling time restriction was imposed at any site.

The results at each sample station therefore represent the pooled results of a variable number of subsamples taken over the whole of the
substratum.

During the same sampling session, records of the site dimensions, maximum water depth, number of vegetation types and major substratum types, were made and subsequently the following physical and chemical parameters were measured using a Waldon E multiprobe unit with appropriate probes:

- water temperature
- oxygen concentration
- conductivity
- light intensity at water surface (expressed as a percentage of the maximum at the nearest open space).
- pH

All the above records were made on cloud-free days during early September, 1979, between the hours of 10.00 a.m. and 3.00 p.m.

Flow was also measured subsequently using either a Kent miniflow meter or a Braystoke BFM .008 Mk. 3 current meter.

Site descriptions were recorded on a shoulder-mounted Philips cassette recorder (E.L. 3302) with lapel microphone and the information subsequently transferred to data sheets.

Identification of the snails was made using the keys of Macan (1969) and the nomenclature revised to follow that of Kerney (1976).

(d) Data analysis

A number of indices have been used to represent the similarity of two sites with respect to their species composition (normal analysis) or the association between pairs of entities with respect to their distribution at a number of sites (inverse analysis). In this study the Index of Similarity (I) is employed because it is least sensitive to sample size, (Mountford, 1962) and has been used
successfully elsewhere for analysing snail faunal composition (Calow, 1973b).

The statistic $I$, is approximately defined by

$$I = \frac{2j}{2ab - (a+b) \times j}$$

where $a$ = number of species in one habitat

$b$ = number of species in the other habitat

$j$ = number of species in common.

The range is from 0 for no relationship to $\infty$ for perfect relationship.

In normal analysis, the matrix is constructed from the species correlation between all possible pairs of samples. The data derived from such a matrix is then used to divide the samples into groups. The theory underlying such normal analysis is that the samples can be regarded as being defined by a small number of critical factors: the species respond to these factors in varying degrees and are used as tests to identify the major discontinuities between groups of samples. (Williams and Lambert, 1961).

For inverse analysis, the matrix is constructed from the same data, but the samples are correlated in all possible pairs and the information derived is used to divide the species into groups. The difference is now that the species can be regarded as being defined by underlying criteria relating to their ecological distribution, and the samples are now used to identify the major discontinuities between groups of species.

These analyses were considered to be useful in defining possible river zones, and identifying snail species groupings. The data were processed on a Honeywell computer using an Olivetti TC 485 at the computer centre of the Hull College of Higher Education.

The difficulty of quantifying species abundance, and the degree
to which this varied during preliminary sampling at Hempholme Lock suggested that the simplest index, the number of species present, would be the most useful in quantifying the relationship between the snails and environmental parameters (Pianka, 1966). This index has been used in previous, similar molluscan studies (Harman, 1972), and is used in the present study to demonstrate the relationship between the snails and the number of plant species present.
1.4 The second level of abstraction: a single site, Hempholme lock

The first section of the study, concerned with the distribution of the different snail species over the whole river, showed that at one particular site, almost all the snail species that occurred anywhere in the system could be found together: co-existence, at this level, was at its maximum. The site was Hempholme Lock, and it was therefore here that attention was focussed, since the range of favourable or limiting factors responsible for snail occurrence should be encountered over a relatively small area. Consequently, regular, more quantitative sampling was necessary in order to follow temporal changes in snail fauna and to make estimates of relative numbers and distribution patterns on a seasonal and annual basis.

(a) Sampling technique

Previous quantitative work on snail populations has entailed three distinct direct sampling techniques. One involves standardizing the number of specimens of each species (e.g. Duncan, 1959, Berrie, 1965) the time spent collecting (e.g. Macan, 1950, Powell and South, 1978), or the area over which the collection is made (e.g. Russell Hunter, 1961a; Heppleston, 1972; Olivier & Schneidermann, 1956; Calow, 1973a, 1974b, Young, 1975). Modifications of the last method were favoured in the present study, for although it carries the disadvantage that in times of scarcity, numbers of rare specimens may fall too low to allow rigorous analysis, it nevertheless produces a picture of the habitat in terms of relative abundance. The alternative of standardizing the number of specimens entails catching an excess of the common ones and by doing so disturbs the habitat. The possibility of standardizing the time was rejected.
because of the vast difference in time involved in extracting snails from weed as compared with rocks. Also rejected were indirect methods listed by Hairston, Hubendick, Watson & Olivier (1958) since these involve capture-recapture techniques inappropriate to a deep, fast flowing river where the bottom is frequently obscured.

In a previous study at this site (Pearson, 1974), all samples were drawn from the bank, just beyond the reinforced west wall. For this study the whole area was sampled, the apparatus used being dependant on whether the substratum was hard or soft. Since approximately half the area was composed of the brick foundations of the first lock and half silt and sand, half the samples at each session, were taken from the soft substratum and half from the rocky zone. Initially ten samples were taken from each zone, but sorting took so long that on subsequent occasions, the number was reduced to between four and eight samples of each.

The apparatus selected for sampling the soft substratum was an Allen grab. This type of grab was suggested by Hairston et al (1958) as being suitable for sampling snails in muddy or silty areas. It carries the additional advantage of possessing sharp jaws which cut through weed, and a box structure that can enclose a standard volume of vegetation.

In places where the substratum was hard, both the Allen grab and a net were tried but found to be unreliable. An air-lift, used throughout the river in earlier studies (Pearson, Litterick and Jones, 1973) was also found to be unreliable against the strongly-attached snails Ancylus fluviatilis Acroloxus lacustris and Theodoxus fluviatilis. Samples were therefore collected by removing whole bricks or stones. In this way all adhering snails were removed. The technique involved placing a net downstream of the brick and in
contact with it. The brick was then gently eased from its position on the river bed into the net and transported to the surface. In this way, snails accidentally dislodged from the surface by movement of the brick or subsequently by sudden exposure to flow were prevented from being swept away. Once landed, the contents of the net, including the brick were emptied into separate buckets of river water and transported, with Allen grab samples, to the laboratory. The depth of the water generally necessitated the immersion of the collector, so a wet suit and face mask were always worn during the sample sessions. Occasionally, when the flow was very strong and the water deep, a boat was needed to raise the samples and transport them to the bank.

In the laboratory, samples were transferred to large, white rectangular dishes (55 cm. x 40 cm.) so that any mud settled as a thin layer. After settling, the trays were tilted and rocked gently and any snails clinging to the walls and base were removed. This process was repeated until no more snails were found. Any stones or weeds were gently brushed and searched. It was necessary to sort the material live, since in certain regions the substratum contained numerous empty, or mud-filled shells. All snails were subsequently transferred to 70% ethanol, identified and measured, using either a grid or travelling microscope. Within each species they were grouped at appropriate size intervals and the information used to construct size frequency histograms.

(b) Frequency and timing of samples

The life cycle of most aquatic gastropods is annual (Boycott, 1936), with breeding in spring, and occasionally, a second period in autumn. Samples were removed in winter (February), spring (April), summer (June) and autumn (October), so that the samples would represent
the main stages in the life cycle. This programme was continued for three years, although the first February sample was not completed until early March 1974.

Because of the large time interval between some sampling sessions, corroborative samples were taken, during the summer of 1979, from a site on Barmston Drain (site 47). This was selected because it was conveniently near to the laboratory, and contained a similar complement of snails to the weed beds at Hempholme. For these samples, 3 litre volume of weed (predominantly filamentous algae) was collected into a bag. The samples were then treated in the same way as those from Hempholme, and 20 were taken during May, June and July.

Although it has been shown that the activity of macroinvertebrates increases at night, (Waters, 1962, Elliott, 1965, Litterick, 1973), both Clifford (1972) and Pearson (1974) found no significant difference between the numbers caught by day and night. Collections were therefore made during daytime, sometimes spread over two days.

c) Data analysis

Comparison of samples can be extremely difficult when the areas from which the samples are taken are different. In this study, where the samples were taken from zones where the substrata were so different that they required different sampling techniques the problem of standardisation is immediately raised. Both techniques employed in this study involved the removal of a known area of substratum, together with the weed growth it supported. But on soft substrata, as with silt in this example, the silt offers a dimension of depth not available to animals on a similar area of brick or stone. For gastropods at least, there is some justification for the adoption of such a method, since most species live on, rather than below the surface. But this still
leaves the problem of plant cover.

Some authors have included an indication of weed quantity, expressing their data in terms of numbers of molluscs/ dry-spun weight of weed (Calow, 1973b) others in numbers of animals/ 10cm. length of leaf (Krecker, 1939). The results can be difficult to compare, however, when the areas sampled contain beds of weed exhibiting different growth forms. Nearest to a solution is the technique of Harrod (1964), in which the actual surface areas of different plant species is estimated. This method was considered to be too time-consuming at this level of abstraction, but is utilised later.

No absolute population densities have been attempted because of the difficulties of standardisation discussed above. Raw data have been standardised so that densities are expressed as numbers m$^2$ by pooling the sub samples from each zone and dividing by the total area of each zone sampled. The area taken into account was that enclosed by the jaws of the Allen grab, and the standard dimensions of the bricks. Although not dissimilar in area from each other, neither takes into account the additional surface provided by plant growths within the sample. The results are used to compare, in broad terms only, seasonal variations at each zone. Comparisons between zones, based on density, are subject to more shortcomings, owing chiefly to the unknown additional surface area provided by the plants, and the conclusions based on such data must be viewed with caution. Standardised densities are presented in FIGS.29-31. Such data should strictly be presented discontinuously, but the points are joined by lines to distinguish them from the overlaid size-frequency histograms.

Relative frequencies, however, are not subject to the same errors inherent in absolute density measurements, and these have enabled comparisons to be made between the population samples. One technique
employed, polar ordination (Bray and Curtis, 1957) was developed and is more usually applied to vegetation cover, but has more recently been used in invertebrate studies (e.g. Rabini and Gibbs, 1980). For this test, the samples are first compiled into a standard community table or primary matrix. It is customary, but not obligatory, to use double standardisation before computing the percentage similarity, which involves converting the importance values of each species into percentages of the maximum value in that row for the species. These standardised percentages are summed in each column, and the values in each column are converted into percentages of the total for that column. Sample similarities are now computed. When the columns in the table are relative importance values, percentage similarity simplifies to

\[ P.S. = \min(x, y) \]

in which \( \min x, y \), is the smaller of the two values for a given species in samples \( X \) and \( Y \). These values, computed in all possible directions between samples are compiled into a sample-similarity matrix. Two samples having the greatest dissimilarity are chosen as the two end points for the axis. The distance between the two end points is the complement of their similarity values, the percentage difference,

\[ P.D. = 100\% - P.S. \]

The values of all the other samples are located along this axis by finding the intersection of the co-ordinates of each sample from both end points. Calculations and results appear in APPENDIX 5 and FIG.25.

Non-parametric analysis was also applied to the raw data. For each pair of summed hard/soft samples at each collection, Kendall's Rank Correlation Coefficient (Siegel 1956) was calculated. These results are presented in FIG.26.
1.5 The third level of abstraction: microdistribution patterns within the rocks and weed beds

(a) The rocks

The results at the second level indicated a separation, at certain times of year, probably at least half, of the snail species into two "communities". During the months of July and August 1979, a more detailed study was made of one of the communities, that on the stones at Hempholme, with a view to determining to what extent spatial separation occurred within that group. The study followed an early summer of high rainfall, and the flow over the weir was already above the figure of 90 m.g./day which was previously correlated with the separation into two communities. Separation was not total, but the group of stone-dwelling, high flow tolerant species (Ancylus, Potamo pyrgus and Theodoxus) was predominant.

The physical appearance of this site, and the presence of the weir, suggested possible patterns of longitudinal zonation. The substratum was composed of inorganic material ranging in size from gravel to large stones, which also gave potential for separation on the basis of different size selection. The bulk of the foundations of the weir was composed of bricks, which provided different aspects for snail colonisation and these three possibilities for microdispersion pattern were investigated at this third level of abstraction.

i. Longitudinal zonation and stone aspect

Samples were withdrawn during daylight from the brick area of the east side of the river between pillar 1-20 (FIG. 4). Sample units were bricks, nearly all of which had been placed in the river twelve months earlier. They were common bricks of standard dimensions (22.0 cm. x 7.5 cm. x 7.5 cm.) with a depression (frog), on one of the two largest surfaces. Although providing a suitable surface for algal
growth, these bricks had not yet been colonised on any aspect by the moss *Fontinalis antipyretica*. Because of the uneven nature of the foundations, each brick provided the opportunity for snail colonisation on any of the six aspects, including the undersurface.

Unfortunately, although the bricks had originally been evenly spaced along the edge of the river, disturbance, probably human interference, had resulted in an irregular arrangement at the time of sampling. Consequently it was necessary to pool the results so that sufficient samples were obtained from each zone. The section of the river from the weir as far as pillar 20 was divided into three zones, 1-5, 6-15, and 16-20. Flow-rates and depth were recorded and presented in FIG. 3. The sampling technique involved shielding the brick from the flow with the legs, and raising it by hand in the shelter thus provided. Whilst every care was taken not to allow snails to be swept away on their journey through the water, some did become dislodged and were not included in the count since it was not possible to tell from which aspect of the brick they had become detached. However, the removal of thirty stones under cover of a net revealed that the highest loss, that of *Potamopyrgus* was less than 5%, and this error is acknowledged. At least five bricks were collected from each zone and the results include a total of 23 bricks for zonation and 19 for aspect. Many bricks provided data for both sections. The number of snails of each species on the bricks, and on each aspect of the bricks was noted and the results presented in Appendices 6 and 7 respectively. The position of the frog was noted at the time of collection, but since approximately half the bricks (8/19) were frog down, 2 frog up and the rest frog sideways, no correction was made for the slight area difference in subsequent calculations.

ii. Stone size selection

Stones were selected and arbitrarily organised into size cate-
gories to cover the main types present, viz.

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
<th>Longest length (cm.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Very small</td>
<td>0-5</td>
</tr>
<tr>
<td>B</td>
<td>Small</td>
<td>6-10</td>
</tr>
<tr>
<td>C</td>
<td>Medium</td>
<td>11-15</td>
</tr>
<tr>
<td>D</td>
<td>Large</td>
<td>16-20</td>
</tr>
<tr>
<td>E</td>
<td>Very large</td>
<td>21-25</td>
</tr>
</tbody>
</table>

Thirty stones of each category (except D) were selected from the sample area. To counteract the possible effect of flow or depth, approximately six stones of each category were removed from the 5 zones identified by pillar numbers as before. This was possible in all cases except for stone category D. Stones of this size occurred in insufficient numbers. The numbers of snails of the three species investigated were recorded and the results presented in Appendix 8.
1.5. (b) Weed beds

A survey of a typically weedy zone of the river was conducted to seek evidence for possible differences in micro-dispersion patterns of the group of snail species commonly found in such areas. The site selected was to have been the 'weedy' zone at Hempholme Lock, to contrast with the rocky zone. However in view of the relative susceptibility of this particular site to alterations associated with the flow regime, and its unavailability at the time required owing to major reconstruction work on the weir itself, a site was chosen on the Barmston Drain. This was site 49 of the first level study, (PLATE 20) which had a similar complement of snail species to that of Hempholme weed beds but was not subject to the same degree of perturbation.

i. Overall occurrence of snails in relation to plant cover

The relative abundance of the various plant species was first estimated using quadrats. Fifty quadrats (size 0.0625m²) were scattered at random along the chosen section and the weed within each quadrat removed, together with the snails it contained. The detailed procedure for each quadrat depended upon the quality and quantity of weed present, but the general sequence was the same. Quadrats were first allowed to settle on the weed or silt substratum. If no weed was present, the area was scrutinised and the surface snails counted. The silt within the frame was excavated to a depth of 2cm. using a D net (mesh size 1 mm.), and the net contents sieved to reveal any snails. At this site the substratum was almost totally silt and yielded very few snails when devoid of weed. When weed was present, any rooted marginal plants which broke the water surface were trimmed off at the water line using scissors. The stems were then cut at their intersection with the vertical projection of the quadrat frame, the sample
within the frame carefully removed and any adhering snails scored. In the beds of filamentous algae, the strands were trimmed along the edge of the quadrat as before, but using shears and the weed sample within the quadrat removed and placed in a polythene bag. The bags were transported to the laboratory and the snails extracted from the filamentous algae by washing. Variations in the amount of weed in each quadrat were considerable. Once the snails had been removed, the weed samples were shaken and spread out on large sheets of absorbent paper. Vascular plants were allowed to dry for 3-4 hours, by which time the surface moisture had evaporated. Samples of filamentous algae were thinned out and left to dry overnight. The surface areas of all samples were then estimated using the technique described below.

**ii. Estimation of plant surface areas**

Watersnails cling to plants by means of their adhesive foot and are reported to feed, not on the plant tissue itself, but on the coating of bacteria, protozoa and particularly algae. It follows that they are very dependent upon the surface of the plants on which they dwell, and that any quantitative considerations must be based on an accurate method of measuring the surface area. The method employed in this study was the technique developed by Harrod and Hall (1962) who demonstrated a relationship between the measured surface area of a plant and the weight of a covering film of solution on its surface. Once standards have been prepared, the surface area of any plant sample of the same species can be read off from the regression, having first determined the weight of the covering solution.

The plants used for standardisation in this study were selected from those which occurred in the 50 quadrats mentioned earlier.
Only four of the five such plants were investigated since two quadrats contained a species of submerged grass that did not strictly qualify as an aquatic plant. In view of the different morphology and growth form of the plant types, three different techniques of measuring or estimating the surface areas were adopted.

**Cladophora sp.**

Almost all the filamentous algae was *Cladophora* sp. and the surface area was measured by removing individual strands and recording their length. Measured units of 5 m. were placed in polythene bags and later pooled to make increasing incremental groups of 5, 10, 15 m etc. In all, 160 m of filamentous algal strands were measured. The diameter of the cells were assumed to be fairly constant, but 10 readings were made using a micrometer eyepiece and the average used in the area calculation. Each group of 5, 10 and 15 metres was dried overnight, then weighed, and immersed for a few seconds in a standard solution (1% 'Tween 20'). The units were then placed individually on a sieve (pore size 250 um) and shaken prior to being reweighed. The difference between the wet and dry weight provided the weight of the surface liquid.

**Veronica beccabunga** and **Myosotis scorpiodes**

These two species had similar growth forms and were treated similarly. Parts of the plants protruding from the water were cut off, as were those covered by silt. Each leafy shoot was removed at its junction with the main stem and the outline of the leaves and petioles traced onto squared paper, starting at the base of the stem and working upwards (FIG.44). The areas of the leaves were determined by doubling the area of the leaf traces. Stems did not taper uniformly, but the internodes appeared to be of uniform diameter. The dimensions of each length of stem of uniform diameter
were recorded on the squared paper, and in the calculations the stems were assumed to be cylindrical.

**Callitrichе sp.**

The samples of Callitrichе were processed similarly, but the area measurements were made after, rather than before the weighings. This was because the leaves were too small to be traced accurately, and it was not possible, particularly at the apex, to distinguish individual leaves without dissecting them out. Surface areas of leaves were measured on excised leaves using a micrometer and eyepiece graticule. Not all leaves on a sample were counted. In this species the leaves are arranged in pairs of equal size, and most of the leaves on the main stem appeared to be of uniform size. Areas of difference were at the apex, and the side branches, and so ten leaves, from different parts of the plant were removed and measured and the average value used to calculate the total leaf area for that sample. The length and diameter of the stems and roots were measured and assumed to be uniformly cylindrical.

All the samples of vascular plants were immersed in acetone and allowed to dry before weighing. They were then immersed in the standard 'Tween 20' solution and shaken before the final weighing.

The time taken to shake excess solution from the weed samples was determined from preliminary trials conducted on average sized sample units of the 4 weed species. In the case of the vascular plant species, the largest samples tended to be multiples of these average sized shoots. Each sample was shaken for periods from 0 to 30 seconds at the rate of one shake/sec., and five replicates were used for each period. Results showed that most solution was lost during the first ten seconds, after which the curve levelled off (APPENDIX 9, FIG.43). A period of twenty seconds was
judged to be appropriate for the range of sample sizes for all weed species. The results also indicated a progressive weight increase within many replicates, possibly due to the accumulation of solution within the plant tissues, so that in the subsequent standardisation, the first result only was used in the regression calculation.

The weighings were made on a balance adjacent to the sink where the solution was applied and errors due to evaporative water loss were ignored.

iii. Microdispersion patterns within single weed species

Some consideration was made of possible differences in micro-distribution of the snail species on the different weed types. Three of the four species of plant had definable regions, e.g. stem, upper and lower leaf surface etc. No attempt was made to delimit areas of the filamentous algae, however, since this formed three dimensional meshes in which the aspects were too numerous and too varied to quantify. Twenty five samples from each of Callitriche sp. and Myosotis scorpiodes were removed and twenty of Veronica beccabunga, because of its comparative rarity. Each sample was cut near to its base, and the positions of each snail recorded whilst the sample was still underwater. This was necessary because the snails frequently became dislodged as the sample was withdrawn from the water. The weed samples were placed in marked polythene bags, returned to the laboratory and their surface areas determined using the method described earlier. This enabled the estimation of snail densities on the various plant species to be made.

iv. Winter distribution patterns

The submerged substratum was devoid of macrophytes during winter, and filamentous algal growth was sparse. The pattern of occurrence of the gastropods was investigated during February, 1981, using the same technique as described in CHAPT.1. 5.i.
1.6 Diet

The purpose of this section was to attempt to find out whether snails were selective in their choice of food, particularly when they occurred in single species clusters, and to observe any differences when they occurred in mixed species groups, or put another way, to compare the diet at times of spatial overlap, with times when spatial overlap did not occur. Such a study provides, incidentally, data on the natural diets of the various species additional to that already published, and a thorough knowledge of the trophic habits is prerequisite for productivity assessments.

The study on diet was conducted at Hempholme Lock during the same period as the second level distribution study. At this early stage the model for distribution had not been formulated and the collections for diet, therefore, do not necessarily follow what would appear, with hindsight, to be the logical progression of matching closely the spatial distribution with that of diet. Nevertheless, the key factors governing snail distribution were operating, even though they were unrealised at the time of collection, and the results of the diet study reflect the situation that pertained at the time, and are interpreted accordingly.

(a) Nomenclature and identification of gut contents

Watersnails generally feed on the algae, bacteria, etc. that coat the surfaces of aquatic plants, rather than the plants themselves (Boycott 1936, Graham, 1955). Such growths occur also on stones and submerged logs, and the literature concerning them is wide and terminology varied. Sládečková (1962), favours the German term "Aufwuchs" or its English synonym "periphyton" to describe all attached flora,
irrespective of the nature of the substratum, but follows the sub-
divisions proposed by Šrůmer-Hušek (1946, 47) based on the substratum
with which the coating is associated. According to this system,
which is adopted for the purpose of the present study, the material
coating stones and bricks is referred to collectively as "epilithon"
whilst that on the submerged macrophytes is "epiphyton".

Of the recognisable components of the periphyton, the Bacillaro-
phyceae were by far the most abundant, and these were identified to
a generic level. Within the genus, occasional size or shape differences
distinguished types below the level of genus, and these were sometimes
designated for example 'Nitschia a' and 'Nitschia b' but in general
the results are presented, for this group, only at generic level. The
same is true for types of filamentous algae, in which cells of different
diameter were distinguished, but which are compounded under the division
'Filamentous algae'. A variety of coloured spherical structures of
various sizes were occasionally present: these were not identified,
but grouped together as "rest" a term generally used for the summed
minor taxa that individually comprised less than 1% of the total sample.
Only one major component was not identified. It occurred on the rocks
in quite large quantities, but in only one group of samples. Multi-
cellular, it is referred to as 'U' in the results.

Although the techniques described are well-tested for algae and
diatoms, the number of unicellular animals occurring in preserved
samples was generally low. Larger invertebrate types, particularly
rotifers, arthropod and crustacean fragments preserved well, but the
presence of fragile unicellular forms with thin or fragile outer mem-
branes remained largely undetected, probably due to the severity of
the treatment prior to scoring.

Because of the difficulty in distinguishing the epilithic and
epiphytic bacteria from the endemic gut flora, no count was made of bacteria in the samples.

Whilst in the spring, summer and autumn most of the material from the snails processed, and that from the weed and rock samples was identifiable, the winter samples did contain large amounts of unidentified, often amorphous material which is probably covered by the term 'detritus'. The origin of this material would be difficult to establish, and its amorphous nature made quantification impossible, at least by observational microscopic means. Because of this, no comparative estimate of detritus was made in this study. Detritus in the form of partly decomposed higher plant material was recognisable however, and was recorded.

(b) Assessment of snail diets

Although the diet of snails, particularly terrestrial pulmonates has been assessed from an examination of their faeces (e.g. Pallant, 1972) and this technique has been employed in his study of Lymnaea and Theodoxus from aquatic habitats by Skoog (1978) it suffers from the disadvantage that it follows the attacks of enzymes and gizzard action, and may not truly reflect the proportions of the ingested components. Diet was therefore investigated using anterior gut contents. Snails were removed from their substratum by hand and immediately placed in 70% ethanol. The shells were cracked prior to fixation to allow penetration. The stomach region (crop, pylorus and gizzard) was dissected out from the pulmonates, and the anterior part of the gut removed from the prosobranchs. A slit was made in the crop, or the most anterior part of the gut in which food could be seen and the contents were squeezed out and mounted on a slide in 50% glycerol/water.

In the case of large, or medium-sized specimens, a measured
area \((57\text{mm}^2)\) was scored under high \((400 \times)\) magnification for
recognisable food components. For small specimens, e.g. \textit{Potamo-
pyrgus} it was sometimes necessary to score the total anterior gut
contents. When large numbers of a snail species were available,
they were pooled in groups of five, and the total of each group
summed to provide the overall total for each species. For small
numbers of snails \((<15)\), each snail was considered separately, each
contributing to the overall total.

(c) Comparison with periphyton

Evidence for selection of particular fractions of the periphyton
was initially investigated by comparing the contents of the gut with
a representative sample of the immediate substratum. A pre-requisite
for such a comparison was local concentrations of a particular species
so that there was no interference from other species. If snails were
too widespread in their distribution, their gut contents could have
reflected differences in local concentrations of diatoms, and this was
found to vary considerably within a small area. Mobility, and hence
catchment area would also have been relevant if the sample area had
been too large.

On occasions when substratum samples were needed for comparison
with gut contents, the sampling method, as with the collection of
snails themselves, was determined by the nature of the substratum.

i. Epiphyton

Weed samples of approximate volume 200 ml. were shaken then
squeezed over a wide necked funnel and the green exudate collected
initially into Lugol's iodine (Saraceni and Ruggui, 1969) for
identification and subsequently into 70\% ethanol. This method was
devised by West and Fristch (1927) and employed by Calow (1970) in
his study of Lymnaea peregra.

ii. Epilithon

The epilithon was sampled in three different ways, depending upon the orientation, size of the surface and whether it was rough or smooth. Smooth stones were removed to the laboratory and scraped with a plastic blade so that an area of 10 cm$^2$ was removed. The smooth walls of the weir were sampled in situ using a teat pipette. The results of ten collections were combined, and a sub-sample of ten drops scored in the same way as the gut samples.

Rough stones were dehydrated via increasing strengths of ethanol, and finally coated with colloidin. The precise sequence of solutions followed the text of the originator of this technique (Margalef, 1949) and is conceptually similar to that of Sechler and Gundersen (1971) in that the whole epilithic community is surrounded by a fluid film and is removed when the dry but flexible film is peeled off. Rough stones that were too large to be treated in this way were fractured with a cold chisel, and the fragments returned to the laboratory and sampled in the manner just described.

(d) Data analysis

For each sample, the counts of each recognisable food component were summed and expressed as percentage proportions of the total components, viz.

\[
\% \text{ occurrence of type } A = \frac{\text{number of individuals of type } A}{\text{total no. individuals of all types}} \times 100
\]

Samples containing large amounts of the moss Fontinalis antipyretica, as well as diatoms, were adjusted to take into account the area of the components. Since the moss invariably appeared as single celled sheets, the relative areas of the diatoms were measured
and substituted in the formula thus:

\[
\% \text{ occurrence of type } A = \frac{\text{Area occupied by type } A}{\text{Total area occupied by all types}} \times \frac{100}{1}
\]

The results were expressed as a series of bar charts, arranged both above and below the axis when comparison between two sets of data was required, e.g. gut flora and epilithon. In one case, that of *Physa fontinalis*, sufficient data were available to be expressed as a graph, the percentage proportions of periphyton being compared with gut contents for six sampling occasions. Points lying on the 45° slope indicate complete equivalence between samples. A discussion on the interpretation of such graphs occurs in Emlen (1966).
1.7 Radula and feeding tracks

Evidence for selectivity of feeding and the mechanics of food handling can sometimes be obtained from a study of the mouthparts and feeding appendages, which in the case of gastropod molluscs are the jaws but particularly the radula. The molluscan radula has been the subject of widespread attention, and the literature for the studies on prosobranchs is reviewed by Fretter and Graham (1962). Pulmonate literature is more scattered, but Carriker (1945), Hubendick (1957) and Calow (1970) have reported on the functional anatomy of Lymnaea, Merkel (1967) on histology and Runham (1962, 1963, ) on replacement mechanisms. Because of its wide depth of focus, the scanning electron microscope has been utilised and Runham and Thornton (1967), Thompson and Hinton (1968), Runham (1969), Hughes (1979), give examples of its application to radular study, although none of these accounts on fine structure refer to the gastropods in the present study.

The purpose of this section of the present study was to seek evidence for differences in radula structure within the various species, that could have implications with regard to the food taken under natural feeding conditions. A descriptive comparison of their structure was combined with an examination of the feeding tracks made by the same species in the laboratory. The impression made by the radula as it abrades the substratum can provide valuable information complementary to that obtained by studying the organ directly. Such tracks are important for two reasons. They reflect the manner in which the denticles of the radula are applied to a flat surface during rasping, and many surfaces in the natural habitat, e.g. stones and submerged leaves are of this type. Also the individual prints form part of a feeding track, which reveals overall movements of the head, and feeding
patterns, which may provide indications of food detecting mechanisms (Storey, 1971: PUBLICATIONS APPENDIX). In the present study the tracks and individual prints were obtained by coating glass slides with a very thin film of albumen and lightly smoking in a candle flame. These were then presented to the snails which had previously been kept in laboratory culture. When suitably etched, the slides were removed, dried and either photographed or enlarged directly onto light sensitive paper.

Observations on living snails feeding on thin films were made using a binocular microscope. The microscope was focussed on the inside of the glass plates or aquarium wall, so that the mouth and radula of the snails were in focus as they browsed the glass surface. Radulae from all species were removed either by dissection or by warming in potassium hydroxide solution. Prior to being scrutinised, the radulae were mounted in 50% glycerol/water or glycerin jelly to prevent undue distortion. Chlorazol black has previously been reported as being suitable for staining radulae (Verdcourt, 1946a), and was used as a stain in some preparations. Other observations were made on the radulae in situ by carefully removing the head and clearing in Berlese's fluid.

Measurements of the lengths of isolated radulae were made, using an eyepiece graticule. Lengths were taken to be the total, flattened lengths rather than in situ lengths. Preserved wet weights of the snails were measured on specimens that had been rolled once, over their complete body surface, on filter paper immediately prior to weighing.
1.8 Diurnal defaecation and locomotory patterns

Some organisms, overlapping in space and on the same trophic level, avoid competition by possessing different patterns of temporal activity. Hawks and owls are examples, one group feeding by day, the other by night. Although it is more difficult to interpret such strategies in terms of herbivores, subjective observations during day and night collections suggested that there may be some difference in the day and night activity patterns of the various snail species. Two strategies were evolved to investigate this possibility. The first was field based, examining the faeces production as a measure of feeding activity and has previously been employed by Calow, 1975b, in his study on Ancylus fluviatilis. The second was laboratory-oriented, to explore more directly the diurnal patterns of locomotory activity under carefully controlled conditions, (Calow, 1974c).

i. Faeces production (in the field)

Like the faecal pellets of many molluscs (Moore, 1931), those of the pulmonates and Bithynia tentaculata are compressed and consolidated and retain their identity for some time. It was therefore relatively easy to collect, with a pipette, the pellets of Physa fontinalis, Lymnaea peregra and Ancylus fluviatilis, onto a slide, orientate them along their longest axis and total their lengths using a travelling microscope. The pellets of Bithynia tentaculata were more elipsoidal and discrete and were quantified by totalling the number of pellets at each collection. The pellets of Theodoxus fluviatilis were less compact, contained sand and easily disintegrated on manipulation. The amount of faecal material for this species, and for Potamopyrgus jenkinsi was, therefore, determined gravimetrically.

