THE STRUCTURAL AND FUNCTIONAL DYNAMICS OF SELECTED SPECIES-POPULATIONS OF FRESHWATER SNAILS: TOWARDS A SYSTEMS APPROACH.

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ABSTRACT

The structural and functional dynamics of freshwater gastropods at Malham Tarn are examined and detailed information is presented with regards to two littoral species, Ancylus fluviatilis (Müll.) and Planorbis contortus (Linn.), occupying a semi-isolated part of the Tarn.

At all levels, from whole Tarn to micro-situations the snail populations are aggregated. Both P.contortus and A.fluviatilis are semelparous with little overlapping between generations. Their phenological details may vary from year to year depending on external conditions.

A.fluviatilis is a herbivore which feeds on epilithic algae, particularly diatoms. P.contortus is a detrivore which is only able to make use of the bacterial fraction of its food. The functional ecology of these two species is considered in terms of the classical energy budget statement and indicates that mucus secretions are important elements of their function and functioning.

The philosophical implications of the mechano-reductionist, energy budget statement are discussed and criticised. The relevance of Control Theory and the more generalised Systems Theory are examined in terms of the results from freshwater snails. A more realistic, holistic approach is suggested.

PREFACE

An ecologist has two spheres of activity. He seeks to know more about the organisms with which he operates and also more about the general principles of his science. The former may not lead naturally to the latter and indeed some ecologists are content to remain with their particular animals (or plants) in preference to exploring the wider implications of their finding. In this scheme, the present work arose out of an urge to study snails and has only developed, in its later stages, into a more broad-minded approach. As a result, the theoretical implications of the findings presented, are to some extent preliminary and tentative, and this is reflected in the title of the thesis.

Ecology is a wide-ranging topic and this imposes itself on ecological research. The current work is divided into 10 PARTS and those presenting results (i.e. PARTS II - VIII) each deal with a different facet of snail ecology and can either be considered as entities in their own right, or as contributions to the theme set forth in PART I and discussed in PARTS IX and X. It is hoped that the format of presentation, by providing a clear distinction between PARTS and yet maintaining some discursive fluency between them, facilitates a dual appreciation in the terms described above.

The figures and appendices are presented in a separate volume to enable easier cross-referencing. There are two types of appendices. One contains raw data and is called the DATA APPENDIX and the other contains work published or accepted for publication during the preparation of the thesis and is called the PUBLICATIONS APPENDIX. Information contained in the latter is rarely duplicated in the body of the thesis so that the PUBLICATIONS APPENDIX should be treated as an integral part. The papers included and the citations within them are not re-cited in the bibliography at the end of volume I.

P.C.

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PART I

INTRODUCTION

(A Historical Perspective and Statement of Intent)

Ecology is ultimately concerned with understanding the structure and functioning of ecosystems (Odum, 1962). Population ecology operates implicitly within this framework, yet, recognising the complexities of the whole, concentrates attention on the parts. Complete understanding of the whole ecosystem from a knowledge of its parts seems unlikely (Friederichs, 1958) although some insight may be achieved. There may also be some intrinsic value in a "population theory" based on units abstracted from the ecosystem just as there is value in a "physiological theory" based on individuals abstracted from populations.

Structural aspects of this ecological effort are involved with the composition of communities, in terms of species, numbers and biomass. Their frame of reference is both space (e.g. dispersion patterns) and time (e.g. phenology) and a consideration of physical factors is relevant in-so-far as these affect the biota.

Functional efforts have lead to a consideration of energy flow through ecological systems and the concomitant circulation of matter. Here time forms an all important frame of reference. The wide-spread interest which has arisen in this field over the more recent history of ecology is reflected in the reviews of Slobodkin (1962a), Macfadyen (1964), Engelmann (1966), Phillipson (1966), Gates (1968), Mann (1969), and Hunter (1970). Studies have been carried out on whole ecosystems (e.g. Juday, 1940; Odum, 1957; Teal, 1957, 1962; King and Ball, 1967), part ecosystems (e.g. Engelmann, 1961; Mann, 1964b, 1965; Van Hook, 1971), and at the level of the population (e.g. Wiegert, 1964; Comita, 1964; Saito, 1965; Varley, 1967; Hinton, 1971; Lawton, 1971; Meese, 1971). Not surprisingly in view of their well defined, semi-isolated condition, lake systems have played a central role in the accumulation of this functional information. Some useful and stimulating generalisations have also been forthcoming from laboratory experimentation (e.g. Slobodkin, 1959, 1960, 1962 a and b, 1964). The latter parallels the relationship between laboratory and field orientated research in the structural branches (c.f. Park, 1956; and Broadhead and Wapshere, 1966).

Impetus for shifting ecological attention to the dynamic functional properties of ecosystems came initially from the, now classical, paper of Lindeman (1942). Use of the energy concept in, and application of the laws of thermodynamics to biological systems, however, arose far earlier than this and stem ultimately from the philosophical writings

of Déscartes (Traité de l'homme, 1664; Passions de Iâme, 1649[1]). Déscartes founded the mechanistic approach to biology, drawing analogy between physical machine and animal system ("La Bête Machine") and opening the way for physiologists like Rubner[1] (1854-1932) to apply the laws of thermodynamics. Biological energetics is at once identified with the twin philosophies of mechanism and reductionism. The energeticist uses a machine analogy to identify his problem and reduces the complex phenomenon of metabolism into simpler subcomponents of anabolism and catabolism to facilitate investigation. The latter are stated explicitly and separately in both the energy budget statement (Phillipson, 1966) and its derivative, the Pütter growth equation (Pütter, 1920; see also Bertalanffy, 1949, 1951).

Odum and Pinkerton (1955) have reviewed generalities in the animal-machine analogy, particularly from an ecological viewpoint and Scott (1965) has assessed the acquisition and use of thermodynamics data in ecological situations. Hubbell (1969, 1971) has criticised the reductionist approach implicit in the energy budget statement on the grounds that it does not account for the emergence of control in whole, living systems. His arguments derive from the philosophical scheme of General Systems Theory (Bertalanffy, 1971), the basic tenet of which is that the properties of the whole are greater than the sum of the properties of the parts involved.

Systems theory and its particular biological manifestation i.e. Organismic biology (Bertalanffy and Woodger, 1933; Bertalanffy, 1952) are not vitalisms. The former do not intend emergent properties as mystical transcendental entities (c.f. the entelechy of Driesch - Philosophie des Organischen, 1921[2]) but rather as tangible outcomes of interaction which lead to a reduction in the degrees of freedom of the parts involved (Weiss, 1969) and allow for the possibility of control. Since organisation and regulation are fundamental properties of living things our understanding of biological, and in the present context ecological, systems must embody these considerations. In this sense the classical energy budget statement is too simplistic, and a logical extension of its formulation, within the framework of a Systems Theory, would appear to be towards a cybernetic representation (see

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1. These references are not cited in the bibliography. For an appreciation of their impact on biology see Coleman (1971).
2. This reference is not cited in the bibliography. For an appreciation of its content and impact on biology see Sũner (1955).

Hubbell, Ibid.). This is not to reject either the powerful machine analogy or the laws of thermodynamics but rather to make use of more complex (cybernetic) machine theory and to recognise that physical laws provide only general constraints within which biological systems must operate (Polanyi, 1968).

The present work has been involved with both the structure and function of freshwater gastropod populations at Malham Tarn in Yorkshire. These animals are particularly convenient for ecological research because, in the temperate world, they have an annual life cycle with non-overlapping generations (Hunter, 1961 a and b). They also provide few taxonomic difficulties and are easily manipulated under laboratory conditions. Even so, although there is a large body of information regarding their spatial distribution (e.g. Boycott, 1936; Macan, 1950; Hunter, 1957; DeCoster and Persoone, 1970; Marazanof, 1970; Morgan, 1970; Pip and Paulishyn, 1970) and some information on their phenologies based on size frequency analyses (e.g. Berrie,1963, 1965, 1966; DeWit, 1955; DeWitt, 1955; Duncan, 1959; Hunter, 1956, 1957, 1961 a and b, 1966; Pinel-Alloul and Maghin, 1971) quantitative information on their structural and functional population dynamics is limited.

On the structural side, apart from laboratory work (e.g. DeWitt, 1954 a and b; DeWitt and Sloan, 1958) and the quasi-field investigations of Eisenberg (1966, 1970) only the field studies of Gillespie (1969) and Jobin and Michelson (1967) have been truly quantitative. With regard to the functional aspects Burky (1971) has compiled a population budget for Ferrissia rivularis (Say) which is in terms of carbon and Tilly (1968) for Physa integra (Say) which is in terms of energy. The latter forms part of a wider study of a whole ecosystem and is necessarily superficial. Heywood and Edwards (1962) have constructed a partial energy budget for Potamopyrgus jenkinsi (Smith). Two reports have been concerned specifically with freshwater snail production in terms of mass (i.e. Gillespie, 1969; Stanczykowska et. al., 1971) and Mann et. al., 1971 (see also Berrie, 1972) have considered this parameter as part of a study involved with a whole ecosystem.

PARTS III to V of this thesis are concerned with the structural dynamics of freshwater gastropods. These begin with the spatial structure of gastropod populations in general, which is discussed in terms of the physical, chemical and biological characteristics of

Malham Tarn given in PART II, and end with the dynamic structural details of two littoral species, (Ancylus fluviatilis Müll.and Planorbis contortus Linn.), occupying one semi-isolated part of the Tarn. The earlier PARTS (i.e. III and IV) present the logic behind the choice of the two above-mentioned pulmonate species and provide the necessary information for planning a sampling programme. PART V documents and discusses the results obtained from this programme. PARTS VI to IX consider the functional ecology of P.contortus and A.fluviatilis. This is approached in a classical reductionist vein. PARTS VI and VII are concerned with growth and energy inputs (anabolism), PART VIII with energy outputs (catabolism) and PART IX with an integration of these components into an energy budget statement. Throughout these PARTS, however, the application of control theory to the individual and population energetics of the two species concerned is examined. This is drawn together and elaborated in PART X when the relevance of Systems Theory to the development of a sound predictive theory of functional ecology is discussed and a method of approach, based on the findings reported in the earlier PARTS of the thesis and orientated towards the population level, is suggested.

PART II

A DESCRIPTION OF THE HABITAT

1. GENERAL CONSIDERATIONS

Malham Tarn is situated ca. 381m. (1250 ft.) above sea level in the West Riding of Yorkshire. Its general geographical location is given in FIG. 1 and geographical details of the area are presented in FIG.2.

In order to appreciate either flora or fauna some knowledge of the geology of the area is essential. Whilst its basic geology is fairly well defined (Garwood and Goodyear 1924; O'Connor 1964) the surface features are more complicated and only a simplified pattern of these can be given here.

The area is trisected by the North and Middle Craven Faults, both of which run from west to east (FIG. 2). The Tarn lies in the most northerly sector of this system, i.e. in a region of upland limestone overlain by glacial scree. It owes its presence to two factors. The first is an inlier of impervious Silurian rock against the North Fault which forms its bed and the second is a series of morainic ridges containing it to the south.

About 15000 years ago the Tarn covered about twice its present area of 62ha. (153 acres). During this period, however, a large area on the western side of the Tarn became overgrown with vegetation, passing through various stages of fen, and fencarr and laying down vast quantities of peat. Erosion of the containing moraine eventually resulted in a breakthrough and the formation of a stream (Malham Water, see FIG. 3), which became the head waters of the River Aire. The water of the Tarn fell by some 7m. reducing its area to one slightly smaller than the present. The western portion became a raised bog, now known as Tarn Moss (see FIG. 3).

In 1791, Thomas Lister, first Lord Ribblesdale, built a controlled outlet at the southern end of the Tarn, thereby raising its level about 1.2m. (4ft.). This had three major effects. Firstly there was flooding of a dug-out portion of Tarn Moss, resulting in the formation of a distinct semi-aquatic portion with characteristic semi-aquatic vegetation i.e. the Fen (see FIG. 3) and secondly there was the creation of a new shoreline. On a clear day the old shoreline is still visible, particularly on the north and northeast shores, as a submerged hummock of large boulders lying beneath ca. 1m. of water. More will be said about

this feature later. Thirdly, and finally, the controlled outflow of water from the Tarn means that its depth undergoes little seasonal variation and its depth range is limited to ca. 15cms. This is particularly convenient when considering littoral populations, since their habitat extent can be assumed to be relatively stable and constant.

The present Tarn, then, is 62ha in extent and very shallow (see SECTION 3. 1). A rough calculation of the volume of water present has been made by Holmes (1965) and approximated to 300 million gallons. There is one major and several minor inflow streams, and a single outflow. The short major inflow arises from springs near the base of the Great Scar limestone and is consequently rich in calcium, as are the waters of all inflow streams. This feature dominates the biology of the Tarn and will be discussed further in SECTION 3. 3.

The following sections are involved with a description of all those features of the Tarn i.e. climatic (SECTION 2.), physical, chemical and morphometric (SECTION 3.) and biological (SECTION 4.), which either have general relevance to its ecology or have specific relevance with regard to subsequent sections of the thesis.

2. CLIMATIC CONSIDERATIONS

2. 1. Temperature

Tarn temperatures were measured using Berthet's (1960) technique which is based on the rate of inversion of sucrose:

$$\text{Sucrose} + H_2O \longrightarrow \text{Fructose} + \text{Glucose}$$

The rate of inversion is assessed at a constant pH. and the rotation of the solution is determined using a polarimeter. The inversion constant is calculated from the equation:

$$K'T = \frac{1}{t} \log \frac{A_0 - B_0}{A - B_0} \quad \text{.....1 (2.2.1)}$$

where:

t = time of exposure to temperature (days)

A_0 = initial rotation value of the solution

B_0 = complete rotation constant

A = actual rotation value of the sample after exposure.

T = temperature in degrees absolute

The temperature is then calculated from the equation:

$$T = \frac{a'}{c' - \text{Log } K'T} \quad \text{.....2 (2.2.1)}$$

where a' and c' are constants. a' is independent of pH and Berthet's value of 5.854 was used. c' is dependent on pH. A value of 19.2000 ($\pm$ 0.0073), the mean of 30 determinations, was used here.

The sucrose solution was prepared by dissolving 400g. sucrose in 220ml. water and 10ml. 35% formalin (as an anti-biotic), and this solution was filtered. The buffer solution was prepared by adding 3.75g. KCl to 33.9ml. of 1N HCl, and was diluted to 500ml. The prepared solutions were stored at 5°C until required.

Equal quantities of the two solutions were thoroughly mixed and 12ml. of this mixture were transferred into each of five plastic tubes. Two tubes (with solutions for determining A_0) were immediately placed in the deep freeze, the remaining three were transported in a freezing mixture into the field. Location of these tubes within the Tarn is shown in FIG. 3 (marked T.). They were placed under 30cms. of water adjacent to the shore on

which the most detailed sampling programme was to be carried out. After a known period of time (about a month during most of the year, but a fortnight during the summer) the tubes were taken back to the laboratory in a freezing mixture. The rotation of the three solutions was measured using a Bellingham and Stanley, model D, polarimeter.

Measurements were begun in January 1970, and continued until August 1971. Estimated mean temperatures derived from the average rotation of the three replicates are shown in FIG. 4. Errors are not shown but in all cases they were less than 4%. In months where two samples were obtained (i.e. summer months), these have been averaged and corrected to the 28 day interval.

As Berthet (1960) points out the mean obtained from the above method is not a true mean since the effects of higher temperatures is more dominant than lower in obtaining the value. This method of exponential integration is, however, of value in ecology in that most biological reactions have a temperature coefficient of the same order as that of sucrose (Q_{10} = 2.0) and the method has previously been used to advantage in energetics studies in both freshwater (e.g. Lawton 1971) and terrestrial (e.g. Hinton 1971) environments.

Information contained in FIG.4 will be used later for both the interpretation of ecological information and the computation of energy budgets.

2. 2. Wind Action

From an intuitive point of view wind action, by influencing the direction and intensity of water movements, must play an important part in determining lake habitat structure and concomitant composition of zoocoenoses. Its influence on wave action, temperature stratification, and heat production is well understood, as is its general effect, via wave action, on substrate composition and floral and faunal distributions (see general texts: Welch, 1935, Rutner, 1953, Macan and Worthington, 1959, Macan, 1963, 1970). The latter, however, has only been stated in qualitative terms (see Macan 1970, who referring to Lake Windermere has suggested a relationship between wind direction, the distribution of detritus, and the occurrence of his "insect" and "non-insect"

communities).

In this section wind action in terms of the speed and direction operating at Malham will be discussed as preliminary to demonstrating its effects on Tarn, particularly littoral, morphology and snail community structures. Data derives from a 21 month interval between February 1970 and August 1971, during which time routine snail population estimates were being made.

The following data has been obtained from meteorological records kept at Malham Tarn Field Centre. I am grateful to the Warden for allowing me access to this information.

Table 1 indicates occurrence and direction of winds over a 577 day interval between Feb. 1970 and Aug. 1971. Winds are classified as either originating from compass points between 0 - 179° (N →S) or between 180 - 359° (S →N). The logic behind this will be discussed in PART III.

TABLE 1. Occurrence and direction of winds operating over a 577 day interval (Feb. 1970 to Aug. 1971) at Malham Tarn.

Source	N →S (0 - 179°)	S →N (180-359°)	No Wind	Total
No. of days operating	155	356	66	577
% total no. of days observed	26.86	61.70	11.44	100

Out of 577 days observation only 11.44% were devoid of wind. Most arose from the compass points between 180 - 359° i.e. blowing from the western sector on to the eastern shores. Mean wind speeds were 8.290 $\pm$ 1.085 knots (N →S) and 10.796 $\pm$ 1.096 knots (S →N). Confidence limits are two standard errors, and means are based only on days when winds were observed. The means are not significantly different ($d = 1.149$ $p > 0.10$) indicating that when winds blow at Malham, their average strengths are not affected by the direction from which they originate. From a biological viewpoint, however, the time periods over which winds blow, particularly with respect to those capable of inducing significant wave action are likely to be more relevant. Only winds exceeding 5 knots are likely to produce waves (Meteorological Office Handbook 1956).

TABLE 2 contains information based on a 364 day subsample (25/7/70 - 24/7/71) derived from the total 577 day sample described above. It summarises data on the total number of windy days and the total number of days when winds were in excess of 5 knots.

TABLE 2 Average wind speeds, total number of windy days and total number of days winds exceeded 5 knots at Malham Tarn between July 1970 and July 1971 (364 days).

	No. Days	% total days observed	
Total days winds blew	329	90.4	
Days winds blew from :			
S → N sector	212	58.3	
N → S sector	117	32.1	
Days winds exceeding 5 knots blew from :			
S → N sector	129	35.4	49.4
N → S sector	51	14.0	
Total days observed	364	100	

Data from this subsample are similar to the reults obtained from the total 577 day period (see TABLE 1) with respect to the proportion of time winds blew, and the directions from which they originated. Further information summarised in TABLE 2, however, indicates that winds with critical speeds (i.e. > 5 knots) were ca. twice as prevalent from the 180 - 359° sector than from the opposite sector. Thus, although winds blowing from each direction do not differ significantly in their average speeds, they do differ in the frequency with which those speeds are in excess of 5 knots. From this point of view shores within the 0 - 179° sector, the eastern shores, are likely to receive more winds and more waves than opposite shores. It must be remembered, however, in judging these conclusions that observations on wind speed at Malham are made once a day (i.e. at 9.00a.m.) and that the data presented result from a series of samples and not a continuous record of wind activity. Nevertheless, the general conclusions derived do correspond with personal observation.

FIG. 5 shows a monthly breakdown of information contained in TABLE 2 in terms of average wind speeds (5a) and duration of time

over which they blew (5b). Data for different sectors are treated separately and horizontal lines within blocks giving durations, indicate number of days over which speeds were in excess of 5 knots. FIG. 6 shows summed total days over which winds occurred in both directions, and summed total days over which they exceeded the critical value in each month.

With respect to FIG. 6, periods over which wind is experienced at Malham show a surprising consistency from month to month (ca. 24 out of 25 days are windy). The pattern with regard to critical wind speeds is more variable with peaks occurring between 17/10 and 14/11 (1970), 6/3 and 3/4 (1971) and 29/5 and 26/6 (1971). Similarly the pattern is more variable when wind direction is considered as in FIG. 5. Here peaks in terms of total no. of windy days and numbers of days on which winds were in excess of 5 knots occur between 17/10 and 14/11 (1970) for winds arising from the S →N sector and between May and July, for winds arising from the opposite sector. Strongest S →N winds blow between 17/10 and 14/11 (1970) and strongest N →S winds blow between 12/12 (1970) and 9/1 (1971).

The ecological implications of these findings with regard to Tarn morphology and snail community structures will be considered in PART III.

3. PHYSICAL, CHEMICAL AND MORPHOMETRIC CONSIDERATIONS

3. 1. Depth Profile of the Basin

As already noted Malham Tarn is shallow, the maximum depth recorded being ca. 4.25m. (14ft.). Most of the offshore parts, however, are between 2 - 3.5m. (6 - 10ft.) deep. FIG. 3 shows the depth contours of the Tarn and is derived from Philipson (1968). Apart from the littoral region, most of the Tarn bottom consists of a surface layer of flocculent, black mud, rich in organic material and an underlying layer of cream coloured marl (Holmes 1965).

3. 2. Depth Profiles of Littoral Regions and Nature of Substrate

The shores at Malham are varied and have been described in detail by Holmes (1965), who gives schematic profiles of all major types. Most shorelines described slope gently, in conformity with the shallowness of the basin.

The north, northeast and parts of the south shores are rocky, west shores adjacent to the "Tarn Moss" are of peat, and two sheltered bays on the south shores have a sandy substratum. Bays in both the northeast and northwest corners of the Tarn contain beds of Carex rostrata (Stokes) and are surrounded by soft muds. Immediately adjacent to the controlled outlet is an artificial dam wall constructed of stone, and sloping steeply into the water.

Most detailed sampling of littoral snail populations has been carried out on a portion of the east shore of the Tarn immediately adjacent to "Ha Mire" plantation and delimited by two walls which are built into the water to a depth of ca. 1m. (see FIG. 3). This shore is ca. 200m. long and has a solid limestone base with a variable depth of glacial drift and weathering debris over it. Wave action has in fact produced an extremely varied shore composed of stones varying in size from small pebbles to large boulders. These rest loosely on top of one another.

The position and outline of this shore is depicted in FIG.7. A broken line offshore delimits the approximate position of the old shoreline, and two dotted lines set at right angles to the shore indicate the inner boundaries of three sectors (A, B and C) which are delimited for sampling purposes (see PART IV SECTION 4)

Size and shape frequency distributions of stones within each sector have already been described (Calow 1972, see PUBLICATIONS APPENDIX 11). FIGS.8 a, b, and c show depth profiles along three transects taken at points x, y, z (see FIG. 7) in sectors A, B, and C respectively. Sector B has the most gently sloping profile, the smallest stones and greatest concentration of between-stone detritus. These features presumably result from its sheltered embayed situation.

3. 3. Water Chemistry

Lund (1961) presents data on the concentration of the major dissolved ions in the waters of the main inflow of the Tarn and of the Tarn itself. As is to be expected from the geology of the area both are highly alkaline, containing between 8 - 12 times as much Ca^{2+} as the North Basin of Lake Windermere (i.e. according to Lund the Tarn contained on 18/6/58, 2.365 millequivalents Ca^{2+}/L.).

Alkalinity of the Tarn, however, varies considerably during the year but is never as high as in the major inflow stream. In the Tarn, the alkalinity is lowest in summer and highest in winter; in the inflow the reverse prevails. The detailed causes of these cyclic changes are unknown but it is unlikely that they are entirely due to biological phenomena and Lund (1961) suggests that temperature differences between the Tarn and the inflow may be involved.

Cycles also occur in dissolved nitrate nitrogen ($N.NO_3$) and SiO_2 . $N.NO_3$ peaks at ca. 0.4mg./L during spring, when much of the organic N_2 arising from winter mortality of plants and animals has been mineralised, and troughs during winter months at ca. 0.1mg./L. SiO_2 cycles between 2.0 and 0.5mg./L with seasonal variations in diatom production.

Phosphate phosphorous ($P.PO_4$) is almost always at extremely low concentrations and Lund (1961) believes that phosphorous is the major element limiting primary production within the Tarn.

4. BIOLOGICAL CONSIDERATIONS

4. 1. Trophic Classification of the Tarn

Malham Tarn is not easily positioned within the usual eutrophic/oligotrophic system of lacustrine classification. In some respects the Tarn exhibits eutrophic features viz. a high production of submerged macrophytic vegetation (Chara, Potamogeton, Myriophyllum), high nutrient status (apart from $P.PO_4$) and shallow depth. In other respects the Tarn exhibits oligotrophic features, viz. a low phytoplankton production (Lund,1961), the absence of marginal reed beds, lack of thermal stratification and consequently no depletion of oxygen during summer months.

As Round (1953) argues, ".... in many cases it is not possible to divide lakes into well defined types, but only into a series showing numerous gradations between oligotrophy and eutrophy". Malham Tarn appears to occupy an intermediate position within this spectrum.

4. 2. A General Consideration of Organisms Present

The general ecology of both flora and fauna present within the Tarn has been extensively reviewed by Holmes (1965). Specific faunal works include those of Stratton (1956) on the Mollusca (see also PARTS 1 and 111), Reynoldson (1956) on the Triclads, Fryer (1953) on Gammarus, Wilson (1949) and Holmes (1960) on the fish, and Williamson (1968) on the bird communities living in and around the area. Work on the flora includes that of Lund (1961) on the algae, Procter (1960) on the mosses and liverworts and Sinker (1969) on the macrophytes.

In view of the altitude, Malham Tarn is extremely rich in both flora and fauna. This reflects the varied nature of the habitats present and also the relatively high concentration of nutrient salts. As already noted $P.PO_4$ must be considered as one of the major limiting factors operating within the Tarn, but Ca^{2+} ions are in abundance, and this is particularly advantageous from the point of view of the molluscan fauna present.

PART III

THE SPECIES COMPOSITION OF GASTROPOD "COMMUNITIES", IN MALHAM TARN

1. INTRODUCTION

A review of work relating to the general ecology of freshwater molluscs has been given in PART 1. Briefly, Boycott (1936) has surveyed their distributional ecology throughout Britain, whereas Macan (1950) has made a more detailed study in a single area. Other geographical surveys have been made in other parts of the world e.g. Baker (1928) in Wisconsin, Frömming (1936, 1938) in northern Europe, Alsterberg (1930) and Hubendick (1947) in Sweden, Hunter (1957) in Scotland and Benthem Jutting (1959) in the Netherlands. Fewer studies have been concerned with a consideration of the intra- habitat distribution of the freshwater mollusca c.f. Baker (1916, 1918 and 1927) in both Oneida Lake, New York and White Lake, Michigan, Hunter (1957) in Loch Lomond and DeCoster and Persoone (1970) in a swamp region near Ghent. Apart from the latter all of these surveys are expressed solely in qualitative terms.

The first species list for the Mollusca at Malham Tarn was produced by Soppitt and Carter (1888). This has subsequently been amplified and verified by Roebuck (1890), Booth (1910), Fysher (1929) and most recently by Stratton (1956). Boycott (1936) has collected together the species lists given by the earlier workers (p. 157 of his paper) and Stratton's list exceeds the latter by five species only, of which two are gastropods. He describes 13 gastropod species in total.

The diversity of the mollusca at Malham Tarn is unusually high in view of the altitude. This can be accounted for by a high concentration of Ca^{2+} (see PART II SECTION 3. 3.), which is far in excess of 20mg/l quoted by Boycott (1936) as the minimum critical level for the presence of snails.

The following sections provide semi-quantitative information regarding distribution of gastropods in one lake. Factors affecting distribution will be considered particularly with reference to the littoral populations and to the influence of wind and wave action the physical aspects of which have already been referred to in PART II, SECTION 2. 2. This information derives mainly from an initial survey of the Mollusca at Malham begun in August 1968, continued in July and August 1969, and aimed at selecting those populations which would be convenient and suitable

for more detailed dynamics studies. Relevance of this survey to the latter will be discussed in SECTION 6. 2.

2. SAMPLING TECHNIQUES

The survey encompassed both the major weed beds of the Tarn and the rocky shores. The shores have already been described (PART II SECTION 3. 2.). The five major types of weed bed consist of pure stands of Elodea canadensis or Potamogeton lucens or Myriophyllum spictatum or Chara delicatula or Carex rostrata. Only the latter species is emergent. Other species i.e. the moss Fontinalis antipyretica L. and the stonewort Chara aspera Deth. occur patchily on the rocky shores and were not considered. Distribution of the weed beds within the Tarn is given in FIG. 9. The positions of the sampling stations are also depicted. Of the littoral sites only station 1 has not previously been considered. It comprises a stretch of glacial drift ca. 150 - 200m. in length surrounded on all sides by peat.

Sampling technique varied with habitat. On the rocky shores, 50 stones were selected haphazardly at each station, snails were removed and stored en-masse in 10% formalin for counting. All weeds, except the sedge, were sampled by means of a grab-net, similar to that described by Phillipson (1968). The grab enclosed 0.25m^2 of weed bed and yielded between 100 - 500g spun-dry weight of weed. Three samples were taken at each station, and stored in 10% formalin. Snails were subsequently extracted using a water flushing device like that described by Cross and Minns (1969). Comparing the number of animals recovered by hand sorting and extraction the latter workers found that the extractor operated at between 96 - 100% efficiency. Using individuals of all species, marked with red nail varnish, I obtained an efficiency of 100% for all samples. Sedge was sampled using a metal frame with muslin sleeve. The frame enclosed 0.25m^2 of bed and the sleeve projected above the water surface. Emergent shoots were sheared to the water surface and discarded. Submerged shoots and roots were shovelled out of the frame and washed thoroughly in 10 litres of water. Washings were sieved through a 1mm screen and the water remaining within the muslin sleeve was stirred and sieved with a conical pond net (24 strands/cm; pore size 300μ ; type B as supplied by F.W.B.A.). Snails so obtained were bulked in 10% formalin. A total of five samples were obtained, each taken at 1m intervals along a transect passing from the waters edge to the bank.

3. A QUALITATIVE CONSIDERATION OF SPECIES PRESENT AND THEIR DISTRIBUTION

Table 3 shows the distribution of the gastropod species at Malham in terms of their presence or absence in various habitats and is compiled from both the 1969 survey, described above, and from Stratton (1956). The latter worker considered only one shore in detail i.e. station 2, but was able to take samples from the north-west sedge bed. Access to this region is now restricted for conservation purposes, though casual observation was possible. Results from the survey in 1968 are identical to those from 1969 and are not included. No gastropod molluscs were recorded either from the sandy bays on the southern shores, or from the peat shores of Tarn Moss or from silt accumulated around the sedge beds. Absence from silt and sand is almost certainly a result of snail sensitivity to the fouling of their respiratory surface, whereas absence from peat probably results from the reduced pH. A complete species list of gastropod molluscs present at Malham, together with dates on which they were first recorded, is given in DATA APPENDIX II.

A general comparison of Stratton's results with those of the present survey indicates a reduction in number of species, particularly operculates, on the rocky shores but an increase in the number in the weed beds. The total number of species present in the Tarn remains the same. The sedge beds and some of the littoral stations seem to present the most restricted fauna.

At present the most ubiquitous species is P.contortus which ranges throughout all habitats. Moquin-Tandon (1855) describes it as living in still waters on aquatic plants whereas Boycott (1936) associates it both with running and with stagnant situations. Its ubiquity may be a function of its feeding habits since it appears to eat detritus and attached bacteria (see PART VII SECTION 4) which are likely to occur in most habitats. Lymnaea stagnalis is also fairly wide ranging being absent only from the rather restricted Elodea, and sedge beds. Its size is significantly larger in the weed beds than on the rocky shores, (see TABLE 4) and a similar phenomenon is found in L.pereger.

TABLE 3. A Qualitative Illustration of Distribution of Gastropod Species in Malham Tarn.

Station Number	1	2	3	4	5	6	7	8	9	10	11	12	13	Range **
Pulmonata														
A.fluviatilis	+	x+	+	+	+	+	+	+						8
P.contortus	+	x+	+	+	+	+	+	+	+	+	+	+	+	13
P.albus	+	x+				+		+	+	+	+	+		8
P.crista	+	x+				+		+	+	+	+	+		7
P.leucostoma													+	1
L.pereger	+	x+	+	+					+	+	+		x	7
L.stagnalis	+	x+	+	+	+	+	+	+		x+	x+	x+	x	11
L.palustris		x							+	+	+	+	x	4
Ph.fontinalis		+								+	x+	x+	+	4
Prosobranchia														
B.tentaculata		x		+		+			+	x	x+	x+		5
V.cristata		x								+				1
V.piscinalis		x							+	x+	x+	x+	+	4
P.jenkinsi		x							+					
Total No. of Species *	6	7(11)	4	5	3	6	3	4	8	(3)9	(4)9	(4)8	4(3)	

* Stratton's results are in parenthesis

** Refers only to the 1969 sampling survey

x Compiled from Stratton 1956

\+ From 1969 survey

TABLE 4. Comparison of Shell Length (S L*) of L.stagnalis + L.pereger Taken from Weed Beds and Rocky Shores in August 1969.

	Shores (Samples summed from all shores)	Weeds (Samples summed from all shores)
L.stagnalis		
MEAN	8.4mm	21.3mm
No. observed	41	57
Fiducial Limits (2X standard error)	2.1mm	3.3mm
+ d	4.77	
p	0.001	
L.pereger		
MEAN	4.1mm	8.5mm
No. observed	33	39
Fiducial Limits (2X standard error)	1.3mm	1.6mm
d	2.78	
p	0.01	

Holmes (1965) explains these differences in terms of food supply whereas Hunter (1961 a, b) who noticed dwarfism in populations of L.pereger in the rocky littoral situation of Loch Lomond suggested that both food supply and oxygen limitations, during summer months, were probably the cause. The variety of L.stagnalis previously cited as peculiar to Malham (Taylor 1895) with a small, delicate, transversely banded shell was not taken in 1969. This apparently fluctuates in abundance from year to year (Holmes 1965). L.pereger taken were of variety ovata (Drapernaud).

A.fluviatilis is limited to the rocky shores where it is found at all stations. This species is usually associated with lotic habitats, though it has repeatedly been described from the

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* Terminology from Hunter (1961a)

+ significance test based on two large samples (n>30) see Bailey (1959)

rocky littoral situations of lakes (see review by Berg 1952, p.264, and also Geldiay 1956, and Hunter 1957).

P.leucostoma is the most restricted species of pulmonate being limited to the sedge beds. Stratton (1956) also noted its restriction at Malham, although he was unable to find it in the north-east sedge bed. Casual observation has indicated that it is still present in the north-west sedge bed. Boycott (1936) lists it as characteristic of stagnant situations.

Of the operculates, only B.tentaculata was found on the rocky shores in 1969. V.cristata and P.jenkinsi have the most restricted distribution being limited to Chara and Elodea respectively.

* The case of P.jenkinsi is an interesting one. It is the most recent molluscan colonist of fresh waters, making the transition from its original brackish location around the turn of the century. Robson (1923) has discussed reasons for this transition and its history of colonisation is well documented (see Robson 1923 and Boycott 1936 for England, Hunter and Warwick 1957 for Scotland, Bondeson and Kaiser 1949 for Denmark and Hubendick 1950 for the whole of Europe). There are probably several distinct races within the species (Warwick 1944, 1952). Potamopyrgus was not recorded in Malham Tarn until 1950 (Stratton 1956) although it had been found in Coniston Tarn, 6.5 miles south of Malham in 1928. Reduced dispersal of this species seems to be typical of highland regions (Hunter and Warwick 1957). Its subsequent course of colonisation in the Tarn is given by Holmes (1965). By 1954 it had become very abundant on the north shores and in the Chara beds. In 1958 and 1959 its densities fell severely, but since then and up to Holmes' publication in 1965 it was apparently undergoing slow recovery and recolonisation. There are no further records after 1965 until the present survey, when Potamopyrgus was found to be strictly limited to Elodea. During the intervening period its densities must again have fallen. This pattern of rapid invasion followed by dramatic reductions in density and restrictions in distribution seems to have been typical (Boycott

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* The following paragraphs to the end of section 3 have formed the basis of a note to the Naturalist (Hull). See PUBLICATIONS APPENDIX V

1936, Macan, 1950) and may be characteristic of any new colonists whilst finding their ecological place within the indigenous fauna (Elton, 1958).

The present association between Potamopyrgus and Elodea may be significant. The invasion of freshwater in Britain by both these species seems to be related, and Robson (1923) suggests that Elodea may have prepared the way for Potamopyrgus by contributing some factor to its food supply. It should be noted, however, that Elodea appeared within the Tarn in 1962 after the initial invasion of P.jenkinsi (Holmes, 1965) and that Potamopyrgus does not eat Elodea tissue directly, only the encrusting epiphytes (Robson, 1923). The latter behaviour is similar to L.pereger on Elodea (Calow, 1970, see PUBLICATIONS APPENDIX I). It seems likely, therefore, that Elodea merely provides a suitable refuge for Potamopyrgus either from the direct action of predators or from competition with other snails. Although other species of snail do occur on Elodea at Malham, P. jenkinsi is by far the most abundant, (see DATA APPENDIX IIIA) and some snails apparently find Elodea toxic (Gaevskaya, 1966).

4. BETWEEN HABITAT SIMILARITY OF SNAIL COMMUNITIES

Various computational methods are available for comparing fauna in different habitats. These have been reviewed by Mountford (1962) and Southwood (1966). The method used here is the Index of Similarity, I, (Mountford 1962) because it is least sensitive to sample size. A comparison is made between the latter and Sørensen's (1948) Quotient of Similarity, QS, which suffers from the disadvantage of being affected by sample size (Mountford, 1962). The Quotient of Similarity is defined as:

$$QS = \frac{2j}{a+b} \quad \text{.....1 (3. 4.)}$$

when a = number of species in one habitat

b = number of species in other habitat

j = number of species in common

and ranges in value from 0 when there is absolutely no relationship between fauna , to 1 when the correlation is perfect. Mountford's index is defined as:

$$I = \frac{2j}{2ab-(a+b)j} \quad \text{.....2 (3. 4)}$$

whereterminology is as in equation 1 (3. 4.) above and ranges between 0 for no relationship to $+\infty$ for a perfect relationship. This index requires random sampling, and this has been assumed.

The trellis diagram (TABLE 5) shows the Similarity Indices obtained from equation 2 (3. 4.) between all possible pairs of habitats sampled at Malham. FIG. 10 shows the relationship between QS and I for equivalent habitat pairs from the survey, and indicates their non linear relationship. Apart from the theoretical difficulties in applying QS to data obtained in the present context (because of non uniformity in sample size), I has the advantage of increasing the resolution between habitats of close similarity. The non finite end point in Mountford's index is inconvenient.

The dendrogram (FIG.11) is constructed from values given in TABLE 5, according to the method of Mountford (1962). It clearly distinguishes between two clusters of habitats, the weed beds and the rocky shores, and suggests a tighter clustering in the shore than the weed bed stations. In other words the variation

TABLE 5. Similarity Indices Between Sampling Stations at Malham, as Judged by Mountford's I.

Station Number	9	10	11	12	13	1	2	3	4	5	6	7
9												
10	.286											
11	.560	.889										
12	.375	.169	.889									
13	.100	.087	.333	.214								
1	.200	.303	.303	.182	.059							
2	.154	.400	.333	.270	.118	2.00						
3	.100	.182	.182	.100	.082	1.00	.660					
4	.146	.125	.235	.171	.065	.500	.364	2.00				
5	.051	.133	.133	.154	.118	.666	.500	2.00	1.00			
6	.200	.167	.303	.385	.053	.333	.417	1.00	.500	.750		
7	.051	.133	.133	.154	.118	.666	.500	2.00	1.00	+ ∞	.660	
8	.039	.182	.130	.214	.082	1.00	.660	.750	.462	2.00	1.00	2.00

over shore stations is less than that over the weed bed stations. The distinction between shores and weed beds results mainly from the absence of A.fluviatilis from the latter and restriction of L.palustris and most operculates to weed beds.

Reasons for restriction of A.fluviatilis to rocky shores have been discussed by Berg (1952) and are apparently more related to its sensitivity to sediment accumulation than its requirement for either simulated lotic (wave action), or oxygen saturated conditions. Absence of both L.palustris and most operculates from the shore stations is not consistent with Stratton's (1956) results (see TABLE 3) and cannot be explained.

Use of either QS or I, when sample components can be expressed in terms of relative abundance loses information, since both are based on presence and absence data only. The following SECTION considers habitat comparisons based on the semi-quantitative information of relative abundance. Since the present analysis, however, has indicated a clear distinction between weed bed stations and rocky shores these will be considered separately.

5. A SEMI-QUANTITATIVE CONSIDERATION OF DISTRIBUTION

DATA APPENDIX III describes the distribution of snails throughout the weedbed sampling stations(IIIa) and littoral stations (IIIb) in terms of their relative abundance. Relative abundance is calculated as:

$$\frac{\text{Total no. of a particular species in sample}}{\text{Total no. of all species in sample}} \times \frac{100}{1} \quad \ldots \; 2(3.5.)$$

All samples from each weedbed station have been conflated to produce the abundance estimate, since ranking concordance between samples as measured by the Kendall Coefficient of Concordance, W (Siegel 1956) is good. (W_{ELODEA} = 0.56, N = 3, $p < 0.01$; W_{CHARA} = 0.62, N = 3, $p < 0.01$; W_{MYR} = 0.59, N = 3, $p < 0.01$; W_{POT} = 0.65, N = 3, $p > 0.01$; W_{CAREX} = 0.47, N = 5, $p \simeq 0.05$).

5. 1. Snail Communities in the Weed Beds

TABLE 6 contains the order of abundance of snail species in different habitats derived from DATA APPENDIX IIIA, information on the contribution of molluscs to the total fauna present (derived from Holmes 1965), and average densities of molluscs at each station expressed in terms of the numbers Kg^{-1} spun-dry weight of weeds.

Apart from stations 10 and 11 the most abundant species varies with station and this presumably reflects habitat differences, variation in the requirements of the snails and possibly competition phenomena. It should be noted, that information contained in TABLE 6 derives from samples taken at one time of year only and that relative abundances may vary with season. Since all species of snail so far investigated, however, are annual and tend to breed approximately in phase (Hunter 1961a) their order of abundance is likely to be the same throughout the year.

Stations 10 and 11, Chara and Myriophyllum, show greatest similarity in terms of the most abundant snail (L.stagnalis), relative abundance of molluscs in the total fauna and total snail densities. Mountford's (1962) method also distinguishes these habitats as being most similar (see FIG.11), although there is some difference in relative abundance of non-dominant forms. It is interesting to note that Chara and Myriophyllum are dissimilar

TABLE 6. Ranks of Snails in the Various Weed Bed Stations at Malham. Information Derived from DATA APPENDIX IIIA.

Weed Species	Elodea canadensis	Chara	Myrio-phyllum	Potamogeton	Carex rostrata
Station No.	9	10	11	12	13
P.contortus	4	3	8	5	-
P.albus	5	7	3	1	3.5
P.crista	2	2	7	8	-
P.leucostoma	-	-	-	-	1
L.pereger	6	4.5	4	-	-
L.stagnalis	-	1	1	4	-
L.palustris	8	8.5	5	6	-
Ph.fontinalis	-	8.5	6	3	3.5
B.tentaculata	7	-	9	2	-
V.cristata	-	6	-	-	-
V.piscinalis	3	4.5	2	7	2
P.jenkinsi	1	-	-	-	-
% Mollusc of total fauna (expressed in nos of individuals in each weed bed) *	-	45.9% (85%) +	52%	24%	-
Av. Density Molluscs No/Kg. spun dry wt. of weed.	1024	464	446	47	15

* Data from Holmes (1965) derived from samples between July and September (1958 - 62).

\+ Figure in parenthesis includes bivalves(Sphaerium corneum L.) which were extremely rare in all other samples.

in the sense that they are from different taxonomic groups (the Charophyta, or stoneworts, and Hydrophyta, or angiosperms, respectively), but are similar in the sense that their resultant weed beds are dense and thus provide good shelter from wave action. Furthermore, "leaf" structures of these two plants are analogous, in that they are both plumose and spicate. Snail affinities, therefore, seem to depend on the structural rather than the taxonomic similarities of their weed bed habitats, and this conforms to the contention of Shelford (1918) that aquatic macrophytes are of importance to animals only in terms of the substrata they provide (c.f. Frohne, 1956; Gaevskaya, 1966). "Leaf" structure also seems to be important for other aquatic, weed-dwelling animals and weeds with more finely divided "leaves" generally tend to support the densest faunas (e.g. Krecker, 1939; Andrews and Hasler, 1942; Entz, 1947; and Rosine, 1955 for freshwater; Weiser, 1951 for the marine environment). The fact that the Myriophyllum bed sampled is surrounded by Chara may also be significant. The Elodea bed is similarly dense, and also protected in location from wave action. Here, densities of snails are extremely high although ca. 60% are the dominant species, Potamopyrgus. This has already been discussed in SECTION 3.

In contrast, beds of Potamogeton are more diffuse, and plant leaf structures are truly laminate (i.e. flat and large) so that less protection is offered against waves. Consequently, snail density both in absolute terms and also relative to total fauna becomes dramatically reduced, (see TABLE 6).

As already noted, the most specialised weed habitats are the sedge beds. Here the dominant species occupies 95% of the total snail community, and snail densities are lowest. Both sedge beds are dense, they contain an abundance of decaying material and the water surrounding them is relatively still and stagnant. It is not surprising, then, that a Planorbis, with haemoglobin in its blood, should dominate this situation. FIG. 12 shows the distribution of P.leucostoma along the transect taken through the N.E. sedge bed. Clearly its peak density occurs centrally and this may represent some compromise between protection from wave action, and escape from fouling and/or terrestrial conditions.

Finally, it should be noted that all the weed beds except Chara die down during the winter months, re-emerging in spring, and thus necessitating annual recolonisation by both snails and other

animals. What happens to the snails during this period is not known, though Cook (1949) for Viviparus viviparus (L.), Lilly (1954) for B.tentaculata and Cleland (unpublished work cited in Lilly 1954) for Valvata cristata indicate that these species migrate to and live submerged in mud during winter months.