Collections of between 20 and 100 snails were isolated in tanks
with river water but no food. Two replicates were generally used but numbers of Ancylus were so low, only one batch of 20 was used, and for Potamopyrgus jenkinsi, one batch of 100 snails was employed. Tanks were covered to prevent temperature fluctuations caused by rain, and held partly submerged by a frame (PLATE 24a) to help stabilize the temperature near to that of the water. Temperatures were recorded at the beginning and termination of the experiment and never found to differ by more than 0.5°C. This whole procedure, carried out during daylight, was repeated during the hours of darkness, and the time for each run was 5 hours. The run involving the rock dwelling species Ancylus, Theodoxus and Potamopyrgus was conducted at Hemp-holme Lock, and that of the weed beds group, Lymnaea, Physa, and Bithynia at site 49, where the microdistribution patterns were investigated. The raw data for these collections is presented in APPENDIX 16 and the results expressed as percentages in FIG. 67.

ii. Laboratory activity patterns

A previous study, on Lymnaea peregra (Storey, 1970), see PUBLICATIONS APPENDIX, showed that the snails travelled much further during their search for food than when they actually encounter it, at which time rapid forward motion is replaced by wide, zig-zag arcs with the head, resulting in less distance being covered. The feeding tracks obtained during this present study suggested that such behaviour is characteristic of most species and that recording the distance travelled by snails in the absence of food would be a way of quantifying their activity. The distance covered was measured by recording the length of the mucous trail. Since starved snails travel further in their quest for food than fed snails (Bovbjerg, 1965), all experimental snails were kept in conditions of super-abundance of food prior to the experiment. Townsend (1974) has shown that some snails
can and do follow each other's trails, so individual snails were therefore isolated for the purpose of the experiment and their containers cleaned thoroughly between trials. The apparatus in which the stock tanks were maintained and the experiments conducted were a Fison's Growth Cabinet, which had a facility for independent control of light and temperature. The regime was one of alternating 12 hours light and 12 hours dark, the light intensity during daytime set at 30 lux. Most experiments were conducted at a temperature of 10°C., since this was the mean for approximately six months of the year in the field, and because this is the temperature below which the pulmonates do not have to surface for respiratory reasons (Hunter 1978). Some trials were made at 5°C. and 15°C. so that a wide range of field temperatures was simulated. During the preliminary runs the temperature was checked using both a mercury and glass thermometer and thermistor and was found not to vary by more than 0.5°C. in any trial. All experimental snails had previously been kept for at least three weeks in a stock tank adjacent to the experimental vessels, and were thus acclimatised. The experimental period was always commenced one hour after the change from 'day' to 'night' to avoid behavioural alterations associated with the sudden change of light to dark, and the experimental period was usually one hour, since this generally gave a measurable trace, uncomplicated by overlapping trails. At the start of the experimental period, snails were isolated in shallow perspex containers (5" x 3" x 1") with 120 ml. of filtered river water. At the end of the trial period each snail was removed from its dish. Fifty ml. of 0.1% carmine suspension were carefully decanted into the dish and after half an hour, the water and carmine poured away, leaving the mucous trails stained red, (PLATE 24b). After drying, these were traced over a mapping table.
illuminated from beneath, and the track lengths measured, using a rotameter. The results are presented in APPENDIX 17.
CHAPTER 2

Results and discussion at the first level of abstraction:

the whole river system.
2.1 Results at the first level of abstraction: longitudinal distribution patterns.

In all, twenty-one species of gastropod were recovered from the River Hull system. Of these, nineteen can be regarded as truly aquatic, that is to say occurring in the water, rather than on the bank, or water/bank interface. The marsh-dwelling species *Lymnaea truncatula*, classed by Boycott (1936) and Hunter (1978) as primarily non-aquatic is included in the species list (FIG.9), but not in the subsequent analysis. Another reason for its exclusion from the analysis was that although the submerged substrata were sampled thoroughly, the banks above the waterline were not. For similar reasons, *Succinea pfeifferi*, which occurs on overhanging vegetation bordering water bodies and is sometimes recovered from under the water, was excluded from the analysis. It is nevertheless interesting to note that specimens of *L. truncatula* were taken from the mud banks of the river as far downstream as site 2 (FIG.8) < 10 km. from the river mouth, denoting a downstream range far exceeding that of any of the submerged aquatic species.

The complete species list is shown in FIG.9. FIG.10 shows the rank occurrence of all snail species. The percentages do not represent abundance of snails, but the frequency of occurrence of each species expressed as a percentage of all sites. It is clear that *Lymnaea peregra* and *Potamopyrgus jenkinsi* were the most commonly occurring species and that *Physa fontinalis*, *Ancylus fluviatilis*, *Valvate piscinalis*, *Planorbis planorbis* and *Bithynia tentaculata* all figured prominently in the river as a whole. The remaining group of eight species all had restricted overall occurrence (<10% sites) although in some cases they may have been locally abundant.
The number of species present at each site (FIG. 11) when superimposed on the river plan (FIG. 12) shows that it is in Barmston Drain and the middle reaches of the River Hull that the species diversity was highest. This was particularly noticeable at Hempholme Lock, where, with the exception of Anisus leucostoma, all species occurring anywhere in the river system could be found together. From this site there was progressive upstream and downstream extinction. The somewhat complex patterns of occurrence were unravelled by computer analysis, whereby the species were used as indicators to classify the sites. Raw data are presented in APPENDIX 2.

Normal analysis of all site data produced a dendrogram from which certain site groupings, and hence potential patterns of river zonation could be inferred (FIGS. 13-18).

The system breaks down into four major groups which broadly correspond to the developmental status of the river (FIG. 14). The groupings were translated into geographic entities in FIGS. 14-18 by joining sites of equal similarity by thick lines; lines connecting adjacent sites of different similarity meet halfway between the sites. Underlying this extrapolation was the assumption that linked sites were part of a continuum, in terms of species similarity, which in fact might not have been the case. Some irregularities were no doubt produced because at some point there would have been transitional zones between one species grouping and the next. Nevertheless, many stretches of the river appear to change little, and this technique was considered useful in converting mathematical indices into definable geographic zones. Physical and chemical features associated with the geographic zones could then be correlated with the snail groupings and act as indicators of positions along certain niche dimensions.
Because of the initial division, and the subsequent different pattern of clustering, the four parts of the dendrogram were considered separately.

Of the sixty sites sampled, eleven contained no snails, (FIG. 14) cluster D). These were not entered into the computer, but form a group of sites, heterogeneous, and probably not a true cluster in the sense of being the product of the same set of environmental conditions. They can be divided into three groups, (TABLE 1) according to certain consistent features. One group, comprising those sites proximal to the river mouth (1, 2 and 3, PLATES 16-19) were in the tidal, unstable, depositing section of the river, where the flow was swift and strong in both directions alternately, (FIG. 2). The substratum was composed of silt, continually moving, causing considerable turbidity, (PLATES 16, 18 and 19). Salt was also present at one site, the salinity range from 0-70% sea water. Any of the factors alone could be responsible for affecting the gastropod life. However, many of the snails occurring further upstream can tolerate flow of this magnitude, and Potamopyrgus jenkinsi and Theodoxus fluviatilis can tolerate salt. It, therefore, seems likely that it is the presence of the highly unstable substratum that is chiefly responsible for the absence of snails in the River Hull downstream of Beverley, although the possibility of the other deleterious factors acting in combination cannot be ignored.

A second grouping, D2 (TABLE 1) can be formed by the sites which were dry at the time of sampling. Of these, sites 38 and 46 had contained water at some time during the previous months, but the other two, sites 25 and 32 were depressions in the ground, shown on the map to have been part of the river at some time, but now grassed over and showing no sign of aquatic life.

A final cluster of sites without snails can be formed by grouping
the sites with the light reduced either by a tree canopy (site 31) or in sites that were less than 1m. wide, by the emergent vegetation (sites 43, 44, 54, PLATE 8). The effect of reduced light on the growth of algae and aquatic macrophytes is predictable, and in the case of macrophytes, visible ( TABLE 1 ), but sites 31 and 43 had also very high conductivity, and either of these factors, separately or in combination, could have made the sites unfavourable for snails.

All remaining sites, including those which were temporarily dry, harboured snails, (FIG. 15).

**Group A (FIGS. 15, 16 and TABLE 2)**

The sites comprising group A are a compact cluster of seven sites, two pairs of three sites fused at infinity, with the pairs fused at level 1.75, and two sites (11 and 56) which are fused to the rest at a much lower level (0.57 and 0.43 respectively). The compact cluster geographically represent the terminal portions of the river, near to its source, (FIG.16,PL.5-7). The precise unifying physical factor appears to be the temporary nature of such loci, for of those sites comprising the group, two were in fact without water at the time of sampling, several of the remainder had dried up during hot spells in previous years (Dr. G.R. Eastwood, pers. comm.) and sites 23 and 24 dried up during September of the subsequent year. For this reason potential over-riding chemical and physical properties of the water could not be considered for the whole group, and even if they were responsible for the initial gastropod composition, tolerance of drying out would be a necessary attribute for any stable snail community. The tendency to become dry also appears to override considerations of substratum type, since the complete range of sand-stones was found.

With regard to plant growth, again a wide range of quantity occurred from sparse — very dense growth, but the diversity was low,
never exceeding four species at any site. The effect of drying out may well have exerted a determining influence over both plants and snails. No particular snail/plant associations were noted, but *Apium* and *Nasturtium officinale*, both tolerant of drying habitats, were recovered from half the group.

Of the two sites remaining, 11 is fused the higher. The fact that it is linked at a relatively low similarity may suggest that it is transitional between the origins and the faster-flowing tributaries, a point which is consistent with its topographic placement.

Site 56 has the lowest similarity and is most obviously different geographically. It occurs at the anastomosis of two tributaries rather than at the origin. It is assumed to have its independent assortment of snails, which is again consistent with its topographic position.

**Group B (FIG.17)**

The sites collectively called group B, all connected at the level 0.81 were all from the upper reaches of the river, (TABLES 3 and 4) the natural continuation, in fact, of the group A sites just considered, (FIG.15). They all contain between one and five snail species. The fact that like group A, the sites are closely related, suggests that the snails are responding to particular environmental influences, and that these are probably important and few. It is perhaps significant that of the twenty-four sites comprising the group, twenty-three are fused, not together, but in various combinations at infinity, or perfect similarity. The relatively small numbers of snail species involved in these clusters (up to five) may well contribute to their close fusions, and it is interesting to note that *Potamopyrgus jenkinsi* and *Ancylus fluviatilis* in particular, figure prominently in these samples. These two species, either separately or in combination, occur in seventeen
out of twenty-four sites and in combination link the largest group (eight) of those showing perfect similarity.

**Sub Group B₁** (FIGS.13 and 17)

Within this major subdivision of group B₁ (TABLE 3) largest is B₁₁, comprising four sites all characterised by the presence of *Potamopyrgus jenkinsi* alone. This is a diverse cluster and from the standpoint of environmental similarity, hardly a cluster at all. Of the four sites, two (7 and 28) contain virtually no plants at all, whilst the other two (26 and 52) possessed almost 100% cover. The flow ranged from 0 to 0.29 m/sec and no single physical factor united the group. It may be of consequence that the feature they all possess is lack of any other snail species.

Linked to group B₁₁ by virtue of possessing *Physa fontinalis* is group B₁₂ (sites 15 and 60). This could be a false cluster. The sites are geographically distinct, and there appear to be scarcely any factors common to both. Moreover, site 60 falls within the unstable depositing section of the river, where the hold of the gastropods is precarious. It is possible that the combination of *Potamopyrgus/Physa* at this site is a chance occurrence, possibly a result of migration from Aike beck which is only a few metres downstream of this site and where both species occur. It is also possible that these sites are transitional.

Groups B₁₃ and B₁₄ are united at a similarity level of 2.0 and by the possession of both *Potamopyrgus* and *Lymnaea peregra*. B₁₄ is a single site, but B₁₃ contains three. Both groups had relatively low light intensity and B₁₃ had a combination of low light and low conductivity.

**Sub Group B₂** (TABLE 4, FIGS.13 and 17)

The largest group (B₂, eight sites) denoted by the presence of both *Potamopyrgus* and *Ancylus* is one in which several environ-
mental factors were common to the sites. In particular the presence of inorganic substrata in addition to silt and sand. All the sites in question had either gravel, (14, 34) or stones (8, 13) or both (21, 27, 35, 36). The presence of these substrata was correlated in these cases, and probably produced by, the fast flow which for the whole group was swift (0.34 m.sec\(^{-1}\)). Plant growth was neither abundant nor diverse: at the most three plant species, usually two, and the growth of these often sparse. Dimensions of the river at these sites were also within defined limits, except for site 35, which was much larger. (PLATES 9-13).

The same environmental conditions as described for group B2\(_1\) apply to the small group B2\(_2\) (sites 20 and 41) characterised by the presence of Ancylus only, except that flow was absent in one case of the two (41). At this site only a single specimen was taken, and it is possible that its occurrence at this rather shaded site was accidental. It is significant, however, that all sites anywhere in the river harbouring Ancylus contained gravel or stone substrata.

The difference between the common environmental features of the sites comprising group B2\(_2\) just described and those of group B2\(_3\) (sites 29 and 53) is a slightly lower maximum flow rate of the latter (0.376 m.sec\(^{-1}\) compared with 0.774 m.sec\(^{-1}\)). This feature seems to be correlated with the presence of an additional species, Lymnaea peregra, to the Ancylus/Potamopyrgus combination.

Sub Group B3 (TABLE 4, FIGS. 13-17).

At the lowest similarity level (0.81) subgroup B3 join the rest of this group B. Again a decrease in flow could have led to the addition of a further species, Physa fontinalis.

Group C (FIGS. 13, 14 and 18, TABLES 5 and 6)

The remaining sites form group C, and in contrast to the close clustering of A and B, group C are more diffuse, more than half the
fusions (eight out of fourteen) occurring between 0.29 and 0.75. The relatively diffuse branching can be interpreted by the snail species (up to eleven) responding in particular ways to a wider range of environmental conditions. At low similarity levels, these would denote the presence of a set of conditions which embrace all those compatible with survival of all the snails that exist there. Even so, some groups are distinguished and are shown as C₁, C₂, C₃, which contain between 4 - 6 sites linked at relatively high similarity levels (0.5 - ∞), and three single sites (16, 42, 47).

C₁ and C₂ are linked together at 0.51. Both have considerable overlap of diagnostic snails and both exhibit a wide range of size, (TABLE 5). They can possibly be separated on the basis of flow, C₁ having a slightly lower flow rate than C₂ (means 0.061 m/sec.⁻¹ and 0.074 m/sec.⁻¹ respectively, ignoring site 57.) The higher flow rate seems again to have the effect of compressing the sites at closer similarity levels, group C₂ sites are all fused at infinity or 2.0 except site 57, which has the lowest flow rate of the group.

Group C₃, which contains four sites, is one of uniform, slow flow (< 0.063 m/sec.⁻¹, mean 0.016 m/sec.⁻¹) and high species diversity. Of the four sites sampled along Barmston drain, three fall within this group. Despite the apparently high quality of conditions at these sites, and the high species diversity, *Potamopyrgus jenkinsi*, present at so many other sites in the river, is absent from group C₃.

Sites 42 and 47 are grouped, but at very low similarity level (0.466). They are widely separate topographically and are possibly transitional zones, (FIG.13 and TABLE 6).

Site 16 is Hempholme lock, split off by itself from the rest of the group at 0.32. It contains all the species that occur in every other group except for *Anisus leucostoma*. Being a canalised section of the river, of large dimensions, it is not subject to drying out, as
is the case with sites which contain this species. It contains a high species diversity, a wide range of substratum types, and the flow range extends from 0.414 m/sec. close to the weir, to zero in the brick interstices. It, therefore, covers not only the whole range of snails, but also a wide range of conditions (except drying up) that prevail anywhere in the river, (TABLE 6).

**Inverse Analysis**

Inverse analysis produced a dendrogram which generally supported, and in specific instances complemented the findings of normal analysis. Inverse analysis groups species using sites as indicators, and with all the data included, the immediate impression is of low similarity within the species groupings, (FIG.19). There were a large number of possible sites (49) compared with the number of snail species (15) and the closest clusters are biased in favour of the less common species, which were present at very few sites. The generally low similarity levels suggest also that many sites exhibit a wide range of environmental influences to which the snails respond, and that they do not therefore act as precise indicators of discrete snail groupings.

Some groupings are apparent, however, and can be correlated with specific factors. Starting at the lowest level of similarity, three clusters are defined (FIG.19, X, Y and Z). Group Z is in fact not a cluster, but one isolated species, *Anisus leucostoma*. Although occurring at relatively few sites (6.6%), the sites are united by being shallow and with a tendency to dry up. One of the sites (10) was in fact partially dry at the time of sampling. *Lymnaea peregra* has earlier been found to be tolerant of drying loci in this district, (Storey, 1972, PUBLICATIONS APPENDIX), but is not exclusively limited to them, and is therefore not paired with *Anisus leucostoma* by this method of analysis.

Group Y is defined at level 0.065, linking *Potamopyrgus jenkinsi*.
and Ancylus fluviatilis. The sites contributing to this cluster are all fast flowing, over gravel and stones and occur in the upper reaches of the river.

The remaining group, X, contains all the other species, linked mostly at low similarity levels. The relatively high levels of similarity of Gyraulus albus/Acroloxus lacustris and Lymnaea stagnalis/Bathyomphalus contortus may be misleading. The fact that they are rare species, and that of the three sites at which they each occur, two overlap, results in their being associated at an artificially high level. Lymnaea peregra and Physa fontinalis are linked at a lower level, for although they occur in 53% and 31% of the sites respectively, the overlap is only 26.6%. The group X, therefore, comprises: Lymnaea peregra, Physa fontinalis, Anisus vortex, Valvata piscinalis, Bithynia tentaculata, Planorbis planorbis and Bathyomphalus contortus. Gyraulus albus, Acroloxus lacustris, Theodoxus fluviatilis, Lymnaea stagnalis, Valvata macrostoma all occur in the same group, but in less than 5% of the sites.
2.2. Snails and Plant Cover

The exact location of the snails and plants within each sample site was not recorded, but there appears to be no strict correlation between any snail and a particular plant species. A correlation was found, however, between the snail species diversity, and plant species diversity, (FIG. 20). The correlation coefficient of 0.795 could imply a direct relationship, possibly that the diverse plant growth is favourable for many different snail species. Alternatively, the link may not be direct, the correlation being the result of both snails and plants responding in the same way to some favourable environmental factor: what is beneficial for snails is beneficial for plants also. The graph (FIG. 20). shows at least two sites where snails occur despite the absence of any weed beds. This occurrence reflects the well-known substratum preference of Ancylus fluviatilis and suggests that any possible direct involvement with weed beds, indicated by some species, may not be as strong for Potamopyrgus jenkinsi.
2.3 Discussion of results.

Traditionally, the distribution of freshwater snails is explained by properties of the abiotic environment and often some parameter of water chemistry is considered the key factor. Thus in many regions of the world, calcium has been found to influence the density and distribution of freshwater gastropods, e.g. southern Sweden (Hubendick, 1947), Finland (Aho, 1956), Zimbabwe (Harrison and Shiff, 1966, Harrison, Williams and Grieg, 1970, and Williams, 1970, a, b), Norway (Ökland, 1969), Canada (McKillop and Harrison, 1972). However, the absence of such correlations in other regions is noted by Lassen (1971) in Denmark, and Harman and Berg (1971) in New York State. Azevedo et al. (1967) concluded that the relationship was complex and may well depend upon particular species and the geographic region concerned. In the British Isles, relationships have been found between the occurrence of freshwater snails and water hardness, e.g. Boycott, 1936, Macan, 1950, 57, 69, Russell Hunter, 1957, Young and Harris, 1974, and corroborative evidence is available from general invertebrate studies, e.g. Sutcliffe and Carrick, (1973). Although some work has indicated a direct influence of water hardness, (Williams 1970 a and b, and Harrison, Williams and Grieg, 1970) it is difficult to ascertain which parameter of hardness is most important. Calcium hardness and pH usually fluctuate together and were isolated by Dussart (1976) from a range of possible contributary factors, as being those most important in governing the general distribution of molluscs in the north west of England. Macan (1969) suggested that a calcium concentration of about 20 parts/mill. was a critical figure below which a number of species seldom or never occur. With a calcium concentration of 117 parts per million, there appears to be no reason for these water parameters to be limiting for any molluscan species. Most work has indicated, in fact, that hard water
is particularly favoured by most snail species. Dussart (1976) found a slightly higher species diversity in 'medium' hard waters (10-40 mg.l⁻¹ Ca) although the actual densities were higher in 'hard' (>40 mg.l⁻¹ Ca). The general findings of Dussart and others therefore support the occurrence of a broad spectrum of gastropod life in the river Hull. The specific difference is that Ancylus fluviatilis, which occurs throughout the faster, stone-gravel substratum areas of this system, has tended in some studies to be restricted to soft waters only (Dussart, 1976) and is also included in the group of soft water species by Macan (1969) although he states that like Physea fontinalis, Potamopyrgus jenkinsi, Lymnaea peregra, Anisus leucostoma, Gyraulus albus and Bathyomphalus contortus, also present in the river Hull, it is found in hard as well as soft waters. Certainly, both Ancylus and Lymnaea peregra are reported from limestone areas in the north east (Armitage, 1976). Two reasons can be suggested to explain these anomalies. One is the idea embraced both by Ulfstrand (1967) and Boycott (1936), that snails, like other aquatic organisms, respond to combinations of factors in nature, and that suboptimality with respect to one factor can be compensated by a high standard of another. Another possibility is that many of the studies have been conducted on discrete, often small bodies of water, and it has recently been suggested that the colonisation by snails of such habitats is progressive and to some extent, random, primarily dependant on opportunities for dispersal and past history, (Moon, 1957, Powell & South, 1978, Macan, 1980).

Although the basic chemical quality of the water may determine the overall distribution of the snails in the river, it cannot explain their patterns of zonation within it. The precise limiting factors responsible for zonation in the river Hull appear to be different in different parts of the river system. Like many chalk streams (Hawkes, 1975) the river Hull contains sections which tend to dry up. In this
particular system these tend to be the terminal portions, which were noted, but not investigated in an earlier study by Whitehead (1935). Once dry, such areas can become subject to the direct effects of sun and wind, producing extremes (Storey, 1972) which makes life for aquatic organisms at least, difficult.

Gastropods, however, vary considerably in their dependence on water as a medium in which to exist. The pulmonate snails of freshwater are primarily air-breathing and can be ranked as a series showing progressively greater degrees of re-adaptation to aquatic life (Russell Hunter, 1953, 1957). At one end of the series in Britain are the marsh dwelling snails Lymnaea truncatula, L. palustris and Succinea spp. (Boycott, 1936). Intermediate species are those defined by Russell Hunter (1978) as those which are completely aquatic in habit, while retaining the mantle cavity of characteristic 'lung' forms and include the Physidae and most Lymnaeidae. There is a subtle difference between these two groups which may have relevance to the present study. The marsh-dwelling species live normally, both on land and when submerged, and characterise temporary habitats (Macan, 1969). The second group are more strictly aquatic, and when stranded out of water do not continue to live normally, but enter a state of dormancy until favourable conditions return. This is what has been found to occur in Lymnaea peregra from other temporary habitats in this district, (Storey, 1972). Upon becoming stranded, the snails adopt a characteristic posture, which entails the foot turning to face the inside of the shell, only the body wall being visible when the snail is viewed from beneath. In this position the rate of evaporative water loss is reduced, and coupled with a general lowering of metabolic activity, is compatible with survival during periods of up to three months without standing water. This contrasts with other species of Lymnaea considered as those which move in and out of water without apparent change in behaviour. Anisus
leucostoma, found in similar situations to Lymnaea peregra in the River Hull, was the other species that occurred in the temporary habitats elsewhere (Storey, 1972), although no study of its behaviour was conducted. This is one of the species that is reported elsewhere as being more typical of temporary habitats (Boycott, 1936, Macan, 1969), and one again which becomes apparently dormant when out of water.

The temporary stretches of the River Hull are dry only for short periods, and when in their normal state are clear, moderately flowing reaches. This study shows that such habitats may tend to be colonised by well-adapted stream gastropods, which possess the additional capacity to withstand drought by becoming dormant, rather than true marsh-dwelling, amphibious types, that are at home in either environment. Unfortunately, despite the considerable amount of data from such habitats abroad, (references in Storey, 1972) due chiefly to the importance of tropical molluscs as vectors of parasitic disease, there is relatively little published data on their occurrence and behaviour in this country. Some studies that are comparable hydraulically, e.g. that of Hynes (1958), have been conducted on mountain streams where molluscs were absent for reasons of water chemistry, either low pH. or calcium, and that of Moon (1956), on a chalk stream, contains no mention of molluscs.

Further downstream, a combination of increasing gradient and water volume alters the pattern and rate of flow in what appears to be a characteristic sequence. Here the substratum is composed of stones and gravel, Lymnaea peregra and Anisus leucostoma disappear and are replaced by Ancylus fluviatilis and Potamopyrgus jenkinsi. These latter species are paired both by normal and inverse analysis and are the sole gastropod representatives throughout the fast-flowing, stone-gravel sections of the river system. There are indications from the survey of Durrant (1977) that Potamopyrgus and Ancylus may have a
distributional association. N.V. Jones of Hull University in an unpublished observation described the occurrence of *Potamopyrgus* in Susobrin, Shetland, only above and below stations which contained *Ancylus*. Hynes (1970) also groups both species together as being characteristic of stone-gravel substrata. Although Geldiay (1956) found *Ancylus* on hard, clean substrata exposed to high and low water velocities, and Macan (1963) and Hynes (1970) both specified that a hard substratum is essential, Verdcourt (1949) suggested that it was lack of sediment rather than presence of flowing water that determined distribution. Durrant (1977) suggests that reduced densities on sand, gravel and moss-covered substrata may be due to their instability as well as their unevenness. *Potamopyrgus jenkinsi* appears to have less specific demands with regard to substratum type for it was also recovered in large numbers from both weeds and silt at Hempholme lock. Macan (1969) states that it occurs in flowing water of all types, and in this study, was one of the few species to be recovered on its own from some stations. Being parthenogenetic and able to breed throughout the year, *Potamopyrgus* has some attributes of a successful r-strategist, capitalising on opportunities for colonising habitats where other snails have not become established. Although found alone, from a range of conditions in this river system, it is absent from many apparently favourable areas where it may compete less well against other species. Failure of *Potamopyrgus* to sustain initial colonisation, in the presence of other species has been noted elsewhere (Calow, 1973c), but its occurrence may also be restricted to one locality in a river despite an otherwise homogeneous fauna (Adam, 1942, Bondesen and Kaiser, 1949).

Approaching the proximal terminations of these fast-flowing sections and at their transitions to areas of decreased flow, there is a progressive encroachment by other species of gastropod, and it is tempting to suggest a causal relationship between the two. According
to the flow figures, their sequence of appearance, in descending order is Ancylus, Potamopyrgus, Lymnaea peregra and Physa fontinalis. Lymnaea peregra has been found in quite fast flowing sections of waters elsewhere, and Armitage (1976) reports that its occurrence overlaps that of Ancylus in parts of the River Tees, but its largest densities occurred in the less extreme flows. Differences between the genera Lymnaea and Physa, but different species to those of the present study have been discovered by Moore (1964) who found that despite possessing a larger foot area, Physa were less able to maintain their hold in flowing water than Lymnaea, a fact attributed to the feeding behaviour of Physa, which raised the anterior part of the foot in a searching movement which Lymnaea does not.

Although the occurrence of certain gastropods in the upper reaches of the River Hull may be determined primarily by the prevailing physical conditions, particularly desiccation and high flow, this does not appear to be the case in the slower flowing reaches. The diffuse pattern of branching of the dendrogram suggests that the limiting factors are less severe, and a wide range of species occurs. Boycott (1936), observed that good conditions for molluscs were a large volume of moderately warm calcareous water, free from inorganic matter in suspension and from organic pollution, flowing not too rapidly over a shallow bottom, with a moderate but not excessive growth of plants. Such conditions are to be found throughout the middle reaches of the River Hull and since they are favoured by the majority of snail species, (Boycott, 1936) this section of the river would be expected to attract a wide variety of gastropod life. This section of the River Hull conforms with the description of the general pattern of development of rivers given by Carpenter (1927) in the lower reaches, in that the decrease in current is accompanied by a widening of the river and the deposition of silt on the bed. As with rivers elsewhere, and general invertebrate studies on the River Hull, (Pearson, 1974) such changes in the physical charac-
teristics are associated with changes in the community structure, and these are reflected in gastropods, although it is difficult to isolate precisely which of the physical attributes is directly responsible for the appearance of particular species. Increase in size is reported by Macan, (1961), to attract a larger species diversity of Ephemeroptera, and he observed that the gastropod species Bithynia tentaculata and Planorbis carinatus were rarely found in small bodies of water, but it is unlikely that large size as such, is responsible for attracting a wide species diversity. The reduction in flow can permit the colonisation of habitats by snail species that are not flow tolerant, so that a direct link with flow is possible for those species, e.g. Valvata piscinalis (Macan, 1969) that are not flow-tolerant. However, flow also has a direct effect on the substratum particle size and turbulence, both of which influence the quality and location of plant species (Moyle, 1945, Spence, 1967). Harman (1972) whose study of aquatic snail fauna ranged from temporary pools to large rivers demonstrated a progressive increase in snail species diversity which he correlated with increased diversity of substratum pattern. This finding has been substantiated by Økland (1969) in gastropod studies in Norway, and extended to include invertebrates generally by other workers (e.g. Thorup, 1966, Ulfstrand, 1967). Frömming (1956) quotes Gayer (1909) as stating that the increased size of the water body gives an increased nutritional potential by increasing the range of available habitats and hence diets. The build up of plant growths are said by the same author to enhance environmental stability. In his earlier study on the River Hull, Whitehead (1935) observed that the nature of the stream bed was a factor of greatest importance in determining the nature of the invertebrate fauna, acting both directly and indirectly, and he stressed the particular importance of aquatic phanerogams. The present study
reveals that a relationship exists between the species diversity of snails and plants. However, it is generally agreed that local factors, e.g. turbulence and particle size of substratum influence the quality and location of plant species (Moyle, 1945, Spence, 1967) and that a very varied habitat is, therefore, likely to support a wide species diversity both of plants and animals. Because of this it has sometimes proved difficult to establish whether the link between the animals and plants is obligatory, facultative or simply adventitious (Frohne, 1956). This point is discussed more fully in CHAPTER 4. Aquatic macrophytes in any case provide additional substrata, thus extending the vertical range of animals in the water column, and the introduction of plants, into lotic waters at least, is reported to create new niches for the existence of animal species (Rosine, 1955).

Numerous studies have been carried out on the longitudinal distribution of different benthic invertebrate taxa in rivers in various parts of the world. Different patterns of zonation have been confirmed in planerians (Thienemann, 1912; Beauchamp & Ullyott, 1932; Carpenter, 1928; Chandler, 1966); and many examples of similar sequencing of aquatic insects are listed in Hawkes (1975) and Hildrew & Edington (1979). Algae, particularly diatoms, have been found to possess longitudinal patterns that differ either quantitatively (Hynes, 1961), or qualitatively (Schmitz, 1961). Quantitative changes are reported for some invertebrates (Jaag and Ambühl, 1964). Evidence for zonation in molluscs is more sparse, but Clark (1944) has demonstrated its occurrence in the rivers of Ohio, and they are included as part of more general faunal study by Maitland (1966) and Thorup (1966). Unfortunately for those who would seek to use community change as a criterion for classifying river zones, the precise factors underlying zonation appear to be different for different invertebrate
taxa which means that they phase in and out in different combinations. Thus, although some authors have claimed that classification on the basis of community type is possible, others, for the reason given above, disagree. The evidence, for each case, is outlined in Hawkes (1975) who concludes that the degree of success depends upon the purpose for which such classification is to be used. Recent work on chalk streams (e.g. Cooling, 1977) has shown the importance of complex analytical techniques, particularly principal component analysis in evaluating such community data, but here too, absolute distinctions between invertebrate communities were found to be infrequent. As in the present study, the general trend has been one of progressive upstream elimination, but the precise causal environmental parameters have seldom been revealed. In the River Hull system, the composition of the snail groupings appears to be related to quite specific conditions, particularly in the upper reaches. Moreover, because they show a fairly precise and repetitive sequence of zonation qualitatively, they provide a reliable and economic guide to certain prevailing river conditions. Their use as indicators of such conditions, however, may be more precise here in a chalk stream, than in 'poorer' oligotrophic mountain streams that lack the broad spectrum of gastropod types.
CHAPTER 3

Results and discussion at the second level of abstraction:
a single site, Hempholme Lock, the tidal limit of the River Hull.
3.1 Distribution on rocks and weeds

Since all species that occur throughout the system were found at Hempholme lock, the species list is identical to that for the whole river system (FIG. 9). The raw data for the three years are presented in APP.3. The overall relative abundance at this site over three years is shown in FIG. 21. These figures show that at this site, *Potamopyrgus jenkinsi* was predominant in terms of numbers, followed by *Physa fontinalis*. These two species made up approximately 70% of the total snail count. *Bithynia tentaculata*, *Theodoxus fluviatilis*, *Anisus vortex*, *Valvata piscinalis*, *Gyraulus albus*, *Bathyomphalus contortus*, *Lymnaea peregra*, *Acroloxus lacustris* and *Ancylus fluviatilis* were represented in progressively smaller proportions. The numbers of *Planorbis planorbis*, *P. carinatus*, *Hippeutis complanatus* and *Lymnaea palustris* were so small that they would be difficult to distinguish on this scale, and these were combined as 'rest' for the purposes of the diagram (FIG. 21). These latter species were visible when the raw results were presented logarithmically, however, (FIG. 22), and when the abundance of species is ranked, the decline approximates a straight line. No particular significance is placed on this finding, since the sample units from weed and rock may not be strictly comparable. Moreover, although this summed data provides useful indicators of dominance, such overviews mask underlying subtleties of dispersion pattern organisation.

Normal analysis conducted in the same way as in the first level study and applied to the results of a single, early, qualitative sampling session at Hempholme lock revealed the presence of two communities, one associated with the weeds and soft substratum and one with the rocks. The dendrogram is shown in FIG. 23, the raw data in APP. 4, and the exact locations of the samples on the map in FIG. 24.
The groupings indicated a closer clustering of the weed samples (0.539-2.0) than those of rocks (0.285-0.545) which could indicate discontinuity within the rocky substratum. The closest similarity (2) between samples 5 and 7 is noteworthy, since these sites are quite widely separated.

Analysis of this type based on presence/absence cannot be applied successfully to the total sample results, since the occurrence even in small numbers, of certain species will lead to the sites concerned being grouped together. At times of year when minimum overlap occurs, existing site discontinuities may not be apparent after such processing, and relationships become clouded. Percentage similarity takes account of such occurrences, however, and polar ordination, (FIG.25) based on percentage similarity, showed a major separation of seasonal samples into two categories which could again be correlated with the two major substrata, one soft (silt and sand) and one hard (stones and bricks). The only exceptions to this were samples 19 and 21, both of which showed affinities with the hard substratum samples when in fact they had been taken on consecutive sessions from where the substratum was soft. The difference between these two and all the other soft zone samples could have been related to the plant cover, which was for most of that year (1976) a dense blanket of Cladophora extending over both zones. The rate of flow during this period was the lowest recorded and followed the winter maximum of less than half that of either of the two previous years (FIG.6.d). As a consequence, a considerable amount of silting had occurred, even on the rocks near the weir: this was particularly noticeable at a time between the two sample dates, when for the only time during the study period, the flow over the east side of the weir ceased completely. Along the first axis, the rocks seem to be a more stable zone than the silt/sand, the ordination groupings being more closely clustered, indicating close
No other pair of samples gave appreciable separation, and no second dimension was therefore considered. The absence of a clear separation along a second axis suggests that the samples are primarily divided by the factor which produced the first separation.

Some evidence for further separation of the samples is provided by non-parametric tests. These provide ways of comparing samples when the use of parametric tests is questionable, e.g. in the present case when the numbers of snails in the sample units may not be strictly comparable. Kendall's Rank correlation coefficient, calculated for each pair of soft/hard substratum samples showed that at certain times of year the samples were significantly different, at others, they were similar; (FIG.26). February/March were consistently different, whereas October were always very similar. April and June showed some inconsistency, but the total snail counts from June in 1976 were very low (533) until October. When compared with the various environmental parameters taken during the sampling period, (temperature, conductivity, pH) it was the flow which provided the most convenient explanation for these fluctuations. FIG.27 shows the amount of water flowing over the weir with the significance values of the non-parametric test superimposed. From this it seems that a flow figure of approximately 80 m.g./day is the figure above which the paired samples became separated. Below this figure the pairs of samples showed significant similarity, the figures for October being particularly close (p between 0.005-0.0004). This analysis does not include the results of 1976, when the snail counts, particularly in summer, were extremely low in (550) total, possibly reflecting the small quantity of weed that occurred in the samples. With the exception of April, 1975, and those below 50 just mentioned, a seasonal explanation provides a possible, but less plausible alternative. This would indicate the similarity between all autumnal samples, compared with differences between at least some of those of the winter (February/
March). This latter is less satisfactory, however, since subsequent sampling of the rocky zone (the results of which are presented in CHAPTER 4) showed a marked distinction of the rocky zone species as early as July, at a time when the flow was prematurely high. The flow could well be the reason for the partial correlation of the season with the snail fluctuations, since generally the flow was higher in winter than in summer and early autumn.

The relative abundance of all species on the two substrata for the three years from 1974-1976 is shown in FIG. 28. Such diagrams provide useful indications of dominance on the two substratum types over the period, but the fluctuations they demonstrate need to be related to the actual density figures, since a reduction in numbers of one species will inevitably produce a relative increase in the proportion of the others, even though the densities of the latter remain unchanged. On the rocky substratum, the dominance of Potamopyrgus jenkinsi is obvious, and together with the density estimates (FIG. 29.d) reflect the suitability either of the substratum or the flow regime at this zone. Theodoxus fluviatilis, although numerically less important, appeared to have a similar preference. Ancylus fluviatilis (FIG. 31.a), was totally restricted to the rocks. The relative importance of Bithynia tentaculata and Valvata piscinalis fluctuates both on the rocks and on the soft substratum, and the density estimates indicate a transition from one zone to the other in the early summer, at a time when it would be reasonable to assume that breeding occurs. The dominance of Physa fontinalis on the weeds/silt zone is less marked and the relative values of the other species present, particularly the planorbids, Bithynia, Valvata and Potamopyrgus, are distributed more evenly than was the case on rocks. The values for Potamopyrgus are probably overestimated by using numbers, and as can be seen later (section 3.2.), the importance of the smaller species is
less pronounced when biomass rather than numbers are used to construct the diagrams. Nevertheless, the increasing proportion of *Potamopyrgus* during 1976 may be significant since it may reflect an alteration of the habitat as a whole owing to the low flow, consequent silting, and the blanket of *Cladophora* sp. which covered the whole area during most of the year, which proved detrimental to most other species.
3.2. Life cycles: distribution in time

The snails occurring in samples taken during the second level study were measured and used to construct the histograms which are presented in FIG. 29. From these it is possible to make certain deductions about the breeding times and duration of life cycles. Because of the large time intervals between Hempholme samples, additional material on the three main "weed" species was collected during 1979 from site 47 on the Barmston Drain, which contained a similar complement of snails to that of the weed beds at Hempholme. Snails from this site were collected at monthly (28 day) intervals during the critical breeding period between the months of May and September and the results used to corroborate the Hempholme data, (FIG.32).

Physa fontinalis

The life cycle was annual, with breeding in April-May and the young starting to hatch in early June (FIG.29 and 32.b.). There followed a period of rapid growth throughout the summer, which meant that in a 'good' year, some were able to reach maturity and reproduce, so that a second hatch was produced in September. This occurred in 1979 at Barmston Drain (FIG.32.b.). The second hatch was only small, however, and there was never any question of replacement of the first generation by the second within the same summer. There appeared to be little or no growth between October and February in any year. The number of snails was usually lowest in June, when (FIG.29.a.), the adults had bred but the eggs were just beginning to hatch. Peak densities at Hempholme were difficult to pinpoint in view of the large time interval between samples, but the evidence from Barmston Drain suggests that a maximum occurred in July, shortly after the main summer hatch, after which the numbers were drastically reduced (FIG.32.b.). The results from Hempholme are compatible with such a suggestion, but
there is the possibility during the winter of 1974/5, of a secondary increase. One interpretation for a winter increase could have been the hatching during October 1974, of a second summer generation. The highest densities occurred on weeds, rather than on the rocks.

*Lymnaea peregra*

This species too appeared to have an annual life cycle, but a small number of snails may have lasted for a second winter. The numbers present at Hempholme were never very high, but this is to some extent offset by its large size. The shell of *Lymnaea peregra* may be up to 4 times longer than that of some of the smaller species (e.g. *Bathyomphalus contortus* and *Potamopyrgus jenkinsi*) and biomass estimates would probably reflect more clearly the importance of this species. FIG. 33 shows the density figures from the May sample of 1979 from Barmston Drain, with the corresponding preserved wet weight figures. The effect is to reverse the proportions of *Bithynia* and *Lymnaea* and this should be taken into account when assessing relative importance values based on numbers of snails. The snails bred during April-May, and hatching started in May, slightly before *Physa*, but continued until late June - early July. Consequently peak densities occurred before those of *Physa*, followed by a high mortality, as judged by the sample size and the large number of empty shells that occurred in the weed. These occurrences are summarised in FIG. 29.b. and 32.a.

There was no evidence for a second breeding period in autumn, and although the numbers were small at Hempholme, there is probably little growth in winter. At Hempholme too, 1974 appeared to be different from 1975, and 1976, and Barmston Drain in 1979, since the June sample contained snails that were rather advanced for that time of year. It is possible that breeding commenced early that year, but there is no evidence for the same occurrence among the other species, and no reason could be suggested, other than error produced as a result of small
sample size. A bias in favour of a weed substratum compared with one of rock is suggested by the standardised density results, although this is less pronounced than that of Physa.

**Anisus vortex**

This species was also annual, the result from Hempholme, in many respects resembling those of Physa, including its greater occurrence on weed. There appeared to be a steady decrease in the numbers each year, however, and by 1976, when collections at Hempholme ceased, its continued survival at the site seemed precarious, (FIG. 29,c).

**Potamopyrgus jenkinsi**

This species dominated the rocks, throughout the period of study, and occurred also in much reduced density on the weeds (FIG. 29,d). From the histograms it appears that recruitment was occurring mostly during the summer, suggesting that breeding was occurring then also. In view of the rapid growth to reach maturity (possible under 4 months) the distinction of generations is not possible from these size-frequency histograms.

**Bithynia tentaculata**

The bimodal appearance of the histograms from Hempholme (FIG. 30,b) indicated the presence of two generations in each sample, which was interpreted as a partial biennial life cycle. Corroborative evidence from Barmston Drain (FIG. 32,c) indicated a later hatch compared with the pulmonates, the young snails appearing at the very earliest in July, and hatching being complete by September. The probable ages and hatching times are indicated by shading in FIG. 32,c. The young overwinter without apparent increase in size (FIG. 30,b).

**Theodoxus fluviatilis**

Like Bithynia tentaculata, the life cycle was spread over two years, with the characteristic bimodal size-frequency distribution, (FIG 30,a). The numbers of this species diminished in the samples
from March 1974 to June 1975, but recovered thereafter. The vast majority of *Theodoxus* were recovered from the rocks, rather than the weeds. As with most of the other species, very little growth appeared to take place during the winter, between October and February. It appears that during 1974 and early 1975 the numbers of snails of *Theodoxus*, and the other rock substratum dweller, *Ancylus fluviatilis*, decreased progressively but subsequently recovered. The reasons for such losses and similar ones that reduced the numbers of most species except *Potamopyrgus jenkinsi* from 1975 onwards are difficult to isolate, since they may be due to progressive deterioration of the environment, or deleterious factors operating at, or before the main breeding period. The most obvious environmental difference during this period was the very dry and warm summer of 1976 and the low rainfall of the preceding winter altering the flow regime, but the precise influence of these on the snail populations would require more detailed knowledge of the population sizes between the dates sampled.
3.3 Discussion of results

The species diversity of the gastropods at Hempholme Lock was wide and the possibility of different factors influencing their distribution correspondingly high. The large number of species could almost certainly be attributed to the fact that the rejuvenating effect of the weir produced, over a relatively short span, the range of conditions that occurred elsewhere in the river over a very wide one. Of particular importance was the flow regime with its direct effect on substratum composition. Substratum is a significant ecological factor in the distribution of freshwater snails. Harman (1972) has demonstrated a convincing relationship between substratum diversity and species diversity of molluscs and explains how alterations in current velocity alter the substratum pattern, causing a mosaic of molluscan demes throughout a stream. Since his observations, on more than 650 locations in New York, indicated particular substratum/snail associations, the more substrata present, the more molluscan species could be accommodated. Clampitt (1973) observed that in Douglas Lake (U.S.A.) which has a rich molluscan fauna, some species resided primarily on the bottom, others on the vegetation and some adopted a roving commission between the two. These are just two examples of descriptive ecology that point towards the importance of substratum in determining the distribution of molluscs. In some cases, these indications have been substantiated by experimental work, e.g. Vaidya (1979) has established substratum preferences of sand over stones in Viviparus bengalensis and Melania scabra, and Clampitt (1973) has demonstrated substratum selection in five species of gastropod from Douglas Lake.

In terms of substratum selection at Hempholme Lock, the occurrence of Ancylus fluviatilis on hard substrata is well-known and has been discussed in CHAPTER 2. Theodoxus fluviatilis, also characteristic of the rocky zone here, is reported to favour a hard substratum (Boycott,
1936, Fretter and Graham, 1978), and because of its large aspidobranch ctenidium and absence of any ciliary rejection currents through the inhalent opening, it is said to be the least suited of the British freshwater prosobranchs to survive muddy conditions, which accounts for its occurrence on stones and away from silt (Heywood, 1961). Potamopyrgus jenkinsi appears in this study both on the rocks, where it is dominant, and on the weeds also. Its distribution elsewhere in the river emphasised its tolerance of flow (CHAPTER 2) and both these observations are consistent with the report of Fretter and Graham (1978) which stresses the importance of flow for this species, the nature of the substratum being immaterial. By virtue either of their substratum or flow requisites, these three species are confined to the area near to the weir. At times of high flow, during later collection, they may account for 98% of the gastropod community near the weir, (FIG. 34) and their microdispersion patterns within this zone are examined in CHAPTER 4.

In contrast to the species just discussed, the larger group, comprising Valvata piscinalis, Bithynia tentaculata, Physa fontinalis, Lymnaea peregra and Anisus vortex are relatively more numerous in the mud and weed beds, which by virtue of the sampling apparatus, are not distinguished in the present study. The dominant species, Physa fontinalis, was recovered chiefly from the weeds, a situation in which it apparently thrives (Duncan, 1959, de Wit, 1955). Anisus vortex also present in the same samples is reported to have similar preferences (Macan, 1969). Lymnaea peregra was ubiquitous, but seldom very abundant at Hempholme. It occurs elsewhere on plants, stones and submerged objects of all types (Boycott, 1936, Macan 1950) but like Physa fontinalis it is reported to have an aversion to crawling on mud (Young, 1975). The prosobranchs Valvata piscinalis and Bithynia tentaculata appear to have different substratum preferences to those of the
pulmonates, although these may be responses to the flow also. Fretter and Graham (1978) report that *Valvata piscinalis* prefers mud to a hard substratum, and Cleland (1954) suggests that although it lays its eggs on weeds in summer, *Valvata* quickly migrate to the mud to avoid the swifter currents of autumn and winter. Flow rate seems to be quite critical for this species, since it is not common in small, quiet pools, and is most abundant in streams and rivers where there is a gentle current, or in which weeds moderate a rapid one (Fretter and Graham, 1978). *Bithynia tentaculata* seems to have similar requirements to *Valvata*, in that it migrates from the mud to the weeds in summer (Lilly, 1953, Miller, 1977). Heywood (1961) recovered *Bithynia* from the Thames in clean gravel, submerged, man-made articles and weed beds, and of the latter, the mosses *Fontinalis antipyretica* and *Hymnum fluitans* and the plants *Elodea canadensis*, *Rorippa nasturtium-aquaticum* and *Typha latifolia* seem particularly favoured (Fretter and Graham, 1978). Flow again may be important for this species, for it is more abundant in the quieter reaches of rivers (Fretter and Graham, 1978). This group of molluscs, *Physa*, *Lymnaea*, *Anisus*, *Bithynia*, *Valvata*, dominated the more moderate flow/soft substratum community not only at Hempholme, but at many stations on the river where the flow was gentle.

The technique of polar ordination identified the discontinuity within the overall gastropod complement, and identified the two communities just described. The dichotomy on the basis of hard or soft substratum was almost complete, but the nature of the substratum is largely determined by the flow regime. Using different methods of analysis, Calow (1973b) was able to distinguish two "communities" of gastropods at Malham tarn. In that situation the division of the gastropods was also determined by water movement, notably wave action, which separated the tolerant, stone-dwelling species (*Ancylus fluviatilis* and *Bathyomphalus contortus*)
from the rest (which included most of the minor species and all the major species of the weed beds in this study). The clusterings on the littoral (rocky) shores at Malham were closer than those of the weed beds, a finding that was also consistent with the present study, and indicates that in both studies the variation within the rocky communities was less than that between the weed beds. This may be because fewer species were involved in each case. Within the rocky community of Calow's study, *Potamopyrgus jenkinsi* was not present, when according to the results of this study and the derived information from elsewhere, it perhaps would have been expected. This species was at the time, however, a relatively recent colonist of the tarn (Calow, 1973c) and its distribution even in the weed beds there, was restricted. Of the prosobranchs at Malham, only *Bithynia tentaculata* occurred at any of the littoral stations.

As well as the flow tolerance and substratum preferences producing spatial separation of the gastropod species, different seasonal substratum requirements add a further complication. *Valvata piscinalis*, during the winter burrows in the mud (Cleland, 1954) even when there are occasional water weeds on which they could crawl: they inhabit the top inch of mud and are not found elsewhere. Their eggs, however, are laid on weeds or stones (Moquin-Tandon, 1855) and by June the young are on the weeds and mud. The young probably do not remain on weeds for more than a week or two before migrating to the mud (Cleland, 1954). *Bithynia tentaculata* also migrate from the weeds and rocks to the mud and plant roots where they may remain for up to five months (Lilly, 1953). The appearance of these latter species on the rocks at Hempholme during spring was no doubt partly responsible for the significant distinction between the rocky samples and the weedy sample as judged by Kendal's rank correlation test. The concordance between rock/weed samples taken in late summer and autumn, compared with the
significant difference during winter is probably explained by differ­
ences in flow at these times of year. Whitehead, (1935) reports the
flushing out of organisms higher upstream in the River Hull by the
increased flow of autumn and winter.

Although fragmentary, the evidence for phasing of the breeding
period to avoid possible competitive effects, is minimal. The results
indicate that the three most abundant pulmonates (Physa fontinalis,
Anisus_vortex and Lymnaea peregra) show an annual life cycle, and are
thus in agreement with previous work on the same species. (Boycott,
1936, and review by Comfort, 1957). Physa fontinalis showed a partial
autumn generation at Barmston drain and there is some evidence to
suggest that the same occurred at Hempholme in 1974. However, there
is no question of a complete replacement of the summer generation, as
found in populations in Holland (De Wit, 1955), and it was less
important than that which occurred in populations of Physa in Middlesex
(Duncan, 1959). No doubt, as Russell-Hunter (1961,b) suggested, its
importance may vary both from year to year and at different localities.
The relatively low numbers of the other pulmonates (other than Physa,
Anisus and Lymnaea) and of the prosobranch Valvata piscinalis preclude
an accurate analysis of their life cycles, but the data such as it is,
was compatible with their being annual also. The data for Potamo-
pyrgus jenkinsi suggests that recruitment occurs during the summer,
and the density estimates indicate one main hatch per year, in summer.
All-year breeding capacity of this species has been reported by Michaut
(1968) and Winterbourn (1970), but the main breeding period varies from
location to location. The population studied by Michaut, (1968) from
the Cote-d'Or of France had two main reproductive periods, one in
spring and one in early winter. The Hempholme data of this present
study correspond more closely with that of Lumbye and Lumbye (1965-)
and Heywood, (1961) indicating one spring-summer peak per year.
The interval of four months, from October-February each year, between sampling is long enough for some populations of this species to have hatched, grown to maturity and bred (Frömming, 1956) but it is unlikely that this occurred since warm, favourable conditions would have been necessary, and these were not typical of Hempholme in winter. No snails species appeared to grow appreciably during the winter months.

Although the data from both Bithynia and Theodoxus indicated a comparable, at least partial biennial life cycles, the derivative support from published sources has shown that whereas Theodoxus takes two years to reach maturity and breed (Heywood, 1961, Fretter and Graham, 1978), Bithynia may breed within twelve months of hatching, then again a year later, and occasionally a third time (Boycott, 1936, Lilly, 1953). Both Lilly (1953) and Schäfer (1953) found rather more Bithynia survived into their second year than probably occurred here at Hempholme, and in this respect the Hempholme results resemble those of Young (1975) from the Worcester-Birmingham canal, not only in the proportion surviving into a second year, but also in the onset of breeding, which was later than that found by the other authors. Young attributed this to less favourable environmental conditions, and the River Hull and the Worcester-Birmingham canal are sufficiently close for a climatic explanation. Russell-Hunter (1961,b) gives a number of examples of how locality and season influence the detailed timing of the freshwater molluscs; generally the more favourable the conditions in terms of temperature and food availability, the earlier in the season breeding occurs.

From the point of view of niche overlap, the slightly staggered start of breeding in Bithynia compared with Physa and Lymnaea, and the longer period of egg-laying and hatching of Lymnaea compared with Physa would seem to provide evidence for some sequencing in time, reducing the degree of temporal overlap at a time when competition for ovi-
position sites and food for the young snails could be intense. Calow (1972) reports the importance of competition for oviposition sites in laboratory cultures and field experiments of Ancylus fluviatilis and Bathymomphalus contortus, which have distributional overlap at Malham Tarn, Yorkshire. These observations revealed that A. fluviatilis obtains oviposition sites at the expense of B. contortus. Other authors (e.g. Pinel-Alloul and Magnin, 1970, Dussart, 1976), have demonstrated how peak densities of gastropods are generally achieved during the summer, in other localities, and for these reasons it seems probable that any slight behavioural differences which results in the reduction of overlap along any niche dimension would reduce the intensity of potential competitive interactions.

Density estimates and sometimes maximum lengths have been used to compare the relative favourability of different habitats for different snail species, e.g. Young, 1975. Comparative density figures must be viewed with caution, however, especially when the sampled area contains plants, the area of which is not taken into account in the calculation. The data presented here are also subject to the criticism that in view of the time interval between samples, the density estimates may fall short of the maximum for the species at that site because the sample was taken before or after the peak densities had been reached. Since many snail populations experience a rapid, and serious decline shortly after hatching (Boycott, 1936) which may approach 40% (Young, 1975), this could lead to very large differences. The fact that here at Hempholme, Potamopyrgus jenkinsi reached densities of only 6800 m², compared with populations of 74000 m² on the Thames (Heywood, 1961), and 12,500 m² here on the River Hull (at Driffield, Whitehead, 1935), may be construed as it being a site with less favourable environmental conditions, competition with so many other species, errors induced by the sampling technique, or merely reflect the timing of the samples, rather than
any demographic differences. For these reasons, comparative density estimates are not discussed. Reasons for the overall decline in numbers of most species from 1975 onwards are also conjectural, due to the possibility of unrecorded events that could have occurred between the sample dates. There are reports of specific competitive interactions involving the species occurring in this study. Lassen, (1975) for example ascribes the extinction of *Lymnaea peregra* at least partly as a result of competition with *Anisus vortex* in a eutrophic pond in Aarhus, Jutland. The deleterious agent here at Hempholme appeared to affect both these species, and others, however, only the population of *Potamopyrgus jenkinsi* remaining relatively unperturbed. This would indicate possible competition between *Potamopyrgus jenkinsi* and the other species, but more likely, a non-biotic cause, possibly the weather, producing temporarily unfavourable conditions which *Potamopyrgus* was better able to withstand, or from which it could recover.

In view of the low rainfall during this period compared with previous years, it is interesting to note the finding of Hunter (1961,a), who reported how low rainfall in one year adversely affected pulmonate populations the subsequent one in the west of Scotland.

There are, however, periodic fluctuations in the flow at Hempholme which are linked only indirectly to the rainfall. Raising and lowering of the weir in response to various requirements inevitably produces rapid and severe differences in the flow and this would presumably exert a direct influence on the snails at both community and population level. Large changes at these levels would, therefore, at a site such as this, be expected.
CHAPTER 4

Results and discussion at the third level of abstraction:

Microdistribution patterns on the rocks and weeds.
4.1 Microdistribution patterns on the rocks

Despite the fact that the samples were taken in mid-July, the communities had already separated, and the species remaining on the rocks were those which had generally dominated the rocky zones at Hempholme and elsewhere (FIG. 34). If anything, the separation was more pronounced, the numbers of Ancylus being higher, and only residual numbers of the 'weedy community' being represented. The data from which the FIG. 34 was constructed are the pooled result of 20 bricks of standard dimensions. This enabled absolute snail densities for this region to be calculated and these are shown in FIG. 35.

(a) Longitudinal separation

Within the 'rocky' snail fauna there is evidence for some separation of the species along the short length of this sample station. The trend is for large numbers of Ancylus to be near to the weir, the numbers decreasing as the distance from the weir increases. (FIG. 36). Theodoxus and Potamopyrgus both show the reverse trend. The large confidence limits could be due to patchiness of the habitat, since the flow was not constant, but pulsatile, and the disposition of the bricks may have resulted in some providing shelter for others immediately downstream.

Reasons for snail separation could be physical or biotic. Of the probable physical factors, flow and depth both correlate with the zonation described, (FIG. 37). The precise factor may operate indirectly via these parameters, since light decreases with increasing depth, and flow exerts effects on substratum composition. Although not weed-covered, some aspects of the bricks had been colonised superficially by epiphytes and no doubt bacteria, and thus a biotic cause is possible, but this is probably linked indirectly to the prevailing physical conditions.
(b). Stone aspect

These results were derived from samples taken from 19 bricks, in which the surface aspects could quite readily be distinguished. The results are tabulated in APPENDIX 7. The differences between the numbers on the top compared with bottom aspects of the bricks were significant for each species when tested by $\chi^2$ (FIG.38) but the polarisation of Theodoxus was opposite to that of Ancylus and Potamopyrgus. This indicates that whereas Theodoxus occurred more commonly on the bottom surface of the bricks, Ancylus and Potamopyrgus occurred significantly more on the top. The differences shown between the upper and lower surface were reflected also on the side aspects of the stones, which tended to resemble the upper distribution pattern, rather than the lower in all species. (FIG.39). From these results it would appear that Theodoxus was seeking shelter, either from light or flow, or possibly the undersides of bricks were the site of preferred food. However, a second sample of 13 bricks taken during the hours of darkness showed an identical pattern for Ancylus and Potamopyrgus, but a reversal for Theodoxus, which now occurred significantly more on the top than the bottom surfaces of the bricks, (FIG.38). This indicates a negative phototactic response, rather than either a rheotactic or nutritional one.

(c). Stone size

The relationship between the stone size and snail density for the three species considered is shown in FIG.40 and APPENDIX B. As might be expected, larger stones harboured larger numbers of snails, but the precise relationship appears to be different in each species, as judged by the slope of the curve. The rather large confidence limits again suggest patchiness of the habitat, and the sample stretch polarised at least two gradients, flow and depth, either of which could have been a contributary factor. The slope in both Ancylus and
Potamopyrgus would tend in any case to be a curve, whilst that of
Theodoxus approximates a straight line. The stone parameter used
in these figures is maximum length, and since the occurrence of
snails is presumably related to the surface area of the stones,
rather than their linear dimensions, on theoretical grounds, a curve
would be expected when the results are plotted as shown. Failure
of the actual data to correspond in this way could be interpreted as
showing that the expected area/density relationship was suspect, and
that for Theodoxus, some areas of the stones were inaccessible or
uninhabitable. Such a view is compatible with the daytime dispersion
patterns where the aspect to which Theodoxus was restricted was the
dark, sheltered undersurface of the stones.

Extrapolation of the curves to their intersection of the x-axis
indicates that the cut-off size, i.e. the size of stone below which
it is rare to find snails occurring, is higher for Ancylus than
either of the other species. The sharp upward trend to the largest
stone category, the bricks, is particularly pronounced in Ancylus,
indicating that these units provide a particularly suitable substratum
for this species.

(d). Between-stone dispersion pattern

Fig. 41 shows the plot of the mean number of snails per stone against
their sample variance for each stone class considered. P represents
the expected relationship between means and variances assuming random
dispersion. All species considered showed a departure from the
latter and indicate a disproportionate rise in variance with increases
in the mean. These relationships are linearized by transforming
variances to standard deviations (Fig. 42). The regressions plotted by
eye, are shown on the figure, but the aggregation pattern that this
indicates must be regarded with caution in view of the sample sizes
(see discussion).
4.2. Microdistribution patterns within the weed beds

(a) The estimation of plant surface areas

The measured areas of the plant considered correlated well with the weight of the surface films they supported. The relationship was positive and linear in all four cases and correlation coefficients lay between 0.95 and 0.99. (APPENDIX 10, FIG. 45). Regression analysis was applied to the scatter diagrams and from the regression lines actual surface areas of the different plants samples were determined. These are shown in APPENDIX 11 and examples of leaf outlines in FIG. 44.

The estimations of surface area from regressions were straightforward for all but the quadrats containing large quantities of filamentous alga. The amount of time that it would have taken to prepare standards to cover the range of actual sample material would have been unrealistic, and the estimations of surface area were made by extrapolating the standard regression. There seemed no reason, given the closeness of the correlation over the measured range, and the uniformity of structure and growth habit, to assume that this relationship would not hold over larger samples. Moreover, in the case of Cladophora alone, dry weight and wet weight correlated extremely well, (0.98, FIG. 46) and it therefore seems probable that estimates of surface area for filamentous algae could be made directly from their dry weight. This would not be possible with the species of vascular plant.

(b) Overall snail occurrence in relation to plant cover

The quantity of weed present, and the relative abundance of each species was measured by the use of quadrats, and the results are presented in APPENDIX 12 and FIG. 47). The number of snails of each species per quadrat, is also shown, (APPENDIX 13). Of the 50 quadrats
scattered, 31 contained plant material. This would mean that in this particular area, there was approximately 60% plant cover, a finding which was consistent with the general impression of the drain when viewed from above (PLATE 20). Of the quadrats containing aquatic plant material, 19 (61.3%) had filamentous algae alone, and the remainder various combinations of rooted vascular plants, Veronica beccabunga, Myosotis scorpiodes and Callitriche sp. Two quadrats included a species of submerged grass. Only 4 of all quadrats containing weed were devoid of filamentous alga.

The occurrence of snails was linked closely to the presence of weed, for of the 18 samples in which no weed occurred, only one possessed snails and in this the total count was two. On the other hand, all quadrats containing weed except one, contained snails also. The relationship between snails and weed was not confined to presence/absence, but extended to quantity, and is shown in FIG.48. The correlation was not strict, however, (r = 0.59) but shows that there was a tendency for larger weed samples to contain more snails. There is just a suggestion that this trend may continue only up to a certain level, or optimum, above which the relationship breaks down. If true, this would suggest that extra surface provided by larger quantities of weed permits colonisation by more snails until a point is reached of optimal density, after which overcrowding, or compression of the weed itself, makes the situation unfavourable for the snails.

(c) Distribution of the different snail species in relation to plant cover

Qualitatively there appeared to be very little difference between the various plant species and the types of snail they harboured. Valvata piscinalis was the exception, occurring only on the beds of the filamentous alga. The other species, Lymnaea peregra, Physa
fontinalis, Bithynia tentaculata and some planorbids were found on all the plant species sampled. Some differences were found, however, between the relative and absolute densities of snails on the weeds. The relative proportions of each major species on all four weed types are shown in FIG.49. These figures show quite similar complements for the vascular plant species, but major differences, particularly with regard to the relative numbers of Bithynia and Physa in the filamentous alga.

Absolute densities, calculated from the pooled results of single species samples of each weed type showed that the highest snail densities were on Callitricha (434 snails m$^{-2}$, FIG.50) which harboured up to 9 times as many snails per unit area as the other three species. The larger-leaved species, were very similar, (Myosotis 56.51 snails m$^{-2}$, Veronica 57.34 snails m$^{-2}$). Despite the fact that the filamentous alga was by far the most abundant species, and that there appeared to be very high snail numbers within it, the density calculations provide a figure of 71.68 snails m$^{-2}$, only slightly higher than those of Veronica and Myosotis, on which snail numbers appeared to be sparse. Moreover the assumption being made is that snails can use the whole of the estimated surface area of the plants, which in the case of filamentous alga, where the surface is not flat, but a series of narrow cylinders, may be invalid. Larger snails may rely on the network of meshed filaments rather than isolated strands to provide a foothold, and it is possible that the estimate of the surface area, in terms of snail colonisation, is rather high and the actual colonisation low.

Density differences are not shared equally by the different snail species, and these are shown in FIG.50. The dominant species, Lymnaea peregra show a remarkably even distribution on all plants but Callitricha, on which the density increase is almost tenfold. Physa fontinalis shows a similar trend, but in Planorbis spp. and particularly
Bithynia tentaculata, the trend is much less marked. It would certainly appear that some facet of Callitriche is particularly favourable for the pulmonates Lymnaea and Physa. The filamentous alga Cladophora alone provided suitable cover for Valvata, and the other operculate, Bithynia, occurred at its second highest density.