5. 2. Snail Communities on the Rocky Shores

The dendrogram in FIG. 11 indicates a complex picture of classification amongst the faunas of the various littoral stations. Examination of the most abundant species at each station, however, indicates a primary dichotomy which has biological relevance. Information in DATA APPENDIX 3B indicates that either P.contortus or A.fluviatilis is dominant on all shores and demonstrates the complete contiguity of similar shore types.This is depicted schematically in FIG. 13,where the line AB separates "Ancylus" from "Planorbis" shores.

The line of demarcation passes through a sedge bed in the north east and a sandy bay in the south west, thus providing discontinuity in the sense that these regions will form barriers to lateral migrations of both P.contortus and A.fluviatilis. Furthermore, division of the Tarn into two sectors by AB roughly corresponds to the division made on the basis of wind and wave action (see PART II SECTION 2. 2.). Thus shores to the south of AB can be considered as more exposed than shores to the north.

This division provides some difficulties in interpretation, because the limpet is obviously better adapted to exposure than P.contortus. Wind action does, however, have a measurable biological effect in that annual, primary, epilithic algal production is reduced by a half on station 6 when compared with station 2 (see PART II SECTION 2.2), and this can be attributed to the scouring action of waves. Since A.fluviatilis is a microherbivore feeding on epilithic algae (see PART VII SECTION 3), shores to the north of AB are likely to favour its existence. P.contortus, on the other hand, feeds on detritus and epilithic bacteria, (see PART VII SECTION 4) and although there is no significant difference in bacterial production, at least in terms of quantity, between stations 2 and 6 (see PART VII SECTION 6) there is no a-priori reason for considering that food supply would prevent its colonisation of

shores to the south of AB. It tends to avoid wave action by living on the undersides of stones in cracks and crevices (see PART IV SECTION 6).

Thus wind action, by influencing wave action and consequently epilithic primary production, may influence the distribution of A.fluviatilis, limiting it to shores characterised by stations 1 - 4. Absence of Ancylus from shores characterised by stations 5 - 8 seems to allow dominance of P.contortus. These relationships will be considered in greater detail in PART VII SECTION 6, but as further corroborative evidence it is worth noting that detritus (i.e. decaying plant parts; both allochthonous and autochthonous) can collect in various isolated pockets on "Ancylus shores", covering stones and obviously reducing algal production. In these regions P.contortus dominates (see TABLE 7).

That the "Planorbis shores" are detritus dominated (TABLE 7) is obvious from the vast accumulation of decaying debris which collects here by wind/wave action. The food chains in this region are likely to be detritus orientated and it is significant that both detritophage tubificid annelids, and chironomids are far more abundant here than on the "Ancylus shores". On these shores, Ancylus is most abundant at station 6, i.e. Ha Mire Shore. The reason for this seems to be a greater variation of the shore line at this point and this will be discussed in more detail in PART IV SECTION 4 .

TABLE 7. Relative Abundance of Snails on Stones Under Detritus on "Ancylus Shores". Results from ca. 20 Stones Collected Haphazardly in September 1969.

Stations	1	2	3	4
A.fluviatilis	3.5	0.8	19.27	5.4
P.contortus	76.0	55.3	65.14	68.4
L.stagnalis	10.5	22.2	7.34	11.3
L.pereger	4.6	8.3	4.59	2.3
P.albus	5.4	13.4	3.66	12.6

6. DISCUSSION

6. 1. General

The general picture of the molluscan communities at Malham emerging from the above is one of stability. Only 5 species (of which 2 are gastropods) have been added to the list over the past 70 - 100 years (see PART 1) and of the 2 gastropod additions, 1 may have been overlooked by the earlier workers. Only Potamopyrgus jenkinsi can be considered as a genuine innovation. This stability is unusual in that one of the most obvious characteristics (secondary adaptations according to Hunter, 1957) of hololimnic fauna is their tendency towards passive dispersal and colonisation of new situations, (Hubendick 1962). This follows from the usual transitory nature of freshwater bodies when compared with terrestrial and marine environments. That snails conform to this general rule of dispersal and colonisation has been demonstrated by both Boycott (1928) and Hubendick (1962).

From this point of view Malham must be considered as exceptional and this probably derives from its relatively high location. Hunter (1957), for example, has already shown that the dispersal of molluscs through the highlands of Scotland is occurring at a slower rate than in England, and is not complete.

If the comparison between my survey and that of Stratton (1956) is valid, however, there appears to have been considerable fluctuation in snail distribution patterns between habitats within the Tarn. Here the picture of stability is different. The repeated dying down of weed beds in winter may contribute to this feature as may the progressive maturation of the Tarn itself. Of course, human intervention via field courses cannot be excluded.

The Mountford (1962) method of classification indicated a clear distinction between the weedbed and littoral faunas, and a consideration of relative abundance indices has suggested a separation of faunas both within the weeds and on the shores which seems to depend primarily on wave action and thus ultimately on wind. This influence is probably not limited to the molluscan fauna and in the littoral regions appears to affect the form of food chains. Similar observations have been made by Macan (1970) for Lake Windermere, and Slack (1957) for Loch Lomond. Wind via wave action

then, is probably one of the major physical influences in most large bodies of freshwater, particularly with regard to littoral and presumably planktonic associations.

6. 2. With Regard to Species and Site for More Detailed Sampling

Weed beds are relatively inaccessible to quantitative sampling and most are inconvenient because of their temporal discontinuities. Attention has therefore been focused on the rocky littoral situations. Here station 1 is peculiar because of its peat bed surrounds, stations 2 and 3 are heavily worked by field courses and stations 4, 5, 7, and 8 are accessible to either the general public and/or cattle and sheep. Station 6, Ha Mire Shore is, however, more or less isolated from students, the general public and domestic animals. It is also conveniently delimited laterally, by two walls which are built into the Tarn to a depth of ca. 1m and of all shores shows the least differential in density between the dominant P.contortus and A.fluviatilis. More will be said about these two features later.

Detailed sampling considerations have, therefore, been limited to Ha Mire, and consequently to the two species present in greatest abundance, i.e. P.contortus and A.fluviatilis.

PART IV

THE DISPERSION PATTERNS OF ANCYLUS FLUVIATILIS AND PLANORBIS CONTORTUS WITH PARTICULAR REFERENCE TO HA MIRE SHORE

1. INTRODUCTION

PART III was concerned with the major distribution patterns of all gastropod species in the Tarn. Attention was focused on two species, A.fluviatilis and P.contortus, at one locus, i.e. Ha Mire shore. The morphometry of this site has already been discussed in PART II, SECTION 3. 2. of the thesis.

The following sections are involved with a more detailed consideration of the dispersion patterns of the two major species. SECTION 3 is concerned with vertical,and SECTION 4 with lateral patterns. Their purpose is a definition of the overall habitat extent of A.fluviatilis and P.contortus, and they are based on a quadrat sampling technique.

Various methods are available for sampling the fauna in stony littoral situations. Calow (1972; see PUBLICATIONS APPENDIX II) has discussed their deficiencies and limitations, and has proposed a new technique, based on the individual stone as the sampling unit, and resulting in a density expression in terms of stone surface area. Subsequent analysis of data obtained from Calow's method requires some knowledge of the between-stone dispersion patterns of the population(s) involved, and this is considered in SECTION 5.

SECTION 6 considers the on-stone dispersion pattern of snails from the point of view of their effective stone habitat. It defines that part of the stone surface on which snails live and completes the distribution hierarchy study which began with the whole Tarn distribution patterns in PART III.

The results are discussed generally in SECTION 7. 1 and with particular reference to more detailed sampling procedures in SECTION 7. 2.

2. SAMPLING TECHNIQUES

2. 1. Vertical Dispersion Pattern

Sampling was undertaken between August - September 1969, using an interrupted belt transect procedure. Transects, positioned perpendicularly to the bank,were taken at regular intervals on all the shores considered (i.e. 15 on Ha Mire and 3 on other shores; see FIG. 14). Samples were removed from 0 ($\leq$ 5cm.), 15, 30, 45, 60, and 75cm. beneath the water surface on all transect lines.

Beneath the 0 - 30cm. depth contours a 0.25m^2 quadrat was placed on the Tarn bottom, stones enclosed were extracted, and snails were removed for counting. Between the 45 - 75cm. contours all contiguous stones at a particular depth location were carefully extracted by means of a standard pond net (specifications as in PART III, SECTION 2) and after removing snails the bed was reconstructed within the quadrat (0.25m^2) on the bank. Sampling continued until the quadrat was full. This procedure is essentially similar to that of Hunter (1953a).

Systematic sampling beyond the 75cm. contour was impossible. Stones were removed from this region haphazardly throughout the year by means of a tong device (made out of two rakes). Only depths between 90 - 100cm. were considered and ca. 250 stones were collected in this way. All were taken from regions immediately off Ha Mire shore.

Sampling errors,due to loss of snails from stones in transit through the water (at all depths),will have been greatest for P.contortus, since the limpet always adheres strongly to rock surfaces. Nevertheless this is probably not a serious source of error since even P.contortus appears to attach tightly when disturbed.

Transect sampling was repeated on Ha Mire in November 1970 to investigate seasonal changes in vertical distribution patterns.

2. 2. Lateral Dispersion Pattern

Information regarding lateral dispersion patterns on Ha Mire i.e. in terms of sectors A, B, and C (defined in PART II SECTION 3. 2.) has been obtained from the sampling procedures, described in SECTION

2. 1 above. Recognising the possibility of seasonal variations, however, some information has been extracted from data derived from the monthly sampling programme, described in PART V SECTION 2. Here individual stones were selected at random from each sector, once every 28 days (see DATA APPENDIX 1). Data encompassing 20 consecutive samples, each of 100 stones (40 from A and 30 from B and C respectively), between M2 - A21, were used.

2. 3. Between - stone Dispersion Pattern

The most detailed information regarding between-stone dispersion patterns was obtained from a single sample made in August 1971, on Ha Mire shore. Stones were initially and arbitrarily classified into 5 size classes on the basis of their longest length dimension i.e.

	Longest Length. (cm.)
Very Small	0 - 5
Small	6 - 10
Medium	11 - 15
Large	16 - 20
Very Large	21 - 25

Twenty five individuals from each size class were collected at random from sector C only, and all the snails were removed. Random collecting points were designated on the basis of twenty five random co-ordinates (see PART V,SECTION 2), not extending beyond the 45 cm. contour of depth. Five stones, one of each size class, were collected from each point so that the effects of lateral and vertical aggregation patterns were effectively removed and samples from each stone size class are directly comparable.

As in SECTION 2. 2 above, comparative seasonal data were obtained from the monthly sampling programme, and comparative regional data i.e. with respect to station 2 (see FIG. 14), by repeating the above procedure at this location.

The relationship between stone size (expressed in terms of longest length, L; largest perimeter, P, and LP) and snail densities was assessed from an independent sample taken from sector C on Ha Mire in August 1969. Thirty stones of approximately similar size and representing each of four size classes, L = 8.5, 10.5, 15 or 20cm. and P = 27.5, 30, 45 or 50cm. were sampled at random in the

way described above. Mean densities together with variances, for numbers of snails within each stone size class were computed.

2. 4. On-stone Dispersion Patterns

The position of snails on stones was considered with regard to depth, time of day, and time of year. Depth information was obtained from the transect work described in SECTION 2. 1. The position of snails removed from each stone was recorded. Four stone positions were recognised i.e. top (T), top-side (TS), bottom-side (BS), bottom (B), and reasons for this classification will be given later. Diurnal variations were investigated by comparing the above information with data derived from a sample of 25 stones taken between 11.00pm. and midnight on the same dates. Collections were limited within the 0 - 15cm. contour. Seasonal variations have been considered with regard to the monthly sampling programme where stone positions of snails were also recorded. Here 10 monthly samples have been considered i.e. N11 - J20 (see DATA APPENDIX 1).

Floral variations on different parts of the stones were also investigated. Ten stones from each of the three depth zones (0 - 15, 15 - 30, 45 - 60cm.) were collected haphazardly from sector A in September 1969. A small scraping of epilitha was removed from each of the 4 stone positions and stored separately in Lugol's fixative (Saraceni and Ruggui, 1969). Samples from the same stone position in all ten stones were bulked. Different depth samples were stored separately. The extent of the tufal encrustation was also recorded. (Tufa is a calcareous deposition formed on stones usually as a result of the activity of blue-green algae e.g. Rivularia - see Lund 1961).

After thorough stirring (by a magnetic flea) of the algal samples, a drop from each was transferred to a haemocytometer, and the number of quadrats containing each of the following components, i.e. diatoms, blue-green algae, other algal types and detrital particles, was recorded. Twenty aliquots from each separate sample were treated in this way, the total number of haemocytometer quadrats containing each algal group in each sample was calculated, and groups were ranked according to this value.

3. VERTICAL DISPERSION PATTERNS

3. 1. Results and their Statistical Treatment

FIG. 15 shows the effect of depth on the mean density of the Ha Mire populations of both P.contortus (15A) and A.fluviatilis (15B). Density is in terms of numbers per 0.25m.^{2} and vertical lines represent confidence limits (i.e. $ts/\sqrt{n}$, where t = 2.145, for 14 degrees of freedom at the 5% level). Out of the 250 stones sampled haphazardly beyond the 75cm. contour, none bore snails.

All confidence limits in FIG. 15 overlap, so that the mean densities at different depths are not significantly different. The large confidence limits probably result from errors associated with variation in total stone surface area contained within each standard quadrat in different shore positions (see Calow 1972 ; PUBLICATIONS APPENDIX II). Nevertheless,a trend towards a general reduction in density with increasing depth is apparent and confidence in this interpretation is increased by a consideration of concordance of the ranks of depths, at all stations, in terms of snail densities. This has been investigated using the Kendall Coefficient of Concordance (Siegel 1956) which enables a measure of the association of k sets of rankings of N observations and provides an expression for "true" ranking order, from the sums of ranks in each sample.

Results are presented in TABLES 8A and B for A.fluviatilis and P.contortus respectively. Between-transect comparisons at most stations are significantly concordant and indicate a reduction in density with depth. The "true" and significant ranking classification obtained from the various sums of ranks for all samples in the Tarn underlines the generality of this statement. Most individuals of both species occur in the shallows and least under 60cm. of water.

TABLE 9 shows the "true" ranks of the various depth zones on Ha Mire in terms of snail densities as determined in November 1970. Concordance among samples is significant, and the results indicate an offshore movement of both populations with respect to August - September samples. Peak densities no longer occur at the edge but at 15cm. in Ancylus and 45cm. in P.contortus populations.

TABLE 8A. The "true" ranks of Tarn depths in terms of the density of A.fluviatilis.

Station \ Depth cms.	0	15	30	45	60	W	P	k
1	1	2	3	4	-	0.64	*	+
2	1	2	3	4	-	0.78	**	+
3	1	2	3	4	-	1.00	**	+
4	1	2	3	4	-	0.46	*	+
6	1	2.5	2.5	4	5	0.44	**	++
8	1	2.5	2.5	4	-	0.24	*	+
All Shores	1	2	3	4	-	0.59	**	+++

TABLE 8B. The "true" ranks of Tarn depths in terms of the density of P.contortus

Station \ Depth cms.	0	15	30	45	60	W	P	k
1	1	2	3	4	-	0.68	**	+
2	1	2	3	4	-	0.70	**	+
3	1	2	3	4	-	0.60	*	+
4	1	2	3	4	-	0.83	**	+
6	1	2.5	2.5	4	5	0.33	**	++
8	1	2	3	4	-	0.80	**	+
All Shores	1	2	3	4	-	0.69	**	+++

* $p > 0.05$; ** $p = 0.05$, $N = 4$ for all stations except 6, where $N = 5$
+ $k = 3$; ++ $k = 15$; +++ $k = 33$.

TABLE 9. "True" ranks of depth zones on Ha Mire with regard to densities of A.fluviatilis and P.contortus in Nov. 1970 (k = 15; N = 5).

species \ depth zone cm.	0	15	30	45	60	W	P
A.fluviatilis	2	1	3	4	5	.62	0.05
P.contortus	3	2	1	4	5	.57	0.05

3. 2. Discussion

The results indicate a general reduction in snail density with depth in the August - September samples and an extinction point at ca. 75cm. A similar negative correlation between numbers and depth for these species has been demonstrated elsewhere by Geldiay (1956) and Macan (1970) for A.fluviatilis in Lake Windermere, and Humphries (1936) for P.contortus in the same location. The depth effect seems to have applicability to snails in particular (Boycott 1936, p. 144) and littoral species in general (Krecker and Lancaster 1933, Welch 1935, Humphries 1936, and Moore 1950).

Vertical zonations of the above type usually result from vertical gradients in physical conditions and Krecker and Lancaster (1933) consider the gradients of wave action and concomitant distribution of sediment to be the effective agents in freshwater. They propose the following system of classification:

Depth	Effect
0 - 6" (ca. 15cm.)	Constant lapping even on calmest days results in absence of sediment accumulation.
18" (ca. 45cm.)	Ordinary day to day waves prevent all but a slight trace of sediment.
3' (ca. 90cm.)	Strong washing effect from waves is only experienced on rough days - sedimentation is pronounced.
6' (ca. 180cm.)	Markedly disturbed only in times of severe storm - maximum sedimentation.

Thus animals sensitive to accumulation of sediment will become less frequent as depth increases, the favoured region occurring between

0 - 45cm.,where there is most water movement and least sediment. It should be noted, however, that these values are not constant but will depend both on shore morphometry and degree of exposure. Krecker and Lancasters' classification was intended specifically for Western Lake Eerie. That an actual increase in sediment with depth occurs on Ha Mire, however, is shown in FIG. 16. Results were obtained from a series of perspex boxes (plan area, 200cm^2), planted along transect 1 (see FIG. 14) in August 1970. Boxes were left in the Tarn over a two day interval, lids were replaced before box removal, contents were ultimately filtered through weighed filter papers, and dried at 40^0 C to constant weight. Allowance for loss in weight of filter papers on drying was made by the use of controls. Boxes could not be planted within the 0 - 5cm. contour so that data for this region is lacking. The graph shows a general increase in sediment accumulation in the boxes with depth, and also the point (determined on a calm day) when the Tarn bottom was no longer visible. This point moves shorewards on rough days when sediments become stirred up.

Snail sensitivity to sediment accumulation is suggested by their complete absence from regions of the Tarn where fine sediments form the major component of the substratum (see PART III SECTION 3). A.fluviatilis appears particularly sensitive to these conditions (Boycott 1936) and Verdcourt (1949) suggests that it is the absence of sediment, rather than the presence of lotic or wave swept conditions which determines its distribution.

A further effect of increase in depth, and the resultant increase in both sediment and turbidity is a reduction of net, primary, epilithic algal production (see PART VII SECTION6). Ancylus feeds on algae (see PART VII SECTION3) and reduction in primary production may act in conjunction with sediment accumulation in determining its vertical distribution pattern at Malham. In contrast, P.contortus is a detritophage which appears able to make use only of the bacterial fraction of its food supply (see PART VII SECTION 4). Since the bacterial production does not decrease with depth (see PART VII SECTION 6) sedimentation must be invoked as a primary cause of vertical limitations.

The vertical extent of both snail populations at Malham is less than in Windermere, where A.fluviatilis penetrates to ca. 5m. (Geldiay 1957, Macan 1970) and P.contortus to ca. 3m. (Humphries

1933). These differences probably result from greater sediment production and thus accumulation within the more eutrophic Tarn conditions.

Although sedimentation and primary production are clearly involved in determining vertical distribution patterns in Malham Tarn, other factors must also be involved and probably show seasonal variation in their importance. Thus the offshore movements of A.fluviatilis and P.contortus populations in November 1970 probably represent an escape from exposure, since wave action on Ha Mire was greatest during this period. The greater offshore movement in P.contortus reflects its greater sensitivity to wave action (see PART II, SECTION 2. 2.). Eggleton (1931) has demonstrated seasonal variation in vertical patterns for other littoral species in other lakes; Geldiay's (1957) data suggest an offshore movement of A.fluviatilis in winter which he interprets as avoidance of edge-freezing and Hunter (1953a) has shown shoreward movements of adult L.pereger populations in Loch Lomond in summer. The latter represents a response to reduced oxygen tension with high summer temperatures, facilitating aerial breathing by bringing individuals closer to the surface. Reduced oxygen tension is not likely to affect the populations under consideration here since A.fluviatilis cannot breathe air and P.contortus does not apparently do so (see PART VIII SECTION 2.3d). Furthermore, conditions in the wave swept littoral regions at Malham are probably always oxygen saturated.

4. LATERAL DISPERSION PATTERN

4. 1. Results and their Statistical Treatment

FIG. 17A & B show the percentage proportion of P.contortus and A.fluviatilis respectively, collected from sectors A, B, and C in the transect samples taken in August - September 1969. The histograms were produced by summing the number of individuals collected from all quadrats on each of the five intra-sector transects, and dividing by the total number of individuals collected from all fifteen transects taken over the whole shore. In this way samples from each sector can be considered equivalent with regards to the account they make of vertical zonation patterns. All proportions are presented as percentages and suggest that P.contortus was aggregated towards sectors B and C whereas A.fluviatilis aggregated in sectors A and C.

Seasonal variations in latteral patterns were investigated with respect to the monthly sampling programme described in SECTION 2 above. Here numbers of snails collected during each sampling period from each sector were expressed as a percentage of the total number of snails collected from the whole shore during the same sampling period. These values were transformed to arcsines following Fisher & Yates (1953) using the expression:

$$p = \mathrm{Sin}\ \phi \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 1(4.\ 4.)$$

where: $\mathrm{Sin}\ \phi$ (at 90^0) = 100%

p = percentage observed.

prior to an analysis of variance (ANOVAR). Percentages and ratios follow rather unusual distributions which are approximately normalised by arcsine transformation. Normal distribution is assumed in ANOVAR. Data from sector A were based on a sample of 40 stones (cf. 30 for B and C) and were corrected to 30 before the analysis. Transformed values are given in DATA APPENDIX IV.

The ANOVAR indicates whether between-sector variances are significantly greater than between-month variances i.e. whether density levels in each sector remain consistent and independent of time of year. In all cases the 5% level of significance was accepted. Overall significance indicated by the ANOVAR does not necessarily imply significant differences in selected pairs of values within the

total number considered. Here the RANGE SIMULTANEOUS TEST PROCEDURE (RANGE-STP) of Sokal & Rohlf (1969) has been used i.e.:-

$$LSR = Q \sqrt{\frac{MS_{residual}}{n}} \quad \text{.....2(4. 4.)}$$

where Q = critical value of the "studentized range" derived from the tables of Rohlf & Sokal (1969).

$MS_{residual}$ = the mean square of the residual variance.

n = no. of replicates.

L S R = least significant range i.e. the range between any pairs of values must exceed LSR to be significant at the chosen level which is fixed by choice of Q. 5% was used here.

The variance ratio test (F) indicates that the between position variance is significantly greater than between month variance ($F(\underline{P.contortus}) = 8.70$, $p < .01$; $F(\underline{A.fluviatilis}) = 5.92$, $p < .01$). L S R values are 5.16 and 10.5 for <u>P.contortus</u>, and <u>A.fluviatilis</u> respectively. The mean proportions (in arcsines) for all months are plotted in FIGS 18A and B, and indicate on the basis of the LSR values that density levels in each sector with respect to both snail species can be summarised as:

B = C > A for <u>P.contortus</u>

A = C > B for <u>A.fluviatilis</u>

These results are consistent with those based on a single independent sample taken at one time of year (see FIGS 17A and B), providing further confidence in the interpretation, and suggesting that underlying lateral patterns of aggregation are seasonally invariant.

4. 2. <u>Discussion</u>

The lateral dispersion patterns of both species are heterogeneous, and remain seasonally constant.This is not surprising in view of the lateral heterogeneities shown in the morphometry of the shore line itself. Each sector is characterised by a distinct profile (see FIG. 3), a distinct size frequency distribution of constituent stones (Calow 1972, see PUBLICATIONS APPENDIX II) and a fairly distinct shape frequency distribution of the latter (Calow Ibid.). Furthermore, FIG.19 shows that textural differences in stone surfaces occur between sectors and that there are also differences in the degree of detritus accumulation. Textural

differences in stone surfaces were assessed using the same method as for the size and shape frequency distributions discussed above (see Calow, Ibid.), the stones being subjectively classified as having either predominantly rough (R) or smooth (S) surfaces. Sediment accumulation was assessed during the transect sampling of August-September, 1969, by kicking the bed at the 15cm. contour on each transect for 30 seconds, and collecting a 250cc. sample of water over the kicked region. Each sample was subsequently filtered through pre-weighed filter paper and dried at 40°C to constant weight. Loss of weight of filter paper during drying was estimated using controls, and dry weight of sediment on each sample was calculated.

As will be discussed in SECTION 5 below, A.fluviatilis requires smooth whereas P.contortus prefers rough stone surfaces for existence. This may, therefore, account for the aggregation of P.contortus in sector C and A.fluviatilis in sector A. Similar aggregations of A.fluviatilis in sector C cannot be explained in these terms, but may result from increased primary production there. Certainly stones in this region have a richer algal cover than elsewhere on Ha Mire shore,(and this may result from the wave shelter provided by the southern wall).

A casual, subjective comparison of Ha Mire with other "Planorbis" shores suggests that the above morphometric heterogeneity is peculiar to the former. This probably results from the more varied shape of the Ha Mire shoreline (see FIG. 7) providing regions of both extreme exposure and relative shelter and thereby conditions suitable for the existence of both species of snail.

5. BETWEEN-STONE DISPERSION PATTERNS

5. 1. Results and their Statistical Treatment

FIGS 20A and B show plots of the mean number of snails per stone (P.contortus in 20A; A.fluviatilis in 20B) for each size class considered, against their sample variance, S^2. Line P indicates the expected relationship between means and variances, assuming random dispersion, and is derived from the Poisson distribution where means are equal to variance. Actual data for snails show a departure from the Poisson expectation and indicate a disproportionate rise in variance with increases in the mean. As might be expected means increase with increasing stone size.

Mean-variance relationships in August 1971 are linearised when means are plotted against $\sqrt{S^2}$, (see FIGS 21A and B), so that the mean numbers of snails per stone are linearly related with their standard deviations, S. Regression coefficients are b (P.contortus) = 1.07 ($p < 0.05$), b (A.fluviatilis) = 1.33 ($p < 0.05$) when the regression lines are forced through the origins. Also included in FIGS 21A and B, but not used in the regression analysis, are data derived from station 2. These points correspond to slopes based on the Ha Mire samples.

As noted in SECTION 2 above, seasonal variation in dispersion has been investigated with reference to the data derived from the monthly sampling programme. Three distinct periods have been considered, each of which are thought to have some biological relevance, viz:

* M2 - A3 - roughly representing the period when copulation occurs.

J6 - J7 - the oviposition period.

D12 - the overwintering period.

The period of post emergence is represented by the August sample described above. Pooling of data $M_2 - M_3$, and $J_6 - J_7$, was necessary because of the low numbers recorded through these months.

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* See DATA APPENDIX I.

Information on numbers of snails per stone for each month has been reorganised into the same stone classes described above, and means and variances for snails within each group were computed. It should be noted in these instances, however, that there are no a-priori grounds for considering that each group is equivalent with regard to either vertical or lateral distribution patterns (cf. August samples where all stones in each sample were effectively derived from the same place). Nevertheless means versus $\sqrt{S^2}$ plots, FIGS 22A and B, are essentially linear and closely approximate to the slopes derived from the August samples which are also included on the graphs.

5. 2. Underlying Nature of the Between-stone Dispersion Patterns

Analyses on dispersion patterns can be motivated either by statistical necessity and/or a genuine interest in the aggregative tendencies of individuals in a population. The present work was undertaken primarily for statistical purposes (see SECTION I) and has lead, secondarily, to a consideration of the nature and causes of underlying dispersion patterns.

Non random and particularly aggregated (contagious) patterns are the rule rather than the exception in nature (Cole 1946), and may arise from either:-

i) Patchiness of the habitat and/or

ii) Behaviour of the organisms themselves and/or

iii) The sampling method chosen

Groups i and ii correspond to Feller's (1943) category of "true contagion", and are, by definition, contrary to assumptions embodied within the Poisson distribution. Group iii corresponds to Feller's (1943) category of "apparent contagion".

In samples obtained from natural populations all sources of contagion are possible. Various tests and measures of aggregation have been proposed, and the simplest is the Variance: Mean Ratios (also called Coefficient of Dispersion, Blackman 1942, and Relative Variance, Clapham 1936). This test has been used here (see FIGS 20A and B) and has shown that both populations of snail are contagiously distributed on Ha Mire and also the other shores at Malham (FIGS 22A and B).

The positive curvilinearity apparent in FIGS 20A and B could

be interpreted as representing a disproportionate increase in aggregation as stone size increases, but this is complicated because data are based on stones of different sizes and thus both on different sized sampling units, and on different levels of population density. These factors can affect the variance to mean ratio independently of any real change in underlying aggregation patterns (Waters and Henson, 1959, Southwood, 1966, Elliot, 1971). This results from the reduced chance of finding any individuals within samples when either the populations are sparse or the sampling unit is very small.

All the above considerations are implicit to the power law of Taylor (1961), which essentially states that variance is proportional to some fractional power of the mean, or that variance rises disproportionately with the mean i.e.

$$S = a\bar{x}^{b} \quad \text{.......... } 1(4.5.)$$

Since by rearrangement:

$$\bar{x} = \sqrt[b]{\frac{S^2}{a}} \quad \text{.......... } 2(4.5.)$$

then the linear relationship shown between $\sqrt{S^2}$ and means in FIGS 21 A and B suggests conformity to the power law (with b = 2). This implies that the underlying aggregation pattern is constant and that changes in contagion with density and stone size are apparent rather than real (Feller, 1943). Furthermore, the power b appears relatively independent of both spatial and temporal changes. A power value of 2 suggests contagion (Taylor, 1961) and an underlying log-normal distribution pattern (Elliot, 1971).

5. 3. Factors Affecting Between-stone Dispersion Patterns

Stones are not homogeneous units but vary in both physical (i.e. with regard to shape, texture and size) and biological (i.e. with regard to the other flora and fauna they support) terms. Preference of snails for stones of a particular texture has already been suggested (see SECTION4.2) and this has been investigated further by a consideration of the ratio:

$$\frac{\text{mean nos. of snails/smooth stones}}{\text{mean nos. of snails/rough stones}} = \mu \quad \text{.......... } 3(4.\ 5.)$$

over a 12 month period (F1 - D12; see DATA APPENDIX 1). The

information required was derived from the monthly sampling programme and here it was assumed that each random sample of 100 stones from Ha Mire, contained an equal number of rough and smooth stones of the same size frequency distribution. Approximate equality in each sample of stones of different textures is demonstrated in FIG 23A.

FIG. 23B shows that ν for A.fluviatilis remains relatively constant throughout the year and is biassed towards smooth surfaces (i.e. for every limpet found on rough stones, 4 were found on smooth). This is correlated with the shell and foot width of this species being generally greater than width of stone crevices, and the fact that a smooth surface is required to provide uninterrupted contact between the shell margins and the stone during periods of heavy wave action. It should be noted, however, that A.fluviatilis (and Acroloxus lacustris L.)have a thin, flexible, uncalcified outer edge to their shell which allows them to conform to the irregularities of the surfaces on which they live (Hunter, 1961b). Nevertheless, this "skirt" is only a few millimetres wide in A.fluviatilis so that it cannot account for violent stone irregularities.

FIG 23B shows that ν values for P.contortus are generally biassed towards rough stones. This species is not as well adapted (in shell streamlining) as the limpet and presumably seeks out the cracks and crevices of rough surfaces for protection against wave action. Here the shell and foot widths are smaller than stone crevices. In P.contortus, however, ν shows some tendency towards seasonal change and apparently increase during oviposition and emergence periods, suggesting migration on to smooth stones. This is correlated with oviposition site requirements and will be discussed in detail in PART V SECTION 4.4. Since the migration is not monitored by the mean-variance analysis given in the preceding sections, it must either cause no change in underlying contagion or only slight changes which cannot be detected.

The results lead to the conclusion that although A.fluviatilis and P.contortus populations both live in Ha Mire, their habitats are spatially distinct, at least until oviposition.

FIGS 24 and 25 show a linear relationship between mean snail density and various indices of stone size (L, P, LP). Lines are fitted by eye. This implies no snail selection for stones of a particular size class. Extrapolation of lines to zero snail density,

however, suggests absence of snails from stones less than ca. 6cm. long (or ca. 25cm. P; or ca. 100cm. LP) and this has been confirmed by casual observation. It probably results from the greater mobility of small stones during rough conditions, which could have either a crushing and/or a scouring effect on organisms present.

6. ON-STONE DISPERSION PATTERNS

6. 1. Floral Variations with Stone Aspect

FIG. 26 shows a generalised stone from Ha Mire. Although there is considerable inter-stone variability (see SECTION 5,above) most can be divided into four distinct zones, top (T), top-side (TS), bottom-side (BS), and bottom (B). The boundary between TS and BS corresponds to the point of contiguity between adjacent stones.

Each zone is readily distinguished by its colour:

T - green to blue-green

TS - green to brown

BS - brown

B - chocolate brown

and this reflects an underlying variation with stone aspect in the epilithic[1] flora. Floral changes also vary with depth, and both effects are shown in the table associated with FIG. 26. Results are derived from the sampling procedure already described, and concordance between samples in each group has been investigated using Kendall's Coefficient of Concordance (Siegel, 1956). All are significant at the 5% level. No concordance analysis was undertaken when there were two groups of cover or less.

Moving from T to B there is a general reduction in both the quantity and quality of flora and this is probably a function of reducing light intensity. The junction between TS and BS is particularly distinct and represents a point where shading from adjacent stones will markedly reduce the light intensity below. In zones T and TS diatoms are dominant in shallow regions but are replaced by the blue-green algae as depth increases. Blue-greens never penetrate below TS whereas diatoms, although considerably reduced in abundance, are able to exist there and this appears to agree with the contention that diatoms are relatively insensitive to light (Prescott, 1969; Hynes, 1970). No algae are ever found at B, since light intensity is presumably zero, though some fungal hyphae were observed. Otherwise,stone bottoms are exclusively covered with a chocolate brown detrital film. This will be described in greater detail in PART VII SECTION 4. 2.

Tufa is not surprisingly absent from B and BT where the blue-

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1. This term is discussed and defined in PART VII SECTION 6

greens are also absent. It occurs on TS and T but increases in extent with depth, beginning first on the sheltered stone sides (TS) and expanding to envelope both T and TS at depths beyond 45cm. The degree of encrustation seems to be a function of wave action.

6. 2. Other Encrusting Organisms

In the shallow regions, tops of stones may be overgrown with the freshwater moss Fontinalis antipyretica. Attached to the undersides of smooth stones,colonies of the freshwater sponge, Spongilla fluviatilis L., and the encrusting polyzoan, Plumatella repens L. may be locally common. These species increase in abundance with depth. Less frequent and more patchily, collections of Hydra oligactis Pallas may also be observed, and these are occasionally found attached to snail, particularly limpet, shells.

6. 3. On-stone Dispersion Patterns of Snails

TABLE 10 shows the on-stone position of both P.contortus and A.fluviatilis with respect to depth. The majority of both species occur on either the stone sides or bottoms. For A.fluviatilis TS is preferred in the shallows whereas BS is preferred at depths greater than 15cm. This species grazes on algae and prefers diatoms (see PARTVIISECTION 3) so that the vertical shift in aggregation can be correlated with similar shifts in diatom abundance (see FIG. 26). Furthermore,tufal encrustations providing violently creviced surfaces make conditions unsuitable for Ancylus in this region (see SECTION 5 above). For P.contortus TB is preferred in the shallows, whereas B is favoured at depths greater than 15cm. This species is a detritophage (see PARTVIISECTION 4) so that an algal supply is not essential, furthermore, conditions below the TS -TB junction are probably sheltered against wave action. Reasons for downward migrations with depth are unclear, though spatial interactions with Ancylus may be involved. It should be noted, however, that these two populations are partially isolated on stones of different texture (see SECTION 5. 3.). Neither species occur to any appreciable extent on stone tops, and this may represent a negative response to wave action.

TABLE 11 compares dispersion patterns on stones within the

TABLE 10. The proportions of snails (%) on various stone aspects at various depths of submergence in September, 1969.

	A.fluviatilis			P.contortus		
Depth (cm.)	0-15	15-30	45-60	0-15	15-30	45-60
T	8.3	8.6	0.0	0.0	2.1	2.0
TS	78.3	11.4	8.3	0.0	6.1	7.2
BS	10.2	78.2	83.4	93.3	31.3	24.6
B	3.2	1.8	8.3	6.7	40.5	56.2
Total N.	105	109	71	142	121	63

TABLE 11. A comparison between the dispersion patterns of snails, expressed in relative abundance (%) on the surfaces of stones, during the day and night.

	A.fluviatilis		P.contortus	
	Day	Night	Day	Night
T	8.3	10.4	-	-
TS	78.3	65.3	-	-
BS	10.2	24.3	93.3	87.6
B-	3.2	-	6.7	12.4
N	> 100	63	>100	89

N = number of snails involved

0 - 15cm contour at different times of the day. No diurnal variations are apparent.

Seasonal variations in dispersal patterns have been investigated by reference to data from the monthly sampling programme (N11 - J20). The percentage proportion of snails present on each aspect was calculated for each of the ten month periods, transformed to arcsine (see equation 1 (4. 4.))and subjected to ANOVAR. RANGE-STP (Sokal and Rohlf, 1969; see equation 2 (4. 4.)) has been used to compare individual pairs of data. A 95% level was accepted in both the ANOVAR and RANGE-STP. DATA APPENDIX V contains the transformed data. Discussion of each species will be treated separately.

A. ANCYLUS FLUVIATILIS;

In considering the whole 10 month interval, the between position variance is greater than the between month variance ($F = 4.54$, $0.01 < p < 0.05$) so that there must be some real difference in the preference shown by snails for particular stone aspects. TABLE 12, column 1 shows the mean proportions of snails on each aspect (in arcsines) computed for the whole period, together with the L S R and suggests that although F is significant, only T is significantly different from the other positions. It bears less snails.

On the basis of the September sample, no significant difference should be expected between proportions on TS and BS since in the present instance no distinction was made between stones collected from different depth positions. Lack of significance between proportions on B and the stone sides is surprising, however.

There is some evidence to suggest that Ancylus prefers the bottoms of stones for egg laying (see PART V SECTION4.4). This would result in downward migrations during oviposition and could account for the lack of significance between B, ST and SB described above. If eggs are layed at B, spat will also emerge onto this position. To investigate this effect data from periods including oviposition and emergence (M17 - J20)were extracted from the total 10 month interval, and subjected to independent ANOVAR. Here between position variance is significantly greater than the residual ($F = 23.90$, $p > 0.001$). Mean proportions and LSR for this four month period are contained in TABLE 12, column 2 and indicate,as predicted from the oviposition activity,a significant polarity towards stone bottoms. Extraction of data from remaining months, and ANOVAR,

TABLE 12. The proportion of snails (in arcsines) on various stone aspects. The data are derived from a 10 month survey (see text). Columns 1-3 refer to A.fluviatilis and column 4 to P.contortus.

Zone \ Column	1	2	3	4
T	6.32	3.09	7.70	1.10
TS	33.09	16.07	76.09	13.81
BS	36.10	33.71		35.61
B	32.91	48.20	27.36	47.80
LSR	24.79	15.09	8.403	9.63

however, suggest a lack of concordance between individual monthly samples ($F = 2.99$; $p > 0.05$). Inspection of data suggested that this was almost certainly due to variations in proportions between TS and BS. Reasons for this have already been discussed. Combination of TS and BS improves concordance ($F = 208.89$; $p < .001$) and the total period means (TABLE 12, column 3) indicate aggregation on stone sides in this period which conforms with results from the September sample (see TABLE 9).

B. PLANORBIS CONTORTUS:

In this species, ANOVAR over the whole 10 months interval indicates that between position variance is significantly greater than between month variance ($F = 42.71$, $p < 0.01$). Mean proportions of snails within each zone are shown in TABLE 12, column 4, together with LSR and suggest ,as with the September sample, a polarity towards stone bottoms. This can, therefore, be considered as seasonally invariant.

On-stone locations of snails indicate some spatial separation between A.fluviatilis and P.contortus which reinforces separation based on the between-stone patterns. P.contortus prefers stone bottoms, whereas A.fluviatilis prefers stone sides, at least until oviposition when it migrates on to the bottoms. Habitat overlap between P.contortus and A.fluviatilis is greatest during the breeding season.

7. DISCUSSION

7. 1. General

Dispersion patterns at all levels of the distribution hierarchy from major distribution within the whole Tarn to micro-distribution on individual stones show heterogeneities, and aggregations. This situation is typical of natural situations where aggregation seems to be the rule rather than the exception (see general texts of Odum,1953, Macfadyen, 1963, Grieg-Smith, 1964, Elton, 1966). Similar detailed studies on snails in particular and freshwater littoral forms in general are lacking, (Elliot, 1971).

Factors affecting aggregation at all levels seem to stem ultimately from wind and thus wave action, and act via either food supply or the deleterious effects of sediment accumulation. The importance of wave action in large bodies of freshwater has already been noted, and the effects of food supply will be considered in greater detail later (see PART VII SECTION6).

The microdistribution patterns of P.contortus and A.fluviatilis are different. P.contortus lives predominantly on the bottoms of rough stones, whereas A.fluviatilis prefers the sides of smooth stones. This means that although both species live in a common major location (Ha Mire), they are to some extent spatially distinct. This picture changes during oviposition and post-reproductive intervals when P.contortus migrates on to the smooth stones, and A.fluviatilis migrates on to the stone bottoms. During this period the habitat space requirements of both species are the same, and interaction may occur.

7. 2. Relevance of the Results in Terms of More Detailed Sampling Procedure

Vertical dispersion patterns studied in SECTION 3. 2. indicate that neither P.contortus, nor A.fluviatilis populations extend beyond the 75cm. contour. This, therefore, represents the offshore habitat limit of these species and is approximately and conveniently delimited by the old shoreline (see PART II, SECTION 3. 2.). The majority of both species, however, occur within the 45cm. contour and it is this portion which will be considered in greater detail

later.

The walls situated at both ends of Ha Mire shore are built into the Tarn to a depth of ca. 1m. (see FIG. 4) so that in view of the 75cm. limitations described above, they effectively provide lateral barriers to both immigration and emigration of snails. Similarly, both the old and new shores can be considered as dispersion barriers, since landward migrations are unlikely and lakeward migrations, although possible (e.g. via floating weeds), can probably be ignored. Thus, A.fluviatilis and P.contortus populations within the walls are effectively isolated and are, therefore, extremely convenient from the viewpoint of a dynamics study, i.e. immigration and emigration can be ignored.

Lateral heterogeneities between sectors requires a laterally stratified sampling regimen if a true estimate of snail densities on all Ha Mire is to be considered, (Yates and Finney, 1942; Healy 1962). Furthermore since strata (i.e. sectors) vary in their length ratios i.e. approximately 4A : 3B : 3C, stratification must also be affected in these proportions (Wadley, 1952). This procedure is termed self weighting.

The power law value (b = 2) obtained in SECTION 5. 2. indicates between-stone aggregations and suggests an underlying log-normal pattern. In these circumstances logarithmic transformation provides approximate linearity (Elliot, 1971). Calow, (1972, see PUBLICATIONS APPENDIX II) however, has suggested a more direct manipulation of raw data derived from a sampling programme using individual stones as the sampling unit which provides a valid estimate of means and variances. Calow (Ibid.) showed that when standard deviation is linearly related to the mean, sampling statistics are computed as follows:

$$\bar{x} = \frac{\Sigma(x/a)}{k} \quad \text{..... 1 (4. 7)}$$

$$\text{var.} = \frac{\hat{\phi}}{k} \quad \text{..... 2 (4. 7)}$$

where x/a = no. of snails/unit observed stone size

k = sample number

$\bar{x}$ = mean no. of snails/unit observed stone size

var. = variance

$\hat{\phi}$ = constant;

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1 as defined in Calow 1972; PUBLICATIONS APPENDIX II

These statistics will be used in the definitive sampling programme described in the following sections.

On-stone aggregations of both P.contortus and A.fluviatilis have been shown in SECTION 6. Neither species occupies the total stone surface, only selected portions. If populations are biassed towards certain situations, but samples are taken randomly SYSTEMATIC ERRORS will arise (LeRoux and Reimer, 1959). Similarly,if distributions are aggregated, and sample numbers are expressed in terms of a habitat parameter bearing no relationship to the region of aggregation further SYSTEMATIC ERRORS will arise.

All easily measured linear stone parameters (longest length L; largest perimeter P; L x P) however, are highly correlated ($r(L \text{ v } P) = 0.85$; $r(L \text{ v } LP) = 0.80$; $r(P \text{ v } LP) = 0.82$). There is also a linear relationship between snail density and these linear stone size parameters, (see FIG 25 and 26). All parameters can, therefore, be considered as being correlated to the effective habitats of the snails concerned, i.e. B and BS in P.contortus and BS and TS in A.fluviatilis so that the parameter chosen for the density expression will be of little consequence.

PART V

THE DETAILED DYNAMIC STRUCTURAL ASPECTS OF POPULATIONS OF PLANORBIS CONTORTUS AND ANCYLUS FLUVIATILIS ON HA MIRE SHORE

1. INTRODUCTION

PART 1 highlighted the lack of quantitative information regarding the structural ecology of freshwater snails. The fact that most species inhabit complex macrohabitats, in which there is tremendous underlying microhabitat variability, seems to have been instrumental. These places, e.g. weeds and rocky shores, provide technical difficulties in obtaining quantitative samples, and theoretical difficulties in their interpretation. Consequently, quantitative information regarding the invertebrates living in these habitats is generally sparse when compared with equivalent work carried out both in the plankton and on organisms occupying the bottom silts. The latter habitats represent far more simple situations, but are generally devoid of snails. (see PART III, SECTION 3).