(d) Seasonal distribution patterns

In contrast to the similar distributions of snails on the plants during the summer, the winter samples indicated a marked separation. At this time (February, 1981) there was no fresh submerged or emergent vegetation, and although there were traces of decaying plant material of various types, the bottom was predominantly silt. A profile from the eastern margin to the centre of the drain shows that the pulmonate species Lymnaea peregra and Physa fontinalis occurred in largest numbers at the edge, and the prosobranchs were concentrated in the deeper zones (FIG. 52). Although Lymnaea peregra occurred throughout the length of the profile, its density varied with depth, with the optimum at 10-20 cm, and the other three species showed even more marked optimal depth distributions, with Bithynia and Valvata phasing in as Physa became extinguished. Along the profile the sequence from the shore to the centre was Physa-Lymnaea-Bithynia-Valvata. These findings are of interest, since they demonstrate spatial separation within a group of gastropods which occur commonly throughout the slower flowing, silty regions of this river system. They indicate the adoption of different strategies between the winter and summer, which means that the overlap during the summer months was relieved by vertical migration, particularly by the prosobranchs.
4.3. Discussion of results

(a) The rocks

Results of the first and second levels of abstraction and those derived from studies elsewhere, particularly the extensive survey of Durrant (1977 and pers. comm.) all show a distributional overlap of *Potamopyrgus jenkinsi* and *Ancylus fluviatilis*. Their particular environmental requirements were fulfilled by the rocky area at Hempholme Lock and these were presumably similar to those needed by *Theodoxus fluviatilis* which was also abundant in the same zone. The results at the third level of abstraction have shown that spatial overlap is relieved by differences in microdispersion pattern of these three species. The pattern of flow tolerance apparent in the first level survey revealed that *Ancylus* was the best adapted of all the gastropod species, and occurred unaccompanied in flows of up to 0.7 m sec\(^{-1}\). In other situations, it may occur in current speeds of up to 1 m sec\(^{-1}\) (Durrant, 1977). This pattern was reflected, on a smaller scale, at the rocky river edge at Hempholme where it occurred in highest densities near to the weir, decreasing as the distance from the weir increased. The distribution of both *Theodoxus* and *Potamopyrgus* reciprocated that of *Ancylus* in this respect, but the underlying reason for this is complicated by the fact that the depth of the water also increased with distance away from the weir. Although it has been observed that the density of *Ancylus* has a negative correlation with depth in standing water, (Hall, 1949, Geldiay, 1956, Macan, 1970, Calow, 1974,b), in running water the effect is reversed, with the density increasing with increasing depth (Maitland, 1965, Everett, 1973). Negative correlation with depth has been explained in terms of increasing sedimentation (Kreck and Lancaster, 1933, Calow, 1972), and Calow (1974b) has suggested that the cause may be reduction of algal
growth via sedimentation. These latter suggestions seem less likely to be responsible for the decline in the present study, in view of the progressive increasing density of *Theodoxus* which is itself sensitive to sedimentation (Heywood, 1961). Thus at Hempholme, the increasing depth away from the weir would have been expected to favour *Ancylus*, instead of reducing its numbers. This reversal cannot satisfactorily be explained by the deleterious effect of increasing sedimentation, as occurs in standing waters (Krecker and Lancaster, 1933, Calow, 1972) since *Theodoxus* is also sensitive to finely particulate substrata (Heywood, 1961) and yet its density increases further away from the weir. The behaviour of *Theodoxus* is, however, altered by strong flow, and Heywood (1961) has demonstrated under experimental conditions, that it moves less in fast flowing water and remains stationary in current speeds exceeding 10mm/sec⁻¹, which indicates an optimum flow well below that figure.

The fact that during the first level survey the maximum flow in which *Potamopyrgus jenkinsi* was discovered was below that of *Ancylus* also suggests that its optimum flow lies below that of *Ancylus*. From this evidence, a persuasive hypothesis emerges, that the reason for quantitative differences between *Ancylus* and both *Theodoxus* and *Potamopyrgus* is that the positions they occupy in relation to the weir reflect different positions along the flow dimension of their respective niches.

Spatial overlap is further relieved by the apparent selection by the three species of different stone-size categories, particularly the smaller stones (5cm. maximum length). By extrapolating from the field data, it appears that both *Potamopyrgus* and *Theodoxus* occurred on smaller stones than *Ancylus*. This finding is consistent with the pattern of occurrence of *Ancylus* on stones at Malham Tarn, where they
were seldom retrieved from stones less than 6 cm. (maximum length), Calow (1974b), but in his extensive survey, Durrant (1977) reported their occurrence on stones smaller than this and even sand, but in reduced densities. Percival and Whitehead (1930) also found a considerable reduction in density of Ancylus on small stones and gravel. An uneven substratum tends to reduce the adhesive properties of the foot, partly by loss of contact, and partly by exposure of the aperture to the flow, and Durrant, (1977) suggests that these explain the reduced densities on small stones and other unstable substrata. The possibility of being crushed is also greater in gravel substrata, and it is interesting to note that Theodoxus and Potamopyrgus both found on the gravel, have much thicker and stronger shells than Ancylus. Similar observations were made by Hynes (1970) on bivalve molluscs and stream dwelling prosobranchs, both in the U.S.A. and Europe, and it may well be a combination of instability, with consequent possibility of being crushed, that reduces the densities on small stones at Hempholme. The difficulty in traversing patches of sand or gravel to preferred substrata may also account in part for the large confidence limits of the Hempholme data. The bricks which had been introduced into the river a year prior to sampling seemed to provide a particularly favourable substratum for Ancylus, but it may well have been the texture of these rather than their size that was attractive. Calow (1974b) found that stones with smooth surfaces were preferred to those with rough, by a ratio of 4:1. No particular note was made of texture of the bricks at Hempholme but most of the surface being unused, and therefore devoid of mortar, had smooth aspects, with only occasional rough patches, whereas many of the smaller stones were fragmented bricks, with rough surfaces.

With regard to stone aspect, the results of this study are in partial agreement with those on Ancylus reported by Calow (1974b) in
that this species tended to occur in greater abundance on the sides of stones rather than underneath. However, at Malham Tarn, the site of Calow's collections, few Ancylus were found on the exposed top surfaces of the stones, whereas in the present study this appeared to be a favoured aspect. This may reflect different responses to the varied flow regimes, since water movement at the habitat at Malham was wind-induced wave action, or it may reflect the response of Ancylus at Hempholme Lock to the presence of other species of gastropod, particularly Potamopyrgus jenkinsi, with which it may compete for preferred stone aspects. At Malham, only Bathyomphalus contortus was present on the rocks in Calow's study and the dietary preferences for detritus restricted this species to the lower aspects, although the distribution of this food was influenced by the flow. The selection of the underside of stones by Theodoxus was most apparent and gave the impression of gregariousness. Their distribution altered however during the night, at which time their dispersion pattern resembled that of the other species. This was presumably a phototactic response and similar behaviour has been described in Theodoxus populations in the River Thames (Heywood, 1961). At Hempholme it produces spatial separation from the other species, although it is difficult to see how such short term behavioural differences could be of much consequence unless it was synchronised with feeding behaviour, a possibility that is investigated further in CHAPTER 7. The relationship between the size of stone and the number of snails they harboured revealed a difference between Theodoxus and both Potamopyrgus and Ancylus. The slope of the curve representing these relationships was far steeper in the latter species than Theodoxus and this may indicate the importance of the under surface as a daytime retreat for this species. In other words, the selection of stone size by Theodoxus may be determined by the small area of the underside that provides a refuge from the
light, during daytime rather than the total area of its surface.

The variance/mean test, applied to the data from different sized stone categories indicated an aggregated dispersion pattern for all species. A similar pattern was found in the gastropods at the littoral zones of Malham Tarn by Calow (1974). Although sampling error can produce apparent contagion when none exists, aggregation in natural populations appears to be the rule rather than the exception, (Odum, 1971 Krebs 1972). The disproportionate increase in aggregation with increasing stone size indicated by the mean:variance data must be regarded with caution, however, since the samples were based on different sized sampling units and these can affect the mean:variance ratios independent of any real changes in aggregation pattern, (Southwood, 1966).
4.3. Discussion of results

(b) The weed beds

The apparent trend for gastropods as a group to react similarly to favourable conditions (Boycott, 1936, Ökland, 1969) was reflected in the increase in their diversity in sections of this river where such favourable conditions prevailed (See CHAPTER 2) and sample site 49 on Barmston Drain was no exception. The site was one of gentle flow and possessed a variety of plant growth, although during the period of study in summer the site was largely dominated by an extensive covering of filamentous algae. The macrophytes present were chiefly represented by the marginal species and consequently made up only a relatively small proportion of the total floral complement. Several authors have commented on the apparent favourability of submerged vegetation for encouraging colonisation by gastropods, and invertebrates generally (see CHAPTER 3, section 3). Frohne (1956) however, suggested that it was necessary to compare the faunal array in areas which were similar in all respects except for the provision of weed cover, before a more precise relationship between the plants and their fauna could be established. In practice, the difficulty in finding natural areas similar in all respects except for plant cover precludes such an absolute comparison, but during the summer months, the substratum at Barmston Drain did contain areas of uncolonised silt between those covered by plants, which fulfilled the main criteria of Frohne. The results showed a decided selection by the snails, during the summer, of the weed covered areas, compared with areas of barren silt. This indicates that the relationship between the plants and snails was facultative or even obligatory, rather than simply adventitious, although it is possible that the barren silt may have provided a less attractive
alternative than stones, gravel, or man-made debris. Some pulmonates particularly are reported to have an aversion to crawling on certain types of mud, (Young, 1975).

Although some marine and intertidal gastropods have been found to be associated with particular plant types, (Fretter and Manly, 1979), there is little evidence in the literature for any relationship between particular snails and specific plants in freshwater. The reason for the difference may well be that the marine plants usually are algae which are taken as food by gastropods. In freshwater, the vegetation is frequently macrophyte which tends to act in a provendering role (Frohne, 1956), rather than being taken as food itself. It may be significant that the few instances cited of association between a freshwater snail and a particular plant is that between Stagnicola reflexa and the filamentous alga Spirogyra on which it feeds, (Bovbjerg, 1965). In the present study, different plants were found to harbour different relative and absolute densities of snails although qualitatively, the composition of the snail 'communities' on the different plants was very much the same. The plant with the highest snail densities was Callitriche sp. which exceeded by far those on Veronica and Myosotis and the filamentous alga Cladophora. At Malham Tarn, Calow (1973) similarly found differences in snail densities on different plants. He found the beds of Carex and Myriophyllum to be particularly densely populated, and similar relative numbers of the snails they harboured. The similarity in form of these plants prompted the suggestion that snail affinities were dependant more on structural than taxonomic attributes of weed beds, an idea that has been extended to include other invertebrates (Macan and Kitching, 1976). Although the range of plant types was smaller, the results of the present study are consistent with such a suggestion. The leaves of Callitriche were thin and more finely divided than the
flat, circular or hastate leaves of the marginal species. The growth form of *Cladophora* was inconsistent, however, for despite being composed of uniformly constructed thin cylinders, the arrangement of these could vary to produce isolated threads, flat sheets or densely compacted three dimensional networks which may have drastically reduced the suitability of the structure for snail colonisation. It seems quite possible that the individual elements of filamentous algae are too fine to accommodate the relatively large foot area of some gastropods and there may be a lower limit on the degree of substratum dissection below which adhesion is impossible. Plant form and structure seem to be important for other weed-dwelling organisms from ponds and lakes, the weeds with finely divided "leaves" generally harbouring the greatest faunal densities (Krecker, 1939; Andrews and Hasler, 1942; Entz, 1947; Rosine, 1955,) and Harrod (1964), has shown the importance of growth form in the occurrence and distribution of certain invertebrates in lotic waters. She found that different plants offered differing degrees of shelter from flow, thus permitting colonisation which would otherwise not have been possible. Although the data on molluscs is sparse in Harrod's report, her findings could have an important bearing on snail species that are not flow-tolerant and may rely on the cover afforded by plants to hold station. Fretter and Graham (1978) report that weeds can moderate a fast flow and thus permit colonisation by *Valvata piscinalis*, which otherwise tolerates only a gentle flow. Ökland (1969) reports the occurrence of increase in the abundance of *Valvata piscinalis*, *Physa fontinalis* and several other pulmonates in situations where there was diverse plant growth, with a significant decrease of the same species in habitats where the water was flowing, this effect being particularly marked when the flow was strong.

The exception to the qualitative conformity of all the plants at
Barmston Drain with regard to the snails they harboured was the occurrence of *Valvata piscinalis* only on the filamentous algae. *Valvata* has been found to have a restricted occurrence within a habitat at sites elsewhere. Calow (1973b) reported that it occurred only on beds of *Chara* at Malham, when other species of plant were available. It is possible that a similarity in form of both *Chara* and filamentous algae is another example of the importance of this facet of a plant rather than its taxonomy, but another explanation is that it is the depth of the water that was being selected, rather than any particular plant form. Hubendick (1947) considered that 1.5-3m. was an optimum depth for this species, although individuals have been recovered from a depth of 9m. in Lake Windermere (Macan, 1950) and 6m. in Loch Lomond (Hunter, 1957). Frömming (1956) gives the range as between 10-20 cm. and in the Thames it is not found above 10 cm. (Heywood, 1961).

Although no depth is quoted for the results of Calow (1973b), the results on the Barmston Drain are consistent with a preferred depth distribution of *Valvata piscinalis*, since all specimens were removed from the beds of filamentous alga, and none of these samples were taken from depths less than 9cm. and most were much deeper than that. The marginal plants on which it did not occur were all within 1m. of the water's edge and all from depths less than 20 cm. Whatever the precise reason, the restriction of *Valvata* to the filamentous algae provided some evidence for spatial separation between this species and the rest.

Similar spatial separation between *Valvata* spp., *Viviparus viviparus* and *Bithynia* spp. was shown by Heywood (1961) in the River Thames. As in the present study, *Bithynia tentaculata* occurred at all points along a profile from the water's edge to the centre of the river, whereas *Valvata piscinalis* was restricted to the deeper zone beyond the marginal weed beds. Some further separation is described by Heywood but none
of the species involved were common to both studies.

During the winter, the vertical migrations both Valvata and Bithynia lead to almost complete separation of these species from Physa fontinalis, and to a lesser extent, Lymnaea peregra. Such patterns have previously been described by Stanczykowska (1960) for Valvata and by Young (1975) for all species in this study from the Worcester-Birmingham canal, and it may well be that a vertical migration of Bithynia and Valvata (and Viviparus) during the autumn which leaves the pulmonates Lymnaea peregra and Physa fontinalis at the edge, is a general pattern of behaviour for these species. The consequence of such occurrence would be to reduce the duration of spatial overlap to approximately four months of the twelve, and the period during which overlap occurred would be the summer months, when there is reason to suppose that food supply would be relatively plentiful.

It is possible that differences in the periphyton of the plant species (Fig. 51) may be partially responsible for different snail occurrence. Without knowing possible food preferences of the snail species involved, it is not possible to evaluate the importance of these observations. The influence of diet on snail distribution will be discussed in the following chapter.
CHAPTER 5

Diets; results and discussion.
5.1 Major species, considered separately; selectivity

Diets of all species assessed on the basis of gut contents, were found to be microherbivorous, sometimes detrital, and in the case of Lymnaea peregra, occasionally macroherbivorous. The chief constituents were algae, chiefly Bacillariophyceae, filamentous algae, detritus, occasionally fresh but usually partly decomposed macrophyte tissue and there were bacterial and fungal components also. Material also ingested included whole animals, especially rotifers, and parts of other invertebrates, particularly arthropod fragments. Only five species of snail occurred in isolation in sufficiently high density for close comparison to be made of their gut contents with the substratum composition. Where this occurred, the pattern of feeding was different from that when snails were feeding in mixed species clusters. The results are therefore presented for each species, initially in single species situations followed by different species combinations.

Physa fontinalis

This was the dominant or co-dominant species on the weed beds throughout the period of diet study. The slides of gut contents were generally free from the amorphous, unidentified material that characterised some species, PLATE 25. By far the most abundant constituent was diatomaceous, but on occasions, filamentous algae and partly decomposed macrophyte tissue fragments were discovered, (PL.25c). Animal fragments and whole animals (copepods and rotifers) were found also, but because they always occurred in similar abundance in comparable substratum samples, were judged to be accidental inclusions, but not necessarily without nutritional value for that reason. Because of its comparative abundance during the study, Physa occurred in sufficiently high densities, unaccompanied by other species, that on
six occasions the opportunity arose to investigate the possibility of selectivity from among the periphyton. The results are presented in FIGS. 54. Because of the similarity between the gut contents and the substratum periphyton in FIG. 54, Physa would appear to be an unselective microherbivore, ingesting chiefly Bacillarophyceae in the proportion in which they occurred in the natural epilithic and epiphytic communities. However, FIGS. 55, a - d, show that this was not always the case, even when Physa fed unmolested by other species. These results (FIGS. 55, a - d) were from different weed species, but sampled during the same period. They indicate a close relationship between the gut contents of Physa and the epiphyton from Fontinalis antipyretica but less so from the other species of plant, the vascular species Myriophyllum, Ranunculus and Elodea. Those from Elodea (FIG. 55, d) were particularly dissimilar. The fact that the gut contents of Physa in all cases (FIG. 55), was very similar suggests that the rank occurrence was one that reflected some form of positive selection by the snails. This could be a food preference, or possibly reflect the pattern of occurrence of the diatoms on preferred loci of the plants. In this respect the structure of Fontinalis, being uniformly composed of minute, simple, entire leaves, possibly offered least opportunity for microdistribution patterns of the epiphytic diatoms, compared with Myriophyllum, Ranunculus and Elodea, all of which have morphologically distinct leaves and stems. A comparison between the epiphyton of the four plant species growing near to the weir, and that on the same species growing away from its direct influence (FIG. 56) supports this suggestion. Here the epiphyton of Fontinalis appeared to be least affected by the position of the weed relative to the weir, (FIG. 56, a). That of the other species, possibly because of their more diverse morphology, possessed
different patterns of relative abundance of the constituent diatom epiphyton, both from one another, and from the same plant species growing in a different zone.

Other occasions when the gut contents of Physa did not match those taken randomly from the feeding substratum were those when other species of snail were present in the same sample, (FIGS.61,63,64a). These too could reflect selection by the snails of either preferred fractions of the periphyton, or preferred feeding sites. Alternative suggestions are discussed under mixed groups.

*Lymnaea peregra*

Collections for the second level study showed *Lymnaea peregra* to be an ubiquitous, but not very abundant species. Its relatively small numbers at Hempholme were to some extent compensated for by its very large size, and histograms constructed on the basis of biomass rather than numbers would reflect more accurately its trophic importance, (See CHAPTER 4, Barmston Drain, FIG. 33a and b.) On the occasions where numbers of *Lymnaea* were feeding alone, the proportions of the periphyton constituents were strongly reflected in the gut contents, (FIGS.57,a and b). Occasions when this did not happen were when the substratum itself was penetrable by the radula, as was the case with *Fontinalis antipyretica* in which case the plant tissue was taken also. This occurrence was coupled with the presence at the same place, and time, of other species of snail and resulted in fragments of plant tissue forming by far the major constituent of the diet, (FIG.63/4a and PLATE 26, a and b). This was the only species of gastropod found to have pieces of fresh macrophyte tissue forming the bulk of the tissue in the gut, although several species, including *Lymnaea peregra* ingested decaying macrophyte material.

*Anisus vortex*

Initially, in 1975 this species was co-dominant with *Physa* among
the weed beds. Its diet showed considerable variation with regard to
the emphasis of the overall components. In early samples, taken
between January and March 1974, the bulk of the material was amorphous
and mostly unidentified. Some material was readily identified
(FIG. 61), but the detritus was so finely particulate that it was
probably not identifiable by visual means alone. By June of the same
year, however, the major component of the detrital fraction was of
macrophyte origin, identifiable as such by the xylem elements, and
epidermal features, (PLATE 27, a - e). The plates show a representa-
tive sample of the gut contents of eleven individual Anisus, feeding
alone. The size of many of the plant fragments was uniform, (PLATE 27, a,b)
suggesting that they were 'bites'. PLATE 27c is more highly magni-
fied and the cells show the wavy edge characteristic of some types of
epidermis. Epidermis, but of a different sort, is visible in PLATE 27,d.
Siliceous spicules, characteristic of certain monocotyledons, commonly
occurred and are visible in PLATE 27,e. The plates show that these
specimens of Anisus vortex were not browsing on a single plant species,
but probably at least two, probably more. In all the June samples
from Anisus, the proportion of diatoms was reduced to less than 1%.
In contrast to these detritus-dominated results, samples taken in
September of the same year were almost devoid of detritus, being almost
totally diatomaceous, (FIG. 63), but in this case, Anisus vortex
was in a group including other species of gastropod.

Theodoxus fluviatilis

This species was generally found on among the rocks, although
specimens were occasionally removed from weed. The bulk of the diet
was consistently composed of an unidentified multicellular organism (PLATE 28)
which was present on the rocks where Theodoxus browsed. Although it
would be tempting to suggest that this snail species was selective, the
results indicated random browsing of the rock surface, (FIG.58),
although the rock samples used to compile the data were chipped off from larger rock samples, and it is thus possible that the snails were being selective in their choice of rock, or part of rock on which the preferred food was plentiful. It seems likely that this species rasps very hard against the substratum, since the guts of several specimens removed from bricks had minute pieces of red brick packed into them. On the rare occasions when Theodoxus were removed from plant leaves, they appeared to be virtually unselective, (FIG. 63), but the number of animals used to compile this data was small. No trace of fresh higher plant material was evident in any sample.

Potamopyrgus jenkinsi

Only a few specimens were examined, but when removed from uncrowded situations this species, which was by far the most numerous, but also the smallest of the gastropods, removed fractions of the periphyton similar to their relative abundance (FIG. 59). When grouped with other species, however, the results indicated non-random browsing, (FIG. 63,c) at least on weed.

Bithynia tentaculata

The only specimens taken for gut analysis were from weed in September 1975. Since during the period of diet study, Bithynia did not occur in sufficiently large numbers unaccompanied by other species, the results reflect only the diet during a crowded period. The results indicated, as with the other gastropods in the same situation, that browsing was far from random (FIG. 63,d). Lacking data from other situations, particularly Bithynia in isolation, it is difficult to generalise, however, in this one situation the diet was chiefly diatomaceous, particularly the stalked Gomphonema in larger proportion than would have occurred with random browsing. Some detritus also occurred, but this was particulate and un-scored.
Ancylus fluviatilis

This species was present only on the rocks. From the 23 specimens examined, the diet was almost exclusively diatomaceous, and was consistent in its rank order, (FIGS. 61,a, 62). No situations were found in which Ancylus fed alone, so such consistency was unusual, however Ancylus is regarded as a stone specialist, and as such may possess some advantage in the quest for food in such situations. Comparing the gut proportions in January, 1975, with the epilithon (FIGS. 60 and 61,a) there is some correlation, but not as close as that between other species and their substratum samples (e.g. Lymnaea, FIG.57 and Physa, FIG. 54.). One reason for this could be the presence of other, possibly competing snail species, but this did not alter the rank occurrence in the guts. A more likely reason is that the samples of epilithon were taken randomly, from all faces of the brick on which the snails occurred. The higher proportions of some diatom types, particularly Gomphonema, may again reflect selection of a particular part of a stone by both Gomphonema and Ancylus, rather than a dietary selection of particular diatoms.
5.2 Minor species

The only group of infrequently occurring gastropods that were found isolated in a group were specimens of *Succinea pfefferi*. These did not occur in Allen grab samples during the second level study, but were encountered at the edge of the river, and on floating, uprooted vegetation. The crops of the two specimens examined were filled with decaying macrophyte tissue, PLATE 29. Xylem elements are visible in PLATE 29a and b. PLATE 29c is epidermis and both 29d and e are examples of guard cells that were common. Very few diatoms (<1%) were present in these samples and it seemed probable that *Succinea* was feeding on the decaying vegetation at the edge of the river rather than on the submerged epiphyton.

The remaining minor species were found in mixed species groupings and are presented in FIGS. 60-64.
5.3 Mixed species groups

Results of gut analysis in isolated species of gastropod indicate that quantities of the recognisable components ingested were generally proportional to the amount available on the substratum. Studies on distribution of the snails, particularly at the second level of abstraction, indicated that at certain times of year, many species had spatial overlap, and that a brick, or tuft of weed could harbour several different species within a small, defined area. If the species continued to browse randomly over the same area of substratum, they will presumably be in competition, once the food supply became limiting. Mixed species groups of snails were examined for diet on six occasions and the results are shown in FIGS. 60 - 64. The collections during 1974 contain only pulmonates, since the prosobranch species were not examined for gut contents until 1975. In four cases out of the six, it is clear that far from browsing indiscriminately, the snails were involved in some form of resource-partitioning (FIGS. 61, 63, 64a).

January, 1974, rocks (FIG. 60 and 61,a)

Although the combined gut contents of all snails reflect that of the epilithon, different species appeared to be discriminating between the various items, so that the total epilithon was apportioned in different ways in different species.

The gut contents of the limpet-type species were dominated by the stalked diatom Gomphonema, and both contained fewer types of other food categories, being restricted to seven diatom species of the twelve potential classes, available on the rock surface, (c.f. FIG. 60). In the case of the planorbid Anisus vortex this weighting was reversed, with Cocconeis being dominant to Gomphonema, and a slightly wider range of diatoms being present in the gut. In common with both Lymnaea and
Physa a large amount of finely particulate detritus was present which constituted an important, but unquantified difference between the limpet species, Ancylus and Acroloxus, and the rest. Lymnaea and Physa gut contents were less dominated by single diatom types, and that of Lymnaea encompassed virtually the complete range of possible food categories. These latter two species also accounted for the filamentous algae present on the rock. Some more of the relative importance of diatoms to detritus can possibly be gleaned by examining the total numbers of diatom cases per snail, for each of the species investigated. This suggests that Ancylus was browsing the surface of the rock on which the greatest density of diatoms was situated, a suggestion that is consistent both with the results of microdistribution patterns of Ancylus described in CHAPTER 4 and with the notes on distribution on the brick surface made at the time of collection of the diet specimens. The relatively high value of diatoms in the gut of Physa is consistent with those results obtained by the same species in feeding situations elsewhere, and with their occurrence on the top, sides and bottom aspects of the bricks in this present example, but its presence on the rocks at all, as with other pulmonate species except Ancylus was unusual in winter.

June 1974, September 1975, rocks (FIGS. 62 and 64,b)

In contrast to the situation just described, which indicate resource partitioning amongst the different snail species, the summer rock samples indicate considerable dietary overlap. In both these cases, however, the number of snails used to compile the data was small. A possible explanation for the difference, in the June example (FIG. 62), is that the snail populations were low at this time and composed of adults having just migrated to the rocks to oviposit. Diet
in senescent individuals is probably less important, and in view of the relatively low densities, competition may, in any case, have been reduced. Although no rock sample was examined for epilithon, in June, browsing was assumed to be random.

The September sample of 1975 (FIG. 64,b) included the prosobranch species, which the 1974 samples did not. Only three species were involved, browsing randomly (FIG. 64,b) but there appeared to be considerable dietary overlap. The situation was different from that in winter, however, in that the flow at this time of year was low, permitting the non-rocky species to live among the weeds and rocks nearer to the weir than was the case at times of high flow. This could account for why *Lymnaea* was present on the rocks at all, and why *Theodoxus*, normally confined to the sheltered undersides of stones, should be present with *Potamopyrgus* on the top. Nevertheless, the probability that such spatial and dietary overlap would eventually lead to competition indicates the importance of niche segregation for most of the year. As with all cases in the present study, the possibility that differences in diatom proportions occur at species level cannot be ignored.

March, 1974, weeds, (FIG. 61,b).

As with all the group samples from weeds, this provided some evidence for resource partitioning. The results, which include only the pulmonate species, which were dominant on the weed beds examined showed that the planorbids were very similar to each other. At the time of sampling, these were in fact congeners, but owing to reorganisation of the taxonomic boundaries, they are now in different genera, but the same family. The proportions of the gut contents were different from those of *Physa* and *Lymnaea*, both in rank order, and in the case of *Physa*, in the range of diatoms ingested.
September, 1975, weeds, (FIG. 63)

The numbers of the various snail species browsing over a single plant species, *Fontinalis antipyretica*, provided a useful example of resource partitioning over the full range of weed-dwelling species in a zone near to the weir from which they were frequently precluded. This clump of moss provided food for a variety of snails of similar structure and habit. In this instance, *Lymnaea peregra*, (FIG.63e,i) as well as ingesting a small quantity of epiphytes in the proportion in which they occurred on the plant surface (FIG.63,i), were also ingesting the actual plant tissue to which the epiphytes were adhering. Of the other species present in large numbers, both *Physa fontinalis* and *Anisus vortex* were removing the epiphytes which closely parallel those on the plant surface, without removing the plant epidermis. The prosobranch *Bithynia tentaculata* was also removing epiphytes, but in vastly different proportions to the pulmonates. Here the stalked diatoms *Achnanthes* and *Gomphonema* formed the bulk of the ingested material, and here too, there was little evidence for the supporting moss tissue being molested. *Potamopyrgus* appeared to ingest fractions between those of *Bithynia* and the pulmonates. Of the remaining species (FIG.63 f,g,h), *Gyraulus albus* appeared to select more *Gomphonema* than random, and correspondingly more *Cocconeis*. The results of *Theodoxus fluviatilis* reciprocated those of *Gyraulus*, but the numbers of both species were small, particularly *Theodoxus* which was normally restricted to the rocks. *Planorbis carinatus* appeared to browse randomly over the moss, but occasional pieces of moss tissue were also found in the gut.

November, 1975, weeds, (FIG.64,a)

Only three species were recovered in the weed sample, and in two of these the numbers were small. The range of diatoms in *Physa* may reflect a wider range in the diet, or simply a larger sample size. The
proportions of the components reciprocated those of *Lymnaea peregra*,
but the size of the sample makes such conclusions tentative.
5.4 Discussion

There is a considerable amount of general information on the components of molluscan diets and this has formed the basis of reviews by Graham (1955) for all molluscs and both Frømming (1956) and Gaevas-kaya (1966) for aquatic gastropods. Unfortunately the source of information is so varied and widespread that conclusions about the diets of the individual species, other than very broad generalisations, are difficult to make. Moreover, since some of the studies contain conflicting or contradictory information, some preliminary discussion about the possible reasons for these apparent anomalies seems appropriate, since a descriptive study of diet of which the present study forms part, relies on additional derivative support from the published literature, and also because these contradictions are mentioned in other, recent diet publications (e.g. Reavell, 1980).

Some confusion may occur because

i. the material ingested by the animals is not compared with what is absolutely available, although the difficulties of making such absolute comparisons are indicated by McDonald (1969) and Calow (1973d).

ii. the categories under which the components are scored are different, e.g. the study of Reavell (1980) scores 14 possible food classes for *Lymnaea peregra* whereas Calow (1970) for the same species has only 3. Compounding the categories may result in loss of detail, and actual differences in diet between species may become blurred.

iii. methods of determining the suitability of various food items experimentally have resulted in different criteria being used to assess what is "best". For *Lymnaea peregra*, for example, Calow (1970) used gut analysis and choice chambers, whereas Skoog (1978) used growth rates and fecundity.
iv. conditions of feeding, particularly the presence of other possibly competing species is not known, or is not recorded.

These variations may be confused further by intrinsic alterations in diet during the life span of an individual species. Skoog (1978) found that diatom diets produced the highest growth rates for juvenile *L. peregra* but blue-green algae were "best" for adults. Various foods may also differ in the effect they produce. For cultures of *L. peregra* spinach gave relatively poor growth rates, but better fecundity than other foods (Skoog, 1978). The results of the present study can be viewed from two standpoints. The first is to see to what extent the natural diets of the species are compatible with the work already published, bearing in mind the points iv above. The second is to observe differences in diet between the species when they exhibit spatial overlap.