Methods of extracting samples from stony substrata have been reviewed by Macan (1958), Cummins (1962) and Schwoerbel (1970). Most techniques suffer from the disadvantage of relating density of organisms to the area of the bottom, not to the actual area available in terms of stone surface. Although snails do not occupy total available stone surfaces (see PART 1V, SECTION 6. 3.), their densities (and thus their effective habitats) are related to stone linear parameters (see FIGS. 24 and 25) and these in turn to stone surface area (Calow, 1972, see DATA APPENDIX II). Because the stone surface area contained within a standard square metre of the bottom may vary haphazardly from place to place, expression of density in these terms automatically introduces an extra element of variance. This phenomenon probably applies to all samples of stone-dwelling invertebrates (Usinger and Needham, 1954) and the sampling variances so introduced are neither of interest nor are usually identifiable.

Calow (Ibid.) has suggested a new technique which allows relatively simple and rapid estimation of true stone surface area. On the basis of this method a sampling technique using the individual stone as the sampling unit was suggested, and this in conjunction with detailed information on microdispersion patterns (e.g. PART 1V SECTIONS 7. 2.) allows truly quantitative density estimates to be made.

Similar trends towards quantifying the effective habitat have also been made in weed bed situations. Thus Krecker (1939) expressed density in terms of plant length, Entz (1947) in terms of a quotient

related to plant surface and Rosinè (1955) in terms of actual surface area.

The following sections present quantitative information regarding the structural ecology of A.fluviatilis and P.contortus populations on Ha Mire shore. Calow's technique has been employed and details of the method are given in SECTION 2. SECTION 3 presents the resultant information regarding phenologies. Natality is discussed in SECTION 4, and mortality in SECTION 5.

2. DESCRIPTION OF THE SAMPLING PROGRAMME

2. 1. Manipulative Details

Samples were taken at 28 day intervals over a 21 month period between February 1970, and August 1971. Sample dates, together with the definitive code which has been used in the text, are given in DATA APPENDIX 1. Individual stones were used as the sampling unit, and the sample size comprised 100 units. Stones below 6cm., L were not considered (see FIGS. 24 and 25).

Units were obtained at random within the 0 - 45cm. contour (see PART 1V, SECTION 7. 2) by reference to co-ordinates selected from random number tables, (Fisher and Yates, 1963). The random points so defined were approached via fixed lanes set at right angles to the shoreline and 2m. apart. This minimised disturbance to the substratum by treading, and stones from the lanes were not included in the sample. Lateral dispersion patterns necessitated stratification of samples with regard to the size of sectors (see PART 1V, SECTION 7. 2.). Forty stones were taken from sector A and thirty from sectors B and C respectively. Blind insertion of a pole at the defined sampling point provided the final decision as to which particular individual was to be removed, as the representative unit. A pond net (size and specifications as in PART 1V, SECTION 2. 1.) was carefully positioned beneath the stone, and was used to hoist it out of the water.

Both the net and the stone were subsequently searched for snails and other invertebrates. All were stored in 70% alcohol, each stone complement within a separate specimen tube. Positions of snails on rocks prior to removal, stone texture and stone size in terms of L and P were also recorded.

Counting was carried out later, when snail sizes were also estimated. A single linear dimension was used for each species i.e. aperture length (AL) for A.fluviatilis and maximum diameter (MD) for P.contortus (terminology after Hunter 1961a). Measurements were made to the nearest 0.05mm. using a dial micrometer fitted to a binocular dissecting microscope, and information was sorted into 0.10mm. intervals. Data for all snails from one sample were pooled to produce a mean and error estimate. This never involved less than 50 individuals and when sample yields were short of this figure

numbers were increased by individuals collected on equivalent dates from the shores immediately adjacent to Ha Mire.

Particular techniques relating to the estimation of natality and mortality will be described in the relevant sections below.

2. 2. Statistical and Computational Details

The underlying, lognormal, between-stone dispersion pattern demands special treatment of raw data for the purposes of estimating means and variances (see PART 1V, SECTION 7. 2.). Data can either be transformed to logarithms, or be treated according to the more direct method of Calow, 1972, PUBLICATIONS APPENDIX II (see equations 1(4. 7.) and 2(4. 7.)). The latter has been employed in the present instance. The information so obtained is in terms of numbers per linear stone parameter. All easily measured linear parameters (L, P, LP) are correlated with the snail effective habitats (see FIGS. 24 and 25), so that all could be employed with equal validity. Nevertheless, Calow (Ibid.) has shown that LP is most significantly correlated with total stone surface area on Ha Mire by the regression equation:

$$y = 2.22\ (\pm .26)\ x \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ 1(5.\ 2)$$

where y = surface area in $cm.^2$

x = LP in $cm.^2$

so that LP was preferentially used.

Equation 1(5. 2) provides the facility for converting density estimates in terms of LP to estimates in terms of surface area by:-

$$\bar{X} = \frac{\bar{x}}{b} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ 2(5.\ 2)$$

where $\bar{x}$ = mean no./LP

b = 2.22

$\bar{X}$ = mean no./surface area

and a direct conversion to numbers $m.^{-2}$ is effected if linear parameters are expressed in 10,000 LP units. Although stone surface area is correlated with snail effective habitats, snails do not occupy the total area theoretically available to them, so that density expressions in terms of area provide a diluted estimate with regard to effective habitats. Consequently, density has been expressed as

numbers/10,000LP until comparisons with other parameters and/or other workers' data were required.

The raw data were stored on computer file. Computation of population statistics, conversion to area and data sorting were accomplished by computer programmes effected on an "English Electric" KDF9 machine.

3. GENERAL PHENOLOGICAL INFORMATION

FIGS. 27 and 28 show the monthly mean density fluctuations in Ha Mire populations of P.contortus and A.fluviatilis respectively. Confidence limits represent two standard errors. Temperature fluctuations are also included. FIGS 29 and 30 show the monthly variations in size frequency distributions.

Periods over which eggs were observed in the field are represented as horizontal, arrowed lines in FIGS. 27 and 28. These extend over two, isolated, two-month periods in 1970 and 1971. Young (spat) appear immediately following that sample date on which eggs were first observed, and are easily recognisable, as distinct from adults, on the following criteria:-

i) Smaller size
ii) Corrugated shell in the case of A.fluviatilis spat (cf. adults which have a smooth shell)
iii) A lighter orange, translucent shell in P.contortus (cf. adults in which the shell is opaque and dark brown).

Distinction between older spat and adults is more difficult, but is nevertheless possible on the following criteria:-

	A.fluviatilis	P.contortus
1.	Adults possess a single growth ring, marking the transition between slow winter and rapid spring growth. (Hunter, 1953a)	Adult shell less transparent than young
2.	Adult shells more worn and usually covered with a dense algal growth. The latter occurs to a greater extent in A.fluviatilis.	

The greatest difficulty of distinction between adults and spat occurred in sample A8 for P.contortus. Here separation was effected on the basis of two methods, i.e. firstly,the subjective technique described above and secondly,the more objective graphical technique of Harding (1949). The subjective technique suggested that adults comprised 29% of the total sample. The graphical technique illustrated in FIG. 31 indicates that 25% of the total sample were adults. The latter value has been accepted but is close to the subjective estimate, so that the subjective method was used to deal with similar difficulties in sample J20.

That part of the curve representing spat in FIG. 31 may also be polymodal. This is to be expected, because eggs are laid over the whole period M5 -J7 and M17 - J19 (see SECTION 4. 3A) so that emergence will be staggered. There is no suggestion of polymodality in sample S9 (see FIG. 32) and it is assumed that all the adult generation have died by this time. Clearly, in both species, three distinct generations have been considered (hereafter called 1, 2, or 3, see DATA APPENDIX 1). Life cycles are annual, and there is a minimum generation overlap of 3 months. Adults die 1 - 2 months after the cessation of oviposition.

Annual life cycles seem to be the rule rather than the exception in freshwater pulmonates both in this country (e.g. Duncan, 1959; Hunter, 1957, 1961a and b) and in other parts of the temperate world (DeWit, 1955; DeWitt, 1955; Gillespie, 1969). Exceptions can occur (Berrie, 1963, 1965), although the original contention of typical biennial cycles (e.g. Cooke, 1895; Pelseneer, 1906; Baker, 1911) is erroneous. Patterns in the tropical regions are more complex (e.g. Schiff, 1964; Pringle and Msangi, 1961; Jobin and Michelson, 1967; Berrie, 1969) as probably are the phenologies of the temperate operculates (e.g. Lilly, 1953; Schäfer, 1953).

Previous work on populations of A.fluviatilis (Hunter, 1953; Geldiay, 1956) have indicated semelparity (terminology after Cole, 1954), and the North American ancylid Ferrissia rivularis (Say.) also shows this property (Burky, 1971). No direct comparative information is available for P.contortus, although the data of DeCoster and Persoone (1970) are suggestive of an annual life cycle. Similarly, P.albus populations in Loch Lomond are semelparous (Hunter, 1961a). Thus both the A.fluviatilis and P.contortus populations on Ha Mire shore are typical.

Although the major pulmonate breeding periods occur in spring, a second,less intense breeding phase may occur in late summer if conditions are good (Hunter, 1961a). A.fluviatilis populations in certain parts of Windermere may show this phenomenon (Geldiay, 1956). Summer breeding did not occur in Malham populations, however, and its absence may be a function of the altitude. Breeding periods in both species on Ha Mire are coincident although they occur earlier in 1971 than 1970. The intensity and timing of oviposition will be discussed in greater detail in SECTIONS 4. 3A and 4. 5.

The double sigmoid pattern of growth in individuals of A.fluviatilis on Ha Mire is similar to that recorded for other populations of this species (Hunter, Ibid.; Geldiay, Ibid.). P.contortus patterns are similar, but the winter plateau is longer and extends up to the oviposition period. Growth in length continues, in both species, through the reproductive phase and up to death and this seems to be typical (Van Cleave, 1934, 1935; Hunter, 1961b). More will be said about growth patterns in PART VI.

Adult freshwater pulmonates die after oviposition (Fischer, 1950). The advantages of this phenomenon, by preventing deleterious inter-generation interactions, are obvious. Hunter (1961a and b) has suggested that environmental conditions are instrumental so that "endogenous senescence", in the sense of Comfort (1956, 1957), appears to play little part. Calow (1972 - see PUBLICATIONS APPENDIX IV.) reasoning on a-priori grounds, has suggested that reproduction and parental death are intimately inter-related. It was suggested that the reproductive processes in semelparous organisms, including snails, are not subject to strict control and that this renders the parental system more sensitive to environmental perturbations, thus increasing the probability of parental death. Here endogenous events would affect the system's sensitivity to exogenous exigencies.

The pattern, intensity and possible agents of pre-ovipositional mortality are discussed in SECTION 5.

4. SPECIFIC INFORMATION ON NATALITY

4. 1. Copulation

The earliest copulations in A.fluviatilis (FF, see FIG. 28 and DATA APPENDIX 1) were observed on sampling occasion A3 for generation 1 and M15 for generation 2 i.e. just two months before the first eggs (FE) appeared in both cases. This process continued until the end of the oviposition period apparently becoming more frequent as time proceeded. Chain copulation, as described originally by Geldiay (1956) for A.fluviatilis was also recorded at Malham.

Copulation in P.contortus was never observed either in the field or in the laboratory. This is not to say that cross fertilisation does not occur since it appears to be a pre-requisite for oviposition within the Planorbidae (Bondesen, 1950) and reciprocal fertilisation has previously been recorded in P.contortus by Hazay (1881).

4. 2. Description of Reproducta and Definition of Terminology Used

A. MORPHOMETRIC CHARACTERISTICS OF THE REPRODUCTA

The form of the gonadial products of freshwater pulmonates has been extensively investigated and reviewed by Bondesen (1950), and the following information is derived mainly from him. Generally speaking the reproducta consist of one or more eggs[1] enclosed within a capsule[1] of which several to many may be layed by one individual. The total number of egg capsules produced by a single individual is called the OVIPOSITION ACTIVITY[2] (C), whereas the total number of individual eggs produced is called EGG PRODUCTION[2] (E) and these two parameters define CAPSULE SIZE[2] (E/C). In the present context the adjective "STANDARD" will be used to denote these parameters when based on average values.

Egg capsules of all pulmonate species are similar (see FIG. 33) but differences do occur with respect to shape. Indeed the Pulmonata can be divided into two distinct groups on this criterion alone, i.e.:

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1. Terminology from Bondesen (1950).
2. Terminology from Mooij-Vogelaar et.al. (1970).

i) those producing globose capsules (Physidae, Lymnaeidae)

ii) those producing flattened capsules (Planorbidae, Ancylidae, and Acroloxidae)

and this dichotomy reflects a basic difference in capsule formation. In group ii) the foot is directly involved in the formative process whereas in group i) it is not involved at all. Thus the Ancylidae and Acroloxidae produce a distinct quaternary membrane of foot origin (see FIG. 33). This is absent in the Planorbidae, but members of the genera do produce a foot secretion which hardens the tertiary capsule membranes. Use of the foot requires smooth, flat surfaces for oviposition in the group ii) species and the ecological significance of this will be discussed in SECTION 4. 4. Both the hardening secretions of the Planorbidae and particularly the quaternary envelopes of the Ancylidae have adaptive significance providing increased protection against predation, but also physiological difficulties concomitant with the cleidoic habit. The former will be discussed in SECTION 4. 6., the latter in PART VII, SECTION 3. 2. Distinction between the capsules of P.contortus and A.fluviatilis was made using Bondesen's (1950) key. Basically, capsules of A.fluviatilis are larger, more yellow, and more flattened than those of P.contortus.

TABLE 13 compares various egg case parameters previously described by other workers (cited in the TABLE) for P.contortus and A.fluviatilis with those obtained on cases collected from Ha Mire. Information for Ha Mire populations derives from two field samples made on sampling occasions J6 and J7 and consisting of 50 and 60 capsules respectively. Data from the two samples were pooled for estimating mean linear dimensions, but treated separately in considering capsule size, C. The weight and calorific information was obtained from an independent sample taken in 1971, and this, with the techniques involved, will be described more fully in PART VI, SECTION 3.

Capsule parameters on Ha Mire are similar to those described by other workers for other habitats. A comparison of the results for P.contortus with those for A.fluviatilis indicates that both the actual egg and the total capsule sizes are larger in A.fluviatilis, that standard C is significantly greater in P.contortus ($d_{(J6)} = 13.00$, $p < 0.05$; $d_{(J7)} = 12.50$, $p < 0.05$), and that caloric densities are greater in the limpet. These differences are consonant with

TABLE 13. A comparison of several egg capsule parameters obtained from the literature with those derived from capsules taken from Ha Mire shore. Information on egg mass and potential energy content is also included.

	P.contortus		A.fluviatilis	
Linear Dimensions of Capsule	$\bar{L}$(mm.) +	$\bar{B}$(mm.)+	$\bar{L}$(mm.)	$\bar{B}$(mm.)
Ha Mire N=110	1.35(±.04)*	1.23(±0.04)*	3.3(±.01)*	3.2(±.007)*
Bondesen(1950)	2.0	-	3.3	2.8
Moquin-Tandon (1855)	≃ 3.0mm. dia.		-	-
Pfeiffer(1821)$_1$	-	-	≃ 3.0mm. dia.	
Geldiay(1956)	-	-	3.4	2.7

Linear Dimensions of egg	DIA.(mm.)	DIA.(mm.)
Ha Mire N=110	0.545 (± .022)*	0.95 (± 0.07)*
Bondesen(1950)	0.70 x 0.54	1.42 x 1.20mm.
Pfeiffer(1821)$_1$	-	1.9
Moquin-Tandon (1855)	0.50	-
Geldiay(1956)	-	1.38 x 1.23

Ave. No. Eggs/capsule (Standard C)		
Ha Mire J6(N=60)	3.48(±0.07)* range 1-4	2.60(±0.03)* range 0-5
Ha Mire J7(N=50)	3.50(±0.06)* " 1-5	2.53(±0.09)* " 1-4
Bondesen(1950)	max. 8	2.60 (max. 10)
Moquin-Tandon (1855)	6 - 8	-
Lehman (1873)$_1$	6 - 8	-
Precht (1936)$_1$	3.4 (range 2-5, N, 19)	-
Pfeiffer(1821)$_1$	-	3-5
Bauchard-Chanteraux(1832)$_1$	-	4-6
Geldiay(1956)	-	3.99(nature) 4.27(aquarium) range 0-11

TABLE 13 continued over page.

TABLE 13 - Continued

	P.contortus	A.fluviatilis
Mass and Energy Values		
A.F.D.W. ** Egg	0.083mg.	0.121mg.
% Ash	5.3	6.6
A.F.D.W. ** Egg Capsule Membrane	0.025mg.	0.045mg.
% Ash	11.5	10.0
Cal. val. kcal./g. A.F.D.W.		
Egg	4.55 Kcal.	6.630 Kcal.
E.C.M.	4.48 Kcal.	4.571 Kcal.

+ $\bar{L}$ = longest linear dimension. $\bar{B}$ = shortest linear dimension perpendicular to $\bar{L}$. Confidence limits represent 2 S.E.

* Confidence limits = 2 standard errors.

1 Authors cited in Bondesen (1950).

** A.F.D.W. = ash-free dry weight.

E.C.M. = egg capsule membrane

N = number of capsules involved.

Bondesen's (1950) description of Ancylid egg capsules. They result from adaptations to life under relatively harsh (lotic, or wave swept) environmental conditions where there is a premium on the production of well developed emergent young, requiring longer developmental time in the egg (see SECTION B, below), and consequent provisioning with rich yolky stores. These stores have been recognised in A.fluviatilis by Lacaze-Duthiers (1899), and Ebner (1913), and their presence is indicated by the high egg calorific densities, presented in TABLE 13. Reduction of standard C automatically follows from the better chances of offspring survival and/or increased energetic efforts involved in yolk production. From this point of view P.contortus is less well adapted to exposure than Ancylus though it has a lower standard C and a higher calorific density than equivalent Lymnaeid capsules also collected from Ha Mire (i.e. Lymnaeid standard C = 176.36 $\pm$ 18.20, N = 25; calorific density of egg = 5.050, N = 1). Hunter and Apley (1966) and Hunter (1970) have suggested that a complete gradient between small, poorly provisioned and large yolky eggs occurs in the freshwater Pulmonata. The former condition appears to be primitive, and evolution has apparently moved towards suppression of free larval stages and reduction of the temporal extent of immature growth, necessitating yolky stores. On this sequence, P.contortus stands closer to the ancylids.

B. EMBRYOLOGICAL OBSERVATIONS

Embryological observations were made on 25-30 egg capsules of each snail species, collected in the laboratory within one day of oviposition. Reproducing adults had previously been collected in the field during the oviposition period. Egg capsules were kept individually in small perspex tubes ($2cm^3$.), containing dechlorinated tapwater which was replenished daily. Cultures were maintained at 15°C, i.e. close to the field temperatures operative during oviposition. Observations on gross embryonic changes were made mainly in-vivo. An occasional capsule was removed, dehydrated in alcohol and cleared and mounted in glycerol for more detailed observation.

Average hatching times at 15°C were found to be :-

i) 13.3 ($\pm$ 1.1) days for P.contortus

ii) 25.8 ($\pm$ 1.8) days for A.fluviatilis

Previous workers have reported a 25 day hatching time for A.fluviatilis (Hunter, 1953a; Bondesen, 1950) and although comparative

TABLE 14. Chronological sequence of gross embryological changes in P.contortus and A.fluviatilis

Stage	A.fluviatilis Description	A.fluviatilis Ave. Time from oviposition (days)	P.contortus Description	P.contortus Ave. Time from oviposition (days)
A	egg cell not cleaved	1	egg cell not cleaved	1
B	egg cleavage and gastrulation	1-10	egg cleavage & gastrulation	1-4
C	Embryo swells into yellow ball, albumen cells distinct	10	foot and shell become distinct, heart beats, shell patelloid not coiled	4-7
D	foot and shell become distinct, heart beats	10-23	shell begins to coil	8-11
E	spat released from egg into capsule chamber	ca.24	spat released to capsule chamber	12
F	Eclosion	ca.25	Eclosion	ca.13

data for P.contortus is lacking, Hunter (1961a) reports a 14 day hatching time for the related P.albus. The longer developmental period in A.fluviatilis reflects its greater yolk complement. Approximately 75% of all the eggs used completed development.

The chronological sequence of gross embryological change is represented in TABLE 14. This crude classification has been used to distinguish between old and freshly laid eggs in field samples (see SECTIONS 4. 3A and 4. 5A).

4. 3. Temporal Description of Oviposition

A TEMPORAL EXTENT OF THE OVIPOSITION PERIOD

FIGS. 27 and 28 show that egg capsules occur in the field over 2,two-month periods in 1970 and 1971, and that these periods are coincident in both species. Specific differences may occur with respect to the rate of capsule production (capsule chronology[1]) within these periods and this will be discussed in SECTION 4. 5. On the basis of information given in TABLE 14 it was possible to distinguish between freshly laid and old eggs in each sample, and the former were found throughout. Thus eggs would have persisted in the field for a minimum of 13 or 25 days,in P.contortus and A.fluviatilis respectively beyond the last sampling date on which they were observed. Failure to find limpet eggs on sampling occasions A8 and A21 must either mean that no eggs were laid after sampling dates J7 and J19 or that the numbers subsequently produced were too low to be monitored by the sampling procedure. Quantitative information on egg case production and loss is given in SECTIONS 4. 5. and 4. 6. respectively.

Bondesen (1950) suggested that the breeding season in A.fluviatilis was shorter than for most other freshwater pulmonates. Hunter (1961a), however, has demonstrated that apart from L.pereger, which has an extended oviposition period, the two-month interval seems to be typical. The present results support Hunter's (Ibid.) statement.

B INITIATION OF OVIPOSITION AND ANNUAL VARIATIONS IN ITS ONSET

Oviposition periods in the two years observed were not coincident (see FIGS. 27 and 28), and occurred one month earlier in 1971 (Generation 2). As already discussed in SECTION 3, the majority of freshwater pulmonates possess an annual life cycle. Within this basic

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1. Terminology from Bondesen (1950)

pattern, however, two variants,with regard to growth and the onset of reproduction,can be distinguished (Duncan, 1959; Hunter, 1961a and b) i.e. :

TYPE 1: considerable growth of snails in spring and early summer before a relatively late summer reproduction period. Reproductive apparatus can function only after winter.

TYPE 2: prewinter growth of snails to near adult size, spring breeding following little post-winter growth. Reproductive apparatus can function throughout winter.

Neither patterns are species specific and both may occur in different populations of the same species (e.g. Hunter, 1953, 1961a and b; Hunter and Hunter, 1956; Geldiay, 1956). Both patterns have never, previously been recorded, however, in the same population in different seasons (Hunter, 1961a and b).

Even when gonads are mature exogenous cues are required to initiate oviposition. The most important of these seems to be temperature change (Boycott, 1936; Bondesen, 1950; Cheatum, 1951; Duncan, 1959), there being a minimal value below which oviposition will not occur irrespective of gonadial state. Thus sexually mature individuals of both A.fluviatilis and P.contortus extracted from Ha Mire on 25/5/71 would not oviposit at 4°C, but would lay eggs at 10 and 18°C. This result conforms to the minimum critical value of ca. 7.5°C recorded for A.fluviatilis in particular (Bondesen, 1950; Geldiay, 1956) and for other species in general (Duncan, 1959) in other places. Thus,environmental temperatures must rise above 7.5°C before oviposition can occur. Other factors have also been implicated in inducing egg production e.g. water change in aquariae (Bondesen, 1950) and exudates from water plants (Raven, 1948).

In the present study eggs were observed in field samples, for both species in both seasons, immediately after the mean monthly temperature had risen above 7.5°C (i.e. the trigger temperature marked T in FIGS 27 and 28). Delay of oviposition during 1970 could therefore be accounted for solely in terms of the slower spring rise in temperature in this year as compared with 1971. It was also noted, however, that individuals extracted from the field on sampling occasions M2 and M15, and transferred to a laboratory temperature of 18°C would only oviposit on the latter occasion. Furthermore, the extent of preoviposition spring growth is greater in 1970 than 1971.

On this basis it is proposed that GENERATION 1 (both species) showed a type 1 life cycle whereas GENERATION 2 (both species) showed a type 2 life cycle and that this reflects some adverse pre-winter conditions in the late summer of 1969. Here both types of cycle occur in the one habitat. This may be more typical of marginal situations.

Parental size at oviposition was ca. 2.75mm., M.D. and ca. 4.75mm. A.L. (see FIGS 29 and 30) in P.contortus and A.fluviatilis respectively. The value for the limpet is lower than the minimum ovipositional size quoted by other workers i.e. 6 - 7mm. in other situations (Hunter, 1953; Geldiay, 195). Hunter (1961a) has already pointed to the possibility of both inter- and intra-population variations in this parameter, and has suggested that its magnitude is probably a function of the level of food supply over the preceding year. This hypothesis is consistent with the marginal nature of Ha Mire with respect to primary production, and the size at breeding is significantly greater in populations occupying the more productive north shores at Malham Tarn (see PARTVIISECTION 6).

C DIURNAL VARIATIONS IN EGG PRODUCTION

Thirty snails of each species were brought into the laboratory from Ha Mire on 20/06/71 and put at 18°C under a natural illumination regimen in 2 litres of dechlorinated tap water without food. Observation on egg production at different times of the day were made over one,24 hour interval and the results (in terms of % total number of egg capsules produced) are contained in TABLE 15.

TABLE 15. Egg Production (% total number produced) of A.fluviatilis and P.contortus over a 24h. Interval (T = 18°C; Light Regimen = Natural).

Time Period	P.contortus	A.fluviatilis
6a.m.-12 noon	2.85	2.30
12 noon-9p.m.	0.00	4.20
9p.m.-12 midnight	5.44	10.00
12 midnight-6a.m.	91.71	83.50

Most eggs were laid during the night in both species and this seems to be the general state of affairs in all freshwater Gastropoda so far investigated (Clapp, 1921; Cole, 1925; Krull, 1931; Pesigan et.

al., 1958; Joy, 1971a and b).

4. 4. Spatial Description of Oviposition

A BETWEEN-STONE AND ON-STONE EGG CAPSULE DISPERSION PATTERNS

A haphazard collection of both rough and smooth stones (50 of each) from Ha Mire on 21/05/71 enabled an estimation of the between- and on-stone dispersion patterns of egg capsules with regard to stone texture and aspect. Results are expressed as percentages in TABLE 16, and indicate that most egg capsules were recovered from the undersides (B and BS terminology defined in PART VI SECTION 6) of smooth stones. This pattern is more sharply defined in A.fluviatilis capsules than P.contortus .

Oviposition site selection was also investigated under laboratory conditions. Twenty sexually mature individuals of each species were put separately in glass tanks (30 X 20cm. plan and 15cm. deep) containing equal areas of smooth and frosted (fough) glass surfaces. Tanks contained aerated tap water, were held at 18°C, and had a natural illumination regimen, and were examined after 24h. for numbers and positions of egg capsules. The experiment was also repeated using a mixture (20:20) of both species in one tank. Results are presented in TABLE 17. Columns 1 and 3 present information on position of egg capsules when species were separate and indicate that both species prefer smooth walls. This conforms to the field observations presented in TABLE 16. Furthermore, adult orientation for oviposition is retained with regards to vertical location, i.e. the lower sides of the vertical walls are preferred even in the presence of constant laboratory conditions when wave action and predators are absent. This either represents some form of orientational habituation similar to that found in coelenterate actinians (Bohn, 1908) or a genotypically determined behavioural response. Columns 2 and 4 of TABLE 17 will be discussed below (in B).

On the basis of both the field and laboratory analysis the preferred oviposition sites of both species can be defined as B and BS of smooth stones. Both Bondesen (1950) and Geldiay (1956) have also noted that Ancylus egg capsules are found in these locations. This position does not correspond to the usual adult habitat locations of either P.contortus (B and BS of rough stones) or A.fluviatilis (BS and TS of smooth stones), and changes of between- and on-stone

TABLE 16. The dispersion pattern of egg capsules on- and between-stones in May, 1971.

Stone Texture	Stone Aspect	% A.fluv.	% P.cont.	% A.fluv.	% P.cont.
Smooth	T	0	0	76.0	97.2
	TS	0	0		
	BS	5.5	17.6		
	B	94.5	82.4		
Rough	T	0	0	24.0	2.8
	TS	0	0		
	BS	0	0		
	B	100.0	100.0		
Nos. collected	-	496	723		

TABLE 17. Distribution of eggs (represented as % total numbers laid) in various positions in a laboratory tank. (V = vertical; H = horizontal; S = smooth; R = rough; U = upper surface; L = lower surface).

	1	2	3	4
	A.fluviatilis	A.fluviatilis with P.contortus	P.contortus	P.contortus with A.fluviatilis
VSU	10.0	9.8	9.4	24.6
VSL	81.5	87.7	80.5	9.1
VRU	0	0	0	15.8
VRL	0	0	0	31.8
HS	0	1.5	0	14.2
HR	8.5	1.0	10.1	4.5
Total no. of adults present	20	40	20	40
Total no. of eggs	93	122 (80 A. fluviatilis)	101	122 (42 P. contortus)

dispersion patterns of adults during oviposition, and spat after emergence have already been noted (PART 1V SECTIONS 5 and 6). This situation requires preovipositional migrations of adults and this takes them and their resultant spat out of the context of their usual habitat requirements, so that considerable selective advantage must accrue from these movements in terms of the success of viable egg production.

According to Bondesen (1950) the egg capsules of the Planorbidae are not flattened on laying, but become so after application of the foot, and this process requires a plane smooth surface. Furthermore, flattening of capsules is pre-requisite of the viability of the contained egg cells. Thus Bondesen (Ibid.),reviewing Dumortier's (1837) observations,noted that capsules of P.carinatus (Müll.) were infertile unless flattened and that flattening caused spacing of the contained egg cells. Overlapping eggs developed abnormally and did not hatch. These requirements also apply to A.fluviatilis and explain the necessity for smooth ovipositional surfaces. Laying eggs on the undersides of stones probably confers some protection against wave action and predation.

B POSSIBLE INTERSPECIFIC COMPETITION FOR OVIPOSITION SITES.

For most of the year the niche requirements of both P.contortus and A.fluviatilis are distinct in terms of both food and space. During the breeding season, however, when ovipositional and living space requirements are similar in these species, niche overlap occurs and competition in accordance with the Gause Hypothesis becomes, at least potentially, possible.

The outcome of the potential competitive interaction for ovipositional space has been investigated both under laboratory and quasi-field conditions. Laboratory methods have been described in B above and the results are contained in TABLE 17, columns 2 and 4. Field experiments were carried out in population cages (construction described in SECTION 4. 5a), containing 6 stones of approximately equal size, and comprising equal quantities of rough and smooth surfaces. Three cages were used, two containing either P.contortus or A.fluviatilis (30 individuals) and one containing both species in equal quantity (40 individuals). Cages were left submerged on Ha Mire (under 40cm. water) for one week in May, 1971. Following this period the contained stones were carefully examined for egg capsules.

Their numbers and positions (with respect to both stone aspect and texture) were recorded, and the results are presented in FIG. 34 A, B, C and D.

Both laboratory and field experiments suggest that A.fluviatilis obtains oviposition sites within the preferred zone at the expense of P.contortus, whose eggs become distributed throughout sites not used in isolation. Furthermore, under conditions of interspecific interaction, the egg capsule production of P.contortus becomes reduced whereas that of A.fluviatilis remains roughly constant. Thus A.fluviatilis appears to be the most successful competitor, and this may result from its better adaptation to life on smooth surfaced stones. During oviposition it finds itself less out of context with respect to its usual habitat requirements than P.contortus.

The extent to which these factors apply within the field populations on Ha Mire is conjectural and must ultimately depend on the extent to which the required resource i.e. smooth bottom stone surface is limiting, the limiting resource being the basic requirement for operation of the Gause Hypothesis (Gause, 1934). Neither the laboratory nor the field experiments can be taken as proof of a field resource limitation since snail densities were almost certainly higher than in the natural situation. Furthermore, the naturally low end of season densities and lateral isolations (see PART 1V SECTION 4. 2.) would tend to mitigate against competition. Nevertheless, the possibility of competition is real, and the hypothesis provides a useful means of explaining some aspects of whole-Tarn snail distribution patterns (see PARTVIISECTION 6).

Finally,if interspecific competition were operative on Ha Mire shore, it would still be possible to postulate stable coexistence of the species involved by a balance of advantages (Ullyet, 1950; Park, 1956; Broadhead and Wapshere, 1966). A.fluviatilis has the advantage in procuring oviposition sites during the breeding season and co-existence would only be possible if a density dependent mechanism equilibrated the population of A.fluviatilis at a level comparatively lower than that of P.contortus over the rest of the year. Here the advantage of survival would be in favour of P.contortus and this seems to be the case on Ha Mire (see PART VIISECTION6). This condition may not always apply, and here either the extinction of P.contortus may occur (see PART V1 SECTION 5. 3.) or other mechanisms may be involved (see PART VIISECTION6).

C THE WITHIN-OVIPOSITION-SITE DISTRIBUTION OF EGG CAPSULES

Results based on the dispersion pattern of eggs in a laboratory situation suggest that even within the preferred oviposition site (i.e. the bottom of smooth surfaces) individual egg capsules may be non-randomly distributed. Mature individuals (20) of both species were placed separately in 2L. beakers containing tap water and were left for 2 days at 18°C under a natural illumination regimen, without food. Following this period egg capsule positions were mapped out using tracing paper.

The total number of capsules layed was 83 and 91 for P.contortus and A.fluviatilis respectively, and the majority (ca. 90%) occurred on the lower halves of the vertical walls. Less than 1% in both instances occurred on the beaker floor. Field orientation behaviour is again apparently retained under laboratory conditions (see A above).

The mean number of egg capsules per 16cm.^{2} of the lower vertical surfaces (i.e. 400cm.^{2}) with their associated variance-mean ratios were 2.30 ($S^2/\bar{x}$ = 6.20), and 2.71 ($S^2/\bar{x}$ = 6.35) for P.contortus and A.fluviatilis respectively when the total available area was sampled systematically. These mean-variance values indicate aggregation and, as would be expected, egg capsule distribution patterns diverge significantly from the Poisson series (χ^2(P.contortus) = 130.72; χ^2(A.fluviatilis) = 113.56; $p < .001$ in both cases). Thus, aggregation occurs under relatively constant conditions so that it must result from the behaviour of the snails themselves. Intraspecific interactions are probably involved.

4. 5. A Quantitative Description of Egg Laying

A STANDARD OVIPOSITION ACTIVITY (C)

Numerous records on the oviposition activities of freshwater gastropods are given in the literature (see review by Bondesen, 1950), but most are based on laboratory observation which cannot be extrapolated directly into the field situation. Three independent estimates of C exist for A.fluviatilis, each is based on independent methods of estimation and each contains certain errors of assumption.

Bondesen (1950) estimated an upper limit of 10 capsules/individual limpet. His methods were based on laboratory observation.

Geldiay (1956) estimated an oviposition activity of between 10-20 capsules/individual limpet based on field observations, in which the number of capsules found at one time on 16 stones obtained from two sampling stations were divided by the total number of adults present at the same time, on the same stones. This method assumes that adults are immobile and stay on the stones on which their eggs were laid, that each adult has laid its total egg complement and that capsule loss and adult mortality are balanced. Hunter (1961b) estimated an oviposition activity in A.fluviatilis of 12 capsules/ individual. This estimate was based on an observed linear relationship between adult and capsule standing crop at one time (the end of May) over several habitats and encompassing several years observations. Unlike Geldiay (Ibid.), Hunter (Ibid.) took account of the eggs produced and hatched prior to the fixed sampling date, by the introduction of a correction factor calculated on the basis of personal experience. The latter technique, however, still fails to account for capsule loss through mortality. No comparable data are available for P.contortus.

The field estimates of Geldiay (Ibid.) and those of Hunter (Ibid.) are based on the relationship between adult and egg standing crop at one date and are, therefore, of questionable significance. In an attempt to obviate some of these difficulties, an experimental field approach has been used here. This involved weekly estimates of individual egg production from a haphazard sample of 30 individual snails kept in isolation under field conditions. The haphazard collection ensured that the size distributions of the isolated sub-populations were approximately equivalent to those of the free field populations, and summation of the weekly values for individual egg production consequently provides an estimate of standard oviposition activity in individuals with a mean life span. The estimates were carried out in population cages ($30cm.^3$) consisting of rubberised wire netting surrounded by coarse muslin (pore size, 300μ) sufficient to prevent escape of the contained snails, and access of other invertebrates. Each week during the egg laying period of 1970 snails of each species were collected haphazardly from the Tarn and placed, on the stones on which they were originally found, in the cages (ca. 4 - 5 stones were used on each occasion). Prior to insertion, capsules already present were removed, as were other visible invertebrates. The latter represents an attempt to remove potential egg predators. After sealing, cages were submerged under 40cm. of water, either on

Ha Mire shore (suspended from the north wall - see FIG. 4) or on the north shore (suspended from trees on "Three Trees Point" - see FIG. 3). Two cages were used in each habitat on all occasions, and contained either P.contortus or A.fluviatilis.

Following the 7-day interval, cages were lifted, and the number of capsules contained (i.e. either on the stones or the cage material) together with the number of surviving adults were determined. An 80% adult survival was usual. Standard C was determined as follows :

$$\frac{\text{Total egg capsules present}}{0.5\ (N_1 + N_2)^{*}} = C \text{ individual}^{-1} \text{ week}^{-1} \ldots\ldots 1(5.\ 4.)$$

This technique is essentially similar to Burky's(1971) but was developed independently from him. Average weekly temperatures over the period were also estimated, using the technique of Berthet (1966, see PART II, SECTION 2.I), from sugar solutions contained within cages on Ha Mire.

Results from each station are presented in histogram form in FIGS. 35 A, B, C, and D and summed values for total oviposition activity are included in parentheses. FIG. 35E shows the weekly fluctuations in average temperature.

Oviposition in both species at all stations began only after the mean weekly temperature had risen to 7.5°C. This is in-keeping with the results presented in SECTION 4. 3B. above. Oviposition as monitored by this technique extends over a three-month interval in most instances (cf. extent of interval as deduced from monthly sampling, FIGS. 27 and 28, where the latter part of the A.fluviatilis egg producing interval on Ha Mire was not monitored in the monthly sampling programme). The chronological pattern of capsule production (capsule chronology) indicates an increase to some optimum rate followed by a decrease, and this is typical for most species of pulmonate (Bondesen, 1950). Nevertheless, the detailed pattern of capsule chronology varies with both species and habitats. Thus patterns on the north shores are fairly similar in both species and relatively evenly distributed around capsule production optima, whereas on Ha Mire shore patterns are dissimilar and unevenly distributed being skewed to the left in P.contortus and to the right in A.fluviatilis. Peaks for both species coincide. That these patterns are real is suggested by their consistent maintenance over a fairly long interval of time. They may possibly be explained in terms of food supply, and

* where N_1 and N_2 = the no. of adults present at the beginning and end of the week respectively.

competition for oviposition sites.

Feeding conditions are good for both A.fluviatilis and P.contortus on the north shore whereas food supply on Ha Mire is poorer with respect to A.fluviatilis (see PART VII SECTION6) and this may retard its initial rate of oviposition. The food supply of P.contortus on Ha Mire is similar to that on the north shores and it is tempting to suggest that here the more rapid rise in capsule production rate represents an opportunistic attempt at competition avoidance. It should be noted, however, that the experimental situation excluded the possibility of interspecific interaction by the isolation of each species in different cages, so that it is necessary to postulate some endogenous origin of the opportunistic behaviour. If, however, competition does occur, and A.fluviatilis is the most successful competitor, then selection would favour any slight genetic modifications in P.contortus which had the effect of reducing the intensity of the deleterious interaction. Furthermore, short term,minor genetic variability in semi-isolated races of hololimnic species seems to be characteristic (Hubendick, 1962) and has previously been demonstrated specifically in freshwater snails (Hunter, 1957, 1961a and b; Hunter et. al., 1967, 1970; McMichael, 1967). Isolation of Ha Mire populations has already been suggested (PART IV, SECTION 7. 2.).

Considering the total standard oviposition activities of both species (in paranthesis in FIGS. 35 A, B, C, and D), values appear to be lower on the north shore situations. The significance of this is unclear and cannot be explained in terms of food supply since north shores represent the most favourable situations for A.fluviatilis and bacterial production is similar here to on Ha Mire. Perhaps an inhibiting effect is involved on the limpet since north shore densities are higher than on Ha Mire (see PART VII SECTION6). Hunter (1961b) has suggested that this phenomenon may occur in some Scottish populations of A.fluviatilis.

Using the total standard oviposition activities from Ha Mire, and assuming oviposition in population cages reflects the behaviour of free snails in this situation it is possible to erect two equations expressing the fecundity of both species in terms of capsule production :

$$(\text{Total } C_{PC}) = 9.72\, N_{PC} \quad \ldots\ldots 2 \text{ (5. 4.)}$$

$$(\text{Total } C_{AF}) = 12.16\, N_{AF} \quad \ldots\ldots 3 \text{ (5. 4.)}$$

where :

N = mean number of adults over the oviposition interval (subscripts denote species).

Total C = total oviposition activity for the whole oviposition interval (subscripts as above).

B STANDARD CAPSULE SIZE (E/C), TOTAL EGG PRODUCTION AND SELECTION RATIOS

Standard capsule sizes, i.e. the average number of eggs per capsule on Ha Mire are given in TABLE 13 for both species on two dates. Methods of estimation have already been given in SECTION 4.2A. Dates of estimation correspond to periods in the middle and at the end of the oviposition interval and the values obtained are not significantly different (d (P.contortus) = 0.28, $p > 0.05$; d(A.fluviatilis) = 1.02, $p > 0.05$). This is contrary to the laboratory findings of Bondesen (1950) which suggests that changes in mean capsule size occur, and are related to the pattern of capsule chronology.

Using the average of both monthly E/C values it is possible to erect two simple equations to represent the relationship between total egg production of GENERATION 2 A.fluviatilis and P.contortus populations on Ha Mire and their adult densities :

$$(\text{Total } E_{PC}) = (9.72 \times 3.49)\, N_{PC} \quad \ldots\ldots 4(5.\ 4.)$$

$$(\text{Total } E_{AF}) = (12.16 \times 2.57)\, N_{AF} \quad \ldots\ldots 5(5.\ 4.)$$

where Total E = total egg production over the whole oviposition period.

N is defined for equations 2(5. 4.) and 3(5. 4.) above.

From these equations it is possible to see that a standard individual in GENERATION 2 lays a total number of 33.23 and 31.25 eggs in P.contortus and A.fluviatilis respectively. Thus,fecundity in both species, on Ha Mire, is remarkably similar. Since all predators may not have been excluded from the population cages (e.g. non-visible micro-predators may have been overlooked) both these estimates and those given by equations 2 (5. 4.) and 3 (5. 4.) above must be considered as minimum.

P.contortus and A.fluviatilis lay considerably fewer eggs than most other freshwater pulmonates. Hunter (1961b) has defined the "annual ratio of selection" as that, which for the known potential reproductive capacity, would allow the population to remain stable

as regards population density from year to year. Assuming that Ha Mire populations are in steady state, selection ratios are in the order of 30:1 for both the species considered. This falls within the range of values previously reported, i.e. 18:1 and 47:1, for A.fluviatilis by Bondesen (1950) and Hunter (1961b) respectively. Similar low values have been obtained by Burky (1971) for the North American ancylid, Ferrissia rivularis. Higher values occur in other species of pulmonate, 1400:1 for L.pereger and 1000:1 for Planorbis corneus (both from Hunter, 1953). All these values contrast markedly with that of 50,000:1 for the primitive salt marsh pulmonate Melampus bidentatus (Hunter et. al., 1966; Apley, 1970; Apley et. al. 1967) which is amphibious and produces small aquatic eggs which hatch as planktonic larvae.

Low selection ratios in the Ancylidae are supposed to be related to a higher degree of structural specialisation and a comparatively low degree of variation (Hunter, 1957). If this is the case, these characteristics can also be applied to P.contortus (and also P.crista, selection ratio - 30:1, Boycott, 1936). They are not, however, relevant to all the Planorbidae (see selection ratio quoted above for P.corneus), and this may depend on adult size. The species consisting of larger individuals having a higher selection ratio than those consisting of smaller individuals.

C FACTORS AFFECTING FECUNDITY WITH A NOTE ON PREDICTABILITY

Various factors, both exogenous and endogenous, are known to affect fecundity in freshwater snails. Van der Steen (1967) has reviewed the effects of physical conditions; Jobin and Michelson (1967) have demonstrated an inverse relationship between fecundity, habitat size and density levels and a direct relationship involving food supply; Calow (1972, see PUBLICATIONS APPENDIX 1V) has shown that fecundity in P.contortus is to some extent independent of food supply; Mooij-Vogelaar et. al. (1970) have found a relationship between fecundity and density level changes, and Bondesen (1950) has suggested that E may vary with individual size.

Clearly equations 2(5. 4.) to 5(5. 4.) can only represent simplistic descriptions of fecundity in P.contortus and A.fluviatilis, at one time in one habitat. Erection of predictive equations would require far more information than is at present available (see Watt, 1969).

4. 6. Egg Mortality

A. METHODS OF OBTAINING THE RELEVANT INFORMATION

Between oviposition and eclosion some of the reproducta (eggs or whole capsules) may be destroyed either as a result of predation or from adverse physical conditions. To investigate the extent and nature of this loss, egg capsules on the stones removed from the population cages were marked by scraping a line around them with a sharp scalpel. Each stone was replaced in the Tarn, bottom downwards, at a depth of between 20-40cm., and marked by an attached buoy. Following one week, marked stones were recovered and the extent of whole capsule loss and damage to remaining capsules was assessed.

Thirty to forty freshly laid capsules of each species were treated weekly in this way and where material from the cages was insufficient, numbers were made up from freshly laid capsules extracted directly from the Tarn. Estimations which were based on fewer than 30 initial capsules will be indicated. Observations were repeated weekly on Ha Mire, through the whole oviposition interval of each species. No attempt was made to follow mortality for longer than 1 week since hatching complications, particularly in P.contortus, then became apparent. Two assumptions are implicit in these estimations:

i) that mortality on marked stones is a faithful index of the natural mortality occurring elsewhere on the shore.
ii) that susceptibility of eggs to destruction does not change with age.

Results from the above estimations in terms of percentage egg capsule loss for each weekly sample are presented in FIGS. 36 A and B. Consonant with the earlier cessation of oviposition in P.contortus observations on mortality in this species do not extend as long as those for A.fluviatilis. Blocks marked with an asterisk are based on ca. 15 original capsules, and are a result of low production rates in the preceding weeks. In no case was there any apparent damage to parts of a capsule or to individual eggs. The significance of this observation will be discussed later.

From the information contained in FIGS. 36 A and B on capsule mortality, FIGS. 35 A and B on capsule production, and FIGS 27 and 28 on adult densities over this period, it is possible to calculate an expected estimate of egg standing crop on Ha Mire for each week

of oviposition by use of the following assumptions:

i) half the eggs laid in any one-week period are oviposited on day 1 and half on day 7.

ii) the mortality operating within any one-week period is taken as intermediate between that observed at the end of the preceding and the present week.

iii) loss to eclosion is accounted for with regard to assumption i) and by further assuming an approximate developmental period of 14 days in P.contortus and 28 days in A.fluviatilis. These are slightly longer than the laboratory estimates given in SECTION 4. 2B, but are more convenient for calculation.

Results from these calculations are contained in FIGS. 37 A and B for A.fluviatilis and P.contortus respectively in terms of expected numbers of capsules per 10,000 LP. Also included are estimates for mean egg case densities derived from the monthly sampling programme described previously in SECTION 2. Vertical bars represent 2 standard errors. Both the means and variances were obtained using equations 1 (5. 2.) and 2(5. 2.), and the computer programme. Correspondance between observed and expected estimates is close and this gives added confidence in the estimates made on the above assumptions, the mortality rates on marked stones being equivalent to natural rates and the oviposition activity in the cages reflecting the normal activities of free individuals.

B. INVESTIGATION OF THE REGULATORY NATURE OF EGG MORTALITY

Information on egg capsule standing crops calculated in A above and presented in FIGS. 37 A and B has been employed to analyse the possibility of regulation, through mortality, in the egg stage of the life history. The form of the data allows the use of two related methods of detection :

I. involving logarithmic regression between the predicted number of capsules entering each weekly interval with those surviving to the end of the interval, making due allowance for hatching.

II. involving a regression analysis between the logarithm of numbers entering a particular weekly interval, with the difference between the logarithm of numbers entering and logarithm of numbers surviving to the end of the interval.

TECHNIQUE I

FIGS. 38 A and B represent the raw, untransformed data. Numbers of capsules entering an interval are represented as No; whereas those surviving to the end of the interval are represented as Ns. In order to exclude hatching complications from the mortality estimate, Ns includes those eggs which would have hatched over the interval.

FIGS. 39 and 40 represent the logarithmic plots. Raw data was multiplied by 10 prior to transformation to alleviate difficulties caused by negative logs. Regressions of Y or Ns against X or No (b_{YX} in FIGS. 39 and 40) are the ones of immediate interest, and regression lines calculated according to the method of least squares are specified as follows :

$$\text{Log } (Ns \times 10)_{PC} = 0.144 + 0.90 \text{ Log } (No \times 10)_{PC} \ldots\ldots 6(5.4)$$
$$(r = 0.95;\ t = 1.064;\ p > 0.1 \text{ when null hypothesis is } b = 1)$$

$$\text{Log } (Ns \times 10)_{AF} = 0.065 + 0.98 \text{ Log } (No \times 10)_{AF} \ldots\ldots 7(5.4)$$
$$(r = 0.98;\ t = 0.973;\ p > 0.1 \text{ when null hypothesis is } b = 1)$$

where No and Ns are defined above, and subscripts denote species.

Density dependence is represented by a disproportionate rise in mortality or reduction in survival as density increases and therefore by regression coefficients based on the above procedure, which are significantly less than 1. Coefficients actually obtained are equivalent to 1 in both species, suggesting that capsule mortality is of a non-regulatory form. Inspection of the raw data for A.fluviatilis supports this outcome whereas inspection of raw data for P.contortus is suggestive of density dependence (see FIGS 38 A and B).

Technique 1 is similar, but not directly analogous, to the method suggested by Morris (1963) as part of his "key factor" analysis. It has been advocated by Soloman (1964) as a simple test for regulation. Salt (1966), however, has criticised the method on several grounds, and has suggested that it may have only limited sensitivity. Furthermore, Technique 1 is only sensitive to prompt density dependence and will not demonstrate lagging effects since the regression coefficients remain at 1 even when lagging occurs. For these reasons Technique II has also been employed.

TECHNIQUE II

The second technique is directly analogous to the "k-plot" method of Varley and Gradwell(1960). "k-plots" are presented in FIGS. 41 and 42 where the logarithm of numbers of egg cases entering a particular interval (No) are plotted on the X-axis and the difference between the logarithm of numbers entering and leaving the interval (k) are plotted on the Y-axis. Regression equations relating k to log No, for each species, and calculated by the method of least squares are :

$$k_{PC} = -0.1461 + .1010 \log (10 \times No)_{PC} \quad \ldots\ldots\ldots\ldots\ldots\ldots 8(5.\ 4)$$
$$(r = .63;\ t = 2.29;\ p = 0.05 \text{ when null hypothesis is } b = 0)$$

$$k_{AF} = -0.0479 - .0606 \log (10 \times No)_{AF} \quad \ldots\ldots\ldots\ldots\ldots\ldots 9(5.\ 4)$$
$$(r = -0.0379;\ t = 0.995;\ p > 0.10 \text{ when null hypothesis is } b = 0)$$

where terms are defined in the text and subscripts denote species. Lines are denoted as b in the figures.

In these plots direct density dependence is represented by a positive regression coefficient which is significantly different from zero; inverse density dependence by a significant negative coefficient and density independence by a coefficient not significantly different from zero. Equations 8(5. 4) and 9(5. 4) above suggest density independence in A.fluviatilis and slight direct density dependence in P.contortus. A low value of the regression coefficient with respect to 1 indicates under-compensation.

Significance tests carried out on the "k-plots", and indicated in the present case in parenthesis below the equations, are not strictly legitimate because k and No are not independent (Varley and Gradwell, 1968). Significance can be tested, however, by considering whether regression lines expressing the relationship of log No on log Ns and their reciprocal plots are significantly different from, and lie on the same side of, one.

The formal tests are in fact represented in FIGS. 39 and 40. Regressions b_{YX} have already been considered in equations 6(5. 4) and 7(5. 4) and their reciprocals, b_{XY} , indicated as a broken line in the figures are specified by :

$$\log(No \times 10)_{PC} = 0.040 + 1.013 \text{ Log } (Ns \times 10)_{PC} \quad \ldots\ldots 10(5.\ 4)$$
$$(t = 0.80;\ p > 0.10 \text{ when null hypothesis is } b = 1)$$

$$\log(No \times 10)_{AF} = 0.019 + 1.001 \text{ Log } (Ns \times 10)_{AF} \quad \ldots\ldots 11(5.\ 4)$$
$$(t = 0.62;\ p > 0.10 \text{ when null hypothesis is } b = 1)$$

Thus equations 6(5. 4) + 7(5. 4) and 10(5. 4) + 11(5. 4) suggest that coefficients given in equations 8(5. 4) + 9(5. 4), are not significantly different from zero, so that the apparently significant coefficient for P.contortus in equation 8(5. 4) cannot be accepted. Nevertheless the possibility of delayed density dependence still remains.

Delayed density dependence may be investigated by chronological linking of points in the "k-plots", rather than treating them as scatter diagrams (Varley and Gradwell, 1965). In these instances, delayed density dependence is suggested by an orderly rotation of the point sequence. This has been carried out in FIGS 41 and 42, (see arrowed lines), and indicates a regular anticlockwise and clockwise rotation in P.contortus and A.fluviatilis respectively. Anticlockwise rotation is suggestive of true, delayed or lagging density dependence when the mortality rate of egg capsules lags behind their density fluctuations, whereas clockwise rotation suggests a leading phenomenon when capsule mortality falls prior to the establishment of peak densities.

Neither Techniques 1 nor 2 indicated prompt density dependence in the egg capsule mortality of either P.contortus or A.fluviatilis on Ha Mire. Chronological linking of points in the "k-plot" analysis, however, suggested delayed density dependence of the usual lagging type in P.contortus and of a less usual, hitherto undescribed, leading type in A.fluviatilis. It is possible that both these processes are linked via some common predator, so that at low total egg case densities (i.e. at the beginning of oviposition), A.fluviatilis capsules suffer greater and apparently more direct mortality than P.contortus. This may be a result of the larger, more conspicuously coloured nature of capsules in the former species (see SECTION 4. 2). As time proceeds, however, and even though P.contortus capsule density falls, this species suffers to a greater extent than A. fluviatilis. Reasons for the shift are unclear, but may result from a greater susceptibility of P.contortus capsules to predation either as a result of their lack of a protective quaternary envelope or if competition for oviposition sites is operative, due to their less favourable situation in the face of the greater egg laying pressures being exerted by the limpet.

Both of the above explanations can be reconciled within the

theoretical frameworks provided either by the "specific searching image" concept of Tinbergen(1960), or the"profitability" concept of Royama (1970). In Tinbergen's sense one could envisage the "searching image" being initially fixed on the most conspicuous and later on the most easily accessible capsules. Royama's (Ibid.) profitability concept represents the amount of prey (in terms of biomass) which a predator can collect in a given hunting time and is defined by :

$$M = W.a.D.T./(a.h.D. + 1)$$

where M = profitability

W = biomass (wt. or cals.) of an individual prey

D = prey density

a = area of discovery

h = time spent handling each victim

T = total time spent hunting

Clearly profitability will be determined by 3 different factors viz.:

i) the predator's ability to find the prey

ii) the handling time

iii) the prey returns in terms of biomass

A predator will operate so as to optimise M.

In the present instance one could postulate that at low total egg capsule densities it would be more profitable to eat A.fluviatilis capsules because they are more conspicuous and return more calories per capsule (see TABLE 13) even though time spent handling them, as a result of their quaternary envelope, may be longer than that for P.contortus. At higher capsule densities, however, ease of handling the capsules of P.contortus as a result of their lack of a quaternary envelope, and possibly their less favourable siting, could shift optimum profitability in their "favour". More information is required on the nature of the predator (see C) before these questions can be fully answered.

C POSSIBLE SOURCES OF EGG CAPSULE MORTALITY

Bondesen (1950) has noted the relatively well protected condition of the ancylid egg capsules. He suggests that this results from them being laid on the underside of stones, and the protective nature of their quaternary envelope. Planorbis capsules will be

similarly protected, but possibly to a lesser extent by their foot secretions. In conjunction with the protective outer capsule membrane in the Ancylidae, Bondesen (1950) observed that parasites such as rotifers and infusoria, which are often found inside the capsules of Lymnaeidae and Physidae are absent from those of the Ancylidae. Observations have confirmed these conclusions for beth A.fluviatilis and P.contortus on Ha Mire.

Information regarding the possible predators of freshwater snail eggs is both sparse and fragmentary. The list given in TABLE 18, together with literature sources summarises the available information. Only one of the groups listed, i.e. the caddis larvae, are present on Ha Mire to any appreciable extent. Oldham (1930) has described the Trichopteran attack as involving larvae clinging to egg cases with their feet, gnawing a hole in the capsule wall, and extracting the contents. This is apparently inconsistent with the observation that egg cases only, were removed from stones on Ha Mire. Nevertheless, ruptured capsules of both P.contortus and A.fluviatilis become extremely flaccid and would easily be completely removed by wave action. Other species, which cannot be neglected as potential predators, are leeches and flatworms. These species peak in abundance during the oviposition interval (see FIGS. 51 A - D). Casual observation in the laboratory, however, has yielded no positive evidence for their implication in egg capsule predation.

Sources of mortality other than predation are also feasible. Thus, Bondesen (1950) has recorded the occurrence of various embryonic abnormalities, particularly in A.fluviatilis, where 20% of all eggs laid under laboratory conditions, develop abnormally and do not complete development. It is not known to what extent this occurs in the field.

Overgrowth by epilithic algae may also contribute to egg capsule destruction. This occurs to a considerable extent on the north shores, (particularly "Three Trees Point") at Malham, but is not apparent on the less productive Ha Mire situation. Neither embryonic abnormalities, nor mortality through algal overgrowth, would have been monitored in the present work.

TABLE 18. A list of potential predators of egg capsules.

Predator	Prey	Literature Source
1. Hydrophilus spp.	unspecified	Bateman (1902) +
2. Disticus spp.	"	Boycott (1936)
3. Trichopteran larvae *	P.corneus	Oldham (1930)
4. Proales gigantea	Lymnaea	Nekrassov (1926) +

* found on Ha Mire.

\+ cited in Boycott, 1936.

4. 7. Recruitment of Spat on Ha Mire

A. SIZE OF SPAT ON HATCHING

The sizes of spat hatching from the experimental group of eggs described in SECTION 4. 2B were measured using a dial micrometer attached to a X40 binocular, dissecting microscope. All measurements were made within 24h. of eclosion. Results expressed in mm. were 0.98 (± 0.11) AL for A.fluviatilis (N = 70) and 0.68 (± 0.09)MD for P.contortus (N = 63). The confidence limits represent 2 standard errors. Hunter (1953a) reported a spat size of 1.05mm., AL for A.fluviatilis. Similar comparative data are lacking for P.contortus but Hunter (1961b) reported a spat size of 0.57mm. MD in the closely allied P.albus. Hunter's data and those reported here are, therefore similar.

An independent estimation of the size of spat on hatching in the field can be obtained from an analysis of their size frequency distribution during recruitment. This information, derived from the sampling programme described in SECTION 2, is contained in histogram form in FIGS. 43A, 43B, 44A, and 44B. FIGS. 43 A and B refer to the months within the oviposition interval (i.e. J6, J7, 1970; M18, J19, 1971) for P.contortus and A.fluviatilis respectively, and FIGS. 44 A and B refer to that sampling occasion immediately following the last date on which oviposition was observed (i.e. A8, 1970; J20, 1971) for both species. The laboratory results in terms of mean size are included as inverted arrows.

As expected, histograms are polymodal and the extent of this polymodality increases as time proceeds. This phenomenon results from the hatching of successive cohorts of eggs laid on successive nights (see SECTION 4. 3C) throughout the oviposition period. On later sampling occasions, however, the polymodality becomes obscured (see FIG. 32), presumably as a result of differential individual growth rates. In consequence, the total adult population present at any one time has been assumed to be homogeneous in terms of both age and size. In FIGS. 43 and 44 there is also a progressive shift of modal peaks to the right as time proceeds and spat grow. Arrows representing mean laboratory spat sizes apparently shift to the left with respect to the frequency distributions.

Use of Harding's (1949) technique did not allow separation of modes. Nevertheless, the earlier peaks can be identified with the

modal size of spat on hatching. These correspond closely to the laboratory predictions only in the case of P.contortus. In A.fluviatilis the modes are generally deflected to the left of the arrow (cf. sample J 19) except in the later months (A8 and J20).

Bondesen (1950) has noted the tendency of A.fluviatilis individuals to produce dwarf eggs particularly at the beginning of oviposition. These develop into dwarf spat and he attributed this to insufficient albumen. Dwarfism may be occurring on Ha Mire and its extended nature in 1970 is probably a result of harsh preceding conditions (see also SECTION 4. 3). Dwarfed individuals probably have lower chances of survival than normal spat.

B. SURVIVAL OF SPAT ON HATCHING

A numerical solution to equations 6(5. 4) and 7(5. 4) (where No = 9.72 N_{PC} or 12.16 N_{AF} for P.contortus and A.fluviatilis respectively) and using mean adult densities over the whole oviposition period as operators (i.e. N_{PC} = 16.00 or 11.00 for 1970 and 1971 respectively; N_{AF} = 1.83 or 2.83 for these two years) provide estimates of total egg capsule production and percentage loss to mortality. Results are contained in TABLE 19.

TABLE 19. Capsule Production and Survival in P.contortus and A.fluviatilis in 1970 and 1971

Species	Date	Capsules Produced (per 10,000 LP)	Capsules surviving (per 10,000 LP)	% Mortality
P.contortus	1970	155.50	129.60	16.7
	1971	106.90	93.35	12.7
A.fluviatilis	1970	22.25	21.20	4.7
	1971	59.88	56.02	6.4

Using the above figures in association with the standard capsule sizes of 3.49 and 2.57 for P.contortus and A.fluviatilis respectively, the total spat production (No./10,000 LP) can be calculated (see column 1, TABLE 20). Comparing these data with the mean numbers of spat per 10,000 LP actually observed on the first sampling occasion after complete hatching (i.e. A8 and J20 in P.contortus and S9 and

A21 in A.fluviatilis, see column 2, TABLE 20) gives an estimate of spat mortality within the oviposition period.

TABLE 20. Estimates of Spat Mortality Following Hatching

Species	Date	Predicted nos. of spat/10,000 LP	Actual nos. of Spat/ 10,000 LP	% Spat Mortality
P.contortus	1970	452.30	67.10	85.2
	1971	325.80	87.00	73.3
A.fluviatilis	1970	54.48	35.70	34.5
	1971	143.97	38.20	73.5

The figures presented in TABLE 20 indicate a relatively high spat mortality during the breeding season which is considerably greater than loss during the egg phase. This outcome was intuitively stated both by Boycott (1936) and Bondesen (1950) and probably accrues from what has already been said about the protective nature of the egg membranes. On the basis of these limited observations it is difficult to make any categorical statement regarding the regulatory nature of this spat mortality. Nevertheless,the percentage mortality increase during years of greatest spat production (see particularly A.fluviatilis) is suggestive of density dependent regulation. Possible sources of spat mortality will be discussed in SECTION 5. 2 below.

4. 8. Recruitment of Spat in Different Habitats and the Regulatory Nature of the Recruitment Phase of the Life Cycle

Recurrent observationsover several generations at one site are necessary to investigate the possible regulatory nature of total spat recruitment with respect to adult density in the preceding generation (Watt, 1968). In the absence of this information the relationship can be considered in terms of different populations, occupying different habitats during one season. The latter technique is obviously less satisfactory than the former.

The different habitats approach has been used here. Data were obtained from several habitats in the Malham area, and these are

listed in FIG. 45. One of the sites i.e. the River Wharfe, at Pool is situated in the lowlands (ca. 10 Km. from Leeds). The pre-ovipositional adult densities were estimated in April 1971 and the resultant spat densities were estimated in August 1971, except for the lowland site which was sampled one month earlier. Here egg laying and hatching occur at an increased rate. All densities are expressed in terms of nos./10,000 LP, and were calculated using equations 1(4. 7) and 2(4. 7) and the computer programme (see SECTION 2).

The plots of adult,versus resultant spat densities are contained in FIGS. 45 A and B for A.fluviatilis and P.contortus respectively. Lines are fitted by eye. These plots clearly indicate a proportional decrease in the recruitment of spat as adult density increases and therefore suggests density dependence, Hunter (1961b) has found a similar phenomenon for A.fluviatilis populations in the West of Scotland.

Recruitment of spat will depend basically on 3 components, which have previously been discussed separately with regard to the Ha Mire populations i.e. :

i) adult fecundity and oviposition activity
ii) egg and capsule mortality
iii) spat mortality on emergence

Each may be subject to density dependent control. Identification of the "key factor" (see Morris, 1963) would demand more information than is at present available.

5. SPECIFIC INFORMATION ON MORTALITY

Investigation on the pattern and causes of mortality (post-embryonic) have been limited to GENERATION 2 since complete information on the relevant population statistics is only available in this instance (see FIGS. 27 and 28). The starting dates for this cohort have been taken as sampling occasions J7 and A8 for P.contortus and A.fluviatilis respectively. Selection of these dates was based on :

i) peak oviposition activity occurring 4-6 weeks after the initiation of oviposition in P.contortus and 6-8 weeks after the onset of oviposition in A.fluviatilis (see FIGS 35 A and D)
ii) development in the egg being twice as rapid in P.contortus as A.fluviatilis (ca. 2 and 4 weeks respectively, see SECTION 4. 2B) so that peak spat recruitment should occur 6-8 weeks after initiation of oviposition in the former and 10-12 weeks in the latter species. The nearest sampling occasions corresponding to these estimates are those given above, and use of these dates assumes that the pattern of capsule production was the same in 1970 as 1971. Starting densities are taken from TABLE 20, column 1, and are therefore based on standard oviposition activities, standard egg capsule sizes, and estimated egg mortality. It is assumed that immigration and emigration do not occur (see PART 1V, SECTION 7. 2).

5. 1. The Form of the Survivorship Curves

FIGS. 46 and 47 show the survivorship curves of each species over GENERATION 2. That of P.contortus (FIG. 46) closely approximates to the Deevey type 3 curve (Deevey, 1947) otherwise known as the Slobodkin type 4 curve (Slobodkin, 1962à),in which mortality mainly affects the young individuals, mean life expectancy increases with age and the median life expectancy is smaller than the mean. In contrast, the survivorship curve of A.fluviatilis more closely resembles the Deevey type II (Slobodkin type III) curve in which the rate of mortality and the mean life expectancy are constant throughout life.

FIGS. 46 and 47 indicate variations in the extent of absolute mortality with time. Of greater significance, however, are changes in the proportion of the populations dying per unit time. This is

examined by plotting the logarithm of population density (lx) against time (FIGS. 48 and 49). As expected from a Deevey type III (Slobodkin type IV) curve, the logarithmic plot of P.contortus remains curvilinear, whereas the Deevey type II (Slobodkin type III) curve of A.fluviatilis becomes approximately linear.

The straight line relationship in A.fluviatilis is represented by the equation :

$$\log y = 1.6040 - 0.0041x \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 1(5.5)$$

($t = 3.08$; $p \simeq 0.01$ when null hypothesis is $b = 0$)

where y = numbers surviving/10,000 LP after a given time (X)

x = time in days starting from A8 (22/08/70).

Inspection of the data, however, suggests a certain degree of curvilinearity which could be reconciled into two linear phases, the first extending from A8–M15, the second from A16–J20. The representative regression equations of these two periods are :

$$\text{A8–M15; } \log y = 1.721 - 0.0055x \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 2(5.5)$$

($t = 6.40$; $p < 0.001$ when null hypothesis is $b = 0$)

$$\text{A16–J20; } \log y = 1.082 - 0.0021x \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 3(5.5)$$

($t = 4.00$; $p \simeq 0.05$ when null hypothesis is $b = 0$)

where the terms are defined above for equation 1(5. 5). The latter interpretations account for 39.7% more of the total sums of squares than the single linear representation and the break between the earlier steep phase, and later shallow phase corresponds to the onset of spring conditions. All the linear semilogarithmic representations of A.fluviatilis allow a description of population survival with time in the form :

$$N_t = N_o e^{-mt} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 4(5.5)$$

where N_t = population density (no./10,000 LP) after time t (days)

No = original population size

m = instantaneous rate of mortality

(N.B. this equation could be written far more generally to account for the instantaneous birth rate, but since birth is limited to one isolated part of the life cycle this can be ignored and set to zero for most of the time). Taking natural logarithms and rearranging equation 4(5. 5), gives :

$$-m = (\ln N_t - \ln N_o)/t \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 5(5.5)$$

Reference to FIG. 49 and using equation 5(5. 5) gives values of m of

0.0153, 0.0030, and 0.0130 for phases A8-M15, A16-J20, and A8-J20 respectively, where t is in days. These values are within the range reported by Gillespie (1969) for pulmonate populations in the Madison River (i.e. for Physa gyrina Say m ranges from 0.0453-0.0002; for Gyraulus deflectus (Say) m ranges from 0.0323-0.0002).

The simple exponential model (equation 4(5. 5)) cannot be applied to the population data of P.contortus because of the curvilinear nature of the semilogarithmic plot (see FIG. 48). This indicates a progressive reduction in the proportion dying per unit time, and a double logarithmic plot of lx versus time enables investigation of the form of this reduction (see FIG. 50).

All the points, except the first, in FIG. 50 lie on a straight line described by the equation :

$$\log y = 2.898 - 0.749 \log x \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 6(5.5)$$

($t = 11.18$; $p < 0.001$ when the null hypothesis is $b = 0$)

where terms are defined for equation 1(5. 5).
Such a linear relationship suggests a constant rate of reduction in the proportion of the population dying per unit time. That the initial change in density is not accounted for by the straight line must mean that individuals pass through some critical phenological stage during the first 28 days of life. Prior to this time they are susceptible to a greater and possibly different form of mortality than later. This could result from changes in the characteristics, either of the organism concerned or their environment, and it may be significant that during the initial period young spat migrate from the more exposed smooth stone surfaces to the more protected creviced regions (see SECTION 5). Similarly, spat are more susceptible to predation than adults (see SECTION 5. 2). Both these factors may be related.

5. 2. The Role of Predators in Mortality in the Ha Mire Populations of P.contortus and A.fluviatilis

A. POTENTIAL PREDATORS PRESENT ON HA MIRE

The potential predators which are most abundant and most intimately associated with snails on Ha Mire are the leeches and flatworms. There are three species of leech, Erpobdella octoculata (L.), Glossiphonia complanata (L.) and Helobdella stagnalis (L.)

and one species of flatworm, Polycelis nigra (Müll.). Data on the monthly density levels of these 4 major predator species are contained in FIGS. 51 A-D, and are derived from the monthly sampling programme described in SECTION 2. Confidence limits represent 2 standard errors. Breeding periods are denoted by horizontal bars and are specified on the basis of the appearence of cocoons on submerged stones for P.nigra and E.octoculata, and the presence of larvae attached to the ventral surfaces of adults in H.stagnalis and G.complanata.

Of general significance is the close similarity between the phenologies described here and those described in other habitats by Mann (1953, 1957a and b) for the leeches and Reynoldson (1967) for the flatworms. In accordance with the snail data, however, (see SECTION 4. 3B) breeding in the leeches appeared later in 1970 than normal (cf. Mann, Ibid.) and cocoon production in P.nigra is typical of highland populations, (Hynes reported in Reynoldson, Ibid.). In most of the species considered, there is an immediate increase in density levels following each breeding occasion whereas in G.complanata there is a lag phase of 1 month between these two processes. Mann (1957a) also described this phenomenon and showed that it was due to the emergent larvae migrating from large stones into the surrounding gravel where they spend the first month of their lives before returning to the larger stones as adults. Of more specific interest from the point of view of the present work is the fact that peak, potential predator densities are roughly coincident and correspond both with the egg and spat phases in the snail life cycles. Results from laboratory experiments on the predatory effects of leeches and flatworms on snails is given in B below.

Neither the density levels of other potential predators on Ha Mire nor their predatory effects were quantifiable. Circumstantial evidence, however, suggests that they are of little importance with respect to snail mortality. Crayfish are present on Ha Mire and Eisenberg (1966) has suggested that they may eat snails, but Holmes (1965) analysing the stomach contents of 20 individuals taken from the Tarn in general found no evidence of snail remains.

The two most abundant littoral fish species at Malham are the Bullhead (Cottus gobio L.) and the Stoneloach (Nemacheilus barbatula L.). These fish live between and beneath stones and are likely to come into contact with stone-dwelling snails. A casual collection of 121 specimens of both species (i.e. mainly C.gobio ca. 85% of the sample)

and the subsequent analysis of gut contents over one year revealed only a single specimen (captured 10/10/70) containing snails (i.e. 3 P.contortus) and none containing A.fluviatilis. The bulk of the diet appears to be composed of chironomid larvae. Other large fish species in the Tarn i.e. Perch (Perca fluviatilis L.) and Brown Trout (Salmo trutta L.) can eat snails (Holmes, 1960) and have been implicated elsewhere in snail density regulation (Macan, 1966b) but they are precluded from the shallow littoral reaches, and probably obtain most of their molluscan food supply from the weed beds at Malham (Holmes, 1965).

The predatory effects of species living on and around the Tarn e.g. birds and semi-aquatic mammals is even more difficult to assess. Boycott (1936) has implicated these animals in possible snail predation, but their effects on the two species under consideration here must remain uncertain. The situation of P.contortus and A.fluviatilis on the less exposed sides and bottoms of submerged stones and their relatively small sizes probably precludes significant mortality from these sources.

Snails may be generally and extensively parasitized with cercariae of trematode flatworms. The extent to which these organisms affect the survival of their hosts is unknown (Wright, 1966) though heavy trematode infection must have some deleterious effect and host pathology has been observed (Rothschild, 1962; Wright, Ibid.; Moore, 1971; Sweeting, 1971). Cercarial release from individuals of P.contortus and A.fluviatilis taken from Ha Mire, however, was never observed and dissection of the hepatopancreas in freshly killed specimens also failed to reveal infection. Larger species of snail i.e. L.pereger and L.stagnalis taken from Malham Tarn were infected, however. These observations tend to support the postulate that cercarial infection is size-limited, being impossible in small individuals of large species and small species in general (Cort et. al., 1957; Sweeting, 1971).

Sciomyzid flies have recently received a good deal of attention with regard to their feeding habits. They appear to be specific predators of both terrestrial and freshwater snails (Berg, 1964). Adults and larvae of this group have been found in Malham Tarn area (Disney- pers. comm.) but no evidence for their existence or activity on Ha Mire has been found during the present study.

B. LABORATORY EXPERIMENTS ON THE PREDATORY EFFECTS OF LEECHES AND FLATWORMS

The possibility of predation by the four major invertebrate species listed above on P.contortus and A.fluviatilis was investigated in the laboratory. All potential predators and snails were collected from shores adjacent to Ha Mire. Each individual predator was starved and acclimated in 250ml. of aerated tapwater at 10°C, for 7 days prior to use. After acclimation five individuals of either P.contortus or A.fluviatilis were introduced into each beaker containing a single predator and were observed daily over a 7-day interval. No cover was introduced and experiments were carried out at 10°C. Loss of whole snails or their parts was interpreted as predatory mortality.

Three size categories of snail were used :

Species	Large	Small	Spat
A.fluviatilis	4-7	2-3.9	< 1
P.contortus	2-4	1-1.9	<1

where dimensions are in mm. AL or mm. MD for A.fluviatilis and P.contortus respectively. Size specifications of the predators used (in cm. length)were :

E.octoculata - 1.0-2.5 cm.
H.stagnalis - 1.0-1.5 cm.
G.complanata - 1.5-2.0 cm.
P.nigra - .5 cm.

All experimental combinations of predator and prey were replicated 10 times.

One experiment designed to investigate the possible interaction between larval leeches and snail spat involved use of a mixed species group of predators since larval leeches could not be distinguished to species. Ten leeches were associated with 25 spat of either P.contortus or A.fluviatilis. Experiments were carried out in 100 ml. aerated tapwater at 10°C. Other experimental specifications were as described for the adult predators above.

TABLE 21 indicates % snail survival after a 7-day association with potential predators in the above experiments. Of the predatory species chosen, only one, P.nigra, failed to take any live specimen of either snail species although it would apparently feed on

TABLE 21. % survival of snails after a 7-day association with some potential predator.

Prey	Predator \ Snail size class	Large	Small	Spat
P.contortus	E.octoculata	100	76	28
	G.complanata	100	83	66
	H.stagnalis	96	82	80
	P.nigra	100	100	100
	Larval Leeches	-	-	53
A. fluviatilis	E.octoculata	100	100	100
	G.complanata	96	76	88
	H.stagnalis	98	84	72
	P.nigra	100	100	100
	Larval Leeches	-	-	77

crushed individuals. Under the experimental conditions used, all leech species fed on either P.contortus and/or A.fluviatilis, though a preference for the smaller prey individuals, particularly the spat, is apparent. Only E.octoculata was species specific, being limited to P.contortus. This species of leech has not previously been recorded as a mollusc feeder, (Mann, 1964) its diet generally consists of aquatic insect larvae which it swallows whole. In the present experiments it was similarly observed to swallow whole prey and this behaviour probably accounts for its size and species preferences, being limited to small, easily obtained and easily swallowed prey types with a thin shell. Both G.complanata and H.stagnalis have previously been recorded as snail feeders (Mann, 1964). TABLE 21 shows that they feed on both P.contortus and A. fluviatilis. They never swallowed snail shells and in the case of the limpet also rejected the muscular foot.

The mixed species group of leech larvae were observed to feed on snail spat. Both species of snail were taken, though P.contortus was apparently preferred. Shells and feet were usually rejected.

The results embodied in TABLE 21 cannot be applied uncritically to the interpretation of field data. The experimental conditions theoretically provided optimum opportunity for predation since the predators were hungry and the prey had no cover. Absence of predation in the laboratory, therefore implies absence in the more complex field situation whereas the demonstration of predation only suggests its possibility in the field. Young snails appear to be particularly sensitive to both adult and larval leech predation and P.contortus seems most attractive. The correlation between leech and snail phenologies (see A above) is therefore advantageous to the predators. Growth of P.contortus beyond the 2mm. size class confers on it a greater degree of immunity to predation. This critical size is reached within the first 28 days of life in the field (see FIG. 29) and may, in conjunction with the exposure of spat on smooth rock surfaces, account for the different rate of mortality before this time (see SECTION 5. 1).

C. A SUMMARY OF THE EFFECTS OF PREDATORS ON THE POPULATION DYNAMICS OF P.CONTORTUS AND A.FLUVIATILIS

Laboratory experiments described in B, and snail survivorship curves presented in FIGS. 49 and 50 strongly suggest the implication

of both larval and adult leeches in snail spat mortality particularly in P.contortus. The fact that peak leech densities and the occurrence of breeding are correlated with peak spat densities is also suggestive. The flatworm, P.nigra only eats dead snails and may possibly make use of the leech feeding remains e.g. snail feet.

The extent to which leeches make use of adult snails in nature is uncertain. Results contained in TABLE 20 demonstrate the feasibility of predation, but also suggest that snails become more immune as their size increases. Furthermore, total leech densities on Ha Mire are relatively low. The effects of other vertebrate predators, trematode parasites and Sciomyzid predators and parasitoids is probably insignificant.

Adult snail mortality is in all certainty brought about by a number of agents, both physical and biological, of which one may be predation by leeches. It has already been suggested that the A.fluviatilis population on Ha Mire may be food limited (see PART III SECTION 5. 2) and evidence will be presented later (see PART VII, SECTION 6) to indicate that this may be involved in adult mortality.

6. GENERAL DISCUSSION AND SUMMARY

Use of the sampling procedure proposed by Calow (1972 - see PUBLICATIONS APPENDIX II) has enabled a quantitative description of the phenologies of two littoral species of snail over a 21 month interval. It has also provided density estimates and life history descriptions of the leech and flatworm populations and these represent one of the first truly quantitative studies of population dynamics in littoral stone-dwelling invertebrates. In most cases, standard error estimates are within 10% of the mean. This level has been accepted as sufficient by most workers (Harcourt, 1969).

Snail life histories are of a typical annual form with no late summer breeding phase. Specific differences in phenological detail may occur from year to year particularly with regard to the initiation of breeding. The most detailed analysis has been carried out on GENERATION 2 for which the most complete information is available.

Inter-habitat comparisons between mature adult densities and the density of resultant spat have suggested density dependent regulation of spat recruitment. This could result either from density dependent regulation of fecundity and/or egg capsule mortality and/or the mortality of spat on hatching. Evidence has been presented to suggest that egg capsule mortality is of an underprompt (lagging) or overprompt (leading) regulatory nature (see FIGS. 40 and 41) and data in TABLE 20 suggest that spat mortality is of a density dependent kind. Leech and flatworm predators have been implicated as instrumental in the latter. Destruction of egg capsules by a common predator is likely though it has not been possible to provide any positive identification.

Although no direct evidence is available, information in the literature suggests that adult fecundity is influenced by various factors (see SECTION 4. 5C), of which the negative effects of high densities and low food supplies would allow density dependent regulation. Furthermore, requirements for specific oviposition sites, which in an absolute sense must be finite and therefore ultimately limiting, provides for the possibility of control via both intra- and interspecific interaction.

Factors affecting adult mortality are uncertain. Predators may be involved though other factors and perhaps food supply limitation in A.fluviatilis are almost certainly instrumental. Survivorship

curve patterns are distinct in both snail species considered and this emphasises their basically different ecologies. P.contortus suffers heavy initial mortality, but thereafter population densities remain relatively constant whereas mortality rate is constant throughout the entire generation in A.fluviatilis.

All adult snails die shortly after breeding. It is suggested that endogenous events associated with breeding render the parental population more susceptible to exogenous perturbation and increases the probability of parental death, (see PUBLICATIONS APPENDIX IV). This is thought to be typical of annual species in general.

Any statement on either total population stability or the critical parts of the life cycle involved in regulation would require more information than is at present available.

PART VI

SOME SNAIL SIZE PARAMETERS AND A CONSIDERATION OF INDIVIDUAL GROWTH

1. INTRODUCTION

Few adequate studies on pulmonate growth rates either in the field (e.g. DeWit, 1955; DeWitt, 1955; Hunter, 1961a and b; Berrie, 1965, 1966) or in the laboratory (e.g. Turner, 1926; Crabb, 1929; Baily, 1931; Imai, 1937) have been reported. Two studies have been involved with growth rates in field populations of A.fluviatilis (i.e. Hunter, 1953; Geldiay, 1956) but none has been concerned with P.contortus. Information is similarly lacking for terrestrial species.

Most of the previously documented growth curves are expressed in terms of linear shell parameters. Such representation can provide a general index of total body growth but is inadequate in any attempt to assess growth in terms of organic biomass. Furthermore, linear changes may not always provide a reliable index of body potential energy or mass increments (Cole and Waugh, 1959; Sitaramaiah, 1966; Hunter et. al., 1968). In an attempt to overcome these difficulties Hunter (1961b) expressed snail size in terms of crudely estimated tissue volumes and Hunter et. al. (1968) advocated the expression of snail growth in terms of total organic carbon estimated by use of a 'wet-oxidation' procedure. The latter technique has been used to advantage by Burky (1971).

In the present work the relationship between snail length and mass, and snail mass and potential energy content are considered in SECTIONS 2 and 3 respectively. The correlations thus obtained have been used to provide growth representations for Ha Mire populations of P.contortus and A.fluviatilis expressed in terms of length, mass and potential energy. These are presented and compared in SECTION 5.

Various environmental factors are known to affect growth in freshwater pulmonates (see review by Wilbur and Owen, 1964). The influence of food and temperature on individual growth of laboratory populations of P.contortus will be considered in SECTION 4. Attention will be focused on the regulatory nature of individual growth.

2. LENGTH-DRY WEIGHT RELATIONSHIP.

2. 1. Introduction

The term, "length-dry weight relationship", as used here, refers to the relationship between snail tissue dry weight and a more easily measured linear shell parameter. The most convenient linear shell parameters were found to be aperture length (AL) and maximum diameter (MD) for A.fluviatilis and P.contortus respectively (terminology after Hunter, 1961b). The major purpose of these investigations was to obtain working equations suitable for subsequent use in length-dry weight conversions, The form of the relationship obtained, however, has some theoretical interest and this will also be discussed.

2. 2. Methods

All estimates were made on samples taken from shores immediately adjacent to Ha Mire. Snails were killed in the field by an instant freezing procedure involving an ice-salt freezing mixture.

After measuring the relevant linear shell parameters (to 0.1mm.) using a dial micrometer, snails were decalcified using 1.0 N HCl and dried to constant weight at 40°C on preweighed coverslips. Periostraca were removed before drying. The small error introduced by the acidic destruction of organic carbon (Richards and Richards, 1965) was ignored, as was the error due to possible loss of volatile organic compounds at the temperature of drying. Ash contents of tissue were estimated separately and will be described in SECTION 3.

The relationship between snail lengths and dry weights was investigated using linear regression analysis. The regressions are based on one major sample taken in February, 1970 and consisting of 60-75 individuals. This is compared, however, with several smaller samples consisting of 15-30 individuals taken at frequent, but irregular times throughout the year. All individuals within each of the smaller samples were of approximately the same length. Size specifications and sampling dates are presented in FIGS. 54 and 55.

Spat were treated separately. Three bulked samples consisting of ca. 200 individuals collected from shores adjacent to Ha Mire were decalcified and dried to constant weight using the above procedures.

Linear size characteristics of individuals within each group were 0.75mm. and 1.00mm. for P.contortus and A.fluviatilis respectively. Groups have, therefore, been considered homogeneous and representative of the spat on hatching.

The relationship between shell length and shell weight has been investigated by reference to a single sample of 50 snails for each species. Snails were killed within the field and lengths were measured as before. After cleaning (by vigorous brushing), shells were separated from snail tissue by picking with a pin. This process was greatly facilitated by the initial freezing. Separated shells were dried to constant weight at 40°C, bulked into a pre-weighed silica crucible and ashed in a muffle furnace at 450°C for 12 hours. Weight loss during muffling was taken to represent loss of shell scleroproteins i.e. periostracum.

2. 3. Results and Discussion

TABLE 22 indicates the initial dry weight of individual spat in both snail species. The spat of P.contortus weigh considerably less than those of A.fluviatilis. This difference presumably results from the longer developmental time and larger yolky stores in the latter species. Larger spat must have greater chances of survival in harsh wave swept environments and the general trend within the freshwater snails seems to have been towards a more extended egg stage, greater provisioning of the egg with albumen and the consequent production of larger emergent spat (see also PART V, SECTION 4. 2A). From this point of view, limpet spat can be considered better adapted to life on the exposed Ha Mire shore, than the spat of P.contortus. This may contribute to the greater initial reductions in spat density in the latter species (cf. FIGS. 46 and 47)

TABLE 22. The Dry Weights of Spat on Hatching

	Dry Wt. (mgm.)	5% Confidence Limits (corrected for small sample nos. N)	N*
P.contortus	0.012	± 0.002	3
A.fluviatilis	0.040	± 0.003	3

* Each sample contains ca. 200 individuals.

When plotted on double logarithmic scales the relationship between snail length (mm.) and dry weight (mgm.) in the Feb. 1970 sample is linear (see FIGS. 52 and 53).

Regression equations are :

	b	a	
for <u>A.fluviatilis</u>	$y = 3.210(\pm 0.210) X$	$- 4.114$	.... 1(6. 2)
	($p < 0.05$ when the null hypothesis is b=0)		
for <u>P.contortus</u>	$y = 1.942(\pm 0.203) X$	$- 2.250$	.... 2(6. 2)
	($p < 0.05$ when null hypothesis is b = 0)		

where y = log (10 x dry weight in mg.) and x = log (10 x length in mm.). Coefficient b in equation 1(6. 2) is not more than 2 standard errors greater than 3.0 so that these two values are not significantly different. Similarly, coefficient b in equation 2(6. 2) is not more than two standard errors greater than 2.0 so that these two values are not significantly different. Using b = 3.0 and b = 2.0 in equations 1(6. 2) and 2(6. 2) respectively and adjusting the a-values accordingly gives :

for <u>A.fluviatilis</u> $y = 3.0x - 3.762$ ..... 3(6. 2)

for <u>P.contortus</u> $y = 2.0x - 2.331$ ..... 4(6. 2)

where y and x are defined above. The theoretical implications of these two formulations will be discussed in SECTION 2. 4.

Lines predicted from equations 3(6. 2) and 4(6. 2) are plotted together with their 5% confidence limits in FIGS. 54 and 55. Also included within these figures are the means and fiducial limits of the smaller seasonal samples. Confidence limits for the point and regression estimates of $y \mid x$ overlap and are, therefore, not significantly different. It will consequently be assumed that the snail length-dry weight relationships are seasonally invariant. This is not absolute proof and is in contrast to the seasonal variations found in the bivalve <u>Scrobicularia plana</u> (Da Costa) by Hughes (1970). Nevertheless, since all point estimates fall close to the regression line, and since the size classes employed approximate to the seasonal mean values (cf. FIGS. 29 and 30) any errors associated with the above assumptions will be small.

The relationship between shell length and dry weight is also linear when plotted on double logarithmic co-ordinates (see FIGS. 56 and 57) and is described by the following equations :

	b	a
for A.fluviatilis	$y = 1.931(\pm 0.33)x - 1.574$	..... 5(6. 2)
	($p < 0.05$ when the null hypothesis is $b=0$)	
for P.contortus	$y = 1.51(\pm 0.30)x - 0.783$	..... 6(6. 2)
	($p < 0.05$ when the null hypothesis is $b=0$)	

where y = log (shell dry weight in mg. x 10) and x = log (shell length in cm. x 10)

The theoretical significance of each b value will be considered in SECTION 2. 4.

The ashing procedure indicated that 4.909% and 5.080% shell dry weight was organic in A.fluviatilis and P.contortus respectively. A working average of 5% will be employed in both species. The organic shell component is probably predominantly protein (cf. SECTION 3). It constitutes the outer periostracum of the shell, but also the inter- and intra-crystalline organic matrix (Saleuddin, 1971). The proportion of combustible organic material contained within the shells of P.contortus and A.fluviatilis reported above falls within the range of the freshwater limpet Ferrissia rivularis (i.e. 2.46 - 7.58% - my calculation from Burky's (1971) data), but is high when compared with the usual value for marine species (i.e. ca. 1.0%; Vinogradov, 1953; Hughes, 1971). Marine molluscs generally have a thicker and heavier shell than freshwater or terrestrial species and this may be a result of the rougher marine conditions, and/or the richer mineral composition of seawater. It should also be noted that both the shell and the total body calcium content may vary in freshwater species both with the calcium concentration of the habitat (Hubendick, 1947) and also haphazardly (Hunter et. al., 1967). The latter workers have attributed these haphazard variations to the occurrence of genetically distinct physiological races.

2. 4. Length-Dry Weight Relationships and some Geometrical Considerations

Equations relating body and shell weight to shell length (i.e. equations 1(6. 2) - 6(6. 2)) are of the general allometric form :

$$w = kl^b \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 7(6.\ 2)$$

where log. k = a (defined above)

This relationship between organismic length and weight is typical

and the coefficient b usually ranges between 2.5 and 3.5 (Winberg, 1971). The coefficients reported for P.contortus and A.fluviatilis above, however, show an atypical range i.e. 1.5 - 3.0 and it is the aim of this section to reconcile these values with snail shell geometry.