The results of gut analysis of the major species in the present study indicated ingestion of a broad range of food materials and thus a mixed, possibly balanced diet for most species. The wide range of diets is commonly reported from natural situations elsewhere (e.g. Boycott, 1936), and may be necessary for maximum growth. In the experimental studies of Reavell (1980), *Planorbarius corneus* was found to have a better growth rate on a mixed diet rather than eutrophic or oligotrophic detritus, and Frømming (1956) stressed the effect of a varied and balanced diet on increasing the growth rate of the same species. Similar findings are reported by Favier-Gamulin (1969) on the ancylid *Gundlachia weuteri*. Calow (1974a) on the basis of bacterial choices made by *Bathyomphalus contortus* suggested that a range of materials may be necessary in the diet if each provides essential, but different micronutrients. Eisenberg (1966, 1970) has suggested that food quality rather than food quantity may be important
in limiting growth and population size in *Lymnaea elodes* and presents some evidence to suggest the involvement of accessory growth factors. It would, therefore, appear that narrow food specialisation is not generally the case with freshwater gastropods. This, however, does not imply the selection of identical proportions of each foodstuff by the different gastropod species. In the present study, *Ancylus fluviatilis* consistently selected diatoms, rather than other green algae or detritus, and of the diatoms, *Gomphonema* was consistently the commonest. These findings match perfectly the field and laboratory results of Calow (1973d) and are also consistent with the same sequence marked on physiological grounds (Calow and Calow, 1975). In situations elsewhere, however, *Ancylus* has been shown to feed on *Verrucaria* (Schmid, 1932) but the ingestion of this food has been correlated with lower growth rates and may not be an optimal food for these gastropods (Calow, 1975a). Such contrasting results may be an example of when different field results are reflecting differences in local availability of preferred food, for under conditions of food shortage, *Ancylus* becomes less discriminating and ingests a far wider range of foods than when satiated (Calow, 1973a). Although the evidence from the present study is sparse, partly due to low numbers of individual snails and partly to the difficulty of scoring detritus in its various forms, there is good reason to believe from the literature that some planorbid species select more of the detrital fraction of the food spectrum than other species (e.g. Heidemanns, 1924, Shuskina, 1949). Calow (1974a) has found that *Bathyomphalus contortus* selectively prefers the bacterial fraction of this material, whereas there is evidence that the larger planorbids (e.g. *Planorbus planorbus* and *Planorbarius corneus*) have a more active cellulase than other gastropods and may be able to make use of the non-living, i.e. cellulose, component of the detritus (Boettger, 1944,
Calow, 1974a). In laboratory experiments, *Gyraulus albus* was not attracted to algal food (Reavell, 1980) and in the present study *Anisus vortex* consumed large quantities of finely particulate detritus during winter, and decaying macrophyte material during early summer, when there is reason to believe that fresh algal material would have been available. The latter finding could, however, be due to opportunistic feeding by a local group of *Anisus*, and certainly the early autumnal samples contained large numbers of diatoms. The situation in both winter and autumn samples was, however, complicated by the presence of other gastropod species in the same situation, a feature that is discussed later. *Lymnaea peregra* in this study ingest more filamentous alga when it is available, than other gastropod species, when it is in mixed snail groups. Reavell (1980) found that the same species, recovered with *Ancylus fluviatilis* from the River Lowther, was the only one to ingest filamentous alga. Calow (1970) has also shown that *Lymnaea peregra* seeks out, prefers and is able to digest green algae with thick cellulose walls and that this preference is reflected in their digestive enzymes, (Calow and Calow, 1975). Although in the laboratory Tsikhon-Lukanina (1958) reared *L. peregra* on macrophytes, gut analysis from natural situations elsewhere has seldom revealed that this forms the bulk of the material ingested, (e.g. Boycott, 1936, Reavell, 1980). This is despite the fact that fresh macrophyte material was considered to be the optimum food for *L. stagnalis* (Frömming, 1956) and that for other species of *Lymnaea* there are indications that fresh plant material is more nutritious than material which is partially decayed (Tsikhon-Lukanina, 1958). From this summary of the Russian literature, Gaevskaya (1966) considered that fresh, higher plant material is more important in the nutrition of *Lymnaea peregra* and *L. stagnalis* than in other lymneids, although
possibly to a lesser extent than higher plants in a moribund state, and algae. In other lymnaeids and Physa acuta, the higher plants are said, by the same author, to be less important, with the role of dying plants and algae increasing proportionately. These reports on the diet of L. peregra from the Russian literature conflict with the observations of Calow (1970) in England, who found no trace of higher plant tissue in the guts of L. peregra removed from beds of Elodea. One reason for this anomaly could be that the physical and possibly chemical nature of Elodea make it unattractive to snails even when no other food is available (Turner, 1927, Sushkina, 1949, Frömming, 1956). A further possibility is that the considerable plasticity in feeding behaviour described by Hunter (1953, 1957 and 1961a) results in differing proportions of the various foods being taken, depending upon the substratum type and particular food availability. The results of the present study indicate that Physa fontinalis may also be showing a preference, in this case for diatoms, especially Cocconeis, for although feeding substrata from which the snails were removed contained this diatom in larger numbers than others, the proportion ingested by Physa was in some cases greater than that which would have been expected with random browsing. The proportions of Naviculoids appeared to reciprocate those of Cocconeis. The position of the points in relation to the line of equivalence (Fig. 55) could be interpreted as active selection of Cocconeis at the expense of Naviculoids. Although the number of replicates is small, it is interesting that these results are similar to those in a report on Physa fontinalis conducted at the same site three years later (Fairweather, 1978, Unpublished Bachelor's thesis). There is little evidence for a change in diet of Potamopyrgus jenkinsi in this study, but Calow & Calow, (1975), found populations at a certain site which were feeding chiefly on detritus, whereas at other sites, the food ingested was chiefly diatomaceous. This may again serve to
illustrate the point that a wide range of foods is acceptable to some snail species and to support the contention that although some foods may be preferred, snails will, when unsatiated, feed on alternative food types.

The results of the present study suggest that despite the wide range of materials found in the guts of many species, the proportions of these may vary from species to species, a feature that is particularly noticeable during periods of spatial overlap. There are some indications that the diet differences may reflect differences in microhabitat rather than strict dietary preferences, but the precise importance of these two factors is problematical and their isolation would require critical experimentation. The same sort of experimentation would also be necessary to discover whether the food selected by certain species is affected by the presence of other snail species. Such studies could resolve the problem of whether apparent coexistence is achieved by a change of behaviour, i.e. character displacement, as has been shown to occur in mud snails (Fenchel, 1975) or whether the snails occupy different positions along this particular niche dimension. One aspect of the latter possibility was investigated and forms the basis of the following chapter.
CHAPTER 6

Radulae and feeding tracks:

results and discussion.
6.1 Structure in relation to individual radula prints

Results

The descriptions presented here are those made on specimens taken during the present study, with additional derivative support from the authors quoted. These form a background against which the radula print observations, made totally during the present study, can be viewed. From both a structural and functional point of view the radulae of all the snails were divisible into two groups, which corresponded to the taxonomic divisions, Prosobranchia and Pulmonata.

(i) Prosobranchs

The prosobranch radulae are similar in that they are characterised by the presence of a bending plane marked by the anterior horns of the cartilages of the buccal mass (Fretter and Graham, 1962), and that they bear a central row of rachidian denticles which are immovably fixed to the radular membrane of which they form part. Lateral and marginal denticles are borne on struts and articulate at their point of attachment with the radular membrane. Of the four species of prosobranch, one, *Theodoxus fluviatilis*, is basically Rhipidoglossan (FIG.65a and PLATE 30a, b and c) and the other three, *Bithynia tentaculata*, *Potamopyrgus jenkinsi* and *Valvata piscinalis* are Taenioglossan (FIG.65b, and PLATE 31a - d).

There are three types of denticle in *Theodoxus*. Those which are very numerous, have long stalks and sweep lightly in an arc are called marginals (PLATE 30b and c). Because of their fine cusps they were designated Randbursten, (Brush-border) by Ankel (1938). During feeding, they execute an outward sweep on passing forwards over the bending plane, and an inward sweep on being withdrawn. The marks left by these denticles are shown on the feeding trace (PLATE 32).
The median, rachidian denticles bear no cusps, are small (PLATE 30a) and appear not to function in the removal of food from the substratum, since they leave no impression on the feeding traces. Their role is probably to collect material already gathered by the marginal denticles rather than to remove food themselves. On each side of the rachidian, *Theodoxus* bears a row of lateral denticles which are extremely well developed. In this respect the radula differs from those described for other rhipidoglossan types. The denticles are strongly constructed, are brown in colour, hard, and bear numerous cusps which show signs of wear. In contrast to those types described by Fretter and Graham (1962) the lateral denticles on the capituliform tooth (FIG. 65a and PLATE 30a) would almost certainly be capable of rasping with considerable pressure, certainly more than the marginal denticles. This implies that the radula could be used not simply as a light brush, sweeping loose detritus, but also as a rasp to abrade the substratum. It is likely that the wider, parallel bands on the feeding trace (PLATE 32) are the result of pressure exerted by these denticles. The position of the mouth is different from the other prosobranchs, being ventrally placed on a broad head, rather than terminally on a snout.

The radulae of *Bithynia tentaculata*, *Potamopyrgus jenkinsi*, and *Valvata piscinalis* are very similar and conform to the basic plan described for the Taenioglossa by Fretter and Graham (1962). The detailed arrangement is shown in FIG. 65b, and reflects the change in emphasis from a multitude of marginal denticles and under-developed rachidian of the Rhipidoglossa to a reduced number of marginals and more highly developed rachidian denticles of the Taenioglossa. The species mentioned here also lack the hard, well-developed lateral denticles of *Theodoxus*. Feeding traces reveal that the only denticles serving to scratch the substratum are the marginals and laterals, and
they appear to be less effective as sweepers than their rhipidoglossan equivalents (c.f. PLATES 32 and 33a and b). The lateral and marginal denticles of *Bithynia*, *Valvata* and *Potamopyrgus* are stalked with the spoon-shaped tip serrated to form numerous cusps (PLATE 31b, c and d). The position they occupy relative to one another in the resting position gives the appearance of a zig-zag, (PLATE 31b and d) and is apparent also on feeding traces, (PLATE 33a). Generally the pressure of the jaw obliterates the fine, oblique striations of the individual cusps, but these are apparent in some traces (PLATE 33c). The traces of *Bithynia* and *Potamopyrgus* (PLATES 33a and b) reveal that the denticles that make contact with the substratum do so for only a short part of their swing, in marked contrast to those of *Theodoxus* where the trace is broad, and the scratches long and parallel. This indicates that the denticles operate as scoops rather than brushes or sweep gently rather than rasp. This is also indicated by the shape of the tips, which show little sign of wear. *Valvata* produced no traces on carbon, despite repeated trials. This could mean that the radula denticles make only very light contact with the substratum, or perhaps that the carbon was not palatable to the snails. The latter suggestion seems unlikely since *Valvata* appears to rasp continuously irrespective of the substratum, and the action is visible through the plain aquarium wall.

All three taenioglossan species possess a row of large, median rachidian denticles (PLATE 31a), each bearing a large central cusp flanked by numerous others. The fact that the cusps occur at different heights and angles is inconsistent with their being used simultaneously for abrading. Their spacing and orientation suggests that their potential lies in scooping and lifting, a possibility which is substantiated by the feeding traces, which, in contrast to those of other species, (Fretter and Graham, 1962) show no impression by rachidian denticles.
Characteristic of the three taenioglossan species is the position of the mouth, which although ventral, is carried on a snout. This is noticeable in both Bithynia and Potamopyrgus and most obvious in Valvata where the snout is narrow and proboscis-like and the mouth terminal.

(ii) Pulmonates

The pulmonate radula shows variety in shape, denticle structure and some differences in its mode of application to the substratum. Unlike the prosobranchs, the radula of the pulmonates operates as a single unit, moving forwards with its supporting structure, the odontophoral cartilage. When the mouth is opened and the buccal bulb orientated prior to the feeding stroke the radula denticles present a formidable battery of spikes with which the snails abrade the substratum (PLATE 34). Immediately prior to making contact the radula is U-shaped, but the shape of the radula, its denticle complement and its subsequent movement cause the prints to be characteristic for each genus and in most cases is species diagnostic. (PLATES 34 and 35).

Lymnaea. The radula has a complex, characteristic shape in cross section anteriorly. The U-shape is retained when the radula is pressed against the substratum, producing a semicircular base to the print (PLATES 35b, 36d). The denticle complement is similar to that described by Carriker (1946) and Calow (1970), there being a central row of rachidian denticles flanked on each side by 12-14 rows of lateral denticles. At each lateral edge there occur marginal denticles which differ in structure from the lateral denticles. Lateral denticles (PLATE 36c) are supported by a basal strut and terminate in what starts as a tricuspid working part. With continued use, the dominant central cusp in particular wears down and becomes confluent with its smaller neighbours (PLATES 36a and b) so that the
dentine becomes shaped more like a chisel than a spike. The fact that all the cusps show signs of wear in those denticles that are worn at all indicates that the denticles are not held vertically when in contact with the substratum, but are angled. The repercussions of this would be that attached material could be removed more effectively from a hard surface and that the denticles could penetrate the surface of softer tissue.

The marginal denticles (PLATE 36e) have a thinner stalk than the laterals, lack the supporting basal strut and bear smaller, equally sized cusps which are both more numerous and closely spaced. From these observations it would seem likely that the lateral denticles, angled, sharp-edged, and applied to the substratum with considerable pressure would serve as the major instruments for rasping and cutting. Slender stalked marginal denticles would presumably be less effective in coarse abrasion or cutting, but could be effective in brushing or sweeping finer material.

This suggestion is borne out by the feeding traces (PLATES 35b and 36d) and corroborate the findings of an earlier study (Storey, 1971, PUBLICATIONS APPENDIX) which drew attention to the major role played by the lateral denticles in Lymnaea peregra. PLATE 36d shows the difference between the marks etched by the lateral compared with the marginal denticles, and PLATE 36c, the actual spacing of the denticles.

The way in which the radula is applied to the substratum is not always the same, and this may affect the quality of the food ingested. On occasions, the trace from L. peregra resembled that characteristic of L. stagnalis, being in the form of a horse-shoe: the converse was also true on occasions (PLATE 37). The difference, also noted in
the earlier study, relates to the shape of the radula, which takes up its customary u-shape, but more extreme: this results in a change in emphasis from lateral denticles to marginals clearing a somewhat larger area. No reason could be attributed to this apparent change of habit, nor was it possible to confirm that such a change occurred under natural conditions.

Physa fontinalis The odontophoral cartilage differs from those of other pulmonates in being not single, but composed of two sections joined at the centre by a muscle. The denticles are of one type only, having a slender stalk, and resembling the marginal "sweepers" already described for Lymnaea in possessing numerous even cusps, (PLATE 38). The denticles, which resemble combs, lie in parallel rows across the radula and are characteristically shaped at the median line where the rows join (PLATE 38a).

As with other species the denticle cusps show signs of wear, (PLATES 38b and c). When the large, curved radula contacts the surface the denticles produce a characteristic trace, which is round­oval with the upper sector between eleven and one o'clock missing, (PLATE 35a). By comparison with other species, the area covered with each feeding stroke is very large.

Planorbidae The radulae were generally long, and of constant width, resembling in shape those of Acroloxus and Ancylus. The denticles were similar in structure from species to species, and there appeared to be little division of labour. Each denticle possessed a long strut, which terminated in a hook with a serrated margin. In the resting position the strut lies in a plane parallel to the radular membrane, the cusps at right angles to it (PLATE 39). Towards the lateral margins the length of the strut decreases, and the extreme edges the supporting strut is short; the transition is gradual,
however, and it would be difficult to define any line of demarkation between lateral and marginal denticles as is possible with *Lymnaea*. Although there is little inter-specific difference in denticle structure, the feeding traces of various planorbids (PLATE 35) indicate a difference in radula shape on initial contact with the substratum. The denticle structure is consistent with their being used for scratching the substratum in a superficial way. The long strut of the bulk of the denticles would enable the cusps to remain in contact with the substratum even if this were to be rough, but the shorter struts at the edge would presumably sacrifice some of their flexibility for strength, a supposition substantiated by the feeding traces, which were frequently thinner around the centre than at the edge, (PLATES 36, 37, 38).

*Ancylus* The radula is slightly V-shaped when isolated, and the strong denticles, (PLATE 34) appear to be abrasive. The V-shape appears to be retained whilst the radula is in contact with the substratum, since the pattern traced by the rows of denticles is this shape also. The distance apart of the etched lines remains constant, indicating that the radula is dragged evenly over the surface and that there is no denticle modification. There are approximately ten bands of parallel V marks, presumably indicative of alternate light and heavy pressure, (PLATE 35c). Pressure must be greater than in other pulmonates, since the short rachidian denticle is apparently in contact with the substratum and removes carbon, (PLATE 35c).
6.2 Relative radula size

The length of the radula may provide an indication of the amount of work involved in collecting food, and Fretter and Graham (1962) quote comparative ratios of radula length/shell length for several species of prosobranch derived from studies by Fischer-Piette (1935), Pelseneer (1935), Eslick (1940) and Evans (1953). Shell length, however, has been found to be a generally unsatisfactory parameter in comparative molluscan studies owing to interspecific differences in shell geometry (Calow, 1975a) and in the present study, the preserved wet weight was substituted for shell length in the calculation of the ratios. The results are presented in APPENDIX 15 and the means (in rank order) for the prosobranchs are:-

*Theodoxus* (137) *Potamopyrgus* (87) *Bithynia* (45) *Valvata* (17).

These results corroborate the observations on radula morphology and feeding traces which indicated that *Theodoxus* possessed the most strongly constructed denticles and those best suited to sweeping and rasping roles. The structure and relative length of the radulae of *Bithynia* and *Potamopyrgus* suggests that they perform similar roles to each other, but the traces (PLATE 41a and b) indicate that *Potamopyrgus* removes more carbon, possibly because it rasps with more pressure. Although the denticle components of the radula of *Valvata* are similar to those of *Bithynia* and *Potamopyrgus*, its relative length is very much shorter, indicating that it rasps with less pressure than the other species and that its food, or the substratum from which its food is taken, is softer.

The three pulmonate species investigated showed a similar progression, with *Ancylus* possessing the highest value by far in the sequence:-

*Ancylus* (267) *Lymnaea* (49) *Physa* (48).
The order is compatible with that which would have been produced on the basis of feeding traces, with *Ancylus* rasping the hardest, even the rachidian removing carbon. Parity between *Lymnaea* and *Physa* is somewhat surprising however, since the structure of the denticles of *Physa*, particularly their narrow stem, would suggest that they are incapable of rasping as hard as the lateral denticles of *Lymnaea*. It is possible, in view of the very different outline of the print, that the orientation of the odontophoral cartilage in *Physa* augments the pressure throughout the stroke, a situation analogous to the start of the stroke in *Lymnaea*, where the weaker marginal denticles are pressed into service and help to produce the characteristic semi-circular base to the print (PLATE 35a and b).
6.3 Feeding tracks

Feeding traces such as those described, more frequently than not form part of a feeding track which is zig-zag and characteristic of grazing gastropods (Ankel, 1938, Markel, 1958, Southward, 1962). In a previous study (Storey, 1971, PUBLICATIONS APPENDIX), on Lymnaea, a relationship was found between both the width of the track and the rate of progress, and the presence of food. In the absence of food the snails moved rapidly over the substratum, with a narrow zig-zag, alternating left and right in the manner Hubendick (1957) describes for Lymnaea stagnalis. On encountering food the track immediately broadens so that the pattern forms a series of arcs. This finding lead to the suggestion that in Lymnaea the substratum was tested ('tasted') by the alternate application of radula to left and right. On encountering food, the amplitude of the swing increases spontaneously as true feeding begins.

The results of the present study show that the wide feeding track of Lymnaea is found in all species studied with the exception of Theodoxus and Valvata (PLATES 40-42). Despite the fact that identically prepared substrata were presented to the snails, the amplitude of a single track was found to vary (e.g. PLATE 42a). It is possible that the degree to which the carbon was palatable to the snail varied or that some facet of the surface, the presence of bacteria for example, discernable to the snails prompted a change in swing amplitude. From observations through the glass aquarium wall, together with feeding tracks, it is tentatively suggested for all species except Theodoxus, and possibly Valvata which left no trace at all, that the food detecting mechanism is similar to that already described for Lymnaea, namely by contact chemoreception via the mouth. However, the obser-
observations that Theodoxus makes side-to-side movements of the head, unaccompanied by mouth movements, indicates that the site of chemoreceptors may be located elsewhere.
6.4 Discussion of results

From a study of the mouthparts during feeding, by examination of radula morphology, and by indirect methods using feeding traces some facets of the working of the mouthparts of the various species of watersnail were revealed. Aspects of ingestion providing a basis for inter specific differences were found to occur under the following headings:

1. Shape of the radula.
2. Number and structure of the denticles.
3. Spacing of the denticles and their orientation during feeding.
4. Pressure exerted by the radula on the substratum.

The radulae of many of the different species of gastropod from the River Hull are structurally different from each other and this may have functional implications with regard to the food taken in nature. Dentine specialisation could permit the different radulae to perform in different ways, and in species possessing different types on the same radula, division of labour is possible. This is particularly noticeable among the prosobranchs: less so the pulmonates where denticle specialisation was minimal. From the evidence available, denticles were capable of performing a number of roles, which are summarised with examples in FIG.66.

The operation of the buccal mass can be likened either to the arms of two rotary polishers or a flexible toothed file, the former analogy pertaining to the prosobranchs, the latter to the pulmonates. Of the prosobranchs only the radula of Valvata failed to make an impression on carbon, and coupled with the much lower radula length/body weight ratio is designated a sweeper. The combined action of the marginal and lateral denticles probably function in the same way as those of Bithynia and Potamopyrgus but with less pressure. The
cusps on the rachidian denticles of all three species seem to be concerned with grasping the material already removed from the substratum rather than with its actual removal, since no marks appear in traces in the position where they would be expected. This finding conflicts with the observations of Ankel (1938), who obtained traces of the rachidian denticle from other taenioglossan species feeding on algal-coated glass plates. In both Bithynia and Potamopyrgus there is evidence that the contacting marginal and lateral denticles do so with sufficient pressure to remove the carbon from a smoked slide for at least part of their sweep, although the overall impression is not as consistent as that from Theodoxus, and the amount of wear shown by these denticles is very small. The denticles of Theodoxus resemble the general plan described for Rhipidoglossa by Fretter and Graham (1962) except that the pair of lateral denticles is much more strongly constructed and more highly developed. As a consequence, the status of the animal could well be raised from detritivore, which typically bears sweeping denticles, to micro-herbivore, and it would not be surprising to find components in the gut more solid and recognisable than amorphous detrital material. It is interesting to note that although the pendulum movement of the head, characteristic of the other species, occurs in Theodoxus, the accompanying continuous radula action does not. This species seldom exposes more than the tentacles when active, and these make frequent contact with the substratum. These observations led to the tentative suggestion that Theodoxus detects food, presumably by means of chemoreceptors, located possibly in the tentacles.

Fretter and Graham suggest that the length of the radula is related to the amount of work which has to be done during feeding: where wear is extensive, a long radula is present, where less wear
occurs (because the food is softer) the length of the radula is much reduced. The lengths of the radulae considered in this study were largely within the range of those quoted for the same species in earlier studies (e.g. Verdcourt b, c, d, e), with the exception of Valvata, in which the values in the present study were lower than those in Verdcourt's study. The reason for this is that the mean size of Verdcourt's specimens was approximately 5 mm (shell height) whereas that of the present study lay between 3 and 4 mm. The rank order of all gastropods, as judged by their radula length/body weight ratios is:-

Ancylus, Theodoxus, Potamopyrgus, Lymnaea, Physa, Bithynia, Valvata,

but in view of the different modes of application of the radulae to the substratum in the two taxonomic groups, the combination of all species to form such a sequence may be questionable. Nevertheless, with the exception of Potamopyrgus, which on structural grounds would be expected to rasp with less pressure than the larger Lymnaea and possibly Physa, the sequence meshes comfortably with that which would be expected on the basis of structural and experimental grounds. Possible reconciliation of the differences is discussed in CHAPTER 8.

With regard to food detection, the evidence offered is that provided by the feeding tracks. In his review of chemoreception in gastropods, Kohn (1961) states that in the pulmonates which do not possess rhinophores, the structures most exposed to the environment are typically the tentacles, siphon and foot. Pieron (1908) offered experimental evidence suggesting that the anterior edge of the foot possessed a capacity to distinguish noxious from inert substances, a facility that the mouth did not possess. On this basis, he suggested that the primary site of chemoreception was the anterior
edge of the foot and that a reflex kept the radula working most of the
time. An alternative suggestion was put forward (Storey, 1971, PUBLI-
CATIONS APPENDIX) on the basis of feeding tracks, which explained the
continuous radula and mouth operation of *Lymnaea* during feeding as a
testing, or 'tasting' operation, which implies the presence of chemo-
receptors in the mouth. The feeding tracks of all species made
during the present study, except *Theodoxus* are compatible with both
hypotheses. The materials used by Pieron (1908) were however not
specifically related to the actual foods encountered in nature, and
Carriker (1946) reported that there were distinct periods during which
the radula of *Lymnaea stagnalis* did not operate. The work of Bovbjerg
(1965, 1968) indicated that aggregations of the pulmonate *Stagnicola*
reflexa on filamentous alga could be explained in terms of a "kinesis
to optimum", the snails detecting plant food by contact chemoreception.
Townsend (1973) has criticised the lack of sensitivity of the technique
of Bovbjerg, and has found that some species of snail detect plant food
at a distance, albeit a short distance, using a tactic response rather
than by kinesis. Townsend also suggested the possibility that the
pendulum movement of the head during feeding could be involved in such
a tactic response and that synchronised mouth movements indicated that
this could be the site of chemoreceptors. Evidence in support of this
suggestion is provided by Nisbet (1953) who indicated that chemoreceptors
are present within the buccal cavity of *Monodonta lineata* (da Costa).
It therefore seems possible that the behaviour of the gastropods of this
present study on the basis of their feeding tracks, was part of some
food-searching quest involving a "tasting" response. The behaviour of
*Theodoxus*, particularly the lack of continuous radula action, and the
frequent contact by the tentacles with the substratum is not compatible
with this hypothesis. The presence of chemoreceptors of one type in
a certain part of the body does not preclude the possibility of others
elsewhere. It seems quite possible that chemoreceptors located in different parts of the body may differ in their specificity.

Differences between the spacing of adjacent denticles is probably much less significant with regard to diatoms and unicellular algae than bacteria, since very few algal or diatom types could slip between the narrow gaps shown on the feeding traces. By far the majority of aquatic bacteria are saprophytic on dead material of plant or animal origin and therefore frequently occur in aggregations associated with detritus particles (Rheinheimer, 1974). Individual bacteria, small enough to escape the attention of the radula would therefore be the exception, rather than the rule. The relative pressure exerted by the radula and buccal mass may be more important, since material adhering tightly to the substratum could escape the attention of the radula in cases where the denticles sweep only lightly over the surface.

The length of the denticles and their shape is also thought to be important in governing the potential food ingested. The depth of penetration into a substratum is presumably governed to a large extent by the size of the vertical component of the denticle, which is small in all pulmonate species except Physa and Lymnaea, since in nearly all other species the denticles are short or hooked. The shape of the radula of these two species is complex and the area covered per bite is larger than other pulmonate species. The pronounced horse shoe shape may be significant. Runham (1969) has described a similar shape for Agriolimax reticulatus which he has found makes it possible, when combined with strong, cutting teeth for the animal to penetrate and remove the plant tissue, rather than slide along its surface. The radula size and shape, both in Lymnaea and Physa bear resemblance to that of Agriolimax but with regard to
the denticles, only those of *Lymnaea* could operate functionally in
the same fashion, the denticles of *Physa* being solely of the sweeping
and fine rasping type, probably incapable of penetrating anything but
the most fragile of plant tissue. Differences of this type would not
be apparent when the snails were browsing stones or other impenetrable
surfaces, so that the substratum, as well as the food it harbours, may
exert an influence on the type of food ingested.

Suggestions for possible foods of the snails, based on radula
studies alone, cannot be too specific. The fact that little, or no
morphological and spatial difference occurs between denticles is not
to say that no selection is possible. Within the limits imposed by
their radula structure, snails may well be exercising discretion over
the type of material they ingest on the basis of its taste, texture
or some other criterion. Moreover, the radula is not the sole food
gathering organ, at least in all species. The ability of several
freshwater prosobranchs to filter material held in suspension in the
water has been shown by Schäfer (1952), Lilly (1953) and Cleland (1956).
That this material is ingested and can alone supply the total nutri-
tional needs of the animal has been established by Tsikhon-Lukanina,
(1961) for *Bithynia tentaculata*, and *Valvata piscinalis*. Moreover,
Zylstra, (1972) has shown that the pulmonate *Lymnaea stagnalis* can
take in particulate matter directly via the epidermis by pinocytosis.
7.1 Faeces production under field conditions

Casual observations, during field work at night, suggested an increased activity level of *Potamopyrgus jenkinsi* and *Theodoxus fluviatilis*. Both species were found attached to the submerged parts of sampling apparatus when this was left standing temporarily in the water at night, an occurrence less apparent during daylight. The possibility that such activity could be related to feeding is supported by the quantity of faeces produced during the two periods. The results (APPENDIX 16 and FIG.67) which were obtained for each species during consecutive periods within 24 hours in the field, show a clear difference between these two species compared with *Bithynia tentaculata* and all the pulmonates which produced faeces in approximately equal quantities, irrespective of daylight.
7.2 Diurnal activity patterns

The casual field observations, in which Theodoxus and Potamopyrgus appeared to be more active during the night than by day, were confirmed for Theodoxus by recording the mean distance travelled under controlled laboratory conditions. No experiments of this sort were conducted on Potamopyrgus. The results (APPENDIX 17(a) show that there is a difference between the mean distance travelled by Theodoxus in darkness, compared with the light. These differences are significant ("t" test, p<0.05). For Lymnaea peregra the trend is reversed, with the mean distance travelled during the light period being significantly greater (p<0.001) than that travelled during darkness (PLATE 24 and APPENDIX 17(b)).
7.3 Discussion of results

The results, both of faeces production and locomotory activity, suggest that *Theodoxus* forages and feeds at night, rather than during the hours of daylight. Despite the fact that all sets of results were derived from snails in aquaria and which were therefore isolated from the flow, the behaviour between the trial periods produced clearly defined differences, suggesting that light rather than flow was of prime importance in determining the behaviour patterns observed. The fact that the activity experiments were all conducted during daylight hours, the cabinet timer being adjusted so that its light and dark periods were out-of-phase with natural day-night regime also suggested that it was the direct influence of light or darkness that prompted the behaviour of *Theodoxus*, rather than some endogenous biorhythm. Although no activity experiments were performed on *Potamopyrgus*, it seems probable, in view of the faeces results, that it too feeds and chiefly forages during darkness. The behaviour of the pulmonates *Lymnaea peregra*, *Ancylus fluviatilis* and *Physa fontinalis* and of *Bithynia tentaculata* is quite different, in that the quantity of faeces they produced was not affected by the day-night regime. Additional locomotory experiments conducted on *Lymnaea* only, did not totally corroborate these findings, but suggested that *Lymnaea* was active (i.e. travelling the furthest distance) during the light period. This could indicate constant feeding (or constant gut movement) but intermittent foraging activity. It is also possible, in view of the fact that the same snails were used in both experiments, that handling during the first trial affected the behaviour of the second. If the behaviour was in fact due to increased foraging activity, perhaps in an attempt to seek optimal feeding sites, then the diurnal
pattern of *Lymnaea* and *Theodoxus* complement each other. The indirect evidence of faeces production would in any case reduce the overlap between the species combination *Theodoxus-Potamopyrgus* and *Bithynia-Ancylus-Lymnaea-Physa*. Observations on diurnal activity of water-snails are reported by Calow (1975b) on *Ancylus* and Fretter and Graham (1978) on *Theodoxus* and both are consistent with the results of the present study. The study of Calow (1975b) was based on faeces collections, whilst that of Fretter and Graham (1978) included the general observations of Heywood (1961).

In some respects, it is the behaviour of the pulmonates and *Bithynia* that is unusual. Aquatic invertebrates are generally more active at night (Clifford, 1972) and terrestrial pulmonates, too, tend to be nocturnal (Newell, 1966) although the latter may be a response to increased humidity rather than reduced light intensity, (Lewis, 1969). No clear reason emerges for the activity of the pulmonates and *Bithynia* during daylight, for even though some have behavioural defence mechanisms (e.g. *Physa*, (Townsend and McCarthy, 1980) all species have similar protective shells for defence against predators.
CHAPTER 8

General discussion
8. General discussion

Theoretically, there must be a minimum ecological difference between resource limited species if they are to coexist in the same community (May and MacArthur, 1972). The observations in the present study show that gastropods in the River Hull, and particularly at Hempholme Lock, its tidal limit, exhibit differences along several resource dimensions. Distribution patterns suggest that most gastropod species overlap spatially only for relatively short periods during the year. This was true at all observational levels, from the zonation in the river as a whole (CHAPTER 2), to micro-dispersion patterns within a zone (CHAPTERS 3 and 4). Seasonal displacement of certain species (CHAPTER 3 and CHAPTER 4, section 2.d) and probable diurnal feeding patterns (CHAPTER 7) provided further ecological distinctions and even when the snail species overlapped in time and space, there is some evidence of dietary separation between them (CHAPTER 5, section 3). The major features of these ecological differences are summarised diagrammatically, in a set mode of representation (Hutchinson, 1957), in FIG.68. Discussion of the separate facets is presented under the relevant chapter headings, however some areas of investigation corroborate the findings in other areas and these are united in the following section, together with concluding comments on the interpretation of the study as a whole in the light of the competitive exclusion principle.
8.1 Spatial separation and diet

The results of the diet study (CHAPTER 5) suggest that despite the wide range of food materials found in the guts of many gastropods, the proportions of these vary from species to species, a feature that is particularly noticeable during periods of spatial overlap. There are some indications, however, that the diet differences may reflect habitat differences rather than strict dietary preferences. The diet of Ancylus, for example, remained remarkably stable. The dispersion pattern of this species (CHAPTERS 2, 3 and 4, section 1 indicates that it is usually found on the exposed parts of rocks in the flowing water, and there is some evidence (CHAPTER 5 and Calow, 1973a) that these are also the sites where the preferred food is found. Most other species removed from rocks for gut analysis at the same time, and showing different proportions of the epiphyton would, from the evidence on their distribution in this study, have been confined to the more sheltered parts of the rocks, out of the immediate influence of the current. Different spatial patterns, correlated with different gut contents, have been discovered for Ancylus and Bathyomphalus contortus (Calow 1974b) Ancylus and Lymnaea peregra (Reavell, 1980) and Viviparus viviparus and the pulmonate species Lymnaea stagnalis, Planorbis carinatus and Anisus vortex (Reavell, 1980). The first example (Calow, 1974b) indicates that for certain water bodies, particularly lotic ones, the flow dictates the spatial position of the snails, and by doing so imposes dietary restrictions on certain species. This cannot be the total picture, however, since when kept under identical conditions in the laboratory, Ancylus still selects diatoms and Bathyomphalus still selects detritus (Calow, 1973a). Under certain exceptional conditions, however, food becomes of secondary importance. Russell-Hunter (1953)
has shown how juvenile *Lymnaea peregra* in Loch Lomond migrate to the water's edge so that their respiratory needs can be satisfied, even though this removes them from their food supply.