The simplest geometrical model accounting for snail shell shape is the equiangular spire. The properties of this figure have been thoroughly discussed by Thompson (1917) and more recently by Raup (1966 and 1967). It essentially comprises a coiled cone and results in the maintenance of continued similarity in shape even though size may increase. Defined formally, an equiangular spire would be formed by a point (P) moving along a uniformly rotating radius vector (r) at an ever increasing velocity. The origin of the radius vector (O) may either be fixed or move in a vertical plane. In the former case a plano-spiral or discoidal shell would result (e.g. Planorbidae, Nautiloids and Ammonites), whereas in the latter case a turbinate spiral would be described (e.g. Lymnaeidae, Physidae). Successive whorls may either intersect (e.g. Nautilus) or may remain distinct and far apart. The most extreme examples of the latter case are the Patelloids (e.g. A.fluviatilis) and the bivalves. The extent to which intersection occurs depends on the apical angle of the original cone (α).

In order to predict a theoretical value for the coefficient b, it is first necessary to investigate how the linear shell parameters measured, are related to the geometry of the spiral shells. This is depicted in FIGS. 58 A - D where the relationship between the estimated linear shell parameters and both whole, and conceptually "unrolled" spires are illustrated. AL of the patelloid type is simply defined as the diameter (d) of the cone base (assuming circular cross-section). MD and SL of the discoidal and turbinate forms respectively are more difficult to conceive but consist of a number of lines (a, b, c, d, etc.) intersecting the uncoiled cone at each θ° rotation (see FIG. 58D). Properties of the equiangular spire demand that distances a, b, c, d, etc. and oa, ob, oc, od, are in geometric progression.

Using dimensions analysis the theoretical value of b in equation 7(6. 2) can be defined for the patelloid, turbinate, and discoidal cases. Reference to FIG. 58 shows that discoidal and turbinate types are essentially analogous and these are treated together. The analyses are carried out in DATA APPENDICES VI, A - B. Analysis

based on the less typical model of an "Archimedes" spire has also been considered. The geometry of this family of spires is defined in DATA APPENDIX VI C.

Equations 3(6. 2) and 5(6. 2) for A.fluviatilis conform to the theoretical predictions contained in DATA APPENDIX VI, A. Equations 4(6. 2) and 6(6. 2) for P.contortus do not correspond to predictions based on the equiangular model given in DATA APPENDIX VI, B, but tend more closely to predictions provided by the "Archimedes" model in DATA APPENDIX VI, C.

FIG. 59 represents a semilog plot of the size of successive radii (r) versus number of turns in the spire (n) for P.contortus. Radii are measured in micrometer units and each point (marked x) represents the mean of 30 measurements, made on snails with the same number of whorls (5) and approximately the same MD, (i.e. 4.0mm.). Also shown in the figure are the cumulative widths (Σ w) of successive whorls measured along the same radius. Points (marked with a solid spot) are the mean of 15 measurements made on shells initially embedded in wax and subsequently bisected through their radii (i.e. from shell centre to aperture). The wax provided support and bi-section was achieved with a sharp scalpel. Measurements are in micrometer units.

In the case of a true equiangular spire :

$$r = \Sigma w \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 8(6.\ 2)$$

FIG. 59 indicates that this is not the case in P.contortus. Furthermore,geometrical properties of the equiangular spire require that

$$\log r(\text{or } \Sigma w) = Kn \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 8(6.\ 2)$$

where K is a constant, so that plotting log r (or Σw) versus n should always give a straight line relationship. Lines A and D in FIG. 58 fitted through the first two data points for r and Σw respectively, represent this prediction and indicate that Σw behaves in the expected way but that log r does not. Curves B and C are constructed on the basis of properties of the "Archimedes" spire (i.e. of arithmetic rather than geometric progression). B begins with whorl 1 as the origin, C with whorl 2. The behaviour of log r clearly follows curve C. Thus, apart from initial shell changes, r increases in an arithmetic fashion. Reasons for change in growth form after the first whorl are probably connected with shifts from embryonic (protoconch) to adult shell morphology.

From these considerations it is possible to postulate that the shell geometry of P.contortus corresponds to a coiled, truncated, ellipsoidal cone in which the cross sectional plan of each whorl tends to an elipse.. The shape of this configuration in coiled and unrolled form is illustrated in FIG. 60 together with an actual cross sectional representation of P.contortus. Both the hypothetical and actual figures (A and B) are extremely similar. Dimensions analysis on the relationship between MD, body and shell weight with respect to the truncated, ellipsoidal cone formulation is presented in DATA APPENDIX VI D. In this case theoretically predicted values for b in equation 7(6. 2),relating to both body and shell weight,conform to actual values obtained in equations 4(6. 2) and 6(6. 2). It should be noted that distinction between the "Archimedes" and truncated ellipsoidal cone cases rests on the value of coefficient b in equation 7(6. 2), when expressing the relationship between shell length and weight. Coefficient b is 1 in the former and 2 in the latter instances. The actual value of b obtained in equation 6(6. 2) is not significantly different from either of these values. Evidence presented in FIG. 59, however, supports the truncated, ellipsoidal cone interpretation. The theoretical analysis provides confidence in the obtained empirical relationships and justifies the use of the hypothetical b-values in equations 3(6. 2) and 4(6. 2). It also underlines the utility of a consideration of length-dry weight and subsequent regression analysis on logarithmically transformed data in defining and investigating shell geometry.

For the sake of completion length-dry weight relationships have also been considered with respect to the turbinate case using L. stagnalis. Specimens were collected from Malham and techniques used were the same as those described in SECTION 2. 2 above. Thirty five individuals were used and the equations obtained were :

	b	a
for the soft body tissue	$y = 3.035(\pm 0.131)x - 10.182$	...9(6. 2)
for the shell	$y = 2.847(\pm 0.143)x - 7.536$	...10(6. 2)

Both regression coefficients are significantly different from zero ($p < 0.05$), but not significantly different from 3.00 ($p > 0.05$). The former coefficient is expected but the latter diverges from the theoretical prediction (i.e. 2.00) probably because shell thickness cannot be assumed as uniform. This assumption becomes more tentative

as shell thickness increases, and data from Thompson (1917) and Franz (1971) suggest coefficients in the order of 3.0 for thick shelled Clausilia spp. and Urosalpinx cineria respectively. When compared with the latter species, shells of A.fluviatilis and P.contortus are thin.

TABLE 23 shows the values of coefficient b obtained by other workers for various aquatic and terrestrial mollusca. Both dry weight and wet weight estimates have been included since although the emphasis in the present work has been on dry weight, the results obtained from the dimensions analysis in DATA APPENDICES VI A - D, should apply equally well to all forms of mass estimation. As well as discoidal, turbinate, and patelloid forms, bivalve types are also included. Here the dimensions analysis on the patelloid case is applicable. The extent to which the variation in coefficients contained within TABLE 23 is significant is difficult to assess in the absence of error estimates. Consequently values above 2.5 have been taken as corresponding to the equiangular spire model, and are marked with a single asterisk, whereas values below 2.5 have been taken as corresponding to the ellipsoidal, truncated cone model and are marked with a double asterisk. It may be significant that the species listed in the latter category have laterally compressed whorls, as in P.contortus and it is tempting to suggest that this characteristic and perhaps also dorso-ventral constriction (e.g. P.crista and P.vortex (L.)) may generally result in conformity with the ellipsoidal , truncated cone model. This model may, therefore, have more general applications. Most species considered in TABLE 23 show characteristics typical of the equiangular spire model. The value reported for Tegula funebralis is difficult to reconcile with any of the models so far proposed.

From the above it is clear that the models based on geometrical reasoning contain a number of assumptions (postulates) regarding shell shape which can be put to empirical test using the double logarithmic regression of length versus weight. From this point of view polynomial curve fitting techniques (e.g. Eckbald, 1970) are less instructive.

TABLE 23. A review of allometric coefficients (b) relating shell length to body weight in various species of molluscs

Shell Form	Species	b	Dry(D) or Wet(W) wt.	Fresh-water F Marine M Terrest-rial T	Source
Discoidal	* Vitrea contracta	2.41	W	T	Mason(1970)
	(Westerlund)	3.05	D	"	"
	* Retinella pura	2.54	W	"	"
	(Alder)	2.68	D	"	"
	* Oxychilus cellarius	2.82	W	"	"
	(M.)	2.88	D	"	"
	* Oxychilus allarius	2.92	W	"	"
	(Miller)	2.82	D	"	"
	* Discus rotundatus	2.78	W	"	"
	(M.)	2.66	D	"	"
	* Vitrina pellucida	2.45	W	"	"
	(M.)	2.58	D	"	"
	* Hygromia striolata	2.80	W	"	"
	(Pfeiffer)	3.63	D	"	"
Turbinate	* Physa hawnii (Lea)	2.50	D	F	Daniels & Armitage (1969)
	* Viviparus malleatus (Reeve)	2.50	D	F	Stanczy-kowska et. al. (1971)
	* Carychium tridentatum	2.62	W	T	Mason(1970)
	(Risso)	2.63	D	"	"
	* Acanthinula aculeata	3.02	W	"	"
	(M.)	3.24	D	"	"
	** Cochlicopa lubrica	2.11	W	"	"
	(M.)	2.05	D	"	"
	** Ena obscura	1.63	W	"	"
	(M.)	1.59	D	"	"
	** Marpessa laminata	2.42	W	"	"
	(Montague)	2.41	D	"	"
	** Clausilia bidentata	2.68	W	"	"
	(Ström)	2.37	D	"	"

TABLE 23 - Continued.

Shell Form	Species	b	Dry(D) or Wet(W) wt.	Fresh-water F Marine M Terrest-rial T	Source
Turbinate	**Euconulus bidentata (M.)	2.68	W	T	Mason(1970)
		2.37	D	"	"
	Tegula funebralis (Adams)	3.70	D	M	Paine(1971)
	*Nucella lapillus(L.)	3.072	D	M	Hughes(1972)
Patelloid	*Ferrissia rivularis (Say)	2.79-2.68	W	F	Burky(1971)
	*Fissurella barbadensis(Gmelin)	3.2756	D	M	Hughes(1971)
Bivalve	*Modiolus demissus (Dillwyn)	ca.3.0	D	M	Keunzler (1961)
	* Anodonta anatina(L.)	"	D	F	Gavrilov & Arabina(1967)
	* Sphaerium corneum (L.)	"	D	F	"
	* Scrobicularia plana (da Costa)	"	D	M	Hughes(1971)

* General conformity to equiangular spire model.

** Possible conformity to ellipsoidal, truncated cone model.

3. CALORIFIC VALUES OF SNAIL TISSUES

3. 1. Methods

Calorific values of snail tissues were determined using a version of the Phillipson, oxygen micro-bomb calorimeter (Phillipson, 1964). Pre-treatment of tissues was carried out as follows :

A. SNAIL FLESH : tissue samples were prepared, after the removal of the shell (technique as in SECTION 2. 2.), by homogenising 100-200 individuals and making 3 pellets from the resultant homogenate. These were subsequently dried to constant weight at 40 C. Samples were betwwen 15-30mg. dry weight. The remainder of the homogenate was used, after drying in a silica crucible to constant weight, for independent ash determinations.

B. PERIOSTRACUM : this material was separated from the inorganic shell matrix by acidic decalcification (see SECTION 2. 2). The resultant organic residue was made into a pellet and dried (as in A above) after thorough washing in distilled water. The ash content of calcified periostraca was negligible and has been ignored.

C. REPRODUCTIVE PRODUCTS : egg capsules were obtained in the laboratory. Mature, adult snails obtained from shores adjacent to Ha Mire were brought into the laboratory and placed in aerated tapwater (10 snails/ litre) contained in smooth walled beakers, at 18°C under a natural illumination regimen. Only capsules laid in the first 24h. were used, and each was collected within 12h. of laying. Removal of capsules from the beaker walls was achieved using a sharp scalpel. Whole capsules and their external membranes were determined separately. Separation of the membrane fractions was carried out by perforating the capsule walls with a fine needle and squeezing out the contents. Approximately 250-350 capsules were treated in this way to provide a single sample of ca. 10mg. dry weight and ca. 200 whole capsules were used to produce a single sample of 12-24mg. dry weight. Samples were dried as above in A.

Unless otherwise stated, all snails were obtained from shores adjacent to Ha Mire, at monthly intervals between September, 1970 and August, 1971. Samples were taken within three days of the first day of each calender month. In those months, when individuals of two generations, i.e. adults and emergent spat were sometimes present,

separate samples were taken from each. Spat were treated separately and were collected from both field and laboratory sources.

The methods of calorimetry employed were as specified by Phillipson (1964) with the application of standard corrections for burning of the platinum wire and acid production (Paine, 1964). No correction for endothermy (Paine, 1964, 1966) was used because of the relatively low ash contents of snail, shell-free tissues.

Except in the case of egg capsule estimates,where insufficient material was available, independent estimates were made on ash contents. Samples were ashed in a muffle furnace for 12h. at 400°C.

3. 2. Results and Discussion

TABLE 24 shows the calorific densities (K.cal./g./ash-free dry weight) and tissue ash contents for the snails at various times of the year. The ash contents of adults vary haphazardly from month to month but show similar averages (worked out after arcsine transformation by $p = (\sin \theta)^2$, see PART IV, SECTION 4. 1) of 10.17% and 10.07% in P.contortus and A.fluviatilis respectively. A common working average of 10% will be used in future calculations. This value is slightly below the range (11-30%) quoted by Birger (1961; cited in Winberg, 1971, p.15) for other species of freshwater mollusc. It should be noted, however, that the ash content of a species may vary considerably and apparently depends on both physiological state and ecological conditions (Hunter et. al., 1970). Spat ash contents are approximately twice those of the adults (ca. 20%). I have found a similar rise in spat ash contents of L.stagnalis, and a working average of 20% will be used in future calculations for P.contortus and A.fluviatilis. The reason for this higher spat value is inclear but may result from the retention of embryonic calcium stores in young snails.

The calorific densities together with their fiducial limits (i.e. t. $s/\sqrt{n}$ where t = 4.303 for n-1 (2) degrees of freedom at the 95% level) also show slight and somewhat haphazard variations from month to month. Monthly calorific values are plotted in FIG. 61 A and B for P.contortus and A.fluviatilis respectively, where it can be seen that although there is a lack of significance between means, there is nevertheless some indication of a slight rise in calorific densities during the breeding season. This trend is most

TABLE 24. The caloric densities and tissue ash contents of snails at different times of the year.

P.contortus	Caloric Density (k.cal./g. ash-free dry weight) ±	Ash (%)
Adult		
Sept. '70	5.676 (0.151)	8.95
Oct. '70	5.736 (0.154)	9.70
Nov. '70	5.640 (0.153)	10.13
Dec. '70	5.648 (0.127)	10.18
Jan. '71	5.616 (0.143)	10.30
Feb. '71	5.500 (0.151)	10.50
Mar, '71	5.478 (0.181)	11.10
Apr. '71	5.590 (0.286)	9.95
May '71	5.885 (0.156)	11.01
June '71	5.740 (0.181)	9.84 *
July '71	5.550 (0.135)	9.91
Aug. '71 (old gen.)	5.543 (0.381)	10.03
Aug. '71 (new gen. >1.0mm. length)	5.674 (0.082)	19.95
Spat		
Field J-A	5.510 (0.061)	20.21
Mean % ash for adults		10.17 ± 0.11
A.fluviatilis		
Sept. '70	5.670 (0.080)	9.01
Oct. '70	5.660 (0.060)	9.93
Nov. '70	5.630 (0.080)	9.98
Dec. '70	5.652 (0.043)	10.36
Jan. '71	5.332 (0.200)	10.21
Feb. '71	5.500 (0.100)	10.11
Mar. '71	5.400 (0.107)	11.03
Apr. '71	5.720 (0.221)	9.98
May '71	6.290 (0.132)	10.91
June '71	6.271 (0.141)	10.01 *
July '71	5.716 (0.142)	9.47
Aug. '71 (old gen.)	5.677 (0.436)	10.09
Aug. '71 (new gen. 1.0mm. length)	5.635 (0.110)	19.01

TABLE 24. Continued.

A.fluviatilis	Caloric Density (k.cal./g. ash-free dry weight)	Ash (%)
Spat		
Field J-A	5.490 (± 0.083)	21.36
Mean % ash for adults		10.07 ± 0.42

* Breeding adults

Working mean % ash for adults = 10%

marked in A.fluviatilis although the calorific equivalents obtained for both species during the oviposition period do not differ significantly from the mean values obtained in the immediately adjacent months (see FIG. 61 for significance tests). Since lipid containing albumen is produced during breeding for egg stocking, particularly in A.fluviatilis (see PART V, SECTION 4) the above differences are probably real and the lack of significance may be a function of small sample numbers. In consequence, the average calorific density for non-breeding spat and adults has been calculated separately. These values are contained within TABLE 25 where S.I. (Joule) equivalents are included in parentheses.

The average values quoted for the adults are similar to the average value for gastropod species in general of 5.675 K.cal./g./ash-free dry weight given by Cummins and Wuychek (1971). The average calorific density for all animal species i.e. 5.70 K.cal./g./ash-free dry weight (Paine, 1964) is slightly greater than that for the non-breeding snails given here, but slightly less than breeding individuals. This reflects the lack of emphasis on lipid metabolism in freshwater snails except during breeding. The predominant storage product in these animals is glycogen (Goddard and Martin, 1966).

Mean calorific densities for the periostraca of both species are presented in TABLE 25. These are extremely similar and approximate to 5.0 K.cal./g./ash-free dry weight which will be used as a working average for future calculations. Hughes (1970) has reported a value of 5.037 K.cal./g./ash-free dry weight for the periostracum of S. plana . These relatively low values are in agreement with the fact that the organic matrix of the mollusc shell is not pure protein (when the calorific equivalent would be 5.7 K.cal./g./ash-free dry weight) but also consists of carbohydrate fractions (Grégoire et. al., 1955; cf. Hunter et. al. (1967) and Burky (1971) who suggest that conchiolin is pure protein).

As mentioned in SECTION 3. 1, the calorific densities of reproducta are based on one sample only. The results are contained in TABLE 25, where calorific equivalents are partitioned between whole egg capsules, external membranes and capsule contents. The latter were determined by difference and the methods of calculation are presented in DATA APPENDIX VII together with ash-free dry weight estimates. The significance of these results has already been discussed (see PART V, SECTION 4). It should be noted that the calorific density recorded

TABLE 25. The mean caloric densities of snail tissues in k.cal./g. ash-free dry weight. S.I. equivalents are given in parentheses.

	P.contortus	A.fluviatilis
	k.cal./g.ash-free dry weight	k.cal./g.ash-free dry weight
Non-breeding adults and spat	5.591 ± 0.050 (23.40k.J)	5.584 ± 0.076 (23.38k.J.)
Breeding adults	5.815 (24.342k.J)	6.280 (26.96k.J)
Periostracum	5.004 ± 0.216 (20.95k.J.)	5.010 ± 0.187 (20.97k.J.)
Working average for periostracum		5.000 (20.93k.J.)
Reproductive Products		
Egg	5.455 (22.84k.J.)	6.630 (27.75k.J.)
Egg capsule membrane	4.480 (18.75k.J.)	4.571(19.13k.J.)
Capsule (egg + membrane)	4.571 (19.13k.J.)	5.917 (24.77k.J.)

for snail eggs probably represents an underestimate, because the difference technique employed does not distinguish between eggs and the surrounding gelatinous matrix. The latter probably has a relatively low calorific value.

4. LABORATORY INVESTIGATIONS ON GROWTH IN P.CONTORTUS

Laboratory investigations have been carried out on the effects of temperature and food, on growth in P.contortus. Similar experiments have not been repeated on A.fluviatilis because of difficulties experienced in conveniently simulating optimum laboratory conditions for growth in this species. Attention will be focused on the regulatory nature of individual growth and its implications. It is considered that temperature and food supply variations may form the dominant natural perturbations which snails receive.

4. 1. Methods

A. CULTURE CONDITIONS

All animals used in the following experiments were derived from a laboratory culture, started in June, 1970 from eggs collected in the field. The culture was maintained at 18°C under a natural illumination regimen in a 10 gallon polythene tank containing aerated tapwater. Food was supplied as cooked, rotting lettuce and both the food and water were replenished weekly. Under these conditions the snails grew rapidly and bred continuously throughout the year. Glass plates were arranged within the culture tank so that eggs could be removed at will, when animals were required for experimentation. On removal,these plates were transferred to a 5l. beaker containing aerated tapwater but no food. The first spat to emerge were removed, randomly sorted and transferred to the given experimental regimen.

B. REGIMEN FOR INVESTIGATION OF THE EFFECT OF TEMPERATURE

Snails collected in the above way were transferred in groups of 5 to 2l. pyrex beakers containing aerated tapwater and a 36cm.^{2} portion of cooked, rotting lettuce as food supply. It should be noted that although lettuce was used as the food supply, P.contortus is essentially a bacterial feeder (PART VII, SECTION 4). The lettuce merely provided a convenient substratum for bacterial growth, and after lettuce had remained within the beakers for a few days a white,translucent slime developed on the beaker walls. Snails preferred this region for grazing and snail trails, representing grazing paths, were clearly visible through the slime. Furthermore, snails would not grow on fresh, uncooked lettuce. For this reason beakers

with lettuce were allowed to condition for a few days before allowing access to snails.

Three such beakers containing a total of 15 individuals were maintained at either 4, 10 or 18°C under 12L, 12D lighting conditions. Water and lettuce were changed every 2 days when care was taken not to remove the bacterial film. Snail diameters were measured weekly using a dial micrometer attached to a binocular microscope. Live snails were measured on damp filter paper.

These experiments were repeated on two occasions i.e. August, 1970 and January, 1971 to test for endogenous seasonal differences in growth patterns. The latter group was also used to investigate the effects of temperature change on growth patterns.

C. REGIMEN FOR INVESTIGATION OF THE EFFECT OF FOOD

Several pulse-feeding experiments were performed to determine the short- and long-term effects of discontinuous food availability on growth, as a test of the snails' ability to regulate their growth and "remember" their past nutritional history. Feeding pulses were administered for 24h. once every 2, 3, 4, 6, or 8 days. During starvation intervals snails were kept in groups of 5 in 21. beakers without lettuce. In this situation water was changed daily and beakers were scrubbed. On the day of feeding individuals were transferred to 21. beakers with lettuce which had previously been conditioning for 3 days. All experiments were replicated 3 times and carried out at 10°C under the usual light regimen. A control group in which snails were fed continuously was also used. Pulse feeding was continued over a 28 day interval following which one experimental group of each of the replicates was transferred to a continuous feeding regimen and growth was observed over a further 2 week interval.

4. 2. Laboratory Growth Curves and the Effect of Temperature

Results from the laboratory growth experiments carried out at various temperatures and expressed in terms of MD (mm.) are presented in FIG. 62. Confidence limits represent $t\,(s/\sqrt{n})$ (when $n = 15$, $t = 2.145$ for $p = 0.05$ with 14 df.). Results from the August experiments are represented as solid triangles whereas results from January cohorts are represented as solid squares. Temperature manipulations

are represented by arrows which indicate the direction and extent of the controlled change. These apply to the January group only. Size changes after manipulation are indicated by broken lines. All curves are fitted by eye.

The growth curves depicted are equivalent to the "mass curves" of Medawar (1945), in which each point represents the mean size of a cohort of 15 individuals. The representation of individual growth patterns in terms of the "mass curves", is open to criticism (Medawar, Ibid.) but they are indispensable when the size of individuals being considered is small and when they are difficult to mark, and/or keep in isolation. Furthermore, these curves probably represent the general pattern of growth in "standard" individuals.

The patterns of growth shown in FIG. 62 are sigmoid at all temperatures. This is typical for freshwater gastropods in general (Crabb, 1929: Baily, 1931; Sitaramaiah, 1966) and Bertalanffy (1949, 1951) arguing on metabolic grounds has suggested that this results from snail respiratory rate being intermediate between surface and weight proportionally. The 3 basic temperature curves given in FIG. 62, and marked 4 - 10 and 18°C are replotted on semilogarithmic co-ordinates in FIG. 63. At all temperatures there is an initial exponential "self accelerating" phase of growth and a later "self-inhibiting" phase which progresses to a steady state plateau (terminology after Brody, 1945). The coefficient of exponential growth (k) defined as :

in differential form

$$\frac{dl}{dt} = kl \qquad \text{.....} \quad 1(6.4)$$

in integral form

$$l = Ae^{kt} \qquad \text{.....} \quad 2(6.4)$$

where

l = length, MD (mm.)

A = integration constant

e = base of natural logarithms

t = time (weeks)

and the steady state plateau (l_∞) are temperature sensitive parameters. Values of k (derived from FIG. 63 by eye and converted to natural logs by dividing by 2.303), and crude estimates of l_∞ (see FIG. 63) are contained together with their Q10 values in TABLE 26. In the experimental temperature range considered Q10 values indicate that the coefficient k is highly sensitive to temperature change and shows

under-compensation (Precht, 1958) whereas the final size achieved is less sensitive to temperature change and, at least in the higher range shows partial-compensation (Precht, Ibid.). The evidence presented does not support the view held by Bertalanffy (1949) that whilst growth curves are steeper at higher temperatures, a larger final size is reached at lower temperatures. Differences in l_∞ however, are less than similar differences in k at the temperature considered. Partial compensation in the final size reached between 10 and 18°C indicates that P.contortus is better adapted to life at this temperature (see also PART VIII SECTION 2. 2).

TABLE 26. Estimates of k and l_∞ for P.contortus at Various Experimental Temperatures, Together with Their Q 10 Values.

Temperature (°C)	k	Q_{10}	l_∞ (mm.)	Q_{10}
4	0.158		1.7	
		3.310		2.042
10	0.328		2.6	
		3.467		1.778
18	0.891		4.1	

Returning to FIG. 62, comparison between growth rate of snails in August and January indicates no significant difference in pattern. Individuals extracted from the field in winter and cultured on rotting lettuce at 18°C also begin to grow immediately and may lay eggs (see PART V, SECTION 4. 3B). This evidence suggests that cessation of growth in winter in natural populations is environmentally and not endogenously induced.

Experiments on growth rates after a temperature switch (see FIG. 62) indicate that following a short period of compensation snails grow at a rate which is completely characteristic of the new temperature, and also at a rate characteristic of their size rather than their age at switching. Thus groups switched from a lower to higher temperature continue to grow at a rate characteristic of snails kept at the higher temperature which, although younger, were of the same size. Only one experiment was concerned with a switch from high to low temperature (i.e. 18 to 10°C. See FIG. 62). Here the size of experimental individuals was greater than l_∞ at 10°C and growth ceased immediately on switching. Similar results have been obtained by Osbourne and Mendel (1914, 1915) for the albino rat, and are implicit to the view that growth is dependent on physiological time, which may be delayed or accelerated by external conditions,

rather than on physical time which is invariant (Brody, 1945). On these grounds the latter author has criticised growth equations which represent growth as explicit functions of time.

4. 3. The Effect of Food Supply on Growth

FIG. 64 shows the results of the pulse feeding experiments. The coefficient k (of exponential growth in energy) at 10°C is plotted against the fractional amount of time (in days) that snails were exposed to food. A calorific expression of growth was obtained from the linear (MD) measurements using equation 4(6. 2), and the average calorific equivalent given in TABLE 25. Growth rate coefficients were determined separately for each experimental group (5 snails) under each feeding regimen, and points on FIG. 64 represent the average of these values. Confidence limits are t $s/\sqrt{n}$ (where t = 4.304 for n-1 (i.e.2) df. at the 95% confidence level).

The broken line in FIG. 64 represents growth rate coefficients to be expected if the snails grow at a rate simply proportional to the fraction of time they were exposed to food. This relationship would result if calorific growth were simply the passive outcome of differences between anabolism and catabolism. Values of k actually determined are in all cases significantly greater than this prediction and lie on a straight line (fitted by eye) which progressively diverges from the simple reductionist model of metabolism. This represents a partially successful attempt being made by the snails to regulate their growth rates to some (presumably genetically fixed) "desired" level (i.e. that growth rate level which is manifest under optimum feeding conditions and represented by the dotted line in FIG. 64). Inverted commas are used in the previous sentence to prevent teleological misinterpretation. It is assumed, for the present purposes, that a continuous feeding regimen under the experimental conditions specified in SECTION 4. 1C, represents optimal conditions for growth in P.contortus.

Hubbell (1969, 1971) has obtained similar results in the terrestrial isopod, Armadillidium vulgare (Latreille) and on this basis has challenged the usually employed mechano-reductionist models of individual growth e.g. the energy budget equation and its derivative the von Bertalanffy growth equation (Pütter, 1920; Bertalanffy, 1949) on the grounds that they fail to account for the emergent property

of control in complex organismic systems. This postulate contributes to the more general paradigmatic scheme of Systems Theory (see Koestler and Smythies, 1969).

As a contribution to a more realistic representation of individual growth Hubbell (Ibid.) has proposed a cybernetic model. This is described more fully, and elaborated in PUBLICATIONS APPENDIX IV. A version of this model is presented in FIG. 65 where both the systems variables and parameters are expressed in the complex frequency (S) domain. The transfer function of the model is :

$$H(s) = \frac{AG(s)}{DG(s)} = \frac{KAE+KRE}{s + (KAE+KRE+KRP-KAP)} \quad \ldots\ldots\ldots 3(6.4)$$

so that the system is first order with its eigen value located at :

$$s = KAP-KAE-KRE-KRP \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 4(6.4)$$

The sum of KAE, KRE, and KRP must be greater than KAP for the system to be stable.

Clearly the model consists of two loops i.e. a basic metabolic and a control loop (my terminology). The basic metabolic loop represents metabolism under optimum conditions when there are no environmental disturbance inputs ($D(s) = 0$). Under the more usual conditions of disturbance ($D(s) > 0$), actual growth rate ($AG(s)$) diverges from the desired level ($DG(s)$) and the control loop becomes operational. A central feature of the control loop is the desired growth rate generating subsystem (KDG) which represents an endogenous signal generating device. The magnitude of $DG(s)$-signals produced depends on current size ($AG(s)/s$). This follows from the fact that growth is a size rather than age dependent process (see SECTION 4. 2). The need for correction ($E(s)$) during disturbance is expressed by the difference $DG(s) - AG(s)$, and the correction constant ($KAE+KRE/s = k_{corr}$) expresses the extent to which $E(s)$ is allowed to feedback positively on basic metabolism. The latter is an expression of the systems control limitations and may take values between 1 (in perfect control) and 0 (in no control). Usually its value will lie between these two extremes. Inclusion of an integrator ($1/s$) in the correction constant is commonly used by control engineers to increase the efficiency of feedback (Bayliss, 1966) and in biological terms it can be considered as a memory of past metabolic events (Hubbell, 1969, and 1971). More will be said about this feature below.

The numerical magnitude of the correction constant has not hitherto been evaluated although data contained in FIG. 64 provide the facilities for this calculation under conditions of food supply perturbation. Thus differences between the mean values of k expressed by lines representing zero and perfect control provides a crude estimate of, "the need for control" under various conditions of temporal food availability and differences between mean values of k expressed by the line summarising the observed values and the line representing zero control represents the extent to which control has been effected. FIG. 66 A and B illustrates the relationship between these parameters for P.contortus and A.vulgare respectively. The latter data were obtained from Hubbell's (1969) FIG. 11. k_{corr} is given by the slope of the straight line relationships in FIG. 66 and is 0.404 for the snail and 0.306 for the isopod. It should be noted that these plots do not allow k_{corr} to be partitioned into its subcomponents.

Quite apart from the utility of k_{corr} in the systems model. it has intrinsic interest as an index of an individual's capacity to regulate its metabolic behaviour in the face of environmental perturbation, and could be useful in assessing the criterion of success in competitive interactions. Thus, in the examples given in FIG. 66 the values of k_{corr} suggest that P.contortus can regulate its growth rate, during food supply perturbation, more effectively than A.vulgare and is consequently better adapted to life under conditions of food shortage. Values of k_{corr} may also be expected to rise with level of organisation, perhaps becoming maximal in homeotherms. Information on this parameter will obviously be instructive and more work is required to determine the possible variations in its magnitude with age, species, and quability of disturbance.

As already noted the inclusion of an integrator (1/s) in the correction constant suggests that an animal has a complete memory of its nutritional history over its entire life. Although the presence of a metabolic memory has been demonstrated (Brody, 1945) it is not likely to be indefinite (Hubbell, 1969, 1971).

Evidence presented in FIG. 64 suggests that on a short term basis snails are able to "remember" their nutritional history and attempt to compensate for it. After 28 days of pulse feeding, representatives of all experimental cohorts were transferred to a continuous food regimen (see SECTION 4. 1C). The initial growth rates (i.e. over the first week) in all cohorts after transference were

greater than that in the continuously fed group (see FIG. 67A). Initial growth rates in groups fed every sixth and eighth days were similar and there was no difference in growth rates of any experimental group over the second week after transference (see FIG. 67B). This suggests that after about 7 days of starvation, further starvation cannot significantly increase the snails' compensatory efforts. Excessive starvation would result in system degeneration when all regulatory abilities would be lost. This did not occur in the range of perturbations applied here. Hubbell (Ibid.) has obtained similar results in woodlice although their memory seems to be shorter than snails (i.e. 3-4 days). Accordingly he has modified his simple model by decreasing the integrated growth rate error, at a rate which is proportional to its own size.

4. 4. General Discussion and Summary

Growth in P.contortus is highly temperature dependent, although the size ultimately reached is less dependent on temperature than the rate at which it is approached. Partial compensation of the latter characteristic at higher temperature (10-18°C) suggests that P.contortus is better adapted to life at these temperatures, and evidence presented later supports this.

In contrast, snails are able to exert limited regulation over their metabolic processes in the face of food supply perturbation. This has been demonstrated elsewhere by Hubbell (1969, 1971) for another poikilotherm and seems to be the general rule in homeotherms (Kavanau, 1961; DeRuiter, 1963; Mayer and Thomas, 1967). Indeed, control over this fundamental property of living systems is to be expected particularly since growth represents the operation of a negentropic process within an essentially entropic universe.

Mechanisms underlying the regulatory process will be discussed in PART X, together with the implications of regulation for ecological energetics studies.

5. FIELD INVESTIGATIONS ON GROWTH IN A.FLUVIATILIS AND P.CONTORTUS

5. 1. Methods

Growth curves in terms of MD and AL for the individuals in populations of A.fluviatilis and P.contortus on Ha Mire have been constructed from the data on size frequency distributions given in FIGS. 29 and 30. Only members of GENERATION 2 were considered. The linear size of spat on hatching was taken as 0.98 mm. (AL) in A. fluviatilis and 0.68mm. (MD) in P.contortus so that the production of dwarfed individuals has been ignored (see PART V, SECTION 4. 7A). Starting dates for each species cohort are as given in PART V, SECTION 5.

In adults, transformation to tissue dry weight was effected using equations 3(6. 2) and 4(6. 2), whereas weights of spat were taken from TABLE 22. Shell weights have been ignored in all expressions. The proportion of ash per dry weight was assumed to be 10 and 20% for adults and spat respectively, and calorific transformation was carried out with respect to coefficients contained in TABLE 25.

A comparison of the size of adults at breeding in various local populations of P.contortus and A.fluviatilis has also been considered. The habitats involved are listed in TABLE 27. Samples consisting of 50 individuals were collected haphazardly from each site in May, 1971. All measurements were made using the same methods described in PART V, SECTION 2. 1 and sizes have been expressed in terms of shell length.

5. 2. A Comparison of Growth Curves, Expressed in Terms of Length, Mass and Energy, for Individuals in Ha Mire Populations

The growth curves of A.fluviatilis and P.contortus in GENERATION 2 are contained in FIGS. 68 and 69 respectively. Information is expressed in terms of length (A), mg. ash-free dry weight (B) and calories (C). It has been assumed for purposes of simplification that variations in MD between N11 and M18 in P.contortus, and of AL between D12 and F14 in A.fluviatilis are not significant and the mean level of these parameters for both the stationary periods have been used as operator of the length dry weight conversion equations.

The patterns shown by each differently expressed growth curve

are essentially similar, except that variations present in the mass and energy curves are more violent. Both species grow rapidly after emergence; P.contortus more rapidly than A.fluviatilis.As time proceeds the growth rate reduces and growth becomes stationary during winter months. This stationary phase is maintained up to oviposition in P.contortus when growth resumes, whereas growth resumes earlier in A.fluviatilis. It has already been suggested that P.contortus is less well adapted to low temperature conditions, SECTION 4. 4. Evidence will be presented later to suggest that on the contrary A.fluviatilis is better adapted to low temperatures. The net effect of winter growth cessation is a double-sigmoid growth curve. This phenomenon is typical of the freshwater Gastropoda, see PART V, SECTION 3. Mass and energy curves for the limpet also suggest a surge in growth during reproduction. This is not just a result of the accumulation of reproducta because there is no concomitant fall in size after deposition of eggs. In these cases curves are triple sigmoid. Absence of weight (energy) losses after reproduction suggest that most of the energy incorporated within the reproducta is derived from energy assimilated, not from endogenous stores. Hunter (1970) has reported that in several snail species 87% of the non-respired-assimilation is directed to egg output.

Length curves for A.fluviatilis are similar to those described elsewhere (hunter, 1953a; Geldiay, 1956). Summer growth rates of spat (0.27mm./10 days) are equivalent to those reported by Hunter (Ibid.) of 0.22mm./day for limpets in Craigton Burn. Post-winter rates, however, of 0.14mm./day are far lower than Hunter's value (0.22mm./day) and in consequence the size of adults at breeding are smaller on Ha Mire (ca. 5.0mm.) than in Craigton Burn (ca. 8.0mm.). Indeed the former is the smallest size for breeding limpets recorded in Britain (Hunter, 1961b, p.631; Geldiay, 1956, Fig. 2). More will be said about these differences in SECTION 5. 3.

There are no comparative data for P.contortus. The length curve for P.albus in Loch Lomond (Hunter, 1961b) is extremely similar, however, and shows the same extended winter growth cessation pattern.

5. 3. A Comparison of Snail Sizes in Different Habitats

TABLE 27 presents the mean sizes of both A.fluviatilis and P.contortus in various local populations, estimated from samples

TABLE 27. The mean size of A.fluviatilis and P.contortus in various local habitats in May, 1971.

Habitat	A.fluviatilis	P.contortus
Highland		
1. Station 1$_a$	6.085(±0.202)	2.631(±0.118)
2. Station 2$_a$	6.160(±0.200)	2.632(±0.106)
3. Ha Mire	4.853(±0.208)	2.663(±0.096)
4. Malham Water$_b$	4.846(±0.201)	-
Lowland		
5. R. Wharfe (Pool)$_c$	6.716(±0.305)	-

a -defined in FIG. 9

b -situation shown in FIG. 3

c -defined in FIG. 1

taken in May 1971. Most habitats are from the Malham area and within the 400m. contour. A single sample was taken from a lowland site (i.e. the R. Wharfe at Pool) which is below the 400m. contour. Data for each population are not strictly comparable in the sense that the physiological age of individuals present may vary e.g. the lowland population breeds approximately one month earlier than the highland equivalents. Nevertheless, the figures given do provide a rough basis for comparison.

The sizes of A.fluviatilis are significantly greater on north and west shore populations than Ha Mire ($d_{1,3}$ = 3.09; p = 0.002; $d_{2,3}$ = 3.28, p = 0.001; subscripts denote order presented in TABLE 27). These differences within the Tarn occur in the face of relatively constant conditions of temperature but may be explained in terms of food supply. Thus epilithic algal production (the food source of A. fluviatilis) is greater on northerly shores than on Ha Mire (see PART VII SECTION 6) and larger snails occur in the former positions. In contrast,the sizes of P.contortus throughout all the stations considered are extremely similar. The food (bacterial) production of this species is also more constant in different parts of the Tarn. These conclusions conform to the hypothesis proposed by Hunter (1961 a and b) that the size of snails at breeding may represent a good index of the food production in the previous year.

Sizes of limpets on Ha Mire are not significantly different from snails in Malham Water ($d_{3,4}$ = 0.02, p >0.01) but are significantly different from snails in the River Wharfe at Pool ($d_{3,5}$ = 3.72, p <0.001). Small size characteristics of the Malham Water population is also probably a function of poor food supply, because the contained stones possess a poor algal cover and are usually silted over. Better growth in the lowland populations may be a result of higher mean temperatures experienced in this situation, and/or greater algal production.

It is worth noting at this point that no evidence for the presence of P.contortus in the River Wharfe was.recorded during the present study. However, its presence was noted by Percival and Whitehead (1930). In 1971 A.fluviatilis was the dominant mollusc present and was relatively abundant (see FIG. 45A). If the competition hypothesis presented in PART V, SECTION 4. 4B is accepted local extinctions of P.contortus in the presence of A.fluviatilis can be expected when conditions generally favour the latter species.

PART VII

THE FOOD REQUIREMENTS OF P.CONTORTUS AND A.FLUVIATILIS WITH SOME NOTES ON OTHER SPECIES

1. INTRODUCTION

Surprisingly little is known about the natural diets of many of the more common species of freshwater snail. The previous work reported is both scattered and superficial (see reviews by Boycott, 1936; Boettger, 1944; Graham, 1955; Gaevskaya, 1966). Information, specifically with regards to A.fluviatilis, is confusing. Thus Hunter (1953a) suggested that this species feeds on epilithic algae. Geldiay (1956) found algal cells in their guts, but Schmid (1932) reported that they feed solely on the freshwater lichen, Verrucaria. No specific information is available for P.contortus, though the Planorbidae in general are supposed to be detrital feeders (Boettger, 1944).

Detailed information on natural diets is necessary for a complete understanding of population function. The following sections are, therefore, concerned with this feature of the ecology of A.fluviatilis and P.contortus. SECTIONS 2-4 deal with the qualitative composition of food input and SECTION 5 with the quantitative aspect. The ecological effects of the reciprocal interaction between food supply and feeder are discussed in SECTION 6 and some notes on species other than P.contortus and A.fluviatilis are included.

2. GENERAL CONSIDERATIONS ON THE NATURAL DIET OF P.CONTORTUS AND A.FLUVIATILIS

2. 1. Field Observations

A. METHODS

Gut contents analyses were carried out on an extract of material from the crop-gizzard region of the snails' guts (see Calow, 1970, PUBLICATIONS APPENDIX 1, for position and reasons for selection). Snail samples were collected from shores adjacent to Ha Mire in September, 1970. 100 individuals of each species were involved. Specimens were fixed immediately on collection in 70% alcohol. The crop-gizzard apparatus was later removed and the contents of all specimens were squeezed out into a single 5ml. sample of water containing 2 drops of Lugol's fixative (Saraceni and Ruggui, 1969). After thorough mixing, one drop of the extract was transferred to a haemocytometer. A single transect was delimited randomly for observation and was scanned under high power (X400). Sixty replicate aliquots were dealt with in this way.

Three food-types were recognised i.e. algae, amorphous detrital material and fungi, and their abundance within each sample was scored on the following basis :

Score	0	: scanning revealed	no	representative	food	type
Score	1	: "	"	very occasional	"	" "
Score	2	: "	"	occasional	"	" "
Score	3	: "	"	frequent	"	" "
Score	4	: "	"	very frequent	"	" "

Since each food-type was ranked independently it is theoretically possible for each to have the same high or low rank. The former would be due to the 3D nature of the sample and the latter to its thin, even dispersion.

B. RESULTS

The frequency of food-type scores in the snail gut extracts, together with the average scores obtained for each group are presented in TABLE 28. These results clearly indicate that P.contortus selectively ingests detrital materials whereas A.fluviatilis takes algae. The low average scores for detritus and fungi in A.fluviatilis and algae and

TABLE 28. The frequency of food-type scores in gut extracts from the crop-gizzard region of A.fluviatilis

Snail Species	Food type \ Score	0	1	2	3	4	Ave. Score
P.contortus							
	Algae	0	45	15	0	0	1.2
	Detritus	0	0	0	4	56	3.9
	Fungi	20	40	0	0	0	0.7
A.fluviatilis							
	Algae	0	0	0	18	42	3.7
	Detritus	11	21	28	0	0	1.3
	Fungi	31	29	0	0	0	0.5

fungi in P.contortus indicate that these were only, "very occasional" components of the diet. It can be reasonably assumed, therefore, that these food-types contribute a small, and possibly accidental, portion of total food ingested.

2. 2. Laboratory Observations

The findings elucidated in SECTION 2. 1 have been investigated further in the laboratory.

A. METHODS

Detritus and algae were collected from the field by scraping the relevant portions of submerged stones (see PART VI, SECTION 6. 1). These samples were centrifuged, resuspended in tapwater, and broken up using an automatic stirrer with magnetic flea. The dispersed samples were drawn through filter-papers (Whatman's No. 1), and these were allowed to dry slightly before they were cut into two equal halves. Filter-paper semi-circles (one carrying algae and one carrying detritus) were positioned in feeding chambers in the apparatus shown in FIG. 70. These halves were secured using a polythene washer, and the whole apparatus was carefully filled with tapwater and allowed to condition for 3h. at 10^0C. Six snails of either species were sealed into the feeding chambers with gauze squares, secured by an elastic band. Snails had initially been starved and acclimated at 10^0C for 3 days. Thirty replicates (180 individuals) were used in each species.

Observations on the positions of snails were made at 1, 5, and 12h. after insertion. Only snails on the filter paper were recorded. Following the 12h. interval snails were removed from chambers and the extent of grazing was assessed using the following scoring system :

Score 0 : no obvious grazing
Score 1 : < 0.5 total food removed
Score 2 : 0.5 total food removed
Score 3 : > 0.5 total food removed

Since the lichen (Verrucaria spp.) can occur in small isolated patches around the edge of Malham Tarn the above experiments were repeated for A.fluviatilis using algae/Verrucaria and detritus/Verrucaria choices. The lichen was collected freshly from the field. No snail was used more than once in any experiment.

B. RESULTS

Snail food preferences in terms of mean numbers per filter-paper semicircle are contained in TABLE 29. These results merely provide an index of the time spent by snails on each food choice and suggest that P.contortus spends more time on detritus whereas A. fluviatilis spends more time on algae. Examination of the means and their associated significance tests suggests that in the case of the latter species individuals spend more time on the algal alternatives as the contact time increases. The same trend is apparent in P. contortus but is not as marked.

The above results together with those on the extent of grazing (see TABLE 30) indicate that A.fluviatilis seeks out and prefers to eat algae. P.contortus shows the opposite trait. These results correspond to the field observations (SECTION 2. 2).

The results contained in TABLE 31 concerning both the aggregation pattern of snails after 12h. exposure to the food choices and the extent of grazing suggest that limpets seek out and feed on algae in preference to lichen. When algae are absent, however, and the choice is between lichen and detritus the former is preferred, although it is not eaten to the same extent as algae.

2. 3. General Conclusions

Taking both the field and laboratory evidence together suggests that A.fluviatilis is a herbivore and that P.contortus feeds on detrital material. A consideration of the data contained in TABLE 29 also gives some indication as to the methods of food location. Thus in A. fluviatilis aggregation on algae becomes progressively more significant as the contact time procedes. The variance-mean ratio also reduces indicating that dispersion patterns become more perfectly replicated. These observations conform to the hypothesis that food seeking is by random search and contact chemoreception. Bovbjerg (1965, 1968) has suggested that the same phenomenon occurs in Lymnaeid snails when seeking herbivorous material, and Calow (1970, see DATA APPENDIX 1) has used this hypothesis to explain results obtained from feeding experiments on Lymnaea pereger obtusa (Kobelt). The response of Lymnaeid snails to animal food material is more prompt and occurs via distance chemoreception, Bovbjerg (Ibid.). The response of P.contortus to the experimental choice regimen provided is also more prompt than A.

TABLE 29. The mean number of snails per filter paper semi-circle at various times after their insertion into the feeding chambers.

Time after Insertion	Snail Species	mean no./algal covered filter paper	mean no./ detrital covered filter paper	d	p
1h.	A.fluviatilis	2.8(±1.00)*	2.0(±0.86)*	0.84	>0.100
	P.contortus	1.7(±0.33)	3.5(±0.58)	3.95	<0.001
5h.	A.fluviatilis	3.0(±0.84)	1.8(±0.35)	2.00	≃0.050
	P.contortus	1.5(±0.20)	3.6(±0.69)	6.00	<0.001
12h.	A.fluviatilis	3.6(±0.71)	1.4(±0.33)	2.36	≃0.020
	P.contortus	1.0(±0.18)	3.9(±0.40)	10.00	<0.001

* confidence limits = $2S/\sqrt{n}$, where n = 30

TABLE 30. The extent of grazing after 12h. contact with food as measured by summed grazing scores (see text).

	Algae	Detritus
A.fluviatilis	42	6
P.contortus	10	48

TABLE 31. The mean number of limpets per filter paper semi-circle and summed grazing scores in the algae/Verrucaria, detritus/Verrucaria choice experiments.

	Algae	Verrucaria	Time after Insertion
Mean no./semicircle	3.9(±0.74)	1.9(±0.41)	12h.
Grazing score	36	15	
	Verrucaria	Detritus	
Mean no./semicircle	3.1(±0.69)	2.2(±0.47)	12h.
Grazing score	21	9	

fluviatilis. On this basis it is tempting to postulate that distance reception of food exudates occurs in P.contortus and this reflects a basic difference in the dietary requirements of both the species considered. More will be said about this below.

The results contained in TABLE 31 indicate that A.fluviatilis takes algae in preference to lichen. In the absence of algae, as in Schmid's (1932) situation, however, Verrucaria may be eaten. I have similarly observed a population of A.fluviatilis which fed exclusively on lichen. This was discovered in a small, shallow stream at Burghfield Common near Reading (i.e. Clayhill Brook; Grid Ref. SU650675). Verrucaria was the only epilithic plant present and the submerged rocks were a uniform black colour. Snail gut contents consisted entirely of Verrucaria. It is interesting to note that individuals collected from this site in April, 1971, were 3.54 ($\pm$ 0.39) mm. long as opposed to individuals on Ha Mire which were about 5mm. long by this time (see FIG. 29). It has already been noted that the growth rates of A.fluviatilis on Ha Mire are low when compared with other habitats so that growth rates in Clayhill Brook must be even lower. Thus, although Verrucaria can support a population of limpets which may be quite high (mean density/10,000 LP at Clayhill Brook was ca. 30) it may not allow rapid growth, and in this sense is not as rich a food supply as algae.

In summary the dietary preferences shown by both species of snail considered above may be expressed in the following preference sequences:
for A.fluviatilis

Algae > Verrucaria > Detritus > Fungi ..... 1(7. 2)

for P.contortus

Detritus > Algae > Fungi ..... 2(7. 2).

3. QUALITATIVE DETAILS OF THE DIET OF A.FLUVIATILIS

3. 1. Introduction

The data presented in SECTION 2 indicated that A.fluviatilis is a herbivore which usually ingests epilithic algae. The following sections are concerned with the qualitative details of the algal diet. Reference is made to both field observation, SECTION 3. 2, and laboratory experimentation, SECTION 3. 3. The selection of food in terms of algal size is also considered, SECTION 3. 4, and a seasonal definition of the limpet diet in terms of both algal cell numbers and biomass is presented, SECTION 3. 5.

3. 2. Field Observations

A. METHODS

Monthly analyses on snail gut contents and epilitha were carried out between March, 1970 (m2) and January, 1971 (J13). A distinction was made between stones with (SN) and without (NS) snails, and separate algal samples were taken from stone tops (T), and sides (S = TS+BS). No algae occur on the stone bottoms (see PART IV, SECTION 6. 1).

The epilitha were sampled by scraping the algal cover from the required stone aspect into 50cc. of distilled water. At least 25 stones were used for each sampling category and all extracts were bulked into the same volume of water. Fixation and storage was in Lugol's solution. Extraction of food samples from snail guts was carried out as in SECTION 2 above. At least 30 individuals were involved in each extraction.

The proportions (in terms of cell numbers) of algal types were estimated from a subsample of the gut extract and stone samples using a haemocytometer. Samples were broken up and dispersed prior to the estimation using an automatic stirrer with magnetic flea. A drop of solution was placed in the haemocytometer and the numbers of each representative algal type were assessed by systematically scanning each subsample with reference to the haemocytometer graduations. In all cases 30 replicate aliquots were considered. Within each sample counts were conflated for the separate algal-types and expressed as a percentage of the total numbers present.

Identification of the algae was taken to genera only.

B. RESULTS AND DISCUSSION

TABLE 32 presents information on the relative abundance of epilithic algae on the sides of snail occupied stones at various times of the year. There was a minimum of 17 algal genera present of which 10 occur in the Class Bacillariophyceae, phylum Chrysophyta (diatoms), 3 in the class Chlorophyceae,phylum Chlorophyta (green algae), and 4 in the phylum Cyanophyta, subphylum Homogeneae (blue-green algae). This classification follows Prescott (1969). All the algae which could not be identified were designated "REST", and contributed less than 10% to the total enumerated.

These results show a surprising degree of inter-seasonal stability in terms of the algal community structure. Changes in detail do occur, but the underlying pattern of abundances is approximately constant. In the Tarn sediments, whose flora is similar to the epilitha, fluctuations in the densities of diatom, green, and blue-green algae are fairly well co-ordinated (Round, 1953) and this would result in stability of structure in terms of relative abundance. Furthermore, the generic classification may obscure details in species fluctuations. It should be noted, however, that stability in floral community structures has been observed in other benthic situations (Smyth, 1955; Hunding, 1971).

As already noted diatoms are the dominant group on stone sides (see PART IV, SECTION 6. 2) and of this group Navicula is consistently the most abundant genus. Variations in the epilithic flora with stone aspect have already been considered in PART IV, SECTION 6. 2, and will not be discussed further in this section.

Investigations on the possible effect of A.fluviatilis on the composition of the epilithic flora has been carried out with reference to a comparison between floras on the sides of snail-,and non-snail, occupied stones. The limpet is restricted to this stone aspect (see PART IV SECTION 6. 3). This method is not altogether satisfactory since absence of snails at one time (i.e. the sampling occasion) does not necessarily imply their absence a short time before. Nevertheless, it was considered that the comparison may provide some indication of grazing effects. TABLE 33 lists the Spearman Rank Correlation Coefficients between epilitha on NS and SN at various times of the year. To account for the semi-quantitative nature of the sampling technique and loss of information in the ranking procedure, the null hypothesis (i.e. no correlation) was only rejected at the 99% level.

TABLE 32. The % proportion of epilithic flora on the sides of snail-bearing stones on Ha Mire shore.

	M2	A3	M4	M5	J6	J7 +
Bacillarophyceae						
Navicula	16.40	25.89	30.73	40.57	31.59	18.99
Gomphonema	2.47	2.37	5.21	2.83	4.22	1.20
Amphora	0.18	0.79	-	0.47	0.75	-
Epithemia	-	0.20	-	0.47	-	-
Cymbella	4.59	0.19	3.65	1.42	4.48	2.40
Cocconeis	-	-	-	0.47	1.24	-
Synedra	14.88	19.96	11.98	7.08	1.48	0.96
Achnanthes	13.41	9.29	10.00	14.62	9.45	5.29
Diatoma	1.24	0.40	-	1.42	1.24	0.24
Fragilaria	-	-	-	0.47	0.25	0.24
Total %	53.17	59.08	61.57	69.82	54.70	29.32
Cyanophyta						
Rivularia	39.33	28.46	20.31	13.20	29.61	60.01
Lyngbya	0.88	2.77	2.08	2.83	1.24	1.44
Phormidium	0.18	2.77	-	-	-	-
Oscillatoria	3.53	3.36	4.17	2.36	4.73	4.33
Total %	43.92	37.35	26.56	18.39	35.58	65.78
Chlorophyceae						
Bulbochaete	0.71	2.37	0.52	1.42	0.25	1.20
Ulothrix	-	-	0.52	0.98	0.25	0.24
Spirogyra	-	0.20	-	0.98	0.25	0.96
Total %	0.71	2.47	1.04	3.38	0.75	2.40
Rest *	2.29	3.35	10.93	8.49	8.96	2.40

TABLE 32 - Continued

	A8	S9	O10	N11	D12	J13 +
Bacillarophyceae						
Navicula	27.70	21.77	29.56	25.10	19.00	32.66
Gomphonema	6.20	4.08	3.29	4.05	3.79	3.18
Amphora	-	-	-	-	1.55	0.58
Epithemia	-	-	-	-	0.17	-
Cymbella	4.60	4.08	7.66	7.29	4.30	4.62
Cocconeis	0.70	0.34	0.73	1.62	0.52	1.16
Synedra	2.30	2.38	8.39	12.55	3.10	8.67
Achnanthes	18.60	10.55	12.41	9.72	15.49	15.90
Diatoma	2.30	12.93	5.47	6.88	1.75	0.87
Fragilaria	-	-	-	-	0.17	0.58
Total %	62.40	56.13	67.51	67.21	49.82	68.22
Cyanophyta						
Rivularia	22.50	30.61	19.71	13.77	45.06	23.70
Lyngbya	0.30	1.21	-	2.83	0.69	-
Phormidium	-	-	-	-	2.24	-
Oscillatoria	4.90	3.40	4.75	14.17	-	4.05
Total %	27.70	35.22	24.46	30.77	47.99	27.75
Chlorophyceae						
Bulbochaete	0.30	0.68	-	0.41	-	-
Ulothrix	0.30	0.68	-	-	-	-
Spirogyra	1.00	0.34	1.10	-	0.17	-
Total %	1.60	1.70	1.10	0.41	0.17	-
Rest *	8.50	6.95	6.93	1.62	2.07	4.03

* "Rest" comprises mainly crustose unicellular algae and the occasional Desmid (possibly Cosmarium sp.) which is likely to have been derived from the phytoplankton rain.

+ Sampling dates correspond to those recorded for population dynamics of snails, see DATA APPENDIX I.

TABLE 33. The degree of correlation, as judged by the Spearman Rank Correlation Coefficient (r_s), between epiliths on stones with and without limpets.

	1	2	3	4	5	6	7	8	9	10	11	12
	M2	A3	M4	M5	J6	J7	A8	S9	O10	N11	D12	J13
r_s	.81	.80	.91	.96	.78	.68	.55	.98	.91	.68	.88	.88
$\simeq p$	.001	.001	.001	.001	.01	.01	.05	.001	.001	.01	.001	.001

TABLE 34. The degree of correlation, as judged by the Spearman Rank Correlation Coefficient (r_s), between the gut contents of A.fluviatilis and the flora on the sides of snail-bearing stones.

	1	2	3	4	5	6	7	8	9	10	11	12
	Mar.	Apr.	May	May	June	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
r_s	.86	.47	.73	.60	.74	.40	.79	.82	.83	.61	.72	.86
$\simeq p$	.01	.01	.01	.01	.01	.05	.01	.01	.01	.01	.01	.01

Reference to the TABLE, however, indicates an extremely good correlation of floras throughout the year and in only one month does the correlation fall below the arbitrarily fixed level of significance. The latter may be by chance, and the suggestion is that snails have no effect on the generic composition of epilithic flora. The Spearman Rank Correlation between the crop-gizzard contents and epilithic flora on the sides of snail-bearing stones is similarly good (see TABLE 34). This suggests absence of dietary selection in snails and would result in them having no effect on the composition of the floral community. As is to be expected from the micro-dispersion pattern of snails and flora (see PART IV, SECTION 6) the correlation between snail gut contents and epilitha on the stone tops is not significant (e.g.February 1970, $r_s = 0.35$, $p > 0.10$).

Non-parametric ranking procedures involve a loss of information. FIGS. 71-74 represent an attempt to retrieve some of this lost information. Here the percentage proportions of algae in one location are compared graphically with those in another location. Points lying on the 45° slope indicate complete equivalence between samples. Emlen (1966) has discussed the theoretical significance of these types of plot.

FIG. 71 represents a comparison between the proportions of the major groups of algae available on the stone substratum at various times of the year with those in the snail guts. This indicates that snails take a consistently higher proportion of diatoms and lower proportion of blue-green algae than are available. FIG. 72 compares the proportions of diatom genera available with those taken by snails. Here the picture is less clear, although a consistently higher proportion of Gomphonema and lower proportion of Navicula, in comparison with their proportions on the stones, are taken by the snails. These two figures do, therefore, suggest that the snails possibly show some degree of selective preference and this may be summarised as :

Diatoms > Rest + Greens > Blue-greens ..... 1(7. 3)

and within the diatoms :

Gomphonema > Achnanthes = Synedra = Cymbella = Amphora > Navicula .....2(7. 3)

On these grounds it would be possible for limpets to exert some modifying effects on the community structure of the epilitha. FIG. 73 compares proportions of the major algal types on NS and SN, and FIG. 74 considers this relationship for diatom genera only. Both figures indicate a general absence of variation and again (accepting that SN and NS provide a good index of conditions with and without

snails respectively) suggest no grazing effect. This could either result from a low grazing intensity due to low limpet densities and/or the ability of the algae to compensate for grazing perturbations, as a result of their rapid multiplicative abilities. Kehde and Wilhm (1972) have similarly observed that snails, at relatively high density had no effect on the species diversity of attached algal communities in laboratory streams. Selective, terrestrial grazers may, however, have significant effects e.g. Tomanek and Albertson (1953) and Hazell (1967). This basic difference may be of general occurrence and result from the differences in rates of turnover between terrestrial macrophyte and aquatic algal communities.

3. 3. Laboratory Observations

The conclusions derived from the field observations, described above, have been investigated further in the laboratory. The algae used in the preference experiments, described below, were all derived from laboratory cultures.

A. CULTURE CONDITIONS AND PROCEDURE

Most of the algae used were initially isolated from stones in Malham Tarn. Stones were removed from the Tarn, washed in 5l. sterile distilled water, to remove the free-water planktonic contaminants, and an algal scraping was transferred to either a sterile "grass-cuttings" or "soil extract" medium (Bold, 1942). Subsequent separation of the required groups was achieved by serial dilutions (Lewin, 1959). This was facilitated by encouraging either diatomaceous or blue-green algal growth in subcultures of the original extracts. Silica was added (as 100-200mg. sodium metasilicate/250ml. organic medium) for the diatoms and the blue-greens were encouraged using "soil-extract" at three times the normal strength. Using this procedure it was possible to isolate the following representatives :

Bacillariophyceae	-	Navicula sp.
		Gomphonema sp.
Cyanophyta	-	Rivularia sp.
Chlorophyceae	-	Cladophora sp. (filamentous)
		Scenedesmus sp. (unicellular)

Achnanthes sp. (Bacillariophyceae) has also been used experimentally,

and this was obtained from the F.W.B.A. (Windermere Laboratory). I am grateful to Dr. J.W.G. Lund for this supply.

Following isolation algae were stored in stock in aqueous mineral media, to reduce bacterial contamination. The diatoms were cultured in Allen and Nelsons' (1910) medium suitably modified for freshwater organisms and enriched with sodium metasilicate (200mg./l). Bristols medium (Starr, 1964) was used for the green and blue-green algae. Stocks were maintained at 20^{0}C under a natural illumination regimen and were subcultured routinely at between 2-3 week intervals. All cultures used in the preference experiments were 2 weeks old.

B. EXPERIMENTAL METHODS

Three groups of experiments have been carried out to investigate the limpet grazing preferences. The first investigated snail preferences with respect to paired-choices involving representatives of all the major algal groups i.e. Mixed diatoms (Navicula + Gomphonema + Achnanthes), filamentous green algae (Cladophora), unicellular green algae (Scenedesmus) and blue-green algae (Rivularia). The second investigated snail preferences with respect to paired food choices involving diatoms only (Navicula, Gomphonema and Achnanthes) and the third investigated the snail response to the major algal alternatives using a multiple choice regimen. Paired-choice experiments were carried out using the methods given in SECTION 2 and the apparatus shown in FIG. 70. In order to facilitate comparison, all algal types were compared against a single standard group i.e. mixed diatoms, and Navicula in the first and second experimental series respectively (see also Calow, 1970; PUBLICATIONS APPENDIX 1). Diatom-diatom choices and Navicula-Navicula choices were used as controls. The distribution of snails was recorded after 12 contact-hours when the degree of grazing was also estimated using the scoring procedure given in SECTION 2. Thirty replicates each involving 6 snails were used for each choice.

The multiple choice experiments offered algal alternatives on filter paper strips (5 X 2cm.) in a trough (6 X 2 X 4cm.) containing aerated tapwater. The strips were arranged haphazardly and contiguously along the floor of the troughs. 25 snails, acclimated at 10^{0}C for 3 days, were used as experimental subjects and the determinations were carried out at 10^{0}C for 12h. Each experiment, involving a single replicate, was repeated on snails which had been isolated from food for 1, 3, and 7 days. Snails used in the dual-choice experiments were

all starved for one day.

C. RESULTS AND DISCUSSION

The results presented in TABLE 35, in terms of the mean number of snails/filter paper semi-circle after 12 contact-hours, indicate that more snails were found on the diatom choices than on the other alternatives. There was no significant difference between the control semi-circles which were arranged so that one choice was consistently to the left of the other. Taxic responses were obviously not contributing to the differences found in the other experimental chambers. The indices of visible grazing intensity given in TABLE 36 indicate that snails not only sought out the diatoms, but also devoured more of them. The ratios presented in column 6 of TABLE 35 compare the mean numbers on diatoms with those on the alternative choice, and can be arranged in a sequence which is suggestive of the degree of preference shown by the limpets for each alternative. These ratios increase in magnitude from the top to the bottom of the table. The lower the ratio, the more the diatoms are preferred. From this sequence the order of snail positioning preferences can be written as :

Diatoms > Green Unicellular > Green Filamentous > Blue-green .3(7.3)

and this corresponds exactly with grazing intensity differences expressed between diatoms and algal alternatives in TABLE 36.

Similar results presented in TABLES 37 and 38 with regards to snail preferences for different genera of diatoms are less conclusive. There is a significant difference between the mean number of snails on Navicula and Gomphonema in favour of the latter and this is mirrored by a greater grazing index on Gomphonema. No significant difference occurs in the Navicula/Achnanthes choice although the grazing index is slightly greater in Achnanthes. The preference order thus becomes :

Gomphonema > Navicula ≤ Achnanthes ..... 4(7. 3)

Results from the multiple choice experiments are expressed in histogram form in terms of the percentage number of the total snails used in each food deprivation regimen (see FIGS. 75 A, B, C). At 1 day food deprivation the preference sequence is essentially similar to that expressed in sequence 3(7. 3) above i.e. :

Diatoms > Green Unicellular > Green Filamentous ≥ Blue-green algae ... 5(7. 3)

TABLE 35. The dispersion pattern of A.fluviatilis between 2 food choices in terms of the mean no./ food choice offered (n = 30, confidence limits = $2(S/\sqrt{n})$.

1 Choice regimen	2 Diatoms	3 Other Choice	4 d	5 Sig.	6 Ratio: Choice / Dia.
Diatom/Blue-green	4.1($\pm$ .86)	1.2($\pm$ .40)	4.6	+++	.29
Diatom/green (filamentous)	4.2($\pm$ .92)	1.4($\pm$ .38)	4.4	+++	.33
Diatom/green (unicellular)	3.7($\pm$ .62)	2.3($\pm$ .42)	2.7	++	.62
CONTROL					
Diatom/diatom	2.8($\pm$ .21)	2.6($\pm$ .21)	1.0	+	.92

sig. - +++=$p < .001$, ++=$.01 > p < .002$, += no sig. diff.

TABLE 36. Indices of grazing intensity (i.e. summed grazing scores, see text).

	Diatom	Other Choice
Diatom/Blue-green	69	15
Diatom/green(filamentous)	63	21
Diatom/green(unicellular)	60	27
Diatom/diatom	48	39

TABLE 37. The dispersion pattern of A.fluviatilis between 2 food choices in terms of the mean no./food choice offered (n = 30, confidence limits = $2(S/\sqrt{n})$.

Choice regimen	Navicula	Other Choice	d	sig. *	Ratio: Choice / Nav.
Navicula/Gomphonema	1.9(±.42)	2.8(±.48)	2.00	++	.68
Navicula/Achnanthes	2.3(±.49)	2.8(±.40)	1.11	+	.82
Navicula/Navicula	2.5(±.60)	2.7(±.59)	.34	+	.93

* as defined for TABLE 35

TABLE 38. Indices of grazing intensity (i.e. summed grazing scores, see text).

	Navicula	Other Choice
Navicula/Gomphonema	31	59
Navicula/Achnanthes	37	45
Navicula/Navicula	30	33

As deprivation time increases, however, the degree of selectivity reduces until at 8 days it is lost completely.

Laboratory preference sequences 3(7. 3)-5(7. 3) and field sequences 1(7. 3)-2(7. 3) are essentially equivalent. It would appear, therefore, that even though the ranking analysis given in TABLE 34 indicates that there is no food selection by snails certain differences in detail do occur between the actual food taken and that available. These differences disappear as food deprivation time increases. Snails apparently become less discerning during conditions of hunger. This appears to be a general phenomenon (Ivlev, 1961; Emlen, 1966) and has considerable adaptive significance since animals will be most efficient if they accept all potential food items when food is scarce, but increase their selectivity towards more nutritious material as food becomes more abundant. Changes in selectivity also contribute to the snail homeostatic repetoire involved in growth rate regulation. Furthermore this outcome underlines the dangers of using starved animals in laboratory selection experiments and suggests that completely satiated beasts will be better indices of food preference. If selection is maintained under conditions of starvation it is likely that the choices ignored either cannot be used and/or are toxic.

3. 4. The Size Selection of Food by A.fluviatilis

Algal cells show both inter- and intra-generic differences in size. The purpose of this section is to investigate the possibility of size selection of food particles by limpets.

A. METHODS

Algal cell volume provides a convenient estimate of size and probably the best estimate of algal biomass (Findenegg, 1969). The cell volume can be estimated by assuming that each type approximates to a simple, regular, geometrical solid (see Paasche, 1960, and Nauwerck, 1963). The aspect viewed and the geometrical shapes that have been assumed here for the diatoms are presented in DATA APPENDIX VIII. Two scarce groups of diatoms, which are found occasionally in snail gut extracts are Diatoma and Amphora. These are not accounted for in DATA APPENDIX VIII and have not been estimated directly. Both the blue-green and filamentous green algae have been considered as approximate cylinders and the crustose, unicellular, green algae have

been treated as spheres.

The epilithic samples and snail gut extracts were obtained from the monthly samples already discussed (see SECTION 3) and the relevant algal dimensions were measured at X400 using a dial micrometer. Volumes were calculated in $(\mu m.)^3$. Both the snail and the substrate samples were fixed and stored in Lugol's solution, and it was assumed that volume distortions due to fixation would be equivalent in these two cases.

B. RESULTS

The mean algal cell volumes taken from snail guts and the sides of snail bearing stones (S.SN) are contained in DATA APPENDICES IX and X. Estimates from a single, arbitrarily selected, month's data (J6) are presented. TABLE 39 compares the volumes of algae available on the stony substrata with those taken by the snails, and shows that in all cases there is highly significant difference. Column 4 of TABLE 39 compares the actual sizes of algae taken by the snails with those found on the substratum, and indicates that in most cases the size of algae taken are approximately half the size of those available.

These differences cannot be ascribed to an upper physical limit in the ingestion processes because there is no upper limit in either the cell linear parameters, or the volumes of algae contained in the gut extracts (see DATA APPENDIX X, columns 2, 5, and 6). The smaller individuals may be more susceptible to grazing either because they are less firmly attached to the substratum or because they occur in greater abundance in the outer layer of the algal mat. The latter may be a region of young cell development. Finally, smaller types may represent different species within the main genera which, for some reason, are selectively preferred by the snails. These explanations are not mutually exclusive.

FIG. 76 A and B shows the seasonal changes in mean algal cell volumes on the substratum. Four equally spaced months data have been chosen. Although differences in detail do occur, there is a general synchrony in cell size changes with season, which involves a reduction in volume during winter. This pattern is not repeated in the snail food (see FIG. 77). Furthermore there is no apparent change in cell volume with snail size. Factors limiting the size of cells ingested must be operative throughout the year, and adult ingestion is

TABLE 39. A comparison of data contained in DATA APPENDICES IX and X on the mean cell volumes of algae in snail guts and that available on the stony substrata.

1 Algal type	2 d	3 p	4 Ratio size ingested/size available
Bacillarophyceae			
Navicula	3.61	< 0.001	0.41
Achnanthes	5.31	< 0.001	0.49
Synedra	3.40	< 0.001	0.47
Gomphonema	2.83	< 0.01	0.36
Cymbella	2.55	≃ 0.01	0.63
Cyanophyta			
Rivularia	3.36	< 0.001	0.61
Chlorophyceae			
Unicells	3.70	< 0.001	0.49
Filaments	3.89	< 0.001	0.39
		Average	0.48

distinguished from that in young snails not on the size of algal particles ingested but in the number consumed per unit time.

3. 5. The Seasonal Variation in Dietary Constituents

FIG. 78 shows the seasonal variation in the proportions of the major food constituents in the guts of A.fluviatilis throughout one 12 month interval. The figures are based on algal numbers and do not give a true picture of dietary composition in terms of biomass. FIG. 79 shows the biomass conversion (cell numbers X volume). All the volume estimates, except for Diatoma and Amphora are derived from DATA APPENDIX IX. The latter are assumed approximately equivalent in shape and size to Cymbella and Achnanthes respectively. This approximation is based on general observation.

The two representatives given in FIGS. 78 and 79 are extremely similar except that Synedra occupies a greater fraction of the biomass ingested than is indicated by FIG. 78. This is because Synedra has the greatest cell volume. The average dietary compositions, calculated over the whole year after arcsine transformation are given in the blocks at the end of each figure. Diatoms are clearly the most abundant food types ingested and within the group Navicula and Synedra form the largest proportion, particularly on a biomass basis. Achnanthes and Gomphonema are also important constituents. The information embodied in FIG. 79 will be used further in SECTION 5. 9.

3. 6. General Discussion and Summary

Although A.fluviatilis ingests the total range of algal material available to it in nature, changes in the proportions of the algae taken compared with those available suggests that some types are selectively ingested. Laboratory experiments have confirmed this suggestion and indicate that limpets possess food preferences, particularly under conditions of satiation. Food preferences have also been noted in other species of freshwater snail by Bovbjerg (1965, 1968), Favier Gamulin (1969), Calow (1970), and Roop (cited in Patrick, 1970). These findings are in contrast to the notion held by Boycott (1936) that freshwater snails are generally indiscriminate in their feeding habits. The fact that pure samples of the most desired food types are not taken in nature may either result from intimate intermingling of all algal genera on rocks or from the

undesirability of a monophagous habit. With respect to the latter Favier-Gamulin (1969) has shown that growth, fecundity, and survival of the ancylid Gundlachia wauteri on monospecific, algal cultures is not as good as in the field or on mixed algal populations in the laboratory. Walne (1970), working on growth in juvenile bivalves suggested that different algal species,fed in association, may act synergistically to increase molluscan growth from levels which occur when they are used in isolation.

Terrestrial pulmonates also seem to show preferences for specific types of vegetation (Pallant, 1969; Grime et. al., 1970; Mason, 1970a; Wolda et. al., 1971) and Taylor (1895) has suggested that plant defensive mechanisms may be a key factor in controlling availability and determining selection. By reducing digestibility, the occurrence of tannin for example, seems to be a widespread terrestrial plant defensive mechanism (Feeny, 1971). Calow (1970) has extrapolated these arguments to aquatic snails by suggesting that preference in the Lymnaeids depends on digestibility and that this in turn depends on plant protective devices. This argument will be extended, with quantitative evidence in SECTIONS 5. 6 and 6. 3.

Diatoms form the major dietary component of a large number of aquatic animals e.g. herbivorous cyclopoid copepods (Fryer, 1957), various insect larvae (Douglass, 1958), planktonic crustacea (Vetter, 1937 a and b; Harvey, 1955) and microherbivorous fish (Velasquez, 1939; Fish, 1950). A.fluviatilis also shows this tendency. Calow (1970), however, has demonstrated that diatoms are of reduced appeal in L.pereger obtusa and has suggested that the protective nature of the silicious diatom coats may be instrumental. A.fluviatilis has a more muscular gizzard than the Lymnaeids (personal observation), and is presumably in a better position to deal with the hard diatom coat.

Selection against green algae may also be the result of protective coverings. Green algae have a cellulose coat and are therefore only available as food to organisms having a cellulase. Lymnaeids have a more active cellulase than the ancylids (see SECTION 6. 3.).

Blue-green algae are rarely preferred and some authors have claimed a toxic effect (Prescott, 1948; Ingram and Presscott, 1954; Schelubsky, 1951). Other workers, however, have failed to demonstrate toxicity (e.g. Krishnamoorthi, 1961; George,1962; Ahmad, 1967), and experiments described later on A.fluviatilis support this contention since this species eats more blue-green algae than any other group

when fed on pure cultures in conditions of starvation (see FIG. 90). Digestion of blue-green algae by A.fluviatilis is, however, low (SECTION 5. 6) and Hargrave (1970a) obtained the same result for the benthic amphipod Hyalella azteca (Saussure). He attributes this to cell wall mucopolysaccharide and to other cell wall properties.

From the above discussion it is clear that plant defensive mechanisms are critical determinants in food selection by aquatic animals. Algal cell walls are important elements of defence and the ability of animals to rupture them by either physical or chemical means contributes to their food selection behaviour. The interactions between predators and their prey have been of considerable selective importance in modifying the life-styles and structure of the species involved. The same considerations must also apply in herbivore-plant interactions. Furthermore, plant defensive mechanisms could lead to herbivore food shortage in the presence of an apparent plenty, and adds to the criticism already levelled at the postulate of Hairston et. al. (1960) that herbivore populations are rarely limited by their food supply (see also Murdoch, 1966; Erlich and Birch, 1967; Feeny, 1970).

4. QUALITATIVE DETAILS OF THE DIET OF P.CONTORTUS

4. 1. Introduction

P.contortus is principally a detritophage which ingests the detrital materials found on the undersides of rocks (see SECTION 2). It is the aim of the following sections to define the nature of the epilithic detritus (SECTION 4. 2), and to investigate which of the detrital components, if any, are preferred and taken by snails (SECTIONS 4. 3.-4. 6). Some consideration will also be given to the general nature of detrital utilisation by aquatic animals.

4. 2. Nature of the Epilithic Detritus

Detrital samples were obtained from stones on Ha Mire shore. Thirty stones were selected haphazardly and their bottoms were scrubbed into 2L. of distilled water (this yielded ca. 1.5g. dry weight of detritus). The extract was subsequently concentrated by centrifugation and stored at 0^0C until analysis. Samples were repeated at 4 times through the year (December and March, 1970, and June and September, 1971). Detrital samples for comparison were also taken from the north-east sedge bed (see FIG. 9) and the sediments surrounding the stones on Ha Mire. These samples were extracted by inserting inverted test tubes into the silty substrata. They were taken once only, in March, 1970.

The sequence of analysis of the samples is summarised in TABLE 40. All techniques were essentially by a weight loss procedure in which some solute-specific solvent was percolated through the sample and subsequent weight loss after drying was assumed to be due to the weight of the particular solute removed. The table distinguishes between methods in which the substance to be estimated was removed by the solvent and alternatively methods in which all extraneous materials were removed. The weights of the subsamples involved are also indicated. The literature sources containing details of the techniques used, together with notes on points of particular interest pertaining to them are contained in the key to the table.

Calorific densities of detrital materials were estimated using a microbomb calorimeter (Phillipson, 1964) with cellulose-acetate membrane filters as the packing substance (see also Comita and

TABLE 40 : Procedure and sequence for the analysis of detritus. Techniques A involve removal of the substance estimated whereas techniques B involve removal of extraneous material.

The amounts of subsamples involved are given in parentheses. The literature sources containing details of each technique, together with notes of particular interest pertaining to them are contained in the key below.

Key.

1. N.B. temperature conditions greater than 450^{0}C can result in deliquescence of the contained salts (Grave et. al., 1961).
2. The method follows Bocock (1963). Two fractions were distinguished, i.e. cold-water soluble carbohydrates (mono- and disaccharides, together with some polysaccharides; 6-10 sugar residues usually associated in a single chain), and hot-water soluble carbohydrates (long chain and branched polysaccharides). The cold water fraction was extracted first.
3. The method follows that of Siefken and Armitage (1968).
4. The method follows that of Price (1965).
5. Lignin was assessed by 12h. digestion with hot, concentrated HCl. The acid insoluble fraction was assumed to be lignin (Brauns, 1952) and is treated as such in the text although other inert organic residues (e.g. tannins and keratins), may be present.
6. The cellulose assay used follows that of Norman and Jenkins (1933) which extracts Cross and Bevans (1911) cellulose.

SAMPLE DRIED TO
CONSTANT WEIGHT
(OVEN TEMP. 40°C)

ca. 1.5g.

0.75g.

ASH
(MUFFLE FURNACE
450°C, 12 h.)
[1]

0.75g.

WATER SOLUBLE
CARBOHYDRATES
[2]

A

LIPIDS
[3]

(0.2g.)

(0.2g.)

(0.2g.)

PROTEIN
[4]

LIGNIN
[5]

B

CELLULOSE
[6]

Schindler, 1963). This technique will be elaborated in SECTION 5. 2A. 2-5mg. subsamples were involved.

TABLE 41 contains the results of the biochemical analyses, on detrital samples collected in March, 1970. TABLE 42 indicates the caloric densities of the same samples in terms of both dry and ash-free dry weights. The biochemical analyses accounted for at least 97% of the organic materials.

When compared with the other sediments the epilithic detritus is rich in terms of organic material (i.e. least ash), protein and energy. Lignin and cellulose make up the greatest proportion of the organic fraction of all sediments (ca. 70%). Hargrave (1970b) records a value of 50% lignin and cellulose in the organic component of surface sediments in Marion Lake (British Columbia). Lipids generally contribute least to the organic fraction except in the sedge bed sediment where the higher value results in a higher caloric density in terms of ash-free dry weight.

The caloric density of the epilithic detritus is greater than that of the other sediments when expressed in terms of dry weight, but is less than the caloric density of the sedge bed sediment when expressed in terms of ash-free dry weight. In the marine situation suspended particulate matter generally has a higher calorific value than sedimented material (see review by Kenchington, 1970). Calorific values for epilithic detritus fall more closely into the former category.

FIGS. 80 and 81 show seasonal variations in the biochemical, and energetic constitution of the epilithic detritus. There is a high degree of inter-seasonal stability, at least in relative terms.

The epilithic detrital cover probably represents a primary seral stage in aufwuchs community succession which is never allowed to progress further because of the absence of light. It is well established that the primary fouling film on submerged surfaces consists of a bacterial slime cover which attracts algae and suspended sediments (Sechler and Gundersen, 1971). Further algal developments in the absence of light do not occur. Detrital particles are usually hydrophilic and carry negative micellar charges which facilitate adhesion to solid objects (Fox, 1950). Attraction of suspended particles to the bacterial film would result in the epilithic detritus showing characteristics in common with the suspended sediments. It is, how-

TABLE 41. The biochemical constitution of epilithic detritus, sediments around submerged stones, and around the sedge in the N.E. sedge bed. The material was collected in March, 1970.

Source Det. Compound	Bottom Stones	Around Stones	N.E. Sedge Bed
% Ash	37.34	55.61	90.45
*Carbohydrates			
Cold water sol.	6.28	-	-
Hot water sol.	2.29	0.01	1.89
Total	8.57	0.01	1.89
Lipid	0.80	0.01	2.47
Protein	6.75	0.90	5.56
Lignin	69.32	71.06	61.96
Cellulose	12.56	25.63	27.31
Unaccounted for	2.00	3.20	0.81

* results are expressed as a percentage in terms of ash-free dry wt.

TABLE 42. The caloric density of epilithic detritus, sediments around stones and sediments around sedge. The material was collected in March, 1970.

Source	k.cal./g. ash-free dry wt.	k.cal./g. dry wt.
	** +	** +
Stone bottoms	4.101 ± 0.31 (17.17k.J.)	2.571 ± 0.19 (10.76k.J.)
Around stones	3.890 ± 0.47 (16.28k.J.)	1.732 ± 0.18 (7.33k.J.)
N.E. Sedge bed *	4.715 ± 0.45 (19.74k.J.)	0.450 ± 0.05 (1.88k.J.)

* Decalcified using HCl before calorific determination

** Confidence limits = 2 standard errors

+ S.I. conversion of caloric density

ever, difficult to specify the ultimate source of the epilithic detritus although the high lignin content is suggestive of allochthonous materials.

Egglishaw (1969) has distinguished two sources of food for bottom feeding invertebrates in streams, i.e. algal epilitha and the detritus between stones. The same sources are available in the wave swept littoral regions of lakes. Results presented here suggest that epilithic detritus, which is generally richer than sedimented materials may be more important than the between-stone detritus. In this context it should be noted that freshly synthesised and suspended detrital particles provide a reasonable animal food supply (Gavard, 1927; Bond, 1933; van Heyningen, 1954) whereas sedimented materials are unsatisfactory (Loosanoff et. al., 1951; van Heyningen, 1954).

4. 3. Fraction of the Epilithic Detritus Preferred and Selected by P.contortus

A. MATERIALS AND METHODS

Dual choice experiments were carried out in the apparatus depicted in FIG. 70, and involved 30 replicates each considering the response of 6 individual snails. The potential food was offered on filter paper semi-circles. Observations on the snail positions was made after 6 contact-hours and only snails on the filter paper were recorded. The choices were between normal epilithic detritus (collected from stones on Ha Mire and stored prior to use at 4°C) and sterilised material. Two sterilisation procedures were employed on different sub-samples, one involving a specific fungicide, nipagin (see Shorrocks, 1971), and one involving heat (tyndalisation, see Cruikshank, 1965). Heat sterilisation, at low temperature, by tyndalisation involves less structural disturbance of the materials involved, than autoclaving procedures. Experiments on the heat sterilised/non-sterilised detritus regimen were repeated after the former had been exposed to air for 1 week at 18°C in the dark. Normal/normal detritus choices were used as controls.

B. RESULTS

It was not possible to assess the extent of visible grazing in any of the choice experiments considered so that preference could only be described in terms of the relative amounts of time spent by snails

on each choice. The results for A.fluviatilis , however, suggest that this parameter is a satisfactory index of food requirements and preferences (see SECTION 3).

The results for all three experiments are presented in TABLE 43 and clearly indicate that the non-sterilised detritus is preferred. Heat sterilised detritus, allowed to condition in air at 18°C, however, becomes as attractive as the non-sterilised material. This suggests that snails require some living detrital factor and precludes the possibility that sterilisation alters the physical (or chemical) constitution of the food in such a way that it becomes less attractive. Application of the specific fungicide does not alter the electivity of the detritus, and this finding,together with the fact that snails in nature rarely eat fungi (see SECTION 2),suggests that the bacterial fraction of the detritus is the one of interest. Furthermore, results presented later (SECTIONS 5. 6 and 5. 7) indicate that of all the detrital fractions, bacteria are the only ones P.contortus is able to digest. All controls indicated no significant difference in the choice so that taxic responses can be precluded.

C. DISCUSSION

The utilisation of bacteria as food by freshwater snails has been reported elsewhere (Schmid, 1934; Rodina, 1948, 1951, 1963; Kopsch,1949; Pacaud, 1949 a and b; Favier-Gamulin, 1969; Bryce, 1970). There is some controversy as to whether aquatic detritus can be used directly by animals (see Pütter, cited in Krogh, 1931; Fox, 1950; Wilson, 1955; Bader, 1962) or only after conversion into microbial protoplasm (see Zobell and Feltham, 1938; Nelson and Scott, 1962; Newell, 1965, 1970; Darnell, 1967; Kaushik and Hynes, 1968; Hargrave, 1970 a and b). The present findings support the latter hypothesis, although the two possibilities are not mutually exclusive. The route of energy flow from detrital sediments will probably depend on the nature of the detritovores involved and the quality of the detritus.

4. 4. Nature of the Bacteria Present on the Stones at Malham

A. ISOLATION PROCEDURE

Using all possible precautions (i.e. sterile face mask, gloves and boot covers) stones carrying P.contortus were removed quickly from the Tarn (on Ha Mire shore). Handling was by means of sterile tongs.

TABLE 43. The dispersion patterns of P.contortus on differently treated detrital materials after 6-contact hours. The results are expressed in terms of the mean nos./filter paper semi-circle.

Det. N	X	C	d	p
1. Det. normal/ sterilised Det.	4.40(±.69)	0.88(±.19)	8.1	< .001
2. Det. normal/left to stand, sterilised Det.	2.50(±.36)	2.80(±.41)	0.77	> .05
3. Det. normal/Det. mormal + fungi-cide	2.90(±.50)	2.5(±.32)	0.98	> .05

n = 30.

X = the choice other than normal detritus

On removal the stones were gently washed with 25ml. of sterile distilled water (to remove the free living planktonic contaminants) and a detrital scraping was obtained with a sterile scalpel. This sample was transferred to 10ml. of sterilised, quarter-strength Ringer.

Several attempts at this procedure indicated that the number of species isolated rose after rainfall. This observation is in agreement with the results of Price and Valadon (1970) who suggest that rainwater washes both aerial and terrestrial micro-organisms into bodies of water. In consequence the definitive isolation was made only after 7 rain-free days in November, 1970.

Agitation, using an automatic stirrer with magnetic flea was used to dislodge the bacteria from the detrital particles. Serial dilutions were subsequently made on 1ml.aliquots of the original concentrate (C) in quarter-strength Ringer to obtain a range of dilutions from 10^{0}(C), 10^{-1}(C), 10^{-2} (C)..... 10^{-10}(C). Standard loopfuls of each dilution were plated out on the surface of nutrient agar (pH. 7.0). Three replicate plates were prepared from each dilution and incubated aerobically at either 4, 10, or 18^{0}C. Surface plating, as opposed to "pour plate" methods, increase bacterial counts from aquatic samples (Jones, 1970).

Pure isolates were kept in stock on agar slopes (ph. 7.0) at 4^{0}C in the dark. Each was routinely subcultured at 28 day intervals.

B. IDENTIFICATION PROCEDURE

Bacterial types were separated on the basis of their colony morphologies, microscopic form, Gram stain properties, and various metabolic criteria. Gram stain techniques followed the description of Cruickshank (1965) and were Preston and Morrell's (1962) modification.

The nutrient requirements of the isolates were investigated by noting the extent of growth in a mineral medium (Knight and Proom, 1950) containing either glucose, sucrose, galactose or mannose as the organic source. Each of the organic solutions was 50% w/v and was sterilised by tyndalisation. 0.3ml. of the organic concentrate was used in 10ml. of the mineral medium. Cellulose and lignin, extracted from the epilithic detritus were also used as organic sources (1mg. of each after drying and grinding were added to 10ml. of mineral medium). The fermentation of glucose was investigated using aqueous glucose-peptone medium with phenol red indicator, and inverted Durham tubes as

gas traps. Production of acid and gas indicate fermentation. All tests were carried out at 18^0C in the dark.

Growth at 55^0C (incubation time = 3 days), 0^0C (incubation time = 2 weeks) and survival after 24h. exposure to sub-zero temperatures were also investigated. In these cases bacteria were cultured on nutrient agar at the required temperature.

C. RESULTS

TABLE 44 lists the various bacterial types isolated from epilithic detritus on Ha Mire. A description of colony morphology, cell type, Gram stain properties, the critical dilution (i.e. that at which growth ceases), relative abundance, and possible genus involved are also included. Each bacterial type has been given a working name (letter of the alphabet) which will be used in the following discussion.

Fondén (1969) has claimed that the bacterial types isolated on agar from freshwater represent less than 1% of the total bacteria present in nature. A comparison between the types isolated on agar here with those observed directly on coverslips which had previously been suspended in the Tarn for 3 days (technique described in SECTION 6) showed good agreement, however, in terms of both the quality and the relative abundance of floras. Vibrios and some other unidentifiable types which represented ca. $<$ 1% of the total count were the only ones not accounted for on agar. Thus, although absolute counts may be misrepresented by the agar technique, qualitative, semi-quantitative estimates on the major groups seem unaffected.