The fluctuations of the flow at Hempholme Lock, and the consequent large species diversity this produced led, during one summer period of low flow, to the colonisation by many different gastropods, of the *Fontinalis*-covered rocks. This is an area from which, during periods of high flow, most species would normally have been excluded (CHAPTER 3, section 1 and CHAPTER 4, section 1). This situation which at Hempholme is not exceptional, produced evidence of resource partitioning that was probably not due to microdistribution differences, since *Fontinalis antipyretica* has a relatively homogeneous morphology and therefore probably offers less opportunity for microdistribution patterns within it. Although resource partitioning has been shown to occur in relatively homogeneous habitats elsewhere, these reports are from marine environments and involve predatory gastropod species (e.g. Paine 1963). In the present study the differences in gut contents of the various species can be explained in three ways.

The first makes the assumption that no change in behaviour has occurred and that differences that were observed reflect differences along one aspect of the feeding niche dimension, e.g. food preference or possibly radula differences. The observed coexistence, albeit temporary, can then be explained by the coming together of a random association of species with complementary characteristics. This explanation of resource partitioning is more likely to apply to distantly related species (Townsend and Hildrew, 1979,b).

The second explanation, more characteristic of congeners, or closely related species, involves a change in structure or behaviour (a character displacement) in response to competitive pressure. Such
changes have been reported as occurring in hydrobiid snails (Fenchel, 1975). Although at the time there was little definitive evidence, Weatherley (1972) quotes Hartley (1948) as suggesting that a tendency to change the proportions of dietary constituents is a major method by which fish avoid direct competitive clashes. In potentially competitive situations, the concept of some species seeking alternatives to their preferred food (i.e. a "food refuge") is attractive, and one, it has been suggested, that facilitates coexistence in some freshwater invertebrates including triclads (Reynoldson and Davies, 1970) and net-spinning caddis (Townsend and Hildrew, 1979,8). In view of the apparent plasticity of feeding habit of some species reported in the literature, this explanation is one which could well apply to freshwater gastropods.

Finally, it is also possible, despite the apparently homogeneous structure of Fontinalis, that the differences in diet may be a reflection of unobserved microhabitat selection. Such explanation would then be compatible with the compression hypothesis of MacArthur and Wilson (1967), which predicts that in the presence of competitors, species should become more specialised in their use of habitats rather than their diets.

It seems quite probable that critical experimentation could shed some light on which of these explanations best explains the dietary differences during this period at Hempholme Lock. An experimental approach was beyond the scope of the present study, but the fact that resource partitioning was observed is of significance, even though the precise reasons for its occurrence remain unresolved.
8.2 Radula, diet and substratum

Differences in radula structure were apparent, providing the potential for the organ to be used in different ways (CHAPTER 6). Given the fact that different feeding appendages are possessed by various aquatic invertebrates, it is not surprising that some authors have suspected that these could be links between certain invertebrate taxa and particular fractions of the periphyton. Allanson (1973) for example stresses the importance of complex substratum-periphyton relationships revealed by scanning electron microscope study and those of Wetzel Allen (1970) and Allen (1971). Despite radula differences, the results of gut analysis in the present study revealed a lack of narrow diet specialisation. Generally, the radulae of aquatic gastropods are used for the same basic purpose, which is to remove the material coating the surface where the animals feed. The only evidence for possible selection by the radula of particular fractions of the periphyton was the occasion when several snail species were grouped on Fontinalis antipyretica (CHAPTER 5, section 3). The tendency in this instance for Bithynia to take more stalked diatoms than the pulmonates could be attributed to the structure and mode of application of the lateral and marginal denticles of the taenioglossan radula, which act in a horizontal scything action, rather than the rasp-like abrasion of the pulmonates. The former action may be more effective in separating the main body of diatoms from their stalks, whereas unstalked species, being more closely applied to the substratum are left unmolested until they receive the coarser, more abrasive treatment of the pulmonate radula. This must be a very tentative suggestion, however, in view of the lack of corroborative experimental evidence. In this respect very little supportive
evidence is provided in the published literature, since in studies of diatom selection, such as those of Calow (1973a, 74a) the food was presented on membrane filters. It was thus chemical, i.e. 'taste' selection which was being tested, rather than different radula capacity when foods are being presented in this way. In view of their relative permanence, submerged rocks are more likely than plants to build up periphyton complexes (Allanson, 1973), and Calow (1973d) has suggested that the selection of certain diatoms in the field by Ancylus, may be due partly to their position in such complexes. More definite evidence for differential use of the radula by the weed-dwelling species is provided by Lymnaea peregra, which was the only species, removed from Fontinalis beds, to consume large quantities of the actual moss tissue, rather than the periphyton it supported. The structure of the radula of Lymnaea bears more resemblance to that of terrestrial herbivorous gastropods, than the other pulmonates in this study. An earlier report (Storey, 1970) suggested that inorganic particles found in the gizzard of Lymnaea peregra serve to comminute macrophyte tissue, and it may thus be significant that of the weed-dwelling species, Lymnaea possessed the most discernable gizzard and the largest quantity of inorganic grit. In view of their ability to consume fresh macrophyte tissue and their capacity to survive periods of dryness (Storey 1972) Lymnaea peregra seems to have travelled less far along the path to aquatic re-adaptation than the other pulmonates in this study.

Morphological differences can be used as indicators of position along resource dimensions and the commonest indicator is the size of feeding structures (Schoener, 1971, 74). These are usually correlated with mean food size, or in the case of molluscs, with the work done during feeding (Fretter and Graham, 1962). The sequence of the
gastropods in this study as determined by the radula length/body weight ratio was compatible with considerations both of structure and pressure exerted on the substratum (CHAPTER 6). It is perhaps significant that an even closer correlation was found between the radula size ratios and the sequence of flow resistance derived from the first and second levels of abstraction (CHAPTERS 2 and 3). Flow is extremely important in determining the nature of the substratum, with the hard rock changing to silt in a progressive downstream sequence. The closer matching of the sequences of flow resistance and radula length indicates that the radula length is dictated by the substratum from which the food is taken, rather than the nature of the food itself.
8.3 Spatial distribution and feeding activity

The observations at the third level of abstraction (CHAPTER 4, section 1.b.) concerning the migration of *Theodoxus* from the underside of stones where it appears to spend much of the daylight hours, to the top and sides where it occurs at night are consistent with the activity patterns described in CHAPTER 7, and confirm that this species is largely nocturnal in habit. Although the faeces production of *Potamopyrgus* was greater at night, suggesting that this species too was nocturnal, no experiments were conducted on its locomotory patterns to confirm that this was so. Nor did the microdistribution patterns indicate that *Potamopyrgus* shuns light by migrating to the undersides of stones during daylight. The phasic differences in faeces production of both *Theodoxus* and *Potamopyrgus* compared with *Ancylus*, which appeared to produce faeces irrespective of daylight, does, however, suggest a diurnal separation in feeding activity in this group of flow-tolerant species. This separation could be another factor that relieves potential niche overlap of these species on the rocky substratum, and is one which is apparently common in terrestrial poikilotherms (Schoener 1974).
8.4 Conclusions

Although a number of ecological distinctions between the various gastropods have been observed, there is no certainty that all of these are crucial for their coexistence. In the light of the Hutchinson hypervolume niche theory, it is probable that the snails are separate along other niche dimensions, particularly behavioural ones, that were not investigated during the present study. Competition theory, however, relates only to resource-limited species, and there are a number of ways whereby the populations could be reduced to a level below which competition need not occur. In this event, apparent niche separation may be unrelated to competition (Wiens, 1976) and it seems appropriate that some discussion of alternative possibilities should receive at least cursory consideration.

The River Hull is subject not only to natural climatic fluctuations, but to sudden and sometimes catastrophic changes produced by man. Goulder (1974) has indicated how oxygen depletion, due to pollution and turbidity affects the growth and abundance of bacteria in the River Hull, and dramatic changes in the invertebrate fauna as a result of manipulation of the weir, and weed-cutting are reported by Pearson (1974). These influences could serve to reduce the size of gastropod populations to below the level where interspecific competition would occur, although there are some areas of the river which are more stable, where this would not apply.

Competition for resources is not limited to interspecific competition between gastropods. Diatoms, for example, form the major dietary component of a large number of aquatic animals, including insect larvae (Douglas, 1958) crustacea (Harvey, 1955) and fish, (Velasquez, 1939, Fish 1950). Of these, the invertebrates
are likely to overlap with gastropods along other resource dimensions and the possibility of interactions between such taxa is one which has been totally unexplored in the present study.

Predation provides another natural means of limiting population growth and birds, fish and a number of invertebrates, particularly leeches, are known to prey on gastropods (Boycott, 1936). Examples of most of these predators are present along the course of the River Hull (Pearson, 1974) and some have been shown to feed on certain snails (Whitehead, 1935). There is some evidence that predation may be a significant factor in determining the structure of gastropod communities elsewhere. De Bernardi et al. (1976) have suggested that differences in the proportions of gastropods in Lake Alserio are the result of differential predation by ducks.

The occurrence of competition in natural situations is notoriously difficult to demonstrate (Pianka, 1966) and simple niche overlap can be used as evidence both for and against its occurrence (Colwell and Futuyama, 1971). The importance of interspecific competition in determining community structure of gastropods has been shown in studies by Lassen (1975) mentioned earlier. Harman (1968) described how Bithynia tentaculata has replaced the native pleurocerid species in areas around New York.

Dupouy et al. (1980) report severe competition between prosobranch and pulmonate species in north-west Algeria, and Graber (1900), Madsen (1979) have demonstrated its effect in laboratory cultures of other gastropods. Interspecific competition therefore appears to play a role in the evolution of some gastropod communities and may well be exerting an influence in the River Hull. Without critical experiments, even short-term competitive encounters cannot be shown to occur, and whether 'proof' of long-term competitive theories can satisfactorily be achieved
is problematical. The results of the present study, whilst not identifying the precise reasons, do, nevertheless demonstrate that the gastropods in the River Hull system seldom overlap, strictly, along the vital niche dimensions of space, time and food. The many examples cited by Schoener (1974) in his review of resource partitioning, showed that overlap along one niche dimension is generally compensated by lack of overlap along another, which facilitates coexistence and does not lead to extinction. The results of the present study mesh comfortably with this theory and provide a plausible explanation for the original problem of incompatibility between the principle of competitive exclusion and the co-occurrence of so many gastropods in the River Hull system.

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A study of co-existence of gastropods in the River Hull system

Volume II

Contents

FIGURES .............................................. 182 - 253

TABLES .............................................. 254 - 262

PLATES .............................................. 263 - 309

APPENDICES ............................................. 310 - 342

PUBLICATIONS APPENDIX ......................... 343 - 362
FIG. 1. The River Hull valley

This figure shows the origins of the River Hull, the main place names referred to in the text, but the main drains have been omitted for the sake of clarity.
FIG. 2. Current speeds and direction of flow above and below Hempholme, the tidal limit of the River Hull. (September 1981)
FIG. 3. The River Hull System

Broken lines indicate man-made drains.
FIG. 4. Hempholme Lock  (a) Plan  (b) Sections

The walls are vertical, reinforced metal from the weir as far as the points labelled "R". Interrupted lines indicate the limits of the original brick foundations.

hwm  high water mark (winter)
lwm  low water mark (late summer)
FIG. 5. Current speeds at various stations at Hempholme Lock. The flow over the weir was 91 m.g.day$^{-1}$, and the stations are approx. 1 M. apart.
FIG. 6. Mean monthly values of various physical and chemical parameters of the water at Henpholme Lock during the period 1974-76. Vertical bars indicate maxima and minima.
FIG. 7. Changes in dissolved oxygen at various positions at Hempholme Lock over a 24 hour period. (August, 1975)
FIG. 8. Map of the River Hull System showing the distribution of sample sites. Photographs of selected sites are presented in PLATES 1-23 and Grid references in APPENDIX 1. Scale and orientation are identical to FIG. 3.
FIG. 9.

Complete species list of all gastropods in the River Hull system, based on collections from 1974-79. Unless stated otherwise, all species were recovered during a single sample period, August-September, 1979.

<table>
<thead>
<tr>
<th>Class</th>
<th>Order</th>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gastropoda</td>
<td>Prosobranchia</td>
<td>Neritidae</td>
<td><em>Theodoxus fluviatilis</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Valvatidae</td>
<td><em>Valvata cristata</em> MÜll.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>piscinalis</em> (MÜll.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hydrobiidae</td>
<td><em>Potamopyrgus jenkinii</em> (Smith)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bithyniidae</td>
<td><em>Bithynia tentaculata</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Euthyneura</td>
<td>Physa fontinalis (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Lymnaea truncatula</em> (MÜll.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>†<em>palustre</em> (MÜll.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>†<em>stagnalis</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>†<em>peregra</em> (MÜll.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Planorbidae</td>
<td><em>Planorbis planorbis</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>†<em>carinatus</em> MÜll.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>†<em>Anisus leucostoma</em> (Millet)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>†<em>vortex</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Bathyomphalus contortus</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td><em>Gyraulus albus</em> (MÜll.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>†<em>Arminia cristata</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>†<em>Hippelis complanatus</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ancyliidae</td>
<td><em>Ancylus fluviatilis</em> MÜll.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Acroloxidae</td>
<td><em>Acroloxus lacustris</em> (L.)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Succinea pfeifferi</em> Rossmässler</td>
<td></td>
</tr>
</tbody>
</table>

* Regarded as not truly aquatic

† Occurred only in second level samples at Hempholme Lock
FIG. 10  Percentage of sites at which the various species of gastropod occurred in the first level study.
The species are presented in rank order.

<table>
<thead>
<tr>
<th>Species</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lymnaea peregra</td>
<td>53.0</td>
</tr>
<tr>
<td>Potamopyrgus jenkinsi</td>
<td></td>
</tr>
<tr>
<td>Physa fontinalis</td>
<td>31.7</td>
</tr>
<tr>
<td>Ancylus fluviatilis</td>
<td>26.7</td>
</tr>
<tr>
<td>Valvata piscinalis</td>
<td>21.7</td>
</tr>
<tr>
<td>Bithynia tentaculata</td>
<td>15.0</td>
</tr>
<tr>
<td>Planorbis planorbis</td>
<td></td>
</tr>
<tr>
<td>Anisus vortex</td>
<td>8.3</td>
</tr>
<tr>
<td>Bathymphalus contortus</td>
<td></td>
</tr>
<tr>
<td>Anisus leucostoma</td>
<td>6.6</td>
</tr>
<tr>
<td>Gyraulus albus</td>
<td>5.0</td>
</tr>
<tr>
<td>Theodoxus fluviatilis</td>
<td></td>
</tr>
<tr>
<td>Valvata cristata</td>
<td>3.3</td>
</tr>
<tr>
<td>Lymnaea stagnalis</td>
<td></td>
</tr>
<tr>
<td>Acroloxus lacustris</td>
<td>1.7</td>
</tr>
<tr>
<td>Sites</td>
<td>number of species</td>
</tr>
<tr>
<td>-------</td>
<td>------------------</td>
</tr>
<tr>
<td>16</td>
<td>11</td>
</tr>
<tr>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td>39</td>
<td>7</td>
</tr>
<tr>
<td>47</td>
<td>13</td>
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<tr>
<td>48</td>
<td>15</td>
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<td>56</td>
<td>23</td>
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<td>12</td>
<td>27</td>
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<td>21</td>
<td>4</td>
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<td>51</td>
</tr>
<tr>
<td>29</td>
<td>3</td>
</tr>
<tr>
<td>42</td>
<td></td>
</tr>
</tbody>
</table>

**FIGURE 11**  Species diversity at the sample sites on the River Hull system.
FIG. 12. Map of the River Hull system showing the number of different gastropod species recovered at each sample site.
FIG. 13. Dendrogram resulting from normal analysis of data.
Gastropod species act as indicators of site groupings.
FIG. 19. Dendrogram resulting from inverse analysis of data. Sites are used as indicators of species groupings.
FIG. 20. The relationship between plant species diversity and gastropod species diversity. These data from 47 sites on the River Hull system.

Correlation coefficient $r = 0.79$
FIG. 21. Overall relative abundance of major species of gastropod at Hempholme. (Summed results of all samples from 1974-76, APPENDIX 3).
FIG. 22. Gastropod numbers, expressed on a logarithmic scale, in rank order. The data were derived from the pooled samples over three years (1974-76) at Hempholme Lock. (APPENDIX 3).
FIG. 23. Dendrogram showing the relationship between the various sites at Hempholme Lock. (Data from APPENDIX 4)
FIG. 24. Hempholme Lock with rocky zone, weed beds and positions of 10 samples taken in April 1974.
FIG. 25(a) Samples ordinated along an axis defined by two end point samples. 22 samples have been ordinated along an axis of length 93.7 units between samples 7 and 20 by distance values (100-% similarity) from end point samples. These are derived from the raw data (APPENDIX 3) converted to a primary matrix of abundance (APPENDIX 5a) and a secondary matrix of sample similarities (APPENDIX 5b, and METHODS, CHAPTER 1.4.c).

(b) Completed ordination, along one dimension, of all sites. Circles indicate weed/silt samples, diamonds indicate rock samples.
FIG. 26. Kendall’s Rank correlation coefficient.

In each monthly sample, the pooled collections from rocks are compared with those from weed/silt.

(Data from APPENDIX 3)

<table>
<thead>
<tr>
<th>Sample date</th>
<th>s</th>
<th>n</th>
<th>$\gamma$</th>
<th>p</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 1974</td>
<td>13</td>
<td>12</td>
<td>0.1969</td>
<td>0.1867</td>
<td>different</td>
</tr>
<tr>
<td>June 1974</td>
<td>32</td>
<td>13</td>
<td>0.410</td>
<td>0.025</td>
<td>same</td>
</tr>
<tr>
<td>October 1974</td>
<td>40</td>
<td>13</td>
<td>0.5128</td>
<td>0.005</td>
<td>same</td>
</tr>
<tr>
<td>February 1975</td>
<td>14</td>
<td>11</td>
<td>0.2545</td>
<td>0.1401</td>
<td>different</td>
</tr>
<tr>
<td>April 1975</td>
<td>30</td>
<td>12</td>
<td>0.4545</td>
<td>0.020</td>
<td>same</td>
</tr>
<tr>
<td>June 1975</td>
<td>10</td>
<td>10</td>
<td>-</td>
<td>0.19</td>
<td>different</td>
</tr>
<tr>
<td>October 1975</td>
<td>32</td>
<td>11</td>
<td>0.5818</td>
<td>0.0064</td>
<td>very similar</td>
</tr>
<tr>
<td>*February 1976</td>
<td>13</td>
<td>9</td>
<td>-</td>
<td>0.09</td>
<td>different</td>
</tr>
<tr>
<td>*April 1976</td>
<td>7</td>
<td>11</td>
<td>0.127</td>
<td>0.2946</td>
<td>different</td>
</tr>
<tr>
<td>*June 1976</td>
<td>6</td>
<td>7</td>
<td>-</td>
<td>0.1</td>
<td>different</td>
</tr>
<tr>
<td>October 1976</td>
<td>30</td>
<td>9</td>
<td>-</td>
<td>0.00043</td>
<td>very similar</td>
</tr>
</tbody>
</table>

* Very little/no weed, therefore count low.
Weed beds rock samples show no significant difference.

Total snail numbers below 50.

Weed beds rock samples significantly different.

FIG. 27. The collections of snails from the weeds compared with the rocks during different flow regimes at Hempholme Lock. (Samples compared using Kendalls Rank correlation coefficient - FIG. 26)
FIG. 28. Relation abundance (% numbers) of the various gastropods at Hempholme Lock on (a) Rocks and "Weeds and silt. 
FIG. 29. Size-frequency histograms and standardised density estimates on both weed and rocks, of 4 species of gastropod at Hempholme Lock.

a) Physa fontinalis

b) Lymnaea peregra

c) Anisus vortex

d) Potamopyrgus jenkinsi

KEY
- M March
- A April
- J June
- O October
- F February
- NR No record
- *** Sample too small to permit analysis
- Weed/silt samples
- Rock samples
FIG. 30. Standardised density estimates and size distributions of (a) Theodoxus fluviatilis and (b) Bithynia tentaculata from Hempholme lock.
FIG. 32. Size-frequency histograms of the three commonest gastropods in Barmston Drain between May and September 1979. The shading in (c) denotes the probable generations.

(a) Lymnaea peregra

(b) Physa fontinalis

(c) Bithynia tentaculata

Numbers too low to permit analysis
FIG. 33. The relative abundance of snail species from Barmston Drain expressed (a) as biomass (b) as numbers.
FIG. 34. The relative frequencies of the gastropods on stones at Hemp-holme Lock (site 16) during July, 1979, (20 bricks). The absolute densities and list of species included under "rest" are presented in FIG. 35 below, (from APPENDIX 6).

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (No./m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Potamopyrgus jenkinsi</td>
<td>1950</td>
</tr>
<tr>
<td>Theodoxus fluviatilis</td>
<td>212</td>
</tr>
<tr>
<td>Ancylus fluviatilis</td>
<td>74</td>
</tr>
<tr>
<td>Bithynia tentaculata</td>
<td>12</td>
</tr>
<tr>
<td>Acroloxus lacustris</td>
<td>11</td>
</tr>
<tr>
<td>Physa fontinalis</td>
<td>10</td>
</tr>
<tr>
<td>Lymnaea peregrae</td>
<td>3</td>
</tr>
<tr>
<td>planorbids</td>
<td>3</td>
</tr>
</tbody>
</table>

FIG. 35. Density measurements: The figures are the total number of each species/surface area of 20 bricks, (from APPENDIX 6).
FIG. 36. Distribution of 'rock' species with reference to distance from the weir. Vertical bars indicate 95% confidence limits. (Raw data presented in APPENDICES 6 & 7).
Flow over weir 90 m.g.d.

<table>
<thead>
<tr>
<th>Pillar no.</th>
<th>Water depth (cm)</th>
<th>Current speed cm.Sec(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15.5</td>
<td>17.1</td>
</tr>
<tr>
<td>2</td>
<td>15.5</td>
<td>15.7</td>
</tr>
<tr>
<td>3</td>
<td>15.0</td>
<td>14.2</td>
</tr>
<tr>
<td>4</td>
<td>17.75</td>
<td>8.2</td>
</tr>
<tr>
<td>5</td>
<td>25.4</td>
<td>11.2</td>
</tr>
<tr>
<td>6</td>
<td>28.0</td>
<td>12.7</td>
</tr>
<tr>
<td>7</td>
<td>36.0</td>
<td>11.2</td>
</tr>
<tr>
<td>8</td>
<td>48.3</td>
<td>11.2</td>
</tr>
<tr>
<td>9</td>
<td>52.9</td>
<td>6.5</td>
</tr>
<tr>
<td>10</td>
<td>58.3</td>
<td>6.5</td>
</tr>
<tr>
<td>11</td>
<td>64.5</td>
<td>4.9</td>
</tr>
<tr>
<td>12</td>
<td>73.0</td>
<td>4.9</td>
</tr>
<tr>
<td>13</td>
<td>78.0</td>
<td>4.9</td>
</tr>
<tr>
<td>14</td>
<td>86.0</td>
<td>8.2</td>
</tr>
<tr>
<td>15</td>
<td>87.0</td>
<td>4.9</td>
</tr>
</tbody>
</table>

**FIG. 37.** Variation in current speed and water depth with increasing distance from the weir. The measurements were made at a distance of one metre from the edge, 10 cm. below the surface.
FIG. 38. $\chi^2$ values of stone aspect (top or bottom surface)

Null hypothesis, distribution equal on top and bottom.

<table>
<thead>
<tr>
<th></th>
<th>DAY</th>
<th>NIGHT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ancylus</td>
<td>$\chi^2 = 4.446$</td>
<td>$p &lt; 0.05$</td>
</tr>
<tr>
<td>Theodoxus</td>
<td>$\chi^2 = 58.33$</td>
<td>$p &lt; 0.001$</td>
</tr>
<tr>
<td>Potamopyrgus</td>
<td>$\chi^2 = 380.0$</td>
<td>$p &lt; 0.001$</td>
</tr>
</tbody>
</table>

All top surface

$\chi^2 12.5$ $p < 0.001$

$\chi^2 238.54$ $p < 0.001$

(Data from APPENDIX 7)

FIG. 39. Densities of snails on different stone aspects. (Day)

<table>
<thead>
<tr>
<th></th>
<th>Ancylus</th>
<th>Theodoxus</th>
<th>Potamopyrgus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top</td>
<td>93.41</td>
<td>148.09</td>
<td>2597.40</td>
</tr>
<tr>
<td>Sides</td>
<td>75.57</td>
<td>128.47</td>
<td>1642.10</td>
</tr>
<tr>
<td>Bottom</td>
<td>54.68</td>
<td>423.78</td>
<td>875.80</td>
</tr>
</tbody>
</table>

Densities are expressed as no. snails/m$^2$.

(Data from APPENDIX 7)
FIG. 40. The relationship between the mean number of snails supported by stones of different sizes. (Data from APPENDIX 8).
FIG. 40. The relationship between the mean number of snails supported by stones of various sizes.

(c) Ancylus

STONE SIZE CATEGORY (cm)
(max length)

MEAN SNAIL NOS. PER STONE

10-59  60-109  110-159  160-209  210-259
FIG. 41. Relationship between the mean ($\bar{x}$) and variance ($S^2$) for Potamopyrgus jenkinsi.

A - E are increasing stone sizes categories, very small-bricks. (Actual sizes tabulated in methods).

P denotes the Poisson distribution.
FIG. 41. Relationship between the mean number of snails/stone ($\bar{x}$) and the variance ($s^2$) for Theodoxus fluviatilis.

A - E are increasing stone size categories, very small - bricks (Actual sizes tabulated in methods, APPENDICES 4 - 6).

P denotes the Poisson distribution.
FIG. 42. Relationship between the mean no. snails/stone ($\bar{x}$) and the standard deviation. ($s = \sqrt{s^2}$) for the 5 stone categories A-E.
FIG. 42. Relationship between mean no. snails/stone (\( \bar{x} \)) and the standard deviation (\( S\sqrt{S^2} \)) for the 5 stone categories A - E.
FIG. 43. Relationship between solution lost and period of shaking
(Each point is the mean of 5 replicates) Data derived from
APPENDIX 9. Similar curves resulted when Cladophora sp. and
Veronica were treated in the same way, but these are not presented.

a Myosotis scorpiodes

b Callitriche sp.
FIG. 44. Typical trace of a sample of *Myosotis scorpiodes*, used in the standardised area calculations.
FIG. 45. Relationship between the surface area of plants and the weight of a film of standard 'Tween' solution it supports.
FIG. 45. Relationship between the surface area of plants and the weight of a film of standard 'Tween' solution it supports.
FIG. 46. Relationship between the wet and dry weight of filamentous alga.
FIG. 47. Results of quadrat samples at site 49. Percentage is the number of occasions that the particular substratum type occurred in the total number of quadrats examined. (Data from APPENDIX 12)
FIG. 48. Relationship between weed area and the number of snails.
(Data from APPENDICES 11 and 13) $r = 0.59$. 

$r = 0.59$
FIG. 49. Relative proportions of the gastropod species in weed types from site 49.

(a) Cladophora sp.  (b) Callitriche sp.
(c) Mysotis
(d) Veronica beccabunga

(Data from APPENDIX 11)
<table>
<thead>
<tr>
<th>Plant</th>
<th>Lymnaea</th>
<th>Physa</th>
<th>Bithynia</th>
<th>Planorbis</th>
<th>Valvata</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cladophora</td>
<td>28.68</td>
<td>6.11</td>
<td>26.656</td>
<td>4.85</td>
<td>5.387</td>
<td>71.68</td>
</tr>
<tr>
<td>Myosotis</td>
<td>27.02</td>
<td>12.28</td>
<td>6.14</td>
<td>11.05</td>
<td>0</td>
<td>56.51</td>
</tr>
<tr>
<td>Veronica</td>
<td>28.67</td>
<td>18.24</td>
<td>7.82</td>
<td>2.61</td>
<td>0</td>
<td>57.34</td>
</tr>
<tr>
<td>Callitriche</td>
<td>258.62</td>
<td>122.68</td>
<td>39.79</td>
<td>13.26</td>
<td>0</td>
<td>434.35</td>
</tr>
</tbody>
</table>

FIG. 50. Estimated densities of snail species (snails m⁻²) on the plants: Data from site 49, summer 1980, (APPENDIX 11).
FIG. 51. The periphyton supported by different plant species at Barmston Drain.
FIG. 52. Distribution of the gastropods during winter at Barmston Drain. Depth refers to the height of water vertically above the centre of each quadrat.

Depth (cm)

0-5 6-10 11-15 16-20 40 50 60 70

%  

10%  

Lymnaea peregra
Physa fontinalis
Bithynia tentaculata
Valvata piscinalis
A = Achmanthes sp.
Am = Amphora sp.
An = Animal fragments
C = Cocconeis sp.
Ce = Cells of higher plants (i.e. above status of filamentous alga)
Ct = Cyclotella sp.
Cy = Cymbella sp.
D = Diatoma sp.
De = Desmid
F.a. = Fontinalis antipyretica.
F. = Filamentous alga
Fr = Fragilaria sp.
G = Gomphonema sp.
M = Melosira sp.
N = Navicula sp.
O = Oscillatoria sp.
R = Rest (i.e. total remaining recognisable components)
S = Synedra sp.
U = Unidentified epilithic plant species

FIG. 53. Key to abbreviations used in diagrams of gut contents and periphyton.
FIG. 54(a) A comparison between the proportions of various items of food in the gut of Physa fontinalis and from the surrounding substratum. Each mark represents one trial, consisting of several snails.
FIG. 54(b) The gut contents of Physa fontinalis compared with the epiphyton.

(Weed bed)

Guts  n=40

Weeds

A D C N G E S F C T D E

July 1974 (Weed beds)
FIG. 55. Comparison between the gut contents of Physa fontinalis and the epiphyton from 4 species of weed from which the snails were removed.
FIG. 56. A comparison between the periphyton from 4 different species of plant growing in situations within the weed beds (above the axis) and near to the weir (below the axis).
FIG. 57. The gut contents of *Lymnaea peregra* compared with the epilithon.
FIG. 58. Gut contents of *Theodoxus fluviatilis* and the epilithon compared.
FIG. 59. Gut contents of *Potamopyrgus jenkinsi* and the epiphyton.
FIG. 60. The summed gut contents of 100 snails of various species compared with the epilithon.
FIG. 61. The gut contents of mixed species groups removed from rocks and weeds at Hempholme Lock.
FIG. 62. Gut contents of mixed-species groups of gastropods removed from rocks.
FIG. 63. Gut contents of various gastropod species removed from the same patch of *Fontinalis antipyretica*.
FIG. 64. Gut contents of various gastropods removed from their feeding sites, (a) weeds (b) rocks.
FIG. 65. Arrangement of the denticles on the radula of (a) *Theodoxus fluviatilis* and (b) *Bithynia tentaculata*. (Drawn from a specimen.)
FIG. 66. Radula capacity of certain gastropods based on the evidence of morphology and feeding traces.

M = marginal denticles
L = lateral denticles
R = rachidian denticles

Plant material
Cutting fresh higher

Vegatating careers

Haspung meat
Sweeping loose material
totally removed

Scooping meat

R = rachidian denticles
M = marginal denticles
L = lateral denticles
FIG. 67. The percentage of faeces deposited during day and night sessions by the various species from the rocks and weed beds.
First level of abstraction

Third level of abstraction etc.