All groups grew at the three temperatures employed (i.e. 4, 10, and 18^0C). The most rapid and vigorous growth occurred at 18^0C, so that although organisms spend most of their time, in the Tarn, at temperatures below this (see FIG. 4), 18^0C still seems to be optimum for growth. Brock (1966) has also noted this phenomenon and has suggested that it implies intrinsic limitations in metabolism (possibly diffusion) which even the most evolved organisms cannot overcome.
TABLE 45, columns 9, 10, and 11 indicate the response of the bacterial groups to various extreme temperature conditions. No species grew at 55^0C, all survived exposure to sub-zero temperatures and a single species (B) grew at 0^0C. This indicates that all groups except B were mesophilic. Group B is probably psychrophilic. No species were thermophilic. It is interesting to note that the psycrophile is a Gram

TABLE 44. A list of bacteria isolated from epilithic detritus with some of their characteristics.

Working Name	Colony Morphology	Cell Morphology	Gram Stain Characteristic	Critical Dilution	Approx. Proportion in Sample	Possible Genus
A	Yellow clear	short bacilli	+	C	.1%	?
B	White opaque (tendency to spread)	short bacilli	-	C	.8%	Pseudomonas
C	Citrus yellow	short bacilli	+	C	.1%	?
D	Creamy yellow	small cocci	+	C/100	90%	Micrococcus
E	Pale orange	short bacilli	-	C/10	9%	Pseudomonas

TABLE 45. The metabolic characteristics of bacterial species which were isolated from epilithic detritus.

Type	Glucose fermentation	Glucose	Sucrose	Galactose	Mannose	Cellulose	Lignin	Growth at 55°C	Survival after 24h.at 0°C	Growth at 0°C
A	+	2	3.5	1	3.5	*	**	x	*	x
B	+AG	1	2	4	3	x	x	x	*	*
C	+AG	1	2	3.5	3.5	*	x	x	*	x
D	+	2	1	3.5	3.5	*	**	x	*	x
E	+AG	1	2	3	4	**	*	x	*	x

\+ Growth, A = Acid, G = Gas

* Moderate growth

** Good growth

x No growth

Columns 3, 4, 5, 6 are expressed in terms of ranking order

negative, non-pigmented rod, and that Larkin (1970) found that psycrophiles in Louisiana Waters also showed these characteristics.

The results in TABLE 45 on the utilisation of organic substrates by bacteria are expressed in terms of ranking order of suitability for growth. This sequence is based on a subjective estimation of the degree of growth of each bacterial type in all the sugars involved i.e. the inter-group rankings are independent. All the sugars offered were utilised but with varying degrees of success. Most of the bacterial types, except A, grew most successfully on either glucose or sucrose. The species growing best on glucose were all fermenters. Differences also occur with respect to the utilisation of lignin and cellulose. Only one species, i.e. B, was not able to use either of these materials.

Variations in the ability of bacteria to use certain organic substrates reflects basic differences in their physiological and hence niche requirements. From this point of view there appears to be little niche overlap between the species considered here and this is particularly striking when comparing the two dominant groups (i.e. D and E). It must be noted, however, that although this type of laboratory investigation indicates the nutrients which are potentially of use to microbes it doesn't necessarily demonstrate those which are actually used in nature (Brock, 1966).

The dominant epilithic bacteria present in November are a Gram positive Micrococcus and a Gram negative Pseudomonas. Direct observation of coverslips which had previously been suspended in the Tarn for 3 days (technique described in SECTION 6) suggests that this pattern is seasonally constant (see FIG. 82). Mitchell (1971) has also noted considerable stability in microbial ecosystems and has attributed this phenomenon to foreign microbes being more susceptible to predation than the indigenous flora. The stabalising mechanism must be extremely effective in view of the dramatic influx of foreign forms after rainfall (see A above).

Aquatic bacterial floras are similar to but differ in detail from terrestrial, soil communities. The former have a higher proportion of Gram negative chromogenic forms (McCoy and Sarles, 1969). The epilithic bacteria at Malham are generally chromogenic but Gram positive organisms dominate. Meadows and Anderson (1967 and 1968) have found a similar state of affairs in episamnic communities and at Malham there is some evidence to suggest that snail mucus may be exerting a

modifying effect (see PART VIII, SECTION 4. 4).

4. 5. Selection of Bacteria by P.contortus

A. METHODS

Selection of bacteria by snails was investigated using both dual- and multiple-choice procedures. Bacteria were cultured separately in Knight and Proom's (1950) medium to which glucose (in the concentration already described in SECTION 4. 4A) was added as organic source. After 5 days incubation all cultures were diluted with sterile distilled water to the same approximate turbidity. 5ml. aliquots were passed through membrane filters (pore size: 0.8μm; diameter 5.0cm.) and the retained bacteria were washed twice with 10ml. of sterile distilled water. The utility of membrane filters in offering epilithic food to aquatic animals has already been noted by Calow and Fletcher (1972, see DATA APPENDIX III). Filters retain cells during submersion.

The dual- and multiple-choice experiments were carried out in the apparatus described in SECTION 2. Six animals were used in each dual-choice feeding chamber and 20 in the multiple-choice chambers. The former was replicated 30 times, the latter 10 times. Experiments were run at 10^0C with snails which had previously been acclimated to these temperature conditions on detritus-bearing stones so that satiation was assumed. Six contact-hours were allowed in each regimen, and only snails on filter papers were recorded.

The following paired choices were offered :

Bacterium A v. Non-sterilised detritus
" B v. " "
" C v. " "
" D v. " "
Bacterium D + E v. " "
" A + D + E v." "

In order to maintain approximately natural proportions, cultures containing bacteria D and E were mixed in the ratio of 9D : 1E to produce the D + E complex, and cultures containing A, D, and E were mixed in the ratio 0.2A : 0.8E : 9D to produce the A + D + E complex (cf. FIG. 82).

The multiple choice experiments offered choices between A,B,C,D and E. These experiments were repeated with animals which had been starved

for 1, 4, and 8 days. No replicates were used in these cases.

B. RESULTS AND DISCUSSION

TABLE 46 shows the results of the multiple choice experiments. The proportions of animals found on each food type after 6h. exposure are expressed in arcsines. Once again it was difficult to assess the extent of grazing so that the time spent on each choice is taken as an index of preference. ANOVAR indicates a significant difference between the time spent by snails on the different choices i.e. :

Source	Sum of Squares	df.	M	F	P
Choices	911.71	4	227.9	99.1	> 0.001
Replicates	213.50	9	23.7	10.3	> 0.01
Residual	81.50	36	2.3	-	-
Total	1206.67	49	-	-	-

Replication is poor but accounts for a smaller proportion of the total sums of squares than the choices. Significance between the mean proportions (calculated on the basis of all replicates) was investigated using the Range-STP test (see PART IV, SECTION IV). L,S,R, at the 95% level is 6.5 so that the range between means must exceed this value for them to be significant. On this basis a preference sequence derived from the means given in TABLE 46 can be written as follows :

$$D > E > A \geq B = C \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 1(7.4)$$

The most preferred bacterium is a Gram positive coccus. Gray and Johnson (1970) have also found that coccoid bacteria are preferred by the interstitial marine Gastrotrich, Turbanella hyalina (Schultze) and suggest that these food organisms may be of general ecological importance. Furthermore it should be noted that bacterium D does not ferment glucose (see TABLE 45) and the latter workers have suggested that fermenters may produce materials which are noxious to animals.

TABLE 47 shows the results of the dual-choice experiments. These indicate that when offered separately both bacterium D and E are not as attractive as the non-sterilised detritus, and that bacterium A is less attractive than D and E. A combination of D and E, however, is as attractive as the detrital material and the addition of A does not improve this situation. Gray and Johnson (Ibid.) also found that

TABLE 46. The proportionate distribution (in arcsines) of P.contortus in multiple choice experiments which offered bacteria A-E as food alternatives.

Replicate \ Choice	A	B	C	D	E
1	18.43	-	26.57	39.23	33.21
2	18.43	-	-	50.77	33.21
3	18.43	18.43	-	56.79	18.43
4	-	18.43	-	50.77	39.23
5	18.43	18.43	18.43	45.00	26.57
6	26.57	18.43	18.43	39.23	33.21
7	18.43	-	-	50.77	33.21
8	26.57	18.43	-	39.23	33.21
9	18.43	18.43	18.43	45.00	26.57
10	26.57	18.43	-	39.23	33.21
Mean	19.03	12.90	8.19	45.60	31.01

TABLE 47. The dispersion patterns of P.contortus between two available food choices, one of which was normal detritus the other bacteria of various types (denoted generally as X). The results are expressed in terms of the mean no./ filter paper semi-circle.

Choice	Normal Det. ±	X * ±	d	p
Normal det. v A	4.9(1.29)	0.4(.30)	6.4	> .001
" v D	4.2(.94)	1.3(.41)	4.8	> .001
" v E	4.5(.95)	1.0(.44)	5.7	> .001
" v D+E	2.9(.62)	2.6(.70)	0.4	> .10
" v A+D+E	2.8(.59)	2.3(.63)	1.0	> .10

* Fiducial limits = 2 S/√n.

bacterial combinations were most attractive to Turbanella. The reasons for this are unclear since D and E are digested as well separately as in combination (see SECTION 5. 6). Perhaps each bacterial type contains some unique biochemical factor which is necessary for optimum snail metabolism.

FIGS. 83 A, B, and C summarise the effects of starvation on snail food preference and indicate, as with A.fluviatilis, that the less preferred foods may be taken to a greater extent during starvation conditions. The significance of this phenomenon has already been discussed in SECTION 3. 3.

4. 6. Bacteria in the Guts of P.contortus

A. METHODS

A random sample of 30 individuals, collected from Ha Mire shore in May, 1971, were fixed and stored in 70% alcohol. The gizzard-crop apparatus was subsequently removed, smeared onto a clean microscope slide, heat fixed, and Gram stained. Smears were observed at X1000 using an oil immersion lens and the bacteria present were identified and scored on the basis of their abundance using the following scheme :

SCORE : 5 - present in all fields
" 4 - present in 75% of fields
" 3 - " " 50% " "
" 2 - " " 25% " "
" 1 - " " <10% " "
" 0 - Not present

Fields were selected haphazardly and non-recurrently. Twenty fields per smear and 21 replicates were considered.

B. RESULTS AND DISCUSSION

A large quantity of bacteria was observed in the snail guts. Most of these were closely attached, usually in single-species clumps, to the detrital particles. Types found together with their abundance ratings are given in TABLE 48.

The fact that small Gram positive cocci are most abundant is in keeping with findings from the preference experiments (see SECTION 4. 5). The results presented, however, must be treated cautiously since the bacteria observed could originate from the endemic gut

TABLE 48. Bacteria observed in the gut of P.contortus. The figures represent an arbitrary scale ranging from 1-5 and indicating abundance (see text for further explanation).

Gram +ve			Gram -ve	
Cocci		Bacilli	Bacilli	Curved bacteria (Vibrio ?)
Small	Large			
5	-	2	1	-
5	-	2	1	-
5	-	2	1	1
4	-	-	2	-
4	-	-	2	-
5	-	-	3	-
2	-	-	1	-
3	-	1	1	1
3	2	1	-	-
5	2	-	-	-
3	1	-	-	-
3	1	-	1	-
4	1	-	1	-
5	4	-	2	1
4	3	-	1	-
5	3	-	1	-
5	3	-	3	-
4	3	-	1	-
5	4	-	-	-
3	5	-	-	-
5	2	1	-	-
87	34	9	22	3 Score Totals

flora as well as from external sources. The large Gram positive cocci which were not observed on the natural substratum probably fall into the former category. Nevertheless, the reults do demonstrate that bacteria could be taken as food by P.contortus and the abundance of Micrococci suggests that this is so.

4. 7. General Discussion and Summary

P.contortus is a detritophage but selectively prefers detrital materials containing live bacteria. Evidence presented later indicates that only the bacterial fraction of the detritus-complex can be efficiently assimilated. One species of bacterium, a Gram negative Micrococcus, is preferred more than any other single species, although bacterial species-combinations are preferred even more.

P.contortus responds to experimental food choice regimes more rapidly than A.fluviatilis (see SECTION 2). It was suggested earlier that the former species employs distance and the latter contact chemoreception. This probably reflects basic differences in the quality and quantity of the bacterial and algal cell exudates. In this sense bacterial secretions elicit a response similar to the exudates of animal flesh (see Bovbjerg, 1965 and 1968).

5. QUANTITATIVE CONSIDERATIONS ON THE DIETARY REQUIREMENTS OF A. FLUVIATILIS AND P.CONTORTUS

5. 1. Introduction

A complete definition of the functioning and functional role of natural populations requires information on food input in terms of both ingestion and assimilation. These parameters can be described in various terms but energy is probably the most convenient and generally applicable unit. The calorific values of snail foodstuffs are, therefore, defined in SECTION 5. 2. SECTIONS 5. 3-5. 7 consider the effects of various factors on the rate of ingestion and absorption of food by snails and SECTION 5. 8 provides equations which can predict food energy absorption under natural conditions. The accuracy of the latter in describing field populations is discussed in SECTION 5. 9.

5. 2. The Calorific Values of the Food Materials

A. METHODS

The calorimetric determination of algae and detritus was essentially similar to that carried out on snail tissues (see PART VI, SECTION 3. 1). Bacteria were not determined directly. Beacause it was impracticable to collect the minimum amount of algal material necessary for bombing, and because the epilithic detritus contains a relatively high quantity of ash, which reduces its combustibility, a "filling" substance was employed. The most convenient was found to be cellulose acetate in the form of membrane filters[1]. Algal or detrital solutions were passed through pre-weighed filter papers, and the retained residue was washed 3 times with 10ml. of sterile distilled water, before drying to constant weight at 40^{0}C. Filters were folded into "parcels" before drying and these were convenient for direct insertion into the micro-bomb. Knowing the calorific density of cellulose acetate, the weights of filters employed, and the weight of algae or detritus retained it was possible to calculate the calorific density of the latter. This technique is similar to the one employed by Comita and Schindler (1963) and Moshiri and Cummins (1969) on micro-zooplankton samples.

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1. Millipore filters (produced by Millipore (U.K) Ltd.) were used in the present instance (pore size : 5μm , diameter 25mm.).

The caloric density of uncontaminated membrane filters was determined from 10 replicate bombings. Filter ash contents were negligible and have been ignored. The mean caloric density was found to be 3.201 ($\pm$ 0.130) kcal./g. ash-free dry weight which compares well with the values reported by Comita and Schindler (Ibid.) and Moshiri and Cummins (Ibid.) for the same material. Their values range from 2.935-3.104 kcal. g^{-1} ash-free dry weight.

All the algal cultures used were kept in the conditions specified in SECTION 3. 3A, and were two weeks old on determination. Three replicates were used for each bombing. The caloric densities of mixed natural populations were also determined. Here algae were collected from pots which had been suspended in the Tarn over a two-week interval (technique described in SECTION 6). Material so collected was sufficient for a single determination only. Four separate samples collected in December, March, June, and September, 1971 were considered.

The collection and treatment of materials and the results obtained from detrital analyses have already been described (see SECTION 4. 4). Seasonal variations in the caloric density of epilithic detritus is shown in FIG. 81.

The ash values of all samples are based on estimates made on independent subsamples (see also PART VI, SECTION 3). Ashing was carried out in a muffle furnace at 450°C for 12h.

B. RESULTS

Of the aquatic algae, diatoms tend to have both the highest calorific equivalents and highest ash contents (see the review by Cummins and Wuychek, 1971). The latter is to be expected from the siliceous coat of diatoms, and the former from the fact that they generally store fat. In contrast green algae store starch, and the Cyanophyta, which tend to have the lowest caloric densities, store glycogen (West and Fritsch, 1927). The results presented in TABLE 49A from the present determinations conform to these generalisations and approximate to the general values of 4.78 for the Chlorophyceae, 4.88 for the Cyanophyceae and 5.310 kcal./g. ash-free dry weight for the Bacillarophyceae quoted by Cummins and Wuychek (Ibid.). Joule equivalents are also shown in the Table.

Data obtained on the caloric density of algae in culture cannot be extrapolated directly into the field since the biochemical

TABLE 49A. The calorific and ash values of algae in culture. The caloric densities are expressed in terms of k.cal./g. ash-free dry weight (A.F.D.W.) but S.I. equivalents are given in parenthesis after the average values. N represents the number of replicates used in the determination.

	k.cals./g. A.F.D.W.	Ash %	N
Bacillarophyceae			
Navicula spp.	5.473 ± .210	40.01	3
* Achnanthes spp.	5.499 ± .310	35.70	3
Gomphonema spp.	5.501 ± .297	31.20	3
Mean	5.491 ± .032 (22.99 k.J.)	35.64	
Chlorophyceae			
Unicellular Green			
Scenedesmus spp.	5.472 ± (22.91 k.J.)	8.17	3
Filamentous Green			
Cladophora spp.	5.075 ± .203 (21.24 k J.)	27.23	3
Cyanophyta			
Rivularia spp.	4.927 ± .367 (20.62 k.J.)	30.05	3

* obtained from the Freshwater Biological Association by courtesy of Dr. Lund. Others were isolated from Malham Tarn.

TABLE 49B. The calorific and ash values for epilithic algae collected from Malham Tarn. The caloric densities are specified as in TABLE 49A.

	k.cals./A.F.D.W.	Ash %
December, 1970 *	5.093	46.31
March, 1971 *	5.087	32.20
June, 1971 *	5.191	55.01
September, 1971 *	5.133	52.12
Mean	5.126	46.30

* One sample only

constitutions of algae vary with culture age and conditions (Denton and Kelly, 1970). TABLE 49B shows the calorific equivalents of algae extracted from artificial substrata on Ha Mire shore. It is assumed that these are representative of the natural epilitha. As can be seen there is little seasonal variability, although there is some variability in ash contents.

Insufficient bacterial material was obtained from the laboratory cultures for calorimetric determination. Consequently the mean ash value of 12% (Mayberry et. al., 1968) and the mean calorific equivalent of 5.33K.Cal./g. ash-free dry weight (Prochazka et. al., 1970) have been used.

5. 3. General Methods Involved in Estimating Ingestion and Assimilation

Unless otherwise stated the methods used for estimating ingestion and assimilation rates follow those of Calow and Fletcher (1972: see PUBLICATIONS APPENDIX III) and involve the use of two radiotracers i.e. 14C and 51Cr. The more usual gravimetric and indicator methods, which are reviewed in PUBLICATIONS APPENDIX III, are not applicable to fresh-water pulmonates because it cannot be assumed that all the materials contained within the faeces are derived directly from the food. As much as 20% of the faecal ash-free dry weight in these animals may be mucus or of an excretory nature (see SECTION 5. 9). The applicability of the 14C - 51Cr technique to both P.contortus and A.fluviatilis, however, has previously been demonstrated by Calow and Fletcher (Ibid.).

The food materials used in the feeding experiments were :

for A.fluviatilis

Bacillarophyceae

Gomphonema

Achnanthes

Navicula

Chlorophyceae

Scenedesmus

Cladophora

Cyanophyta

Rivularia

for P.contortus

Bacteria

Species D

Species E

Dead Organic Materials

Lignin

Cellulose

The living materials were cultured according to the methods given in

SECTIONS 3. 3 and 4. 4 and all were found to be capable of sorbing 51Cr. The methods of labelling and food presentation were as described by Calow and Fletcher (Ibid.). All the algal cultures were 2 weeks old on presentation to the snails whereas bacterial cultures were 1 week old.

Cellulose was prepared in labelled form from cultures of the green alga Scenedesmis. Two 500ml. cultures were used and were incubated with $NaH^{14}CO_3$ (1µ Ci/10ml. culture) for a 7 day interval, at 18°C under a natural illumination regimen. The isotope was initially admitted when cultures were 7 days old. After a further 7 days, cultures were passed through a single filter paper (Whatmans no. 1) which was subsequently washed 3 times with 10ml. of distilled water. The filter was air dried, pigments were removed using warm acetone, and cellulose was extracted using the technique described in TABLE 40. The resultant substance was soaked in distilled water (12h.), air dried, and ground down to a fine powder. This technique yielded ca. 2.5g. of cellulose which was derived ultimately from both the labelled algae and the unlabelled filter papers. The specific activity was ca. 2000 counts $g^{-1} min^{-1}$. Ingestion and assimilation of this material was estimated using a radiotracer technique involving ^{14}C only, and this will be described in detail in SECTION 5. 6.

Lignin was prepared directly from the epilithic detritus using the technique described in TABLE 40. This substance was not labelled and its rate of ingestion and assimilation was estimated gravimetrically (see SECTION 5.6).

The shells of all snails used in the feeding experiments were cleaned (with a tooth brush) to remove algal contamination. The latter could cause difficulties in radiotracer determinations.

The 14C - 51Cr techniques allow expression of ingestion and assimilation approximately in terms of ash-free dry weight (see PUBLICATIONS APPENDIX III). These may be transformed to an energetic representation using the information contained in SECTION 5. 2. This transformation will not be carried out until PART IX when the energy input, in terms of food assimilated, is specified for purposes of constructing energy budgets. The physiological inexactitude of using the term "assimilation" to describe absorption has already been noted by Calow and Fletcher (Ibid.) but will be retained here because it has become firmly established in the ecological literature.

Specific methods involved with particular experimental investigations will be described in the relevant sections.

5. 4. The Effect of Food Deprivation on Ingestion and Assimilation

This section is concerned with the effects of food deprivation on appetite, assimilation efficiency and the rate of assimilation. The amount of food ingested after a particular starvation interval provides a good index of appetite (Holling, 1966 a and b) and has been used for this purpose here. Observations have been carried out on 6 separate groups of 5 snails in both species. Each group was subjected to a single deprivation interval of either 6, 24, 48, 72, 120 or 144 hours before being offered labelled food. Snails were individually isolated during deprivation in aerated, filtered tapwater. The faeces were removed frequently and it can be assumed that food deprivation was near to absolute. Following this period A.fluviatilis was offered 14C, 51CR - Achnanthes and P.contortus, 14C, 51Cr - Bacterium D. The food deprivation procedure and the feeding experiments were carried out at 10^0C.

The experimental results are summarised in FIGS. 84 and 85 for A.fluviatilis and P.contortus respectively. In both species appetite, assimilation efficiencies, and thus total assimilation rate increases with starvation time, but at a progressively reducing rate. After 144h. starvation, however, both appetite and assimilation efficiencies become reduced and this probably reflects the onset of some pathological state.

The curvilinear relationship between appetite and starvation appears to be generally applicable in a wide range of vertebrate and invertebrate animals (Miner, 1955; Holling, 1966 a and b; Beukema, 1968; Brett, 1971; Hubbell, 1969, 1971). This derives from the fact that appetite is functionally related to the unfilled volume of the gut (Holling, Ibid.) although endogenous regulation may also exert a modifying influence (Hubbell, Ibid.).

The increased efficiency of digestion following starvation has also been noted for other species (Brett, Ibid.; Windell, 1966) and could result from the exertion of passive and/or active control over the digestive processes. Thus a greater gut space could result in a more effective trituration of the ingested materials, when control would be passive and/or there could be an increase in the level of

activity and rate of secretion of digestive juices as the gut empties, when control would be active. Histochemical evidence indicates that in Lymnaea truncatula (Müll) the concentration of enzymes in the hepatopancreas rises during starvation (Moore, 1971), so that at least part of the regulatory mechanism is under active, endogenous control in this species. Moore (Ibid.) observed the same phenomenon during parasitisation with trematode larvae so that the effects of parasitisation and starvation are similar and probably represent a homeostatic attempt at maintaining constant food energy input in the face of differing forms of environmental, food-supply perturbation. The ultimate effect of enzyme accumulation in the hepatopancreas is "liver" cell autolysis which impairs the digestive processes (Moore, Ibid.). This could account for the pathological state noted in P.contortus and A.fluviatilis after 144h. starvation. Furthermore this critical starvation interval corresponds with the period of metabolic "memory" loss in P.contortus (see PART VI, SECTION 4. 3) and may contribute to the latter.

The fact that the two species considered are able to increase their digestive efficiency during starvation implies some degree of wasteful feeding during normal conditions. This is similar to the concept of "superfluous feeding" described by Beklemishev (1962) in herbivorous zooplankton (cf. Butler et. al., 1970). Both concepts lead to the difficult question - why do animals generally eat more food than they require ? Clearly a gut store would buffer against sudden and temporary food shortage (e.g. when animals migrate accidentally into areas containing little food) and the production of high grade faeces during satiation could enrich the surrounding habitat. Both these effects would have a beneficial feedback effect on the organisms concerned and would be selected for. It is also likely that control over the activity of peripheral energy obtaining subsystems (i.e. those involved with ingestion) is more crude than control over the more central equivalents (i.e. those involved with absorption), and such incompatibility could result in wastage. These explanations are not mutually exclusive.

Lawton (1971) has listed the various possible relationships which can occur between ingestion rate and assimilation efficiency. Assimilation efficiency can either remain constant, reduce or increase with increasing food levels. These are defined as types A, B, and C respectively. Clearly, these responses are related to the behaviour of assimilation under the conditions of starvation which have been

described above. P.contortus and A.fluviatilis can be considered as Type B organisms in this scheme, and this type of response probably represents the optimum adaptation.

As Lawton (1971) has noted, Type B conditions provide difficulties in extrapolating laboratory estimates of ingestion and assimilation into the field. Theoretically the field conditions of food supply must be known. Here it will initially be assumed that field individuals are satiated, or at least only mildly starved, and this assumption will be tested in SECTION 5. 9 by comparing independent laboratory and field estimates of ingestion rates and assimilation efficiencies.

The assumption of satiety, and the possibility of starvation effects on feeding processes demands rigorous control over the experimental conditions. Thus snails in subsequent experiments were acclimated at the appropriate temperature in the laboratory, on stones freshly collected from the field. The acclimation time was arbitrarily fixed at 5 days and snails were maintained at a reduced density (i.e. with respect to the field) of 1-2 individuals per stone in aerated tapwater. The effects of parasitisation have been ignored since cercarial infections have never been observed in either P.contortus or A.fluviatilis (see PART V, SECTION 5.2).

5. 5. Gut Emptying in P.contortus and A.fluviatilis

A. METHODS

Following the suggestion of Calow and Fletcher (1972; see PUBLICATIONS APPENDIX III) 51Cr labelled food material has been used to follow the time course of gut emptying in A.fluviatilis and P. contortus under various conditions. The major food materials used were ^{51}Cr-Navicula and ^{51}Cr-bacterium D for A.fluviatilis and P. contortus respectively. In the case of P.contortus the bacterial food component was mixed with lignin such thatnthe ratio between the dry weights of bacteria and lignin offered was 100:1 respectively (for techniques see SECTION 5. 7B).

The basic experimental procedure involved feeding groups of satiated snails (consisting of 5 individuals) on the labelled food for between 6-12h. Following this interval snails were thoroughly washed in running tapwater and counted en-masse for 5 mins. in a well-type, γcrystal scintillator using a 5 x 1 cm. vial containing tapwater.

After counting, individuals were transferred to non-labelled food of the same type as the labelled material and were recounted at frequent, approximately regular, intervals. The individuals within each experimental group were all of approximately the same size and four size classes were used :

	P.contortus (MD)	A.fluviatilis (AL)
Spat	0.8mm.	1.0mm.
Small	1.5 "	2.0 "
Medium	2.5 "	4.5 "
Large	3.5 "	6.0 "

Experiments were carried out at 10^0C and snails were acclimated at this temperature for 5 days prior to use.

Experimental variations on the basic regimen described above involved :

i) investigations at 4 and 18^0C

ii) investigating the effect of a step-wise rise in temperature by comparing gut emptying rates at 10^0C in snails acclimated to this temperature with snails which had been acclimated and fed at either 4 or 18^0C, but which were transferred to 10^0C for emptying

iii) the use of starved animals (i.e. for 56h. prior to use)

iv) starvation of animals after feeding on labelled food

v) the use of different food types (i.e. bacterium E in P.contortus, and Scenedesmus and Rivularia in A.fluviatilis).

Only large sized P.contortus and medium sized A.fluviatilis were used in these experiments.

In order to investigate the relationship between the pattern of gut emptying and the gut areas involved faecal samples, retained from the above experiments, were examined. Microscopical examination of pulmonate faecal pellets indicates their site of formation within the gut and their routes of exit (Carriker, 1945, 1946; Calow, 1970). Thus gizzard-strings are formed in the crop-gizzard region and pass to the anus without diversion to the hepatopancreas. They contain indigestible particles. Liver-strings are formed in the hepatopancreas from the waste products of intracellular digestion. They represent the undigested component of the potentially digestible particles which are diverted from the direct gizzard intestinal pathway into the hepato-

pancreas. The latter is the major site of digestion in the Gastropoda.

B. THE BASIC PATTERN AND THE EFFECT OF STARVATION

FIGS. 86A and 87A demonstrate the pattern of loss of 51Cr labelled food from the guts of large P.contortus and medium sized A.fluviatilis at 10^0C. The logarithm of the counts remaining in the snails, expressed as a percentage of the original counts, is plotted against time (in hours). Correction for natural decay of 51Cr was by reference to an external source which was counted with the experimental samples, and corrections for background were made in the usual way. Each point estimate is based on the summed loss from all the snails in each group. Three experimental groups are considered i.e. satiated individuals transferred to non-labelled food after labelling (crosses), satiated groups which were starved after labelling (closed triangles), and groups which were starved prior to labelling but fed afterwards (closed circles). These will be designated groups A, B, and C respectively. All lines in the figures were fitted by eye.

It is convenient to begin with a description of group B. Both snail species showed similar patterns of isotope loss and will be discussed together. Three linear phases are discernible in the semi-logarithmic plots i.e. an initial rapid (steep) phase of short duration, an intermediate, less rapid phase of longer duration, and a final phase in which the rate of loss of isotope is extremely low. This suggests a minimum, 3 compartmental separation of 51Cr within the snail. A similar sequence occurred in group C, but the rate of loss over the second phase increased. Comparison of these phases in group B with the cumulative loss of faecal components in the same group (depicted in FIGS. 86B and 87B) gives some indication as to the nature of the compartmental separation involved. The initial rapid rate of isotope loss is clearly associated with gizzard string production and thus gizzard emptying whereas the second, less rapid, phase is associated with the emptying of the hepatopancreas. No faecal losses occur during the third phase although snails do lose caecal string, a thin mucus band, and the occasional liverstring. The defaecation is, however, complete and the final, slow phase of isotope loss must be interpreted as excretion of absorbed 51Cr. Extrapolation of this line to the origin indicates that ca. 10% of the 51Cr offered was absorbed in both species and this corresponds to the value obtained in an independent method by Calow and Fletcher (1972; see PUBLICATIONS APPENDIX III).

Extrapolation of the line representing the second phase provides an estimate of the proportion of material diverted to the digestive diverticulae and was ca. 70% in both species. It should be noted that this value is not equivalent to the assimilation efficiency, since not all the materials diverted are utilised. Furthermore some digestion and absorption can occur in other parts of the digestive tract (Owen, 1966).

Only two linear components occur in group A. The slow component is equivalent to loss of ^{51}Cr by excretion so that the fast component must represent fusion of the gizzard and hepatopancreatic emptying processes. Production of both liver and gizzard strings throughout this period has been observed and confirms this interpretation.

In a continuous feeder, synchrony between the rate of passage of food through the hepatopancreas and crop-gizzard complex is necessary to prevent blockage of the latter. During starvation, however, such synchrony is unimportant but a reduced rate of loss of the potentially digestible material, from the hepatopancreas may be of some advantage in increasing the chances of digestion of food materials present. Reduction of the rate of emptying also occurs in animals starved prior to feeding labelled material, i.e. group C. This may contribute to the increased efficiency of digestion which was observed earlier in starved animals (see SECTION 5. 4). These findings correspond to histological observation. Krijgsman (1925, 1928), for example, has noted a rhythmic activity of secretion in the diverticulae of starved Helix pomatia (Linn.) which accelerated after feeding. Clearly,control on gut emptying during food supply perturbation is exerted mainly at the level of the hepatopancreas.

C. METHOD OF COMPARING GUT EMPTYING UNDER DIFFERENT CONDITIONS

Because the rate of loss of egesta from the gut is exponential in both starved and fed animals there is no theoretical point in time at which all the egesta from one meal has been defaecated. Therefore egestion is best specified by the egestion half life ($E_{\frac{1}{2}}$) i.e. the time taken for half the indigestible material in the gut to be defaecated. This parameter can be delimited graphically and is related to the coefficient of exponential loss (K) by :

$$E_{\frac{1}{2}} = -\frac{1}{K} \ln 0.5$$

$$\therefore K = \frac{0.693}{E_{\frac{1}{2}}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 1(7.5)$$

These parameters are not absolutely satisfactory since gut emptying curves are not pure exponentials. Nevertheless, $E_{\frac{1}{2}}$ occurs approximately within the first linear component in all cases and together with K provides a simple and convenient parameter for comparison.

D. THE EFFECT OF TEMPERATURE

FIG. 88 shows the effect of temperature on K in large snails and indicates that K rises exponentially with temperature in both species. These relationships are represented by the equations :

for A.fluviatilis

$$\log (K \times 100) = 0.144 + 0.028T^0C \quad \ldots\ldots\ldots\ldots\ldots 2(7.5)$$

for P.contortus

$$\log (K \times 100) = 0.549 + 0.035T^0C \quad \ldots\ldots\ldots\ldots\ldots 3(7.5)$$

Q_{10} values over the whole temperature range considered are consequently 1.995 and 2.291 for A.fluviatilis and P.contortus respectively.

TABLE 50 shows the effect of a stepwise change in temperature on the gut emptying rates ($E_{\frac{1}{2}}$) in 4 and 18^0C acclimated individuals.

TABLE 50. Effect of a Stepwise Change in Temperature on $E_{\frac{1}{2}}$ in Large P.contortus and Medium A.fluviatilis

	P.contortus ($E_{\frac{1}{2}}$ - Hours)	A.fluviatilis ($E_{\frac{1}{2}}$ - Hours)
10^0C control	8.50	11.00
4^0C acclimated (switched to 10^0C)	8.29	10.82
18^0C acclimated (switched to 10^0C)	8.61	11.41

There is little evidence of acclimation in the gut emptying process since $E_{\frac{1}{2}}$ values in the control and experimental groups are similar. Lack of acclimation is also suggested by the Q_{10} values reported above. These tend to 2.0

E. THE EFFECT OF SIZE

The coefficient of gut emptying (K) is negatively and ex-

ponentially related to linear body size in snails (see FIG. 89). These relationships are described by the equations :

for A.fluviatilis

$$\text{Log } (-K \times 100) = 2.258 - 0.313\ (AL) \quad \ldots\ldots\ldots\ldots\ 4(7.5)$$

for P.contortus

$$\text{Log } (-K \times 100) = 2.202 - 0.387\ (MD) \quad \ldots\ldots\ldots\ldots\ 5(7.5)$$

Thus as length increases the rate of gut emptying decreases at a progressively increasing rate. Assuming that the rate of gut emptying is dependent on the length of the gut, then increases in the latter must be more rapid than increases in shell length. In torted gastropods like A.fluviatilis and P.contortus the gut is looped and this condition could be instrumental in the necessary shell and gut size allometries.

Weight for weight the rate of gut emptying in P.contortus is more rapid than in A.fluviatilis (cf. K in spat for example). Rapid movement of food through the intestinal tract is probably typical of detritophages (Macfadyen, 1967). The rate of passage of food through the gut in P.contortus, however, is reduced and approximates to the rate in A.fluviatilis when bacteria only are offered as food (see SECTION 5.9). It would appear that the presence of lignin stimulates more rapid food turnover in the gut.

F. THE EFFECT OF FOOD QUALITY

K values for food of differing qualities are presented in TABLE 51.

TABLE 51 K Values for Medium A.fluviatilis and Large P.contortus at 10°C Using Different Food Material

	A.fluviatilis (K)	P.contortus (K)	
Diatoms			
Navicula	0.063	Bacterium D	0.810
Green Algae		Bacterium E	0.807
Scenedesmus	0.077		
Blue-green algae			
Rivularia	0.089		

In A.fluviatilis there is a negative relationship between rate of gut

emptying and order of preference (see PREFERENCE SEQUENCES 1(7. 3) - 5(7. 3)). This is probably related to digestibility, since the most preferred food has the highest assimilation efficiency (see SECTION 5. 6). There is apparently no difference between the two bacterial types ingested by P.contortus and there is similarly little difference in their digestibility (see SECTION 5. 6).

G. GENERAL SUMMARY AND DISCUSSION

The results indicate a fairly rapid and exponentially reducing rate of gut emptying under optimal conditions. Both the pattern and rates may be changed under various conditions of starvation. Rates are also dependent on temperature, the quality of food supply and animal size.

The rates of gut emptying in P.contortus and A.fluviatilis presented here are low when compared with those reported by other workers for other species. Thus Heidermans (1924) suggested that complete gut clearance occurred in 12 minutes in young A.fluviatilis, Rosenbloom (cited in Carriker, 1946) found a clearance time of 2.3h. in L.stagnalis appressa and Cleland (1953) reported a 6h. clearance time in V.piscinalis. The conditions under which gut emptying was measured are not reported by these workers, however, and all values quoted are based on the use of stained food. The rate of passage of dyed food particles from mouth to anus, in animals possessing an efficient gut mixing device e.g. the crop-gizzard complex represents "transit time" which is not necessarily equivalent to complete gut emptying (Balch, 1950; Utley et. al., 1970). The "transit time" based on the first stained food particle to emerge in the faeces is equivalent to a minimum estimate of gut clearance, and it is this parameter which was probably measured by the earlier workers.

5. 6. Food Quality, Ingestion and Assimilation Efficiencies

A. METHODS

The effect of food quality on ingestion rates and assimilation efficiencies was investigated using the following food types :

for A.fluviatilis	for P.contortus
Bacillarophyceae	Bacteria
Achnanthes	Species D
Navicula	Species E

for A.fluviatilis	for P.contortus
Bacillarophyceae	
Gomphonema	
Chlorophyceae	Algae
Scenedesmus	Navicula
Cladophora	Scenedesmus
Cyanophyta	Non-living Organic Material
Rivularia	Lignin
Bacteria	Cellulose
Species D	

Most of the experiments were carried out at 10^0C using medium sized snails (defined in SECTION 5. 5). The effect of size and temperature on ingestion and assimilation was investigated in a separate series of experiments. All snails except those used in lignin determinations were satiated and acclimated to laboratory conditions by keeping them on stones (density ca. 1-2 individuals/stone) for 5 days prior to experimentation. The stones were freshly collected from the field and cultures were maintained at the relevant temperature in aerated tapwater under a 12L, 12D light regimen. The lignin group was starved for 3 days prior to use. Each experiment involved groups of 10 individual snails which were treated en-masse in determining their assimilation efficiencies. All groups were replicated 3 times so that each regimen involved 30 individuals in total.

The sources and methods of cultivation of the living food materials have already been discussed (SECTIONS 3. 3 and 4. 4). In these instances ingestion rates and assimilation efficiencies were determined using the radiotracer technique of Calow and Fletcher (1972, see PUBLICATIONS APPENDIX III). Faeces from all snails in each group were bulked for isotope determination. Preparation of the lignin and cellulose (14C labelled) has also been discussed earlier (see SECTION 5. 3).

Ingestion and assimilation of lignin was estimated gravimetrically. 5ml. of a solution of finely divided lignin, suspended in distilled water (400mg. lignin/Litre) was drawn onto membrane filters (size and specifications as in Calow and Fletcher, Ibid., pore size was 5μm). Snails were fed on these substrata in the feeding chambers described by Calow and Fletcher (Ibid.) for 6h. Three filter discs with lignin

prepared as above, but to which snails were not allowed access, were used as controls and these indicated a weight loss of 2.0% in lignin over the experimental interval. Weight loss in experimental discs corrected for the latter was assumed to be due to snail grazing. Fed snails were removed to clean chambers where they were allowed to empty their guts completely (i.e. over a 5-day interval), and the faeces collected over this time were bulked with those collected from feeding chambers. This sample was digested in concentrated HCl, residues were washed, re-attached to pre-weighed millipore filters, dried (40^{0}C to constant weight) and weighed. The difference between the lignin ingested and that recovered in the faeces after acid hydrolysis, was assumed to be due to the lignin assimilated. Pre-starvation of snails was necessary to prevent contamination of the lignin, extracted from faeces, collected in the feeding chambers and derived from the feeding discs, with the lignin derived from natural dietary sources. The result of this manipulation was probably to increase the rate of lignin ingestion and its efficiency of digestion (see SECTION 5. 4).

The ingestion and assimilation of 14C-cellulose by P.contortus was measured using a radiotracer technique similar to that described by Hargrave (1970a). 5ml. of a solution of finely divided 14C-cellulose powder (2g. cellulose/L. of distilled water) was drawn through millipore filters (size and specifications as for the lignin estimate). These were offered to snails in the feeding chambers which have already been described. Three control chambers were employed each containing food-laden filter papers but no snails. The filter papers were prepared in exactly the same way as the experimental group, and were used to estimate the initial weight of the food material added, together with its specific activity. Feeding was allowed for 6h. when snails were removed to clean chambers for gut emptying (5 days). The faecal material and food discs were removed from the feeding chambers, dried and counted for 14C disintigrations (see PUBLICATIONS APPENDIX III for methods). Faeces from the feeding chambers and gut emptying chambers were bulked and similarly estimated for 14C counts.

Loss in weight of food on membrane filters, as estimated by the radiotracer technique, was assumed to be equivalent to food ingested. The difference between this and cellulose recovered in the faeces (also estimated by the radiotracer technique) was assumed to be due to assimilation.

B. RESULTS AND DISCUSSION

TABLES 52 and 53 show the effect of food quality on assimilation efficiencies in A.fluviatilis and P.contortus respectively. Efficiencies in A.fluviatilis range from 10-60%, the higher values being associated with the most preferred food (i.e. diatoms). There was no significant ingestion of bacterium D. Efficiencies in P.contortus range from 1-75% and again there is a positive correlation between food preference and assimilation efficiency. Diatoms and green algae may be taken by this species but are not digested as efficiently as they are in the limpet. The non-living organic fractions of the detritus are digested with efficiencies of less than 10% and Hargrave (1970a)has obtained similar values in Hyalella. This result suggests that though P.contortus is a detritophage it is only able to make efficient use of the bacterial fraction of its food. Furthermore the bacterial association of species D and E is not assimilated any better than the species in isolation (see SECTION 4. 5).

The range of assimilation efficiencies in A.fluviatilis on diatomaceous, green, and blue-green algae fall within the range reported by other workers for aquatic microherbivorous organisms (cf. DATA APPENDIX XI). It should be noted that not all results presented in DATA APPENDIX XI are comparable since efficiencies are based on various units and that notably the diatom efficiencies are generally expressed in terms of dry weight so that they will be much lower than their ash-free dry weight equivalents. The review suggests no generalisation with regards to the efficiencies in each taxonomic food group except that blue-green algae are associated with relatively lower efficiencies than the other types. The digestive efficiency of a particular food type presumably depends on the physiological make-up of the herbivore concerned and perhaps its ability to cope with the algal cell walls (see SECTION 3. 6 and 6. 3).

Efficiencies in A.fluviatilis and P.contortus on the preferred foods exceed the value of 30% which was the upper limit set by Engelman (1966) for poikilotherms in general. Lawton (1970) has similarly shown that this limit does not apply to poikilothermic predators. Selected efficiencies in terrestrial poikilotherm and homeotherm herbivores (see DATA APPENDICES XII and XIII) show that those in the homeotherms exceed the poikilotherm efficiencies, and comparison with values given in DATA APPENDIX XI indicates that the efficiencies in aquatic grazers range between and beyond these two groups. The wider

TABLE 52. The variation in assimilation efficiencies of medium-sized A.fluviatilis (at 10°C) on different food-types.

Food Type	Assimilation Efficiency %
Bacillarophyceae	
Achnanthes	60.0 ± 3.4 *
Navicula	56.3 ± 3.2
Gomphonema	59.5 ± 2.7
Chlorophyceae	
Scenedesmus	13.9 ± 3.6
Cladophora	10.3 ± 5.0
Cyanophyta	
Rivularia	10.7 ± 5.0
Bacteria	
Species D	+

* Confidence limits = t. S/√n where t = 4.303 for 2(n - 1) degrees of freedom at the 95% level.

+ Quantity ingested too small for estimation.

TABLE 53. The variation in assimilation efficiencies of medium-sized P.contortus (at 10°C) on different food-types.

Food Type	Assimilation Efficiency %
Bacteria	
Species D	76.0 ± 2.9 *
Species E	74.8 ± 3.4
Species D + E	75.3 ± 3.5
Algae	
Navicula	21.3 **
Scenedesmus	9.0 **
Non-living Organic Material	
Lignin	1.0 **
Cellulose	5.3 **

* Confidence limits = t. S/√n where t = 4.303 for 2 (n - 1) degrees of freedom at the 95% level.

** Results from 1 replicate only.

range in aquatic microherbivores reflects the greater structural and biochemical diversity of algae when compared with terrestrial macrophytes. Assimilation efficiencies depend not only on the level of metabolic organisation of the herbivore being considered but also on their habitat situation and food supply.

The efficiencies presented in TABLE 53 regarding bacterial digestion by P.contortus compare favourably with the data of Hargrave (1970a). No other information is available on the efficiency of digestion in benthic bacterial feeders though a limited amount is available on planktonic organisms (see Calow and Fletcher, 1972; PUBLICATIONS APPENDIX III). Here the efficiencies appear to be lower than in the benthic forms. The reasons for this difference are unknown.

TABLES 54 and 55 consider the effects of both environmental temperature and snail sizes on assimilation efficiencies when P.contortus was fed on bacterium D and A.fluviatilis was fed on Navicula. Temperature appears to have little effect on snails and this has also been reported in Calanus (Conover, 1966), Daphnia (Schindler, 1968) and Pyrrhosoma (Lawton, 1970). Widdows and Bayne (1971), however, have found an inverse temperature dependence in Mytilus , and absence of a temperature effect in snails is surprising in view of the usual temperature sensitivity of digestive enzymes.