FIG. 68. Summary of the niche segregation of the major species of gastropod in the River Hull.
Tables 1 - 6

Environmental parameters of sample sites

Abbreviations:

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp.</td>
<td>temperature</td>
</tr>
<tr>
<td>Cond.</td>
<td>conductivity</td>
</tr>
<tr>
<td>St.</td>
<td>stones</td>
</tr>
<tr>
<td>Gr.</td>
<td>gravel</td>
</tr>
<tr>
<td>Sa/si</td>
<td>sand-silt</td>
</tr>
<tr>
<td>Group</td>
<td>Indicator</td>
</tr>
<tr>
<td>-------</td>
<td>-----------</td>
</tr>
<tr>
<td>D1</td>
<td>None</td>
</tr>
<tr>
<td>D2</td>
<td>None</td>
</tr>
<tr>
<td>D3</td>
<td>None</td>
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<td>54</td>
<td>43</td>
<td>44</td>
<td>45</td>
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</tr>
<tr>
<td>0.05</td>
<td>1.0</td>
<td>0.3</td>
<td>1.5</td>
<td></td>
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</table>

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<tbody>
<tr>
<td>32</td>
<td>31</td>
<td>100</td>
<td>25</td>
<td></td>
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<td>100</td>
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<td>4.3</td>
<td>2.5</td>
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</tbody>
</table>

<table>
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<tr>
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<td>100</td>
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<tr>
<td>100</td>
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<td>2.5</td>
</tr>
<tr>
<td>100</td>
<td>1.5</td>
<td>3.0</td>
</tr>
</tbody>
</table>

**Table 1**
<p>| Site | Dominant Species | Water Temperature | Dissolved Oxygen | pH | Flow | Predation | Substrate Type | Light Intensity | Flow Type | Plant Species | Substrate Gravel | Soil Type | Depth (cm) | Table 2 |
|------|------------------|-------------------|------------------|----|------|----------|---------------|----------------|-----------|-------------|----------------|------------|-----------|----------|----------|
| A1   | Anis. leucos.    | 20                | 120              | 1.5| 0.15 |          |                |                |           |             |                |            |           |          |          |
| A2   | Anis. fluv.      | 0.30              | 0.30             | 1.5| 0.15 |          |                |                |           |             |                |            |           |          |          |
| A3   | Anis. leucos.    | 1.0               | 120              | 1.5| 0.15 |          |                |                |           |             |                |            |           |          |          |
| B1   | Anis. leucos.    | 3.0               | 3.0              | 2.5| 0.5   | +        |                |                |           |             |                |            |           |          |          |
| B2   | Anis. leucos.    | 3.0               | 3.0              | 2.5| 0.5   | +        |                |                |           |             |                |            |           |          |          |
| B3   | Anis. leucos.    | 3.0               | 3.0              | 2.5| 0.5   | +        |                |                |           |             |                |            |           |          |          |</p>
<table>
<thead>
<tr>
<th>Group</th>
<th>Indicator</th>
<th>Sites</th>
<th>Light %</th>
<th>Flow Sec.</th>
<th>Substratum</th>
<th>Plant Drying</th>
<th>Predominant spp.</th>
<th>Dimensions Width Depth</th>
<th>Site Parameters</th>
<th>Predicament</th>
<th>snail spp.</th>
</tr>
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<tr>
<td>B11</td>
<td>Lymnaea per.</td>
<td>7</td>
<td>100</td>
<td>12.0</td>
<td>0.50</td>
<td>+</td>
<td>0</td>
<td>W.M. 5.0, 0.75</td>
<td>0.000, 0.000</td>
<td>7.3, 4.2, 10.5</td>
<td>B15, 5</td>
</tr>
<tr>
<td>B12</td>
<td>Lymnaea per.</td>
<td>10</td>
<td>88</td>
<td>10.6</td>
<td>0.000</td>
<td>+</td>
<td>0</td>
<td>W.M. 5.0, 0.75</td>
<td>0.000, 0.000</td>
<td>7.3, 4.2, 10.5</td>
<td>B15, 5</td>
</tr>
<tr>
<td>B13</td>
<td>Potam. jenk.</td>
<td>51</td>
<td>68</td>
<td>1.0</td>
<td>0.000</td>
<td>+</td>
<td>0</td>
<td>W.M. 5.0, 0.75</td>
<td>0.000, 0.000</td>
<td>7.3, 4.2, 10.5</td>
<td>B15, 5</td>
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<td>B14</td>
<td>Potam. jenk.</td>
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<td>66</td>
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<td>0.000</td>
<td>+</td>
<td>0</td>
<td>W.M. 5.0, 0.75</td>
<td>0.000, 0.000</td>
<td>7.3, 4.2, 10.5</td>
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<td>Group Indicator Sites</td>
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<td>Substratum type</td>
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<td>-------------------------------</td>
<td>----------------</td>
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<td></td>
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<tr>
<td>Ancylus 0.25 0.35</td>
<td>6.0 0.80</td>
<td>+</td>
<td>7.6 0.95</td>
<td>7.6 0.95</td>
<td>12.2 7.6 0.560 7.6 0.95 7.6 0.95</td>
<td>+ + +</td>
<td>Ancylus 0.25 0.35</td>
<td>+ + +</td>
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<td>+</td>
<td>7.6 0.95</td>
<td>7.6 0.95</td>
<td>12.2 7.6 0.560 7.6 0.95 7.6 0.95</td>
<td>+ + +</td>
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<td>+ + +</td>
<td>Ancylus 0.25 0.35</td>
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<tr>
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<td>2.0 0.80</td>
<td>+</td>
<td>7.6 0.95</td>
<td>7.6 0.95</td>
<td>12.2 7.6 0.560 7.6 0.95 7.6 0.95</td>
<td>+ + +</td>
<td>Ancylus 0.25 0.35</td>
<td>+ + +</td>
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<td>+</td>
<td>7.6 0.95</td>
<td>7.6 0.95</td>
<td>12.2 7.6 0.560 7.6 0.95 7.6 0.95</td>
<td>+ + +</td>
<td>Ancylus 0.25 0.35</td>
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<td>+</td>
<td>7.6 0.95</td>
<td>7.6 0.95</td>
<td>12.2 7.6 0.560 7.6 0.95 7.6 0.95</td>
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TABLE 6

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Valv.pisc.
Lymnaea p.
Physa font.
Gyr.albus

Valv.pisc.
Valv.crist.
Lymnaea p.
Physa font.
·Gyr.albus
Anisus··: var.

Valv.pisc.
Lymnaea p.
Physa font.
Gyr.albus ·
Anis.·. var.
Plan,. plan
Theod. fl.
Ancylus fl.
Acrolox. 1.
Potam. jenk.
Bith. tent.

Light

67.5

Sites

13. 5

7.5

8.4

8.3
8.8

'

D

7.5

2.5

0.75

D.75

Dry

5

D

Dimensions
Width Depth
M
M

4

D

Plant
si;,p.

D

+

7

Predominant
substratum
St. Gr. Sa/si.

D D

+

+

□.□□□

+

D

0.187

+

1. 5

□ .414

Site parameters
Temp.
Cond.
pH.
Flow
"3 cm-3
oc
M sec- 1

1 DD

%

42

57.5

39.D

18.0

15.4

100

100

47

16


Plates 1 - 23. Selected sample sites from the River Hull system. All photographs were taken during September, 1980, the year following faunal sampling. In each plate the datum pole is marked off in alternate red and white one foot (30.5cm.) bands.
PLATE 1  Hemholme Lock, at the weir:  site 16.

PLATE 2  Hemholme Lock, above the weir, looking upstream.
PLATE 3  Hempholme Lock, looking downstream.

PLATE 4  Hempholme Lock. The brick foundations of the original lock, exposed at low water level.
PLATE 5  Kalk Beck at Kilham: site 23.

PLATE 7  Moor Beck, near Lockington: site 10.

PLATE 8  Overhung ditch, near Old Howe: site 43.
PLATE 9  Beck parallel to Eastburn Beck:  site 34.

PLATE 10  Bryan Mills Beck:  site 8.
PLATE 11  Skerne Beck:  site 27.

PLATE 12  Driffield Beck at Driffield:  site 36.
PLATE 13  Kilnwick New Cut:  site 14.

PLATE 14  Aike Beck:  site 7.
PLATE 15  Kelk Beck, near Frodingham junction: site 18.

PLATE 16  River Hull at Hull Bridge, Tickton: site 3.
PLATE 17  River bank showing silt at low tide: site 3.

PLATE 18  River Hull at Weel (near Beverley): site 2.
PLATE 19  River Hull at Sutton Road, Hull: site 1.

PLATE 20  Barmston Drain at Hull Bridge, Tickton: site 49.
PLATE 21  Barmston Drain at Weel:  site 48.

PLATE 22  Barmston Drain at Dunwell:  site 50
PLATE 23    Tributary of Old Howe: site 42.
Apparatus used to investigate faeces production of snails under field conditions.

Mucus trails of *Physa fontinalis* and *Lymnaea peregra*, after staining with carmine, and drying.

(CHAPTER 5)
PLATE 25 (a)  Smear of gut contents of *Physa fontinalis* showing large numbers of diatoms.  

\[ \times 100 \]

(b)  Smear of gut contents of *Physa fontinalis*.

The dark zones are detritus of unidentified origin.

\[ \times 100 \]
PLATE 25 (c) Smear of gut contents of Physe fontinalis. As well as diatoms and detritus, pieces of macrophyte tissue are visible. ×100

PLATE 26 (a) Large pieces of Fontinalis antipyretica from the gut of Lymnaea peregra. ×40
PLATE 26 (b) Single piece of *Fontinalis antipyretica* from the gut of *Lymnaea peregra*. Also visible are grit particles. ×100

PLATE 27 (a) Plant fragments from the gut of *Anisus vortex*. ×100
Pieces of macrophyte epidermis from *Anisus vortex.*

\( \times 100 \)

Enlarged view (\( \times 4 \)) of one of the pieces from PLATE 27 (b).
PLATE 27 (d)  Monocotyledon epidermis in gut smear of Anisus vortex.  ×100

(e)  Siliceous spicules, characteristic of many gut slides of Anisus vortex, indicating the presence of monocotyledons.  ×100
PLATE 28 (a) Unidentified plant type, common in some *Theodoxus fluviatilis* guts. × 200

(b) Isolated fragment of PLATE 28 (a).
PLATE 29 (a) Smears of gut contents of *Succinea pfefferi*.

Macrophyte tissue made up the bulk of material from this species. Xylem elements are evident in the lower portion.  

PLATE 29 (b) Macrophyte material with xylem elements in the centre, from guts of *Succinea*.  

×100
PLATE 29 (c) Plant epidermis from *Succinea* gut smear.  
×100

(d) Guard cells from *Succinea* gut smear.  
×100
PLATE 29 (e)  Enlarged view (x4) of part of guard cells from PLATE 29 (d).
Radulae and the tracks and individual prints made by the radulae as snails moved over carbon-coated slides in the laboratory. (CHAPTER 6)
PLATE 30 (a) General view of the radula of *Theodoxus fluviatilis* to show arrangement of denticles. ×40

(b) Marginal denticles of *Theodoxus*. ×100
PLATE 30 (c)  Flexed portion of radula of *Theodoxus* to show rotary action of marginal denticles. ×100
PLATE 31 (a) Central portion of the radula of *Bithynia tentaculata* to show central rachidian denticles. 
\*100

(b) Same portion of radula as 31 (a) but focused to show zig-zag arrangement of lateral and marginal denticles. 
\*100
Partly flexed radula of Bithynia to show the shape of the tips of lateral and marginal denticles

Highly magnified view of the lateral and marginal denticle tips to show serrated edge.
Individual radula prints of *Theodoxus*. The very fine striations were assumed to have been made by the marginal denticles. The wider bars (arrowed) were presumed to have been the action of the capituliform denticles.
Radula prints of *Bithynia tentaculata* collectively making concentric patterns on carbon-coated slide. Zig-zag appearance of each side of an individual print reflects the position of the marginal and lateral denticles.

Individual print of *Potamopyrgus jenkinsi*.
Highly magnified individual radule print of *Bithynia*. The fine striations presumed to have been made by the fine serrations on the marginal and lateral denticles, are arrowed.
PLATE 34 (a) Denticles of *Ancylus fluviatilis.* x100

(b) Denticles of *Ancylus fluviatilis.* x100
PLATE 35 (a) Individual radula print of Physa fontinalis.

(b) Individual print of Lymnaea peregra.
PLATE 35 (c) Individual print of *Ancylus fluviatilis*.

PLATE 35 (d) Individual print of *Bathyomphalus contortus*.
PLATE 35 (e) Individual print of *Anisus vortex*.

(f) Individual print of *Planorbis carinatus*. 
PLATE 35 (g)  Individual print of *Gyraulus albus*.
PLATE 36 (a) Unworn denticles of *Lymnaea peregra.* ×100

(b) Worn denticles of *Lymnaea peregra.*
PLATE 36 (c) Median view of the radula of *Lymnaea peregra*.

The radula is folded so that the difference between the lateral denticles (left) and marginal denticles is apparent.  ×100

PLATE 36 (d) Impression of the denticles of *Lymnaea peregra*.

At the base of the print, the spacing of the lateral denticles (centre) is compared with the marginals (left and right).
PLATE 36 (e) Median view of the marginal denticles of *Lymnaea peregra* to show the relatively narrow base, and the broad, serrated tip. ×100
The inter and intra-specific variation in radula print. The two left hand impressions are of *Lymnaea peregra*, whilst those on the right are both *Lymnaea stagnalis*.

PLATE 38 (a) Radula of *Physa fontinalis*. The row of denticles when the two halves of the radula join. × 100
PLATE 38 (b) *Physa* radula showing unworn denticles. ×100

(c) *Physa* radula showing worn radula denticles.
PLATE 39

Denticles of *Bathymphalus contortus* to show characteristic hook-shape. ×100
PLATE 40. Zig-zag traces made by gastropods on carbon-coated slides in the laboratory. (All at same level of magnification)
PLATE 41. Zig-zag traces made by gastropods on carbon-coated slides in the laboratory. (At same level of magnification)
PLATE 42. Zig-zag traces made by gastropods on carbon-coated slides in the laboratory. (At same level of magnification)
# APPENDIX 1  National Grid Reference of Sample sites (1:50,000 metric)

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# APPENDIX 2

**Results of qualitative sampling of the River Hull system.**

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**Totals**: 1138, 915, 231, 912, 419, 780, 336, 201, 415, 787, 823, 2063, 30, 409, 16, 556, 33, 1825, 74, 14.
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Occurrence of Gastropods at Hempholme (March/April 1974)

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APPENDIX 5(a) Primary matrix of species abundance

Percentage occurrences of all snail species, March 1974 - October 1976.

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Percentage occurrences of all snail species, March 1974 - October 1976.

Primary matrix of species abundance

APPENDIX 5(a)
|   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |   |   |   |
| 0.2 | 2.8 | 6.0 | 6.2 | 6.8 | 7.2 | 7.0 | 6.9 | 0.5 | 1.0 | 1.9 | 2.7 | 4.0 | 6.5 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 |
| 3.6 | 5.6 | 7.2 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 2.8 |
| 2.7 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 |
| 3.6 | 5.6 | 7.2 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 |
| 2.7 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 |
| 3.6 | 5.6 | 7.2 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 |
| 2.7 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 |
| 3.6 | 5.6 | 7.2 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 |
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| 2.7 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 |
| 3.6 | 5.6 | 7.2 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 |
| 2.7 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 |
| 3.6 | 5.6 | 7.2 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 |
| 2.7 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 |
| 3.6 | 5.6 | 7.2 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 |
| 2.7 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 |
| 3.6 | 5.6 | 7.2 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 |
| 2.7 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 | 4.7 | 3.9 | 5.6 | 3.9 | 4.2 | 4.0 | 6.5 | 7.2 | 2.8 | 4.0 | 6.5 | 7.0 | 6.9 | 6.7 |

APPENDIX 5(b) Secondary Matrix for sample statements
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Changes in abundance of three species of gastropod with reference to distance from weir. (See FIGS. 34, 35 and 36)
## APPENDIX 7

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**APPENDIX 8(a)  Results of stone size, *Potamopyrgus jenkinsi*.**

(See FIG.40a)

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95% c.l. = 0.553, 1.687, 10.580, 39.5, 28.704

S.D. = 1.156, 4.621, 28.99, 39.5, 78.61

Variance = 1.336, 21.354, 840.42, 1560.25, 6179.532
APPENDIX 8(b)  Results of stone size, *Theodoxus*.
(See FIG. 40b)

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(See FIG. 40c)

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</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

Total  2  2  11  2  196

$\bar{x}$  0.06  0.06  0.36  0.50  8.52

95% c.l.  0.116  0.116  0.423  0.577  5.058
APPENDIX 9

Time needed to remove excess fluid from weed samples.

**Callitriche sp.**  
Dry weight of sample = 0.373 g.  
Time (sec.)

<table>
<thead>
<tr>
<th>Time (sec.)</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>5</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>30</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.203</td>
<td>1.171</td>
<td>0.970</td>
<td>0.909</td>
<td>0.790</td>
<td>0.746</td>
<td>0.685</td>
<td>0.691</td>
</tr>
<tr>
<td>2</td>
<td>1.580</td>
<td>1.204</td>
<td>1.000</td>
<td>0.961</td>
<td>0.772</td>
<td>0.752</td>
<td>0.647</td>
<td>0.661</td>
</tr>
<tr>
<td>3</td>
<td>1.585</td>
<td>1.090</td>
<td>1.035</td>
<td>0.868</td>
<td>0.817</td>
<td>0.714</td>
<td>0.673</td>
<td>0.645</td>
</tr>
<tr>
<td>4</td>
<td>1.743</td>
<td>1.119</td>
<td>1.062</td>
<td>0.840</td>
<td>0.742</td>
<td>0.720</td>
<td>0.681</td>
<td>0.628</td>
</tr>
<tr>
<td>5</td>
<td>1.571</td>
<td>1.085</td>
<td>1.095</td>
<td>0.825</td>
<td>0.754</td>
<td>0.690</td>
<td>0.668</td>
<td>0.649</td>
</tr>
<tr>
<td>X</td>
<td>1.536</td>
<td>1.134</td>
<td>1.032</td>
<td>0.881</td>
<td>0.775</td>
<td>0.724</td>
<td>0.671</td>
<td>0.655</td>
</tr>
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</table>

**Myosotis scorpioides**  
Dry weight of sample = 1.701 g.  
Time (sec.)

<table>
<thead>
<tr>
<th>Time (sec.)</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>5</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>30</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2.606</td>
<td>2.521</td>
<td>2.633</td>
<td>2.326</td>
<td>2.245</td>
<td>2.246</td>
<td>2.225</td>
<td>2.226</td>
</tr>
<tr>
<td>2</td>
<td>3.040</td>
<td>2.646</td>
<td>2.583</td>
<td>2.457</td>
<td>2.372</td>
<td>2.375</td>
<td>2.338</td>
<td>2.333</td>
</tr>
<tr>
<td>3</td>
<td>3.188</td>
<td>2.939</td>
<td>2.762</td>
<td>2.556</td>
<td>2.507</td>
<td>2.456</td>
<td>2.440</td>
<td>2.398</td>
</tr>
<tr>
<td>4</td>
<td>2.453</td>
<td>2.889</td>
<td>2.799</td>
<td>2.688</td>
<td>2.557</td>
<td>2.510</td>
<td>2.471</td>
<td>2.486</td>
</tr>
<tr>
<td>5</td>
<td>3.365</td>
<td>2.842</td>
<td>2.896</td>
<td>2.649</td>
<td>2.500</td>
<td>2.458</td>
<td>2.458</td>
<td>2.430</td>
</tr>
<tr>
<td>X</td>
<td>2.930</td>
<td>2.767</td>
<td>2.735</td>
<td>2.535</td>
<td>2.436</td>
<td>2.409</td>
<td>2.386</td>
<td>2.375</td>
</tr>
</tbody>
</table>

**Cladophora sp.**  
Dry weight of sample = 1.866 g.  
Time (sec.)

<table>
<thead>
<tr>
<th>Time (sec.)</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>5</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>30</th>
</tr>
</thead>
</table>

(See FIG. 43)
Standardisation of plant surface areas and covering liquid film.

(a) *Myosotis scorpiodes*

<table>
<thead>
<tr>
<th>Sample no.</th>
<th>Dry weight (g.)</th>
<th>Wet weight (g.)</th>
<th>Wt. film (g.)</th>
<th>measured area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.1796</td>
<td>0.2691</td>
<td>0.0895</td>
<td>18.40</td>
</tr>
<tr>
<td>2</td>
<td>3.299</td>
<td>3.700</td>
<td>0.401</td>
<td>122.24</td>
</tr>
<tr>
<td>3</td>
<td>7.070</td>
<td>7.833</td>
<td>0.763</td>
<td>258.32</td>
</tr>
<tr>
<td>4</td>
<td>9.660</td>
<td>10.753</td>
<td>1.093</td>
<td>438.60</td>
</tr>
<tr>
<td>5</td>
<td>9.505</td>
<td>11.590</td>
<td>2.085</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>9.741</td>
<td>11.410</td>
<td>1.669</td>
<td>556.85</td>
</tr>
<tr>
<td>7</td>
<td>12.106</td>
<td>14.600</td>
<td>2.494</td>
<td>916.21</td>
</tr>
<tr>
<td>8</td>
<td>20.635</td>
<td>23.711</td>
<td>3.075</td>
<td>1179.90</td>
</tr>
</tbody>
</table>

(b) *Veronica beccabunga*

<table>
<thead>
<tr>
<th>Sample no.</th>
<th>Dry weight (g.)</th>
<th>Wet weight (g.)</th>
<th>Wt. film (g.)</th>
<th>measured area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3.035</td>
<td>3.110</td>
<td>0.075</td>
<td>38.04</td>
</tr>
<tr>
<td>2</td>
<td>7.420</td>
<td>7.910</td>
<td>0.490</td>
<td>141.16</td>
</tr>
<tr>
<td>3</td>
<td>8.620</td>
<td>9.245</td>
<td>0.625</td>
<td>246.48</td>
</tr>
<tr>
<td>4</td>
<td>10.142</td>
<td>10.870</td>
<td>0.728</td>
<td>427.28</td>
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<tr>
<td>5</td>
<td>12.570</td>
<td>13.685</td>
<td>1.115</td>
<td>574.64</td>
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<tr>
<td>6</td>
<td>18.095</td>
<td>19.440</td>
<td>1.345</td>
<td>788.28</td>
</tr>
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</table>

(See FIG. 45, a and b)
APPENDIX 10

Standardisation of plant surface areas and covering liquid film.

(c) *Cladophora* sp.

<table>
<thead>
<tr>
<th>Sample no.</th>
<th>Dry weight (g.)</th>
<th>Wet weight (g.)</th>
<th>Wt. film (g.)</th>
<th>measured area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.0089</td>
<td>0.1056</td>
<td>0.0967</td>
<td>15.7079</td>
</tr>
<tr>
<td>2</td>
<td>0.0200</td>
<td>0.2533</td>
<td>0.2333</td>
<td>31.4158</td>
</tr>
<tr>
<td>3</td>
<td>-</td>
<td>-</td>
<td>0.4035</td>
<td>47.1237</td>
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<tr>
<td>4</td>
<td>0.0435</td>
<td>0.4435</td>
<td>0.4000</td>
<td>62.8316</td>
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<tr>
<td>5</td>
<td>-</td>
<td>-</td>
<td>0.5639</td>
<td>78.5395</td>
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<tr>
<td>6</td>
<td>0.0750</td>
<td>0.7700</td>
<td>0.6950</td>
<td>109.9553</td>
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<tr>
<td>7</td>
<td>0.1136</td>
<td>0.2870</td>
<td>1.1734</td>
<td>157.09790</td>
</tr>
</tbody>
</table>

(d) *Callitriche* sp.

<table>
<thead>
<tr>
<th>Sample no.</th>
<th>Dry weight (g.)</th>
<th>Wet weight (g.)</th>
<th>Wt. film (g.)</th>
<th>measured area (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.0056</td>
<td>0.0160</td>
<td>0.0104</td>
<td>2.899</td>
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<tr>
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<td>0.0299</td>
<td>0.0955</td>
<td>0.0656</td>
<td>5.012</td>
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<tr>
<td>3</td>
<td>0.0132</td>
<td>0.0460</td>
<td>0.0328</td>
<td>4.985</td>
</tr>
<tr>
<td>4</td>
<td>0.0407</td>
<td>0.1209</td>
<td>0.0802</td>
<td>13.130</td>
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<tr>
<td>5</td>
<td>0.0500</td>
<td>0.2609</td>
<td>0.2109</td>
<td>21.230</td>
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<tr>
<td>6</td>
<td>0.0760</td>
<td>0.1929</td>
<td>0.1169</td>
<td>20.625</td>
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<td>0.1845</td>
<td>28.190</td>
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<td>8</td>
<td>0.2892</td>
<td>0.5429</td>
<td>0.2537</td>
<td>40.520</td>
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<tr>
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<td>0.2242</td>
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<tr>
<td>10</td>
<td>-</td>
<td>-</td>
<td>0.4551</td>
<td>71.037</td>
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(See FIG.45, c and d)
APPENDIX 11(a)  
Number of various species of gastropod on 25 samples of *Myosotis scorpiodes*.

<table>
<thead>
<tr>
<th>Weight of film (g.)</th>
<th>Area (cm²)</th>
<th>Lymnaea</th>
<th>Physa</th>
<th>Bithynia</th>
<th>Planorbis app.</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.096</td>
<td>428.125</td>
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<td>0</td>
<td>1</td>
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<td>0</td>
<td>1</td>
</tr>
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<td>0.305</td>
<td>143.750</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0.330</td>
<td>157.000</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
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<td>0</td>
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<td>3</td>
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<tr>
<td>0.779</td>
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<td>4</td>
<td>1</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>0.503</td>
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<td>0</td>
<td>0</td>
<td>1</td>
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<tr>
<td>0.971</td>
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<td>0</td>
<td>2</td>
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<td>2</td>
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<td>0</td>
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<td>0</td>
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<td>0.510</td>
<td>212.50</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<tr>
<td>0.333</td>
<td>157.50</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>0.435</td>
<td>209.06</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>0.325</td>
<td>152.8f</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>0.683</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
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</table>

Total 8140.60 22 10 5 9 46

(See FIGS.49 and 50)
APPENDIX 11(b)

Number of various species of gastropod on 20 samples of *Veronica beccabunga*.

<table>
<thead>
<tr>
<th>Weight of film (g.)</th>
<th>Area (cm²)</th>
<th>Lymnaea</th>
<th>Physa</th>
<th>Bithynia</th>
<th>Planorbis</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.480</td>
<td>220</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>0.437</td>
<td>185</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>0.250</td>
<td>72</td>
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<td>3</td>
<td>1</td>
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<td>5</td>
</tr>
<tr>
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</tr>
<tr>
<td>0.265</td>
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<td>1</td>
<td>0</td>
<td>2</td>
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<tr>
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<td>278</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>4</td>
</tr>
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Total 7673  22  14  6  2  44

(See FIGS.49 and 50)
**APPENDIX 11(c)**

Dry weight/wet weight/surface film weight/area relationships with number of snail species/sample.

Data from quadrat studies, only 20 pure filamentous algae shown.

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(See FIGS.46, 49, 50)
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*Note: Myosotis (Callitriche concealed within filamentous sample)*

*Note: Graminae (grass entwined too intimately with Cladophora to distinguish snail positions)*
APPENDIX 11(e)  Number of various species of gastropod on 25 samples of *Callitriche* sp. of measured area.

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Total 3016 78 37 12 4 131

(See FIGS.49 and 50)
APPENDIX 12  Results of quadrat sampling.  50 quadrats (0.0625m²)

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<th>Quad. no.</th>
<th>Filamentous algae</th>
<th>Myosotis scorpiodes</th>
<th>Veronica beccabunga</th>
<th>Callitriche sp.</th>
<th>Gramineae sp.</th>
<th>Gastro-pods present</th>
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(See FIG. 47)
APPENDIX 13  Results of quadrat samples (gastropods).

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<th>Planorbis spp.</th>
<th>Valvata piscinalis</th>
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APPENDIX 14 Depth distributions during February 1981 of the gastropods at site 49.

The quadrat size was the same as that used during summer sampling (0.625 m²) (see Fig. 92).

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<th>No. of Samples</th>
<th>Vaivata range</th>
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<th>Total</th>
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<table>
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<th>Bithyta range</th>
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<th>Total</th>
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<th>Physa range</th>
<th>Mean</th>
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(See FIG. 92)
APPENDIX 15 (a) *Potamopyrgus jenkinsii*

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<th>Radula length (mm)</th>
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\[ x \approx 87.448 \]
**APPENDIX 15 (b) Theodoxus fluviatilis**

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\[ \bar{x} = 136.672 \]
### APPENDIX 15 (c) Bithynia tentaculata

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\[ \overline{X} = 44.733 \]
## APPENDIX 15 (d) - *Valvata piscinalis*

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\[ \bar{x} = 17.431 \]
## APPENDIX 15 (e) \textit{Ancylus fluviatilis}

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\[ \bar{x} = 266.9 \]
### Appendix 15 (f) Physa fontinalis

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<td>0.0539</td>
<td>2.869</td>
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<td>53.95</td>
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<td>0.0534</td>
<td>2.522</td>
<td>47.22</td>
</tr>
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<td>0.0570</td>
<td>2.783</td>
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<tr>
<td>0.0393</td>
<td>2.130</td>
<td>54.21</td>
</tr>
<tr>
<td>0.1282</td>
<td>3.174</td>
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<td>0.0839</td>
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<td>39.63</td>
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</tr>
<tr>
<td>0.0555</td>
<td>2.739</td>
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<tr>
<td>0.0461</td>
<td>2.695</td>
<td>58.47</td>
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\[ x = 47.92 \]
### APPENDIX 15 (g)  **Lymnaea peregra**

<table>
<thead>
<tr>
<th>Wet weight (g)</th>
<th>Radula length (mm)</th>
<th>ratio</th>
<th>radula length</th>
<th>wet weight</th>
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<td>0.0157</td>
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<td>77.515</td>
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<tr>
<td>0.0169</td>
<td>1.217</td>
<td>72.012</td>
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<td>0.0255</td>
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<td>1.304</td>
<td>50.750</td>
<td></td>
<td></td>
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<tr>
<td>0.0312</td>
<td>1.435</td>
<td>45.987</td>
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<td>0.0353</td>
<td>1.478</td>
<td>41.878</td>
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<td>1.478</td>
<td>58.201</td>
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<td>1.478</td>
<td>41.878</td>
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<td></td>
</tr>
<tr>
<td>0.0382</td>
<td>1.565</td>
<td>40.974</td>
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<td>0.0431</td>
<td>1.478</td>
<td>34.299</td>
<td></td>
<td></td>
</tr>
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<td>0.0437</td>
<td>1.478</td>
<td>33.828</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$\times 10 = 49.549$
### Faeces production: rocky zone species

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Duration (hr)</th>
<th>Repl.</th>
<th>Dark</th>
<th>Light</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Potamopyrgus jenkinsi</em></td>
<td>100</td>
<td>7</td>
<td>1</td>
<td>0.0577 g.</td>
<td>0.0090 g.</td>
</tr>
<tr>
<td><em>Theodoxus fluviatilis</em></td>
<td>25</td>
<td>7</td>
<td>1</td>
<td>0.0540 g.</td>
<td>0.0054 g.</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>7</td>
<td>2</td>
<td>0.0667 g.</td>
<td>0.0013 g.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(\approx) 0.0608 g.</td>
<td>(\approx) 0.0033 g.</td>
</tr>
<tr>
<td><em>Ancylus fluviatilis</em></td>
<td>20</td>
<td>9</td>
<td>1</td>
<td>7.215 cm.</td>
<td>6.560 cm.</td>
</tr>
</tbody>
</table>

### Faeces production: weed beds species

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Duration (hr)</th>
<th>Repl.</th>
<th>Dark</th>
<th>Light</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Physa fontinalis</em></td>
<td>25</td>
<td>5</td>
<td>1</td>
<td>29.315 cm.</td>
<td>33.045 cm.</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>5</td>
<td>2</td>
<td>24.020 cm.</td>
<td>21.190 cm.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(\approx) 26.667 cm.</td>
<td>(\approx) 27.117 cm.</td>
</tr>
<tr>
<td><em>Lymnaea peregra</em></td>
<td>25</td>
<td>5</td>
<td>1</td>
<td>38.335 cm.</td>
<td>36.220 cm.</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>5</td>
<td>2</td>
<td>29.090 cm.</td>
<td>27.255 cm.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(\approx) 33.712 cm.</td>
<td>(\approx) 31.737 cm.</td>
</tr>
<tr>
<td><em>Bithynia tentaculata</em></td>
<td>25</td>
<td>5</td>
<td>1</td>
<td>195 pellets</td>
<td>334 pellets</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>5</td>
<td>2</td>
<td>343 &quot;</td>
<td>297 &quot;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(\approx) 269 &quot;</td>
<td>(\approx) 315 &quot;</td>
</tr>
<tr>
<td>Distance travelled (cm.)</td>
<td>Distance travelled (cm.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------------------------</td>
<td>-------------------------</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.5</td>
<td>7.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11.4</td>
<td>39.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13.3</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>27.8</td>
<td>46.3</td>
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<td></td>
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</tr>
<tr>
<td>2.6</td>
<td>22.2</td>
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<td>11.8</td>
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<td></td>
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<td>65.1</td>
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<td>12.2</td>
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<td>3.7</td>
<td>40.2</td>
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<td>7.0</td>
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</tr>
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<td>23.1</td>
<td>0.6</td>
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<tr>
<td>11.4</td>
<td>10.7</td>
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<td></td>
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</tr>
<tr>
<td>4.6</td>
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<td></td>
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<td></td>
</tr>
</tbody>
</table>

\[ \bar{x} = 1.6694 \times 10^1 \quad \bar{x} = 3.0250 \times 10^1 \]

\[ \text{variance} = 2.7109 \times 10^2 \quad \text{variance} = 2.0522 \times 10^2 \]

\[ \text{S.D.} = 1.6465 \times 10^1 \quad \text{S.D.} = 1.4325 \times 10^1 \]

\[ t = 2.3005005 \times 10^0 \quad (27 \text{ D.F.}) \]

\[ p < 0.05 \]

APPENDIX 17a. Distance travelled by *Theodoxus fluviatilis* in light and dark conditions. (10°C)
**Lymnaea peregra**

(Light) | (Dark)
---|---
Distance travelled (cm.) | Distance travelled (cm.)
94.2 | 14.3
88.5 | 14.4
119.8 | 64.2
111.8 | 69.8
58.7 | 45.4
101.5 | 53.1
73.7 | 27.5
142.1 | 67.1
133.4 | 12.4
79.7 | 28.3
6.7 | 46.6
142.6 | 11.6
114.2 | 10.7
112.0 | 13.6
108.4 | 15.4
116.6 | 43.2
48.5 | 125.8
193.0 | 15.8
102.8 | 31.6
89.0 | 26.7
101.0 | 45.9
91.5 | 40.0
56.7 | 23.1
155.7 | 22.0
| 37.2

\[ \bar{x} = 1.0217 \times 10^{02} \quad \bar{x} = -3.5638 \times 10^{01} \]

variance = 1.4920 \times 10^{03} \quad variance = 6.5654 \times 10^{02}

S.D. = 3.8626 \times 10^{01} \quad S.D. = 3.8626 \times 10^{01}

\[ t = 7.2298886 \times 10^{00} \quad (48 \text{ D.F.}) \]

\[ p < 0.001 \]

**APPENDIX 17b.** Distance travelled by *Lymnaea peregra* in light and dark conditions. (10°C)


THE IMPORTANCE OF MINERAL PARTICLES IN THE DIET OF *LIMNAEA PEREGER* (MÜLLER) 

R. STOREY
Wolfreton School, East Yorkshire

(*Read before the Society, 31 January 1970*)

**INTRODUCTION**

The frequent occurrence of mineral particles in the stomach region of various species of the Lymnaeidae is well known and has been reported by several authors (Owen, 1966). Some disagreement has existed with regard to the degree of importance of such particles in the diet of these snails (Heidermanns, 1924; Boycott, 1936), but the unquestionable need for their presence has been established for *L. stagnalis* by Carriker (1946). Colton (1908) found that with sand present, plant material otherwise untouched by *L. columella* was cut to pieces.

The present study attempts to assess the significance of mineral particles in the diet of *Limnaea pereger* (Müller) by long term and short term feeding experiments on diets with and without sand particles and by examination of faecal pellets and food remains.

**METHODS AND RESULTS**

The source of laboratory cultures of both snails and food was Willow Lane ditch, Beverley, East Yorkshire (Nat. Grid. Ref. 50/035385), an artificial ditch issuing from Cretaceous Chalk underlying Pleistocene boulder clay and by drainage from neighbouring fields harbouring cattle and horses. The ditch bottom is composed largely of silt with occasional sandy patches. In summer there is an abundance of higher plant material consisting chiefly of starwort, (*Callitriche* sp.) and watercress (*Nasturtium officinale* [R.Br.]). The ditch is cleared of much of this material periodically to ensure drainage. Large numbers of *L. pereger* can be seen to browse the bottom mud, the submerged plant material, and the algae which collect in quantity on wood, stones and debris. Occasionally the same species occurs on submerged deposits of treated cellulose, like cardboard boxes and paper.

During the period of study (1967–1970), the alimentary tracts of more than a hundred snails were opened and the contents examined. In all cases, mineral particles occupied the largest volume of the gizzard, crop and pylorus. Inorganic matter also made up the major part of the faecal pellets obtained from most snails collected from various feeding sites in their habitat, and thus it seems likely that this substance comprises the bulk of the material ingested.
STOREY: MINERAL PARTICLES IN DIET OF *LIMNAEA PÆREGER*

For long term experiments, egg masses collected from the habitat were isolated in a glass dish with filtered ditch water, free from mineral particles. Soon after hatching, the young snails were measured using a travelling microscope and then isolated in individual glass dishes containing 50 ml. of filtered ditch water. The dishes were covered and divided into four batches. To each batch was then added one type of food material only. Foods selected for this purpose were those which were available in greatest abundance in the natural habitat: these were fresh dicot. material (leaves of *Callitriche* sp. and *Nasturtium officinale*), filamentous algae (*Cladophora* sp.), non-filamentous algae (chiefly unicellular coccoid forms), and detritus in the form of bark and rotting leaves. The dicot. leaves, filamentous algae and detritus were all thoroughly rinsed and cleaned to remove traces of unicellular algae before being presented to the snails. Acid-washed sand was then added to half of each batch thus prepared. The dishes were inspected at regular intervals and kept replenished with the appropriate foods. Faeces and food remains were examined and the snails were measured at regular intervals and their growth rate and longevity recorded. Two series of experiments were conducted, and in all 59 snails were used. During the course of the experiment the temperature varied from 9°C. to 22°C. Despite all precautions, minute traces of inorganic matter were found in the faeces of a few snails from which it had been excluded in the diet. The results of one of the long term series of experiments are summarised in Figure 1. Each graph represents the growth rate of a pair of snails. Not all the foods offered to the snails were found to be equally acceptable and different cultures of food produced different growth curves. However, it can be seen that in all cases but two the growth rates of the snails with sand present in their dishes are higher than those without sand. In all but one case the snails without sand had died within two months: the snails in the control dishes continued to grow and appeared to be normal in all respects.

A short term experiment, lasting from the time of hatching until six weeks later showed that the mean growth rate for the duration of the experiment was higher by 69% in dishes with sand present in the diet. Only dicot. food was offered during this experiment and twenty-three snails were used.

The faeces produced during the long-term experiments were collected frequently and examined microscopically. Results of these examinations revealed that the material in the pellets from the control dishes was always more thoroughly triturated and generally browner in colour than in that from the experimental dishes without sand. This was particularly noticeable in faeces produced by snails feeding on dicot. material, which was finely shredded in cases where sand had been offered with the food. In the absence of sand the dicot. material occurred in large sheets, appearing to have undergone very little triturition.

Examination of the remains of the food in the control and experimental dishes showed a marked difference. In the batches fed on *Callitriche* sp. the leaves showed obvious signs of wearing, both in dishes with sand and those without. Whereas without sand the leaves had been thinned only in patches, in those
Fig. 1. Results of long-term experiments on *L. pereger* on diets of different foods. Each graph represents a pair of snails. Black line = growth rate of experimental snails; broken line = growth rate of control snails with sand present.
with sand present, frequently the only evidence of plant material was the stumps
of the petiole. More dicot. material was taken by the snails when sand also was
offered. In the additional experiments where filter paper was provided as the
only source of food, the snails with sand in their dishes could derive sufficient
nourishment from the filter paper to grow at a rate comparable with those snails
on more orthodox diets (see Fig. 1). In this case the filter paper was worn away
almost completely. The snail without sand was dead within 10 days, the filter
paper showing no visible signs of wear.

For a second series of long term experiments, the procedure adopted was
exactly the same as for the first series, except that the newly hatched snails were
allowed to feed for 2-3 weeks in a stock tank in which sand and silt from the
habitat covered the bottom. After this period the snails were transferred to
individual dishes prepared exactly as before, with the same foods and controls
with sand. The faeces were removed frequently and examined for traces of
sand using a pair of polaroid filters. The inorganic particles have birefringent
properties and stand out from the organic material when viewed in this way.
After 9 weeks the following results emerged. Of the 24 snails that started the
experiment, 11 had died. Six of these were from dishes in which sand was pro­
vided, five were from dishes in which it was not. Of those snails which survived,
no significant difference in size distinguished those from the experimental dishes
from those from the control. Sand appeared in the faeces of the experimental
snails on rare occasions, and then only in traces. Upon dissection, however, the
stomach regions of the experimental snails which had survived yielded sand.
In 4 out of 6 cases, the sand was abundant in the stomach region. No sand was
found in other portions of the alimentary tract. Since no sand was offered with
the food of the experimental group, it appears that the quantity found in the
stomach was that which the snails had ingestion before isolation, which they had
retained for the nine weeks duration of the experiment.

DISCUSSION

*L. pereger* collected from the natural habitat investigated always have some,
often a good deal of sand or silt in their stomachs. Results of the examination
of their alimentary tract and faeces indicate that such inorganic particles prob­
ably form by far the greatest proportion of material ingested by the snails.
Previous studies (Storey, 1969, unpublished work) have revealed that this species
of snail feeds by sampling the substrate whilst moving along, making slight
pendulum movements with the head until a source of food is detected at which
time the amplitude of the swing increases. A result of this sampling could be
the accidental ingestion of material which might not normally form part of the
diet of the snails if their mechanism of selection were more precise. Thus it is
not surprising to find that inorganic particles form such a large proportion of
the material ingested when this is the chief component of the substrate; nor is it
surprising also that they are the chief constituent of the faecal pellets.
The results of the present study show that the inclusion of mineral particles by *L. pereger* results in more efficient trituration of food materials and influences the rate of growth. In certain circumstances it is possible that the presence of inorganic matter allows this species of snail to utilise materials like paper, which could not otherwise be tackled. For the purpose of the present study, no significance is placed on the different growth rates produced by different foods, as in the case of filamentous algae compared with *Callitriche* sp. or unicellular forms. In such cases the significance lies in the fact that better use was made of the available food in all cases where sand formed part of the diet.

With sand present, dicot. material was taken more readily as food and the quantity ingested was greater.

Additional evidence for the necessity of sand is supplied by the results of experiments showing the capacity of these snails to retain quantities in the stomach region when a replenishing supply is not forthcoming from the habitat.

The long term effect of complete exclusion of sand from the diet of the snails from the time of hatching is that they are unable to derive sufficient nourishment from their food to keep them alive, and a degree of dependence on mineral particles is thus established.

**SUMMARY**

The importance of mineral particles in the diet of *L. pereger* is investigated by long and short term experiments using cultures of food which would normally be available to the snails in their natural habitat.

The presence of sand in the gut, especially in the stomach region, allows food materials to be triturated more thoroughly than would otherwise be the case. Without sand in the diet, the rate of growth of the snails is adversely affected, but its presence may allow the utilisation of a wider variety of foods than would otherwise be possible. Mineral particles are retained in quantity in the gut when an adequate supply is not provided.

The deleterious, and in the end, fatal lack of sand in their diet from birth establishes the need for its presence in the gut of this species of snail.

**REFERENCES**


NOTES

SOME OBSERVATIONS ON THE FEEDING HABITS OF
LYMNAEA PEREGRINA (MÜLLER)

R. STOREY
Wolfreton School, Willerby, East Yorkshire

INTRODUCTION

The mechanism of feeding in a number of molluscs has been studied in detail and recently reviewed (Owen, 1966). Lymnaea pergera (Müller) appears to have escaped attention although the larger L. stagnalis (L.) has been studied in detail by Hubendick (1957) and Carriker (1946, 1947). The present study uncovers some behavioural patterns associated with feeding and reveals some differences between the two species which may be adaptive to the type of food material taken in natural conditions. The feeding of L. peregra was studied by direct observation in the natural environment and in laboratory cultures, and indirectly by examination of feeding traces. The site of field observations and source of laboratory cultures was Willow Lane ditch, Beverley, Yorkshire (Nat. Grid ref. 54/035385), an artificial ditch fed from natural springs. The ditch bottom is composed largely of silt with occasional sandy patches and in summer there is an abundance of higher plant material, chiefly Callitriche sp.

FEEDING MOVEMENTS

Observations on Lymnaea peregra in the laboratory and in the field showed that whilst travelling over different substrates the speed and details of movement varied according to the nature of the substrate. Timed movements of ten snails under controlled conditions in the laboratory and a further thirty-six in the field showed their speed to be at least three times faster over materials devoid of food such as sand and barren stones, than over algal coated stones and the leaves of water plants (see Table 1). Whilst timing was in progress in the field, and during similar laboratory observations, differences in head movement accompanying the changes in speed were noted. It is evident that two basic types of movement occur (Fig. 1). The pendulum head movement reported for other species of grazing gastropods by Ankel (1938) and Hubendick (1947) also occurs in L. peregra. This is the slight side-to-side move-
Table 1. Timed movements of adult *Lymnaea peregra* (shell height 9–11 mm) over different substrates

<table>
<thead>
<tr>
<th>Type of substrate</th>
<th>Speed (cm/min)</th>
<th>No. of snails timed</th>
<th>Total period of timing (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min.</td>
<td>Max.</td>
<td>Mean</td>
</tr>
<tr>
<td>Field record (F)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sand</td>
<td>1·2</td>
<td>3·0</td>
<td>1·8</td>
</tr>
<tr>
<td>mud</td>
<td>1·8</td>
<td>2·1</td>
<td>1·4</td>
</tr>
<tr>
<td>cleaned stone</td>
<td>1·1</td>
<td>2·0</td>
<td>1·4</td>
</tr>
<tr>
<td><em>Callitriche</em></td>
<td>0·2</td>
<td>0·2</td>
<td>0·2</td>
</tr>
<tr>
<td>Field record (F)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>algae on stone</td>
<td>0·1</td>
<td>0·2</td>
<td>0·1</td>
</tr>
<tr>
<td>laboratory record (L)</td>
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<td></td>
</tr>
<tr>
<td>algae on stone</td>
<td>0·1</td>
<td>0·3</td>
<td>0·1</td>
</tr>
</tbody>
</table>

F, Field record; L, laboratory record. Field temperature, 12° C; laboratory temperature, 12–15° C.

The action of the radula associated with the movements described was examined by direct observation through the aquarium wall and by feeding traces obtained on glass slides. The latter were given a thin coating of Meyser's egg albumen and...
smoked or dusted with flour before being presented to the snails. The traces shown in Fig. 1 were made by a specimen of *L. peregrina* on a glass slide coated half with carbon and half with flour. The narrow feeding track was produced by six snails out of seven on carbon substrates and was also noted on numerous occasions as the snails crawled quickly over the clean aquarium wall. The wider zig-zag pattern was obtained from all of eighteen specimens on slides coated with flour or algae, and over such surfaces their speed was correspondingly slower. The food material presumably stimulates a feeding response resulting in a larger area of the substrate being scoured.

It is suggested that for this species of snail the pendulum action of the head when unaccompanied by the side-to-side sweep is merely a testing or tasting action and not feeding. When, by the result of this testing, food is found to be available, feeding begins and the sweep from side to side over a series of progressing arcs ensures that full use is made of the available food.

**COMPARISON WITH *LYMNAEA STAGNALIS***

Some differences between *L. peregrina* and *L. stagnalis* were found to occur in the shape and nature of the individual prints (Fig. 2). The characteristic shape of the prints described by Hubendick (1957) from *L. stagnalis* feeding on the algae on a glass aquarium wall was found to occur in the prints made by ten snails of this species on carbon-coated slides. Fig. 2(b) is typical of the type of trace produced. Hubendick found that at the beginning of the rasping stroke the radula of *L. stagnalis* becomes U-shaped, presenting teeth to the substrate along two lateral margins and

![Fig. 2](image-url)

*Fig. 2. Individual prints from *Lymnaea peregrina* (a, × 24) and *L. stagnalis* (b, × 18). In both the substrate is carbon. In all traces the animal is moving to the top of the page.*
a curved median portion. As the radula is pulled forward, the teeth on the two lateral margins contact the substrate first and are pulled towards the centre, producing the oblique, converging marks at each side of the print. The teeth of the median portion of the radula make contact with the substrate about half-way through the stroke and produce the parallel marks in the centre. The area removed by the teeth of the lateral regions (between 72 and 94%), is greater than that removed by the median part.

The prints made on the same surface by *L. peregra* are less squat than those of *L. stagnalis*. Figs. 1 and 2(a) show traces made by two specimens of *L. peregra* and are representative of the prints made by fifteen in the laboratory. They are characterized by the semicircular base, a result of the teeth of the median and lateral parts of the U-shaped radula being applied simultaneously to the substrate. The parallel, longitudinal marks traced by the teeth of the median section are apparent from the start of the print at the base to its conclusion at the tip. The area removed by these median teeth (between 56 and 84%), is greater than the two areas at each side, composed of oblique marks, removed by the lateral teeth. Whilst it is in contact with the substrate the median section is pressed so hard that the teeth are caused to bend, producing ratchet-shaped marks on the trace. The form of these marks presumably indicates a periodic movement of the teeth producing alternate light and heavy pressure on the substrate, which could be due to intrinsic vibration of the radula or to relaxation oscillations set up by the interaction of teeth and substrate.

Preliminary examination of the gut contents and faeces of seventy individuals of *L. peregra* suggests that food during the summer months consists principally of mineral particles, algae and diatoms, traces of vascular plant material and brown, amorphous material of unidentified origin, in the present study termed detritus.

**DISCUSSION**

The present study reveals that when seeking food *Lymnaea peregra* scoops small quantities of the substrate as it moves along, the head making pendulum movements to left and right. Once the presence of food is detected, feeding commences and the rate of forward progress of the snails decreases considerably. During the feeding period the head and anterior portion of the foot make broad, slow, sweeping movements which, coupled with the action of the radula, result in the food being cleared in a series of wide arcs. When feeding on thin coatings of food on hard surfaces, such as algae on a stone, the radula is applied to the substrate with some force, so that all the material in the path of the radular teeth and too large to slip between them is removed. Successive rasps frequently overlap so that almost all material from the substrate is removed, and such areas in the path of the snail are effectively denuded.

The major role in the rasping process is played by the teeth on the median part of the radula in *L. peregra* and in this respect the process differs from that known to occur in *L. stagnalis*, in which the lateral margins perform the major rasping action.
This difference may be correlated with a difference in diet, as indicated by Hunter (1953) from a comparison of their faeces.

The feeding behaviour described for *L. peregra* could be of selective value. In view of the varied nature of the diet and occurrence in the natural habitat of local deposits and concentrations of food material, the benefit of a technique for rapid searching of barren areas and efficient clearance of fertile ones is apparent.

ACKNOWLEDGMENTS

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DORMANCY IN *LYMNAEA PEREGRINA* (MÜLLER)
DURING PERIODS OF DRYNESS

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*(Read before the Society, 16 October 1971)*

*Introduction*

Like other species of lymnaeid (Cawston, 1929; DeJesus & Mallari, 1937; Henderson, 1932; Mozley, 1928; Olsen, 1944; Patzer, 1927; Ross & McKay, 1929; Shadin, 1926), *Lymnaea peregra* (Müller) is able to survive for periods when its habitat dries up, and is included by Boycott (1936) in his list of British species which tolerate drying loci. Unlike the marsh-dwelling species which are primarily non-aquatic (Hunter, 1964), *L. peregra* is essentially aquatic in habit and when stranded out of water for long periods must enter a state of dormancy in order to survive.

Some of the factors concerned with the dormant state were studied in two natural populations of *L. peregra* occupying habitats which dry up temporarily. The site of field observations was Willow Lane ditch, Beverley, Yorkshire (Nat. Grid ref. 54/035385) and a pool in the corner of a field nearby. The stream is fed by drainage from neighbouring fields and a natural spring, the pool by drainage only. Both have bottoms of silt overlying clay, and both were without standing water for a period of three months. In the laboratory, an attempt was made to reproduce conditions similar to those which occur in the natural habitat. This was done by lowering the water level in large vessels containing the snails until they became stranded on the mud, which then dried. Observations were made on *L. peregra* under these simulated field conditions. Further observations and experiments were conducted on snails which had become dormant on glass slides in the laboratory.

*The dormant state*

In this study the term “dormancy” is adopted in preference to “aestivation” for although in some respects it resembles the condition defined by Wells (1944) as “aestivation”, the period of inactivity does not seem to be directly dependant on seasonal factors. It occurred in the field only when the snails were exposed to prolonged periods of dryness, usually from mid-summer until late autumn; in the laboratory it would occur whenever the aquarium dried up. The dormant state in *L. peregra* was found to be readily recognised by the unusual posture adopted within the shell, which results in the side of the body, not the foot, being visible when the animal is viewed from beneath. This posture, illustrated in Fig.
1.a., instantly distinguishes dormant snails from those which are resting (Fig. 1.b.)
and simply withdrawn.

Field observations

The sites were visited each day, from just before the water had evaporated until ten days after. On each occasion 20 snails, chosen at random from the pool and 10 from each of 5 selected sections of the stream, were examined for traces of dormancy. Mud samples from the same regions were collected in screw-top jars and later analysed for water content.

Initial observations showed that although most adult snails (shell height 11–12 mm.) were concentrated in the residual water, the young ones (shell height 2–6 mm.) crawled away from it and moved around on the wet mud. A small proportion of very small snails (under 2 mm.) had probably hatched directly onto the mud from eggs which had been stranded as the water receded, since some egg masses were found there also. When all the water had disappeared, most of the snails moved actively on the wet mud; this they continued to do for the next two days whilst the mud retained much of its moisture. As a result of their activities, the snails' shells received a coating of mud. By the third day the mud was becoming dry and cracks began to appear. Snails became increasingly difficult to find, since many of the smaller ones sought refuge in depressions and crevices. At this stage 40% of the adults examined were dead. None of the young snails had died however, and by the fourth day some were dormant. By the end of a week all the young examined were dormant and all the adults were dead. These changes are presented graphically in Fig. 2.

Snails did not appear to burrow below the surface of the mud to escape drying out, but to confirm this, quadrat frames (10 cm. x 10 cm.) were scattered at random over the surface of the mud 3 weeks and 3 months after the disappearance of the water. The soil beneath each quadrat was excavated to a depth of 10 cm. and the sample scrutinised at the site for distribution of snails. The results
Capacity for long-term survival

Samples of mud from different sections of the stream were examined for snails 3 months after the water had evaporated. At this time the mud was baked hard and the water content low (11.5%). Snails recovered from these samples were divisible into two groups, probably corresponding to two generations. Live snails were found in the small-sized group (1-6 mm.): all the large-sized group (11-20 mm.) were dead, and assumed to have died when the water dried up. The survival rate of the young snails was related to their size, (Fig. 3) the smallest being the first to feel the effect of long-term drying.

From a total of 278 snails examined, 116 were found to be alive and in the characteristic posture.

Experiments under simulated field conditions

To provide additional information relating the size of snails with their capacity for survival, and to confirm field observations, the following experiment was devised. Large earthenware pots (20 cm. diam.) were filled to a depth of 12 cm. with mud from the stream bottom. L. peregra of 4 size ranges were introduced and the containers flooded so that the snails were covered to a depth of 5 cm. The water levels were maintained by immersing the pots overnight in a large container filled with pond water. The pots were then removed from the vessel and allowed to dry out in a cool room in the laboratory. After 9 days the snails were examined for signs of dormancy, and placed in water to see if they were still alive. Their location in the soil was also noted.

The results (Table 1) again show for adults, increasing vulnerability with

<table>
<thead>
<tr>
<th>No. SNAILS USED</th>
<th>SIZE CATEGORY</th>
<th>MEAN SIZE (MM.)</th>
<th>% SURVIVAL 9 DAYS</th>
<th>% DORMANT 2 MONTHS</th>
</tr>
</thead>
<tbody>
<tr>
<td>50</td>
<td>Large</td>
<td>13.7</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>65</td>
<td>Medium</td>
<td>10.7</td>
<td>47</td>
<td>47</td>
</tr>
<tr>
<td>70</td>
<td>Small</td>
<td>3.8</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>50</td>
<td>V. small</td>
<td>&lt;2.0</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

Relative humidity during experiment 65-80%.

Increasing size, augmenting field findings. Further evidence is the fact that the mean size of the surviving snails from these large and medium-sized groups was smaller than the mean of the groups as a whole, being 10.8 mm. and 7.7 mm. respectively. Long term survival capacity reflected field results.

None of the snails had burrowed into the mud, all being visible at the surface.
of the sampling were as follows. 307 snails from 14 quadrats were recovered from the dried mud, all of them from the surface. Most of them were not visible at first glance, partly because many had withdrawn into small depressions, pulling the edge of the shell into the mud, and partly because of the mud coating, which allowed them to blend with the surrounding soil.

Fig. 3. Relationship between size and survival capacity in *L. peregra*. (Field results.)
STOREY: DORMANCY IN *Lymnaea peregra*

Also their behaviour during drying out appeared to be identical to that observed under field conditions, although the mud coating the shell was in most cases thinner. This last finding was attributed to the faster drying rate in the laboratory compared with the field, and the consequent shorter period of activity prior to dormancy.

Field and laboratory results indicate that:
1. When stranded out of water, the snails move actively on the wet mud; in so doing many receive a coating of mud on their shells.
2. Snails do not respond to the disappearance of water by entering the mud, but seek shelter in existing hollows and become dormant as the mud becomes dry.
3. Adult snails (comprising 10% of the population) do not survive the initial drying up: young and juvenile stages are relatively immune.
4. Over prolonged periods of dryness, the survival rate of young and juvenile snails increases with size.
5. All surviving snails from the habitat are dormant and in a characteristic posture.

*Laboratory experiments on water loss in L. peregra*

In an attempt to relate field behaviour to the degree of water loss, weight losses from *L. peregra* of various sizes and in different phases of activity were measured and compared. Weight losses were determined gravimetrically using an analytical balance measuring to an accuracy of 0.1 mg., and the drying process was accelerated by keeping the snails in an atmosphere of constant saturation deficit, (35% relative humidity). The temperature, although not controlled, did not fluctuate by more than 0.5 °C. during the experiments: mean temperature was 19 °C.

It is well known that slugs and snails undergo periodic fluctuations in weight unconnected with feeding (Howes & Wells, 1934). Such cycles extend over a period of days however, and are therefore thought not to interfere significantly with short term experiments, normally lasting only minutes or hours. All weight losses were attributed to evaporative water loss during the experiment and no corrections were made for minor losses occurring for other reasons.

Weighings were conducted on individual snails during the various phases of their activities. Fig. 4 shows the results of such weighings on a snail of medium height (9 mm.) and is typical of 9 others of the same size. Because of the sensitivity of dormant snails to slight vibrations and even to changes in the atmosphere from room to room (Weals, 1944), weighings of snails in this condition was carried out on specimens which had become dormant on cover slips in the balance chamber itself, the pan and floor having been covered with plastic foam. Results show that the maximum water loss occurred during the initial period of being exposed to a drying atmosphere, when the snails were most active. As they became withdrawn, the water loss decreased, presumably since less of the moist
body surface was exposed to the drying atmosphere. The lowest rate of all was recorded when the foot slid sideways to expose the body wall in the typical dormant condition.

The comparative rates of water loss from *L. peregra* of different sizes are shown in Fig. 5, which represents group weighings of 124 specimens during a one hour period under similar conditions of temperature and relative humidity. During this period most snails were active and the results are therefore comparable. The results shown in Fig. 5 show that the rate of water loss is inversely proportional to the size of the snail. Over prolonged periods of exposure, even with reduced activity, the smallest snails would be at a disadvantage from the point of view of
survival. These results are compatible with field and laboratory records of *L. peregra* stranded out of water for long periods, and indicate that a possible cause of death was desiccation.

Fifty specimens of *L. peregra* of various sizes were allowed to dry out in a desiccator and were found to range in their tolerance between 30% and 60% loss in body weight. Such levels of tolerance are not unusual for molluscs: slugs have been known to lose 50% (Dainton, 1954) and even 80% (Künkel, 1916) of their body weight and still recover.

**Comparative water loss from foot and body wall**

The lower rate of water loss of snails in the dormant posture compared with those simply at rest and inactive has already been shown (Fig. 4). In an additional series of experiments the rate of water loss from the foot was measured and compared with that from an equal area of the body wall. For these experiments the weights of large specimens of *L. peregra* were recorded at minute intervals whilst they were in the drying atmosphere of the balance chamber. The snails were secured so that the aperture faced upwards, and water loss via the shell was prevented by a coating of paraffin wax. Changes in weight were noted when snails were inactive, with only the moist foot exposed, and when they became active to expose both the foot and the body wall: the difference between these two rates was attributed to water loss from the body surface. Computed results showed that the rate of water loss per unit area from the body surface was always less than that of the foot. During one active period of one snail, the area of the body surface exposed was only slightly greater than that of the foot, and allowed a reasonably direct comparison to be made. The rate of water loss during this 24 minute period was calculated as 54.4 mg./hour from the foot compared with 17.3 mg./hour from an equal area of the body surface.

In the interests of water economy the benefit of replacing the foot surface, exposed during resting, by the lower evaporative surface of the body wall during dormancy, is now apparent.

**Other observations**

Like many terrestrial pulmonates (Howes & Welles, 1934), *L. peregra* when dormant secrete a thin mucous veil, which may occlude the aperture completely or partially. In dormant snails removed from their habitat the veil was frequently complete, sometimes incorporating particles of soil or debris. Snails becoming dormant on glass slides in the laboratory were observed to produce copious quantities of mucus which was spread to the edge of the shell, acting as a cement at the shell-glass interface. Block (1971) quotes numerous workers who have found that thin epiphragms have little or no effect on water loss in dormant snails. The function of the mucus in *L. peregra* may well be in anchoring the snail to the substrate.

No measurements were made of the metabolic activity during the dormant period, but its rate was inferred from the following observations.
The alimentary canals of 25 snails were dissected and found to be devoid of food. The only material retained in the gut was a supply of mineral particles in the stomach region. It was not possible to tell whether the lack of food in the gut was due to their deliberately emptying it or simply due to food shortage prior to becoming dormant.

Once dormant snails were activated, breathing movements at once commenced. During a 12-hour period, whilst two snails were under continuous observation, no breathing movements were detected. It is possible that the pneumostome became active for periods after the observation period but this would have been a considerable reduction compared with resting snails in which the pneumostome was active between 1 and 18 exchanges per hour.

On certain snails from which the mud coating had previously been removed the beating of the heart could be observed through the semitransparent shell. The heart rate of 5 newly-activated snails (2.5–3.4 mm.) varied between 48 and 56 beats per minute. No heart beat was observable in the same snails prior to their re-activation and it seems likely that the activity of the heart in these dormant snails if not stopped completely, was considerably reduced either in amplitude or rate or both.

**DISCUSSION**

Studies conducted on two habitats which harbour *L. peregra* revealed some patterns of behaviour associated with the drying up of the water. During the period immediately following the disappearance of the water the snails move actively in the wet mud and in doing so receive a coating of mud on their shells. Behaviour of this type has been described for other pulmonates in drying habitats (Olivier & Barbosa, 1956), and results in their being difficult to see. This concealment could be of selective value, since once stranded on the mud, snails become more vulnerable to attack by predators.

Observations in the laboratory and in the field indicated that *L. peregra* do not burrow below the surface of the mud to avoid desiccation, a finding which contradicts an earlier observation by Cooke (1895), who recovered *L. peregra* from 3 inches below the surface of a dried-up pond at Cambridge. Burial may not favour the snails, however; Cawston (1929) found that *L. natalensis* (Krauss) quickly died when buried in garden soil at a depth of 2–12 inches, and other authors (Olivier & Barbosa, 1956; Perlovagora-Szumlewicz & Oliviera Dias, 1955) report the fatal effect of burial in other aquatic pulmonates.

Both in the natural habitat and in experiments under simulated field conditions the adult snails died shortly after the disappearance of the water. At this early stage, young snails, and those which, because of their small size were assumed to have recently hatched, survived. There can be little doubt that the adults which died, did so prematurely, and that their death was prompted by the drying up of the habitat, although whether the snails themselves died of dehydration or whether this simply accelerated the normal ageing process is problematical. What-
ever the precise destructive agent, it operates on the adults, the young snails being unaffected. Whilst simulated field experiments suggest for adult snails a scale of vulnerability with increasing size, it is worth noting that the intermediate sized specimens used in this experiment were from a different habitat, and that different races of snail can vary in their resistance to desiccation (Olivier, 1956).

In the particular habitat investigated, the period of dryness was quite prolonged, in excess of 3 months, and although occasionally augmented by showers and dews, the amount of soil water was generally low. The smallest snails were the ones first to suffer the effects of prolonged exposure, the tolerance increasing with increasing size: this finding could be broadly correlated with their rate of drying out in the laboratory. Results are in agreement with studies on tropical pulmonates (W.H.O., 1957) which stress the importance of favourable ecological conditions for the survival of the young stages in view of their susceptibility to desiccation.

The ability of L. peregra to survive during periods of dryness was associated with their capacity to become dormant. The posture adopted by the snails during dormancy has not previously been described for this species, but appears to be important in water economy. Water which evaporates from snails is derived not from the body wall directly, but from a superficial layer of mucus (Machin, 1964). The change in partially-dehydrated mucus has been shown to reduce considerably the amount of water lost from the mantle collar of inactive terrestrial snails (Machin, 1966). Whether the reduction in evaporative water loss in L. peregra is due to similar changes in mucus composition is not revealed, but a reduction occurs, and corresponds to the removal from the aperture, of the foot, and its replacement by the side of the body.

Because of its fragility, the thin mucus sheet frequently produced by L. peregra prior to becoming dormant is not thought to be important in water economy. Fragments of the substrate occasionally become incorporated into this veil, an occurrence reported by Shadin (1926) from L. palustris. The adhesive properties of the dried mucus may assist in anchoring the snails to the substrate: dislodgement could result in the more vulnerable parts of the animals being exposed to wind and predators.

A reduction in the metabolic rate, inferred from observations on the heart and pneumostome, would be necessary for survival of the snails during long periods without food and water.

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