Size also appears to have little effect on the assimilation efficiencies in snails although efficiencies are significantly higher in the spat. A number of workers have reported a negative relationship between assimilation efficiency and body size in other invertebrates (e.g. Phillipson, 1960 a and b; Quasrawi, 1966; Schindler, 1968). Other workers, however, have demonstrated a positive relationship (e.g. Wiegert, 1964; Chlodny et. al., 1967) and yet others have shown size independence (e.g. Sorokin and Panov, 1966). The nature of the relationship which applies,presumably depends on age-specific changes in enzyme secretions and the form of the gut surface/body size (e.g. weight) allometry. Age-specific changes in the efficiency of food comminution and the quality of food ingested may also be involved.

FIG. 90 shows the relationship between ingestion rate and assimilation efficiencies of medium sized P.contortus and A.fluviatilis fed on various food types at 10°C. Both species obviously eat more of the less well assimilated food materials when foods are offered in pure culture. Schindler (1971) has shown a similar relationship in the

TABLE 54. The effects of temperature and body size on the assimilation efficiency of A.fluviatilis on Navicula.

Size ** \ Temperature °C	4	10	18
Large	-	56.6 ± 5.0 *	-
Medium	60.0 ± 5.3 *	56.3 ± 3.2	59.0 ± 4.6 *
Small	-	55.6 ± 3.9	-
Spat	-	74.7 ± 4.8	-

TABLE 55. The effects of temperature and body size on the assimilation efficiency of P.contortus on Bacterium D

Size ** \ Temperature °C	4	10	18
Large	-	74.0 ± 3.0 *	-
Medium	76.3 ± 3.2 *	76.0 ± 2.9	78.3 ± 2.62 *
Small	-	76.9 ± 4.0	-
Spat	-	94.0 ± 2.1	-

* Confidence limits = t. S/√n where t = 4.303 for 2 (n - 1) degrees of freedom at the 95% level.

** Size specifications defined in SECTION 5. 5A.

herbivorous zooplankton, Diaptomus,and has attributed this phenomenon to the maintenance of a constant food energy input (i.e. across the gut wall) in the face of variability in the quality of the food supply. The extent to which this control is maintained with time is not yet known.

It has already been noted that the order of food preference is positively correlated with efficiency of digestion in P.contortus and A.fluviatilis. Snails clearly seek out those food types that will provide most energy per mouthful ingested or alternatively the greatest energy returns per energy expended in searching and processing. This strategy is widespread (Ivlev, 1961) and has obvious selective advantages.

5. 7. The Effect of Lignin on the Ingestion and Digestion of Bacteria by P.contortus

A. INTRODUCTION

P.contortus consumes detritus but is only able to make efficient use of the bacterial fraction of its food supply. Nevertheless, in nature, P.contortus must inevitably ingest both the utilisable and non-utilisable detrital fractions because of their intimate intermixture. From this point of view the non-utilisable fraction can be considered both as a "food-carrier" and a "food-diluent". It is, therefore, necessary to consider what effect ingestion of the "food-carrier" has on the utilisation of the true food material i.e. the bacteria. In the following experiments this relationship is considered with respect to an association between bacterium D (true-food) and lignin (food-carrier).

B. METHODS

A single culture of bacterium D in Knight and Proom's (1950) medium was labelled with 14C and 51Cr in the usual manner (see PUBLICATIONS APPENDIX III). After 1 week three 25ml. aliquots were transferred into separate, sterile, conical flasks. A further 10ml aliquot was removed, filtered, dried and weighed to give the approximate concentration of bacteria per unit volume of culture. On the basis of this figure sufficient sterilised lignin powder was added to the three, 25ml. aliquots (held at 4^0C to suspend growth) to provide solutions containing 100, 300, and 500% dry weight lignin to dry weight

bacteria. The filtrates of 5ml. aliquots of the resultant solutions were fed to snails in the usual manner. Groups of 5, satiated, large sized individuals were used at each lignin concentration and estimations were made over a 6h. interval. Feeding was also considered on bacterial filtrates, not mixed with lignin.

A single control filter carrying food but not subject to grazing was used for each solution. These, together with subsamples from other solutions derived from the same original culture, but containing 100, 50 and 0% dry weight lignin to bacteria enabled estimation of the self absorption effect of lignin during G.M.-tube measurements. Self absorption was, in fact, negligible (see FIG. 91) so that specific activities estimated from the original bacterial culture could be used to estimate the weights of bacteria offered (from controls) and subsequently eaten (from experimental discs). Actual gravimetric measurements on dried control and experimental discs after feeding allowed an estiamtion of total food ingested. Assimilation efficiencies of the bacterial food component were estimated using the 14C-51Cr technique.

C. RESULTS AND DISCUSSION

Results from the feeding experiments are presented in TABLE 56. Column 2 gives the average ash-free dry weight of the total food consumed (estimated gravimetrically), column 3 the average ash-free dry weight of bacteria consumed (estimated isotopically) and column 4 the average weight of lignin consumed (estimated by difference). Assimilation efficiencies of bacteria are contained in column 5.

The results indicate that addition of a "food-diluent" (lignin) does not affect the actual input of true food (bacteria). Furthermore the amount of diluent ingested remains relatively constant and independent of the amount offered. Thus snails appear to compensate for the presence of a diluent by increasing their ingestion rate and also by selectively ingesting bacteria. The digestion of bacteria is not affected by the presence of lignin.

In contrast to the above results the addition of diluents to the rations of both sheep and cows seems to reduce voluntary food intake and also the digestibility of the true-food materials (see review by Dinius and Baumgardt, 1970). Indigestible particulate matter, however, stimulates both ingestion and digestion in certain protozoa

TABLE 56 The Effect of Lignin on the Ingestion and Assimilation of Bacteria by Large P.contortus at 10°C over a 6h. Interval. The results are expressed in terms of a single individual.

1	2	3	4	5
% Lignin to Bacteria	Ash-free dry weight (mg.)of total food eaten *	Ash-free dry wt.(mg) of bacteria eaten *	Ash-free dry wt.(mg) of lignin eaten	Assimilation Efficiency
500	58.0 (±4.9)	24.2 (±2.3)	23.8	76.3
300	57.8 (±5.1)	24.3 (±2.1)	23.5	76.2
100	52.5 (±3.3)	26.0 (±2.5)	26.5	76.0
0	-	25.9 (±2.9)	-	76.7

* confidence limits = t. S/√n where t = 2.776 for 4, (n-1) degrees of freedom at the 95% level.

(Rickets, 1972). Interference between diluent and true food during digestion may be avoided in snails by predigestive separation of these fractions at the level of the crop-gizzard complex where ciliary sorting occurs.

The discrimination between bacteria and lignin apparently shown by P.contortus is surprising in view of their intimate association. The question therefore arises as to whether bacterial selection is an experimental artifact. To test whether this phenomenon occurs in the field the relationship between the ratio of bacteria to detritus on the natural substratum at Ha Mire and in the guts of snails collected from the field was investigated. Collections were made in May, 1971. Detritus was extracted from 5 haphazardly chosen stones in the usual way. The gut contents of 30 snails taken from these stones were squeezed out into 10ml. of sterile distilled water and this extract, together with 10ml. subsamples of the stones extract were subject to automatic stirring for 12h. to dislodge bacteria and to provide some consistency in detrital particle sizes.Three smears were made from each sample and these were Gram stained, following heat fixation. Twenty haphazardly chosen, and non-repeated fields were observed and were scored on the presence or absence of bacteria and/or detritus. Refractive calcareous particles were ignored. TABLE 57 shows the summed scores for each sample and indicates that the ratio bacteria/detritus increases in the snail guts. The technique is crude, and

doesn't offer absolute proof, but nevertheless suggests selection of bacteria by P.contortus in nature.

TABLE 57. Comparison of the Relative Proportions of Bacteria and D Detritus in Snail Guts with those Available on the Substratum

	Fields with Bacteria	Fields with Detritus
Stone Extracts	62	91
Gut Extracts	97	33

This species probably selects and ingests detrital portions which are heavily infected with bacteria. Colonial aggregation of bacteria is known to occur on natural substrata (Meadows and Anderson, 1966; Bott and Brock, 1970) and would facilitate this process.

In summary, the presence of indigestible food material intermingled with the digestible fraction does not appear to impair ingestion or assimilation of the latter. Snails accommodate by the selective ingestion of bacterial-rich food portions and by increasing their overall ingestion rate. Interference from the detrital material during digestion is probably prevented by strict separation of digestible from indigestible fractions in the crop-gizzard apparatus.

5. 8. Absorption Rates as Related to Body Size and Temperature

A. METHODS

Ingestion rates and assimilation efficiencies of P.contortus and A.fluviatilis were measured at 3 different temperatures, i.e. 4, 10 and 18°C using 14C-51Cr-bacterium D and 14C-51CR-Navicula as food. At least 30 individuals of varying lengths were used at each temperature. One adult and 5 spat were added to each feeding disc so that ingestion rates of spat represent an average calculated from 5 individuals. All groups were satiated prior to use, and the feeding experiments were carried out over 12 and 6h. intervals in A.fluviatilis and P.contortus respectively. Measurements were made in the summer of 1971, and all experiments were started at 10 a.m.

Ingestion rates have been expressed in terms of μ g., ash-free dry weight/individual/12h., so that a time correction was only necessary for the P.contortus results. The proportion of ash in bacterium D

and Navicula was taken as 12% and 40% of the dry weights respectively (see SECTION 5. 2). Adult snail tissue dry weights were estimated from the shell linear parameters using equations 3(6. 2) and 4(6. 2) and spat-dry weights were taken from TABLE 22. It was assumed that 10% of adult, and 20% of spat tissue dry weights is ash.

B. RESULTS AND DISCUSSION

There is a significant linear relationship between the absorption rate of food and individual size (mg. ash-free dry weight) when each is plotted on logarithmic co-ordinates (see FIG. 92). The equations specifying these relationships are :

for A.fluviatilis

		a		b	
at 4^0C	y =	1.26	+	0.71 ($\pm$ 0.18)x	..... 6(7. 5)
at 10^0C	y =	1.89	+	0.67 ($\pm$ 0.10)x	..... 7(7. 5)
at 18^0C	y =	2.15	+	0.70 ($\pm$ 0.12)x	..... 8(7. 5)

for P.contortus

		a		b	
at 4^0C	y =	1.20	+	0.72 ($\pm$ 0.09)x	..... 9(7. 5)
at 10^0C	y =	1.74	+	0.71 ($\pm$ 0.10)x	..... 10(7. 5)
at 18^0C	y =	2.80	+	0.72 ($\pm$ 0.09)x	..... 11(7. 5)

where y = log (μg. absorption/12h. x 100)

and x = log (tissue ash-free dry weight of snails in mg. x 100)

All the regression coefficients are more than 1.96 standard errors away from zero so that all are significant at the 95% level. None is greater than 1.96 standard errors away from the hypothetical value of 0.67 and cannot be considered as significantly different from the latter. All the regression coefficients are consequently assumed equal to 0.67 and the 'a' coefficients have been suitably modified to provide the following equations :

for A.fluviatilis

		a		b	
at 4^0C	y =	1.56	+	0.67x	..... 12(7. 5)
at 10^0C	y =	1.89	+	0.67x	..... 13(7. 5)
at 18^0C	y =	2.45	+	0.67x	..... 14(7. 5)

for P.contortus

		a		b	
at 4^0C	y =	1.25	+	0.67x	..... 15(7. 5)
at 10^0C	y =	1.78	+	0.67x	..... 16(7. 5)
at 18^0C	y =	2.85	+	0.67x	..... 17(7. 5)

The logarithms of coefficients 'a' in these equations are linearly related to temperature over the ranges considered (see FIG. 93 A and B). These relationships are summarised by the equations :

for A.fluviatilis

$$\text{Log } a = 0.014\ T^0C + 0.135 \quad \ldots\ldots 18(7.5)$$

for P.contortus

$$\text{Log } a = 0.026\ T^0C - 0.005 \quad \ldots\ldots 19(7.5)$$

The Q_{10} values are 1.38 and 1.82 for A.fluviatilis and P.contortus respectively. Both values are less than 2 and suggest partial compensation (Precht, 1958) particularly in the limpet. Widdows and Bayne (1971) have also demonstrated temperature acclimation in the food processing mechanisms of the bivalve mollusc, Mytilus.

A linear relationship between the logarithms of food absorption and tissue weight with a regression coefficient of 0.67 indicates that food input is functionally related to body surface. This was predicted on a-priori grounds by Pütter (1920) and incorporated into his growth equation as the anabolic term. Surface dependence of food input has subsequently been demonstrated empirically in mature millipedes (Glomeris marginata (Villers)) feeding on oak leaf-litter by Van der Drift (1951). He showed that food consumption (in dry weight) raised to the power of 0.67 was linearly related to individual dry weight. The constant of proportionality has been called the, "Van der Drift Constant" by Gere (1956) who found it independent of body size but dependent on temperature in cryptozoic isopods and diplopods. Dunger (1958) preferred the term, "Konsumquotient" (= 100 x "Van der Drift Constant") and again found this parameter independent of size and age, but dependent on environmental conditions such as food quality and temperature. More recently Reichle (1968) has demonstrated the application of the "Van der Drift" constant to a variety of forest floor arthropods. Coefficient "a" in equations 6(7. 5)-17(7. 5) is equivalent to the logarithm of the "Van der Drift" constant, and is temperature dependent, at least to a limited extent.

In contrast to this supporting evidence for surface dependence, Phillipson (1960b) has shown that the "Konsumquotient" changes with age in the phalangid, Mitopus morio (F). Furthermore, although Tsikhonlukanina (1967) demonstrated a linear relationship between ingestion and body weight in terrestrial isopods when these were represented on logarithmic co-ordinates, the value of the regression coefficient was significantly less than 0.67. Clearly the form of the allometric, anabolic term in Pütter's (1920) equation changes with species, conditions and possibly with the units in which body weight is determined (Reichle, 1968).

5. 9. A Comparison of Field and Laboratory Estimations of Assimilation Efficiencies and Rates in A.fluviatilis

A. INTRODUCTION

Absorption rates in the laboratory have been estiamted using a single food source, under constant conditions, and using superabundance of food material. None of these conditions is likely to pertain in the field so that it is necessary to ask to what extent the derived equations (i.e. equations 12(7. 5)-17(7. 5)) can be extrapolated into the field for predictive purposes. Food inputs (assimilation) predicted from equations 12(7. 5)-17(7. 5) have therefore been compared with those actually estimated under field conditions. Because the diet of P.contortus consists of an intimate mixture of true food and 'food carrier' and because the actual ratios between these two components are unknown, field estimation of true food absorption in this species has not been possible.

B. MANIPULATIVE TECHNIQUES

On each sampling occasion (for dates see TABLE 58, column 1) 40-50 snails were collected from Ha Mire shore, washed thoroughly, and transferred to a sealed, clean, plastic container with 2L. of tapwater and no food. The water was at 10^0C and was maintained at this temperature by immersing the plastic container in water at 10^0C in a large vacuum flask for a time equivalent to $E_{\frac{1}{2}}$ for the size class being considered. Snails were chosen so that they approximated to some predetermined, relatively constant length (see specifications in TABLE 58, column 3). Snail shells were quickly scrubbed prior to their insertion into the experimental chamber, in order to remove shell epiphytes. The

temperature of the Tarn water on collection was measured by making several probes with a mercury thermometer and averaging the readings (see TABLE 58, column 2).

Following an interval, equivalent to $E\frac{1}{2}$ at 10^0C snails were removed, faeces were decanted away and the latter were concentrated by centrifugation. The concentrated samples were dried to constant weight (in an oven at 40^0C) on pre-weighed platinum trays and were subsequently ashed in a muffle furnace (450^0C for 6h.).

C. METHODS OF CALCULATION

Assimilation efficiencies were estimated using the method of Conover (1966a) which Mason (1970a) has shown applicable to a variety of terrestrial mollusc species. Conover's determining equation is :

$$\text{Assimilation Efficiency} = \left\{1 - \frac{X/ADE}{Y/ADF}\right\} \times 100 \quad \ldots\ldots\ 20(7.5)$$

where X = wt. ash in faeces
Y = " " " food
ADE = ash-free fraction in the faeces
ADF = " " " " " food

This formulation, however, is not directly applicable to freshwater pulmonates since the faecal ash-free dry weight consists not only of egesta but also of mucus and excreta (Carriker, 1946; Calow, 1970, see PUBLICATIONS APPENDIX 1). Equation 20(7.5) must, therefore, be modified to :

$$\text{Assimilation Efficiency} = \left\{1 - \frac{X/C.\ (ADE)}{Y/ADF}\right\} \times 100 \quad \ldots\ 21(7.5)$$

Where C = proportion of faeces which are egesta.

The correction constant C has been estimated crudely using a radiotracer technique. Snails were fed on 14C-food of known specific activity. The resultant faeces were collected, dried, counted, weighed, and then ashed to determine their ash-free dry weight. Assuming that the specific activity of labelled food is not altered by passage through the gut, then the faecal 14C counts provide an estimate of the ash-free dry wt. of egesta present. The difference between this expected value and the observed ash-free dry weight of faeces represents mucus and excreta. It is further assumed that the latter have a negligible ash content. The value of C based on one experiment involving 30 individuals and at 10^0C was 94.8% for A.fluviatilis and 85.1% for P.contortus. Average

values of 95 and 85% have been used for A.fluviatilis and P.contortus respectively. The significance of this difference will be discussed in PART VIII, SECTION 3. 3). C may conceivably change with food quality and both exogenous and endogenous conditions, so that the estimates given are only crude first approximations.

The ash content of food in nature was obtained from the ash content of epilithic algae which developed on artificial substrata suspended in the Tarn over a two week period, encompassing or near to the period of estimation (see SECTION 6. 2B for techniques).

Field ingestion rates were estimated from the defaecation of ash observed over $E_{\frac{1}{2}}$ at 10^0C. This former quantity was adjusted to field conditions by correcting $E_{\frac{1}{2}}$ to the Tarn temperatures operative immediately prior to collection of the sample (see TABLE 58B column 2). Assuming continuous feeding and remembering that though the pattern of egestion is different in starved and fed individuals, the initial linear phase of gut emptying encompasses $E_{\frac{1}{2}}$ at all temperatures for all size classes of snail and for all conditions of food availability, then the amount of ash egested per day under field conditions is obtained from:

$$\text{Ash egested/day} = \frac{24}{E_{\frac{1}{2}} \text{ (under field conditions)}} \quad \ldots\ldots 22(7.5)$$

Knowing the ash content of the food and its assimilation efficiency then the rate of assimilation of food material (ash-free dry weight) under natural conditions can be calculated.

D. RESULTS

TABLE 58A compares predicted values for assimilation efficiencies with those actually observed. The former have been calculated as weighted averages by use of the following equation :

$$\bar{X} = \frac{W_1 X_1 + W_2 X_2 \ldots\ldots + W_K X_K}{W_1 + W_2 \ldots\ldots W_K}$$

$$= \frac{\Sigma W_i X_i}{\Sigma W_i} \quad \ldots\ldots 23 (7.5)$$

where i = 1, 2, ...K

W_i = % proportion of a particular food item in the snail's diet (derived from FIG. 79)

X_i = assimilation efficiency of a particular food item expressed in arcsines

$\bar{X}$ = average assimilation efficiency

In this calculation all diatoms were considered together and an average efficiency of 59% (derived from TABLES 52 and 54) was used. All blue-green, filamentous algae and unicellular green algae were assumed equivalent to Rivularia, Cladophora and Scenedesmus respectively and the appropriate assimilation efficiencies were extracted from TABLE 52. Increased efficiencies in spat were accounted for by assuming that the proportional increase was independent of food quality and was equivalent to the increased efficiency shown with diatoms as food, i.e. 74.7 or 1.28 times
58.0

TABLE 58A Comparison Between Predicted and Observed Field Assimilation Efficiencies in A.fluviatilis

Date	Observed %	Predicted %
15-1-71	60.0	57.5
16-2-71	60.0	57.0
3-3-71	59.6	46.9
23-5-71	61.0	56.6
23-6-71 *	59.7	52.6
1-8-71 *	65.1	65.8

* Spat

In all cases, except for the spat, predicted values are more variable and lower than the observed values. Mean efficiencies for each group, excluding spat and expressed in angular units, are 50.80, and 47.36 for the observed and predicted results respectively. These are not significantly different at the 95% level but are significantly different at the 90% level (t = 2.05 for 8 degrees of freedom). In consequence the differences are probably real and the lack of significance may be due to the small sample size.

The higher observed assimilation efficiency in A.fluviatilis i.e. 60% (after re-transformation) possibly represents some outcome of interaction between the food types involved and the seasonal constancy may derive from active metabolic regulation on the part of the snail. The Systems Theory principle of emergence seems to have application here (see PARTS I and X), and it may be relevant that Mason (1970a) has also reported efficiencies close to 60% in a variety of terrestrial pulmonates. In the spat, the observed and predicted

efficiencies are similar and are higher than in the adults. Both values approximate to 65% and this will be used in future calculations.

Columns 10 and 11 of TABLE 58B compare the observed rates of assimilation in samples taken from the field populations with those predicted from equations 12(7. 5)-14(7. 5). In the former case, assimilation efficiencies were assumed equivalent to 60%. In the latter case corrections for temperature were effected using equations 18(7. 5). It should be noted that this procedure involves some extrapolation beyond the 4^0C point since this temperature represented the lower limit of laboratory investigation. Columns 4-9 in TABLE 58B explain the methods of obtaining the observed values and here again some of the calculations (e.g. the reults in column 5 on 15-1-71 and 16-1-71) involved extrapolation beyond the 4^0C limit.

All the results compared in columns 10 and 11 are extremely similar except on 23-6-71 when the predicted value is approximately twice the observed rate. This discrepancy occurs at a time when oviposition is over and when adult limpets are in a senescent condition. The latter may be instrumental in reducing food input.

In summary, the major point of interest arising from the above results is that, provided food input is considered in terms of assimilation, then laboratory estimates (based on equations 12(7. 5)-14(7. 5)) provide an adequate description of the field process even though the laboratory conditions may differ considerably from the field. This equivalence must be interpreted as a result of control mechanisms tending to maintain constant assimilation irrespective of environmental variations (e.g. in food quality). The homeostatic mechanisms involved probably include changes in food preferences with starvation (see FIGS. 75 and 83), changes in ingestion rates and digestive efficiency with starvation (see FIGS. 84 and 85) and changes in ingestion rates with food quality (see FIG. 90). All these regulating processes can be considered as being mediated through the "desired" growth rate controlling subsystem (see PART VI, SECTION 4).

The above considerations may have more general applicability particularly since homeostasis is a basic feature of all living systems. If this is the case then estimates of field ingestion rates can generally be based on laboratory observation provided that assimilation efficiencies are measured under field conditions. This would greatly facilitate field estimation of ingestion since, of the elements of the food input processes, assimilation efficiency is the most readily

TABLE 58B The method of obtaining an estimate of field assimilation rates in A.fluviatilis (columns 3-9) and a comparison with the results obtained under laboratory conditions (columns 10-11).

1	2	3	4	5
Date / 1971	Temperature °C	AL mm.	ca. $E_{1/2}$ @ 10°C	$E_{1/2}$ at field temperatures
15 - 1	3.05	4.0	7h.	11.2h.
16 - 2	3.50	4.0	7h.	10.5h.
3 - 3	6.52	4.5	9h. 50mins	11.8h.
23 - 5 (oviposition)	10.10	5.0	14h.50mins	14.0h.
23 - 6 (post-oviposition)	13.21	5.5	19h.50mins	16.2h.
1 - 8	13.01	1.0	48mins	0.7h.

	6	7	8	9	10	11
Date / 1971	Ash egested/$E_{1/2}$ (µg.)	Ash egested/ 24h.(µg)	Ash in Food %	Ash-free dry wt. ingested (µg.)	observed assimilation µg. ash-free dry wt. individual^{-1} h.$^{-1}$	Predicted assimilation µg. ash-free dry wt. individ.$^{-1}$ h.$^{-1}$
15 - 1	6.30	13.41	40.12	20.02	12.01	12.62
16 - 2	14.88	26.11	39.71	26.42	15.85	15.52
3 - 3	11.32	23.11	32.20	48.67	29.20	28.90
23 - 5 (oviposition)	51.35	88.54	50.08	88.25	52.95	54.40
23 - 6 (post-oviposition)	88.70	131.41	55.01	107.47	64.80	129.10
1 - 8	1.84	11.10	51.11	10.62	6.90	6.46

measured under field conditions.

In the snail species being considered here, equations 12(7. 5)-19(7. 5) will be used to predict field assimilation. The predicted value will be reduced by 0.5 in senescent, post-ovipositional individuals, however, and it will be assumed that in this respect P. contortus behaves similarly to A.fluviatilis. In A.fluviatilis a constant assimilation efficiency of 60% will be used except for spat where a value of 65% is more appropriate. It has not been possible to estimate field assimilation efficiencies in P.contortus and the values of 76.3% (average from the results contained in TABLES 53, 55, and 56) and 94.0% (see TABLE 55) will be used for the adults and spat respectively.

5. 10. The Effect of Time of Day on Consumption Rates

In orded to test the possibility of differences in feeding rate with time of day (e.g. as demonstrated by Phillipson, 1960b for Mitopus morio) two groups of medium sized snails (for definition see SECTION 5. 5) were fed on 14C-51Cr labelled food, one beginning at 12 noon, and one at 12 midnight. Pre-treatment of snails and estimation of consumption and assimilation was as previously described. P.contortus was given bacterium D and A.fluviatilis , Navicula. Thirty individuals were considered in each experimental group and measurements were made at 10^{0}C under a natural illumination regimen. The results are presented in TABLE 59 and indicate no significant difference between the daytime or the night-time values for both ingestion rates and assimilation efficiencies.

TABLE 59 Comparison of Ingestion Rates and Assimilation Efficiencies of P.contortus and A.fluviatilis Fed at Different Times of Day

	A.fluviatilis		P.contortus	
Time	Rate of ingestion (µg. ash-free dry wt. individual^{-1} 12h.$^{-1}$	Assimilation Efficiency %	Rate of Ingestion (µg. ash-free dry wt.individual^{-1} 12h.$^{-1}$	Assimilation Efficiency %
	*		*	
12 noon	110.7 ($\pm$6.7)	61.1	61.0($\pm$4.1)	75.9
12 midnight	108.9 ($\pm$7.2)	59.8	59.2($\pm$3.8)	76.3

* Confidence limits = 2. S/$\sqrt{n}$ where n = 30.

The possibility of diurnal variations was investigated further in the field. Thirty individuals of both species were collected haphazardly at 6h. intervals from Ha Mire shore and were allowed to defaecate for a 6h. period in white enamel dishes placed on the bank. The faecal pellets so obtained were collected and their lengths were measured using a dial micrometer. It was assumed that the snail size class represented in each haphazard sample (which were taken on one day i.e. 5-10-70) were the same. Total lengths of faecal string collected, together with the ratio between the gizzard and liver string subcomponents, are listed in TABLE 60. The results again suggest that time of day has little effect on food consumption and the diurnal constancy manifest in the gizzard string/liver string ratios suggest constancy in assimilation efficiencies (see Calow, 1970; PUBLICATIONS APPENDIX I).

TABLE 60 Faecal Production (Length) in Snails Collected from Ha Mire Shore at Various Times Through the Day.

	A.fluviatilis		P.contortus	
Time Collected	Total Length Faeces (from 30 individuals (mm.)	Ratio Length gizzard string (G)/length liver string (L)	Total length faeces (from 30 individuals (mm.)	Ratio G/L
6 a.m.	120.8	0.27	218.1	0.32
12 noon	117.7	0.23	222.3	0.33
6 p.m.	122.5	0.29	220.8	0.35
12 midnight	124.3	0.27	217.9	0.31

5. 11. General Discussion And Summary

The radiotracer technique of Calow and Fletcher (1972; see PUBLICATIONS APPENDIX III) has allowed investigation on the effects of starvation, food quality, temperature, and body size on ingestion and assimilation in snails. Both P.contortus and A.fluviatilis digest preferred food types most efficiently, and when foods are offered in pure culture, eat more of the less well digested food materials. Ingestion and assimilation rates increase with starvation up to some critical starvation state when a pathological condition becomes manifest.

These phenomena are of a regulatory nature and contribute to the metabolic repertoire involved in maintaining a "desired internal-milieu". Apart from their theoretical interest and implications with regards to modelling energy-flow (discussed in PART X) these regulatory processes have practical value in that they contribute to some constancy in energy input (i.e. across the gut wall). The latter suggests the feasibility of extrapolating laboratory estimates on assimilation rates into the field, even though laboratory conditions may only roughly approximate to the conditions which apply in nature. Of critical importance from this point of view is a realistic estimate of assimilation efficiency so that field ingestion rates can be calculated from laboratory determined assimilation rates. This method will be used in PART IX for the species under consideration here.

6. THE EFFECT OF FOOD SUPPLY ON SNAIL ECOLOGY

6. 1. Introduction

A consideration of the effect of food supply on the structure and function of natural populations ideally requires information on the absolute availability of food. It has not been possible to obtain this sort of quantitative information for the two snail populations being considered here because of the complex nature of their diets and the complex inter-dispersion which occurs between their various dietary components on the natural substrata. The latter precludes making estimations on the relative contributions made by individual components of the floral array e.g. diatoms or bacterium D. Nevertheless, some indication as to the factors which influence snail population distribution and also regulation can be attained by comparing the ecological conditions in areas of high and low snail density. Here indices of food supply production in various parts of Malham Tarn will be considered in terms of relevant properties of the associated snail populations. This technique is essentially equivalent to that of Hargrave (1970b). The interaction between food supply and freshwater snails in general will also be discussed (see particularly SECTION 6. 3).

6. 2. The Effect of Food Supply on the Ecology of A.fluviatilis and P.contortus in Malham Tarn

A. THE FOOD SUPPLY NOMENCLATURE

The terminology which has been applied to aquatic algae attached to submerged surfaces is vast and has been extensively reviewed by Sládéckovā (1962). The latter worker favours use of either the term "Aufwuchs" or its English equivalent, "periphyton" as descriptive of all attached flora irrespective of nature of the substratum to which they are attached, but follows the nomenclatorial subdivisions proposed by Šrāmek-Hušek (1946 and 1947) based on the form of substratum involved. This system of classification describes stone dwelling floras as, "epilitha" and this term has been used throughout the present work not only for algae but also for bacteria and detrital materials which are found on submerged stone surfaces.

The trophic position of algae is quite clear. They stand at

the base of food chains, trapping the in-coming light energy and transforming it to organic biomass. They are involved in primary production. The trophic position of heterotrophic bacteria, however, is less clear. In that they use pre-formed organic materials they can be considered as secondary producers, but in the sense that they release energy stores which would otherwise be unavailable for higher trophic levels, they may be considered as primary producers. Since, however, bacterial production occurs intermediate between the primary and secondary types of production and because bacteria act as intermediaries between the living and non-living organic elements of ecosystems the term "intermediary" seems a more appropriate description of their production processes and will be used in the following sections. Bacteria can also be considered as intermediaries in biogeochemical cycles and the use of the term in both these senses is equivalent to its usage in physiology.

B. METHODS

Primary algal production was measured using the artificial substrate technique (see reviews by Blum, 1956; Cooke, 1956; Castenholz, 1961; Sládécková, 1962; Wetzel, 1964). This method involves suspending some artificiel substratum (e.g. a glass slide) in the aquatic habitat to be considered, and measuring the quantity of periphyton which develops on it over a given time. It provides a crude estimate of net primary production i.e. :

(Rate of gross production)-(respiration + decomposition + consumption)

but is also influenced by the rate of inoculation or colonisation of new propagules (Westlake, 1966; Wetzel, 1969). Other factors may also influence these periphytic developments e.g. substrate colour (Godward, 1934), substrate quality and texture (Hohn and Hellerman, 1963), substrate positioning (Newcombe, 1949), and manipulative losses may result in significant errors (Wetzel, 1969). Furthermore the quality of algae developing on artificial substrata need not bear any relationship to that occurring on natural surfaces (Foerster and Schlichting, 1965; Tippet, 1970). These differences are probably more distinct when the natural substrata are living (e.g. as in epiphytic situations) and the artificial substrata employed are non-living materials. Even though the above considerations provide considerable difficulties in interpretation, the production values so obtained may still be useful as indices in comparing the production potential of different locations

and it is in this sense that the method has been applied here.

The technique employed, involved suspension of perspex pots (ca. 160cm.^{2}) in the Tarn for a period of 2 weeks each month (N.B. Szczepański and Szczepańska, 1966, found this period to be optimum for growth in periphyton). Pots were filled with gravel for anchoring purposes, positioned on the bottom between stones (ca. 30cm. depth) and were secured by a terylene cord attached to a stake on the bank. Following the two week interval, pots were carefully removed from the water, sleaved, without touching, in clean 1 litre beakers for transportation, and their outer surfaces were ultimately scrubbed in distilled water to remove the attached algae. The extract was concentrated by centrifugation, dried in a silica crucible to constant weight (at 40^{0}C), and ashed in a muffle furnace for 6h. at 450^{0}C. In this way, net primary production could be expressed in terms of ash-free dry weight per unit area (μ g./cm^2) of the whole pot surface, and results were corrected to a 28-day interval. This procedure provides an index of algal production with respect to total stone surface area. Limited observations have suggested that between 40-50% of this estimate derives from the pot sides. Monthly samples were made on Ha Mire (i.e. between January, 1970 and July, 1971) when 3 pots were randomly positioned in each sector, and on station 2 (see FIG. 9 sampling dates were between January,1971 and July, 1971) when 3 pots were randomly positioned along the length of the shore. The sampling intervals were chosen so that the routine snail population sampling dates (see DATA APPENDIX I) occurred centrally within them.

Bacterial production was measured according to the method of Bott and Brock (1970). This technique is essentially similar to the algal determinations so that the same criticisms can be applied to it and again it provides an index rather than an absolute estimate of net production. Here the artificial substrata were coverslips (20 x 25mm.) which were supported by cork in perforated perspex boxes with blackened sides. Each box contained 4 coverslips and the whole apparatus (after a U.V. sterilisation procedure) was positioned beneath stones at 30cm. depth for 3 days. Following this interval boxes were removed, stored on ice and the surfaces of three of the contained coverslips were ultimately assayed for protein. This is assumed equivalent to the bacterial biomass which had developed during three days exposure. The remaining coverslip was heat fixed, Gram stained, and used for microscopical determinations.

Protein assays followed Bott and Brock's (1970) procedure which represents adaptation from Prices (1965) modification of the colorimetric method of Lowry et. al. (1951) in which the protein is made soluble as well as assayed in alkaline copper tartrate reagent. Colorimetric determinations were made in a Unicam Sp 800 at 750 nm. The extracts from each coverslip were treated separately and bacterial production as ω g. protein/cm.^{2}/day was based on the average protein compliment of the three.

Single monthly determinations were made on Ha Mire shore and these correspond to the dates on which the routine snail population samples were made. Comparative estimations were also made once (28/5-30/5, 1971) on station 2 (see FIG. 9). Here perspex boxes containing 4 coverslips were positioned under stones in the open shore (30cm. depth), and at similar depth locations under stones covered with debris (see PART 3, SECTION 5.2).

C. RESULTS

The seasonal patterns of net primary algal production (as measured by the artificial substrate technique) on Ha Mire shore and at station 2 are shown in FIG. 94. The between-season and between-habitat patterns are similar except that a higher optima occurred in 1970 on Ha Mire and the net primary production is consistently and significantly higher at station 2 (see confidence limits). It is difficult to compare the actual levels of primary production given here with those reported by other workers since the previously determined values are generally in terms of gross production and are not expressed with respect to total stone surface area. Thus the net annual primary production on Ha Mire in 1970 of ca. 591mg. organic material/m.^{2} /yr. (or ca. 236mg. C/m.^{2}/yr. assuming 40% ash-free dry weight was carbon) falls considerably short of the range 8-660g. C/m.^{2} /yr. reported by Allen (1971; see his review table, p. 110) for a variety of periphyton and planktonic "communities".

The seasonal pattern of net intermediary bacterial production is depicted in FIG. 95. There is a considerable degree of inter-seasonal stability during autumn and winter, although oscillations occur during the spring and summer months. Price and Valadom (1970) have shown similar fluctuations in the standing crop of open-water bacteria in Queen Elizabeth II reservoir. In all the bacterial samples from Ha Mire Micrococci (species D) made up at least 90% (in terms of

total numbers of cells) of the flora which developed on the cover-slips. There was no significant difference between protein production on Ha Mire and at station 2 under open water, although protein production on pots positioned under collected, decaying detritus was significantly higher than at both the other sites (see FIG. 96, and confidence limits). Algal production under detritus at station 2 was not measured but the surface colour of stones in this region indicate that algae were generally absent.

There is also some indication that algal production reduces with depth, whereas bacterial production remains relatively constant. This statement is based on one set of observations made in August, 1971, when estimations on algal and bacterial production were measured at 10 and 45cm. depth, on Ha Mire, using the techniques given in SECTION 6. 2B above. Production estimates were $85.6^{\pm}(8.3)$ and $32.7^{\pm}(3.8)$ μg. ash-free dry weight at 10 and 45cm. respectively for algae[1], and $9.9^{\pm}(1.2)$ and $10.3^{\pm}(0.9)$ μg. ash-free dry weight at 10 and 45cm. respectively for bacteria[2]. The former are significantly different, the latter are not (t (algae) = 29.6, $p \simeq 0.002$, for 2 d.f. (n-1 pots); t(bact.) = 0.83, $p > 0.01$ for 2 d.f. (n-1 c. slips)). The reduction of algal production with depth probably results from reducing light intensity. The ecological implications of these findings have already been discussed in PART IV, SECTION 3.1 and will not be discussed further here.

D. DISCUSSION

The results indicate that during 1971 net algal primary production at station 2 was approximately double that on Ha Mire, whereas there was no significant difference in bacterial production between these two situations. The difference between north and east shores at Malham has already been discussed in terms of wind/wave action (see PART III SECTION 5). Basically, the east shores of the Tarn receive a greater intensity of wave action than the north or west shores and this probably contributes to a reduction in primary algal production by scouring (see Douglas, 1958). Bacterial intermediaries, on the other hand, are less susceptible to wave action since they appear to adhere strongly to artificial substrata (Hattori, 1970) and are able to exist in the absence of light, on the protected undersides of stones. A further consequence of wave action is that detrital materials are washed onto the east shores and this phenomenon, in conjunction with the reduced algal production results in detritus-orientated food chains.

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1. expressed over a 28 day interval; 2. expressed over a 1 day interval.

Detritus also accumulates in isolated pockets on the north shores (see PART III SECTION 5) and although algal production is reduced on stones below the debris, bacterial production is increased.

TABLE 61 contrasts various population characteristics of A. fluviatilis and P.contortus in both the algal dominated (station 2) and the detrital dominated (Ha Mire and under debris cover on station 2)parts of the Tarn. Where the parameters given have been defined and presented in other parts of the thesis the PARTS and SECTIONS involved are cited. In fact the only parameter not presented elsewhere is the "condition factor". This is a measure of the extent to which individuals taken from the field can withstand controlled starvation stresses imposed within the laboratory and as such provides an index of the body stores avaialble for withstanding adverse dietary conditions. It is likely that the extent of these stores depends on the availability of external food. The "condition factor" was measured by taking a sample of 30 individual snails, in each species, from the various field locations described above in February 1971, and subjecting each cohort to starvation in the laboratory at 18^0C. All experiments were run concurrently and each cohort of 30 was maintained in 2 litres of tapwater. The water was changed daily and containers were scrubbed out regularly. The mean survival time (in days) was assessed for each cohort.

The physical and chemical characteristics which pertain on Ha Mire and at station 2, as with the other littoral situations at Malham, are probably very similar. Thus the differences presented in TABLE 61 must be considered in terms of wave action, detritus collection and concomitant variations in algal and bacterial production. It is assumed that estimates of the latter parameters on artificial substrata reflect food supply production on the natural stone surfaces with respect to both A.fluviatilis (the algal feeder) and P.contortus (the bacterial feeder).

TABLE 61 shows that A.fluviatilis dominates the gastropod "communities" at STATION 2 but ranks second on Ha Mire shore and its relative abundance is considerably reduced on stones below the debris collections at STATION 2. The absolute density of the limpet (in April) was also highest at STATION 2 and was reduced by about 25 fold in other situations. These differences cannot be interpreted in terms of wave action because of all the British freshwater Gastropoda, A.fluviatilis is best adapted for rough conditions. Its reduced density on Ha Mire shore could, therefore be interpreted in terms of food shortage, a

TABLE 61. A comparison of various properties of populations of P.contortus and A.fluviatilis in different parts of Malham Tarn.

Parameter \ Tarn Location	Ha Mire Shore	Station 2 (No Cover)	Station 2 (Debris Cover)	Location in Thesis
P.contortus				
1. Ranking order (in gastropod"community")	1	2	1	PART III SECTION 5
2. Relative abundance(in gastropod"community")	54.0%	2.4%	29.7%	
3. Density(no./10,000 LP in April, 1971)	11.13±1.51	5.30±0.46	10.21±.82	FIG.45B
4. Natality				
Standard C	9.72	7.62	-	FIG.35
Standard E/C	3.48±0.09-3.50±0.06	3.51±0.07		TABLE 13
5. Recruitment				
Spat density-Aug.'71				
Adult " -Apr.'71	7.90	4.62	-	TABLE 13
6. Body size (mm.MD May, 1971)	2.663±.096	2.632±.106	2.652±.141	TABLE 27
7. Condition factor (mean days survival of a cohort of 30, subjected to starvation at 18°C)	25.5±3.2	24.4±4.1	29.7±6.2	-
A.fluviatilis				
1. Ranking order(in gastropod"community")	2	1	5	PART II
2. Relative abundance(in gastropod"community")	35.0%	70.0%	0.8%	
3. Density(no./10,000LP in April 1971)	3.81±0.77	50.92±2.21	1.1±.21	FIG.45A
4. Natality				
Standard C	12.16	9.13	-	FIG.35
Standard E/C	2.60±.03 - 2.53±.09	2.57±.10	-	TABLE 13
5. Recruitment				
Spat density-Aug.'71				
Adult " -Apr.'71	7.90	4.62	-	TABLE 13
6.Body size(mm.AL-May'71)	4.853±.208	6.16±.200	-	TABLE 27
7. Condition factor(mean days survival of cohort of 30,subjected to starvation at 18°C	10.6±3.1	20.9±5.1	-	-

postulate which is supported by the significant reduction in its body size ($d = 6.45$, $p < 0.001$) and a 2-fold reduction in its "condition factor" in this region. Whereas the reduction in the latter is directly proportional to the reduction in the index of food supply (i.e. net algal production) on Ha Mire when compared with STATION 2, limpet density is reduced by a factor of more than a half and body size by a factor of less than a half. The former can be interpreted as a result of additional deleterious effects of other non-favourable conditions (e.g. the presence of more silt) and the latter in terms of homeostatic mechanisms tending to adjust growth to some desired level irrespective of environmental food supply perturbations (see PART VI, SECTION 4). Indeed the regulatory nature of the growth processes, by disproportionately increasing growth in the face of food shortage, might be expected to reduce individual survival by denying food to less fit individuals through intraspecific competition. The whole problem as to which of the two possible strategies, i.e. the reduction of individual size or the reduction of population density, which can occur in natural populations in the face of food shortage may be reconciled in terms of the relative strengths of the control mechanisms involved at the individual level to produce a "desired" growth rate and at the population level to produce a "desired" density level.

The natality (in terms of Standard C and Standard E) and recruitment (i.e. spat density (Aug. '71)/Adult density (Apr. '71)) in A.fluviatilis are more difficult to explain in terms of the food limitation hypothesis. In both cases the parameters are lowest on shores where food production is apparently greatest. This, however, may result from inverse density dependence since both fecundity and total spat recruitment may be adversely affected by high adult density (see PART V, SECTION 4. 8). It should also be noted that Calow (1972, see PUBLICATIONS APPENDIX IV) has shown on theoretical grounds and also by reference to some empirical evidence (for P.contortus) that fecundity in snails may, to some extent, be insensitive to food supply perturbations.

P.contortus has greatest relative abundance on Ha Mire shore and under debris cover at STATION 2, but has a reduced relative abundance along the rest of STATION 2 and most other north shore situations (see also FIG. 9). Density is similarly reduced on the north shore situations when compared with Ha Mire. These differences cannot be ascribed to food supply limitations since FIG. 97 shows that bacterial

production is similar on Ha Mire shore and at STATION 2, although it does significantly increase under the debris cover. Condition factors and individual sizes at these stations are also less variable than in A.fluviatilis.

It is possible, however, to involve the operation of inter-specific competition for oviposition site between A.fluviatilis and P.contortus to explain the differences in relative abundance and absolute density which occur in various parts of the Tarn. The possibility of competition for oviposition site has already been noted (see PART V, SECTION 4. 4B) and the outcome seems to be in favour of the limpet. It was suggested earlier that the lower density of A.fluviatilis (possibly as a result of food supply limitations) on Ha Mire either reduces the intensity of this competition or lessens its subsequent effect on P. contortus. At STATION 2, however, the situation may be different since A.fluviatilis is more dense and conditions favour its existence. Here competition may be operative and in the absence of a balancing effect (see PART V, SECTION 4. 4B) P.contortus densities would naturally become reduced, perhaps even to the point of extinction, were it not for the refuges provided by the debris-covered stones, which allow escape from competition. In support of this hypothesis observations on egg capsule standing crops on 20 stones (longest length 10cm.) from a portion of STATION 2 covered over with detritus, and an adjacent portion which had no cover but which was at the same depth (20cm.) indicated a higher density of P.contortus capsules under the debris (24.9 ($\pm$ 4.8)/debris covered stone : 9.9 ($\pm$1.3)/non-covered stone) and a greater proportion of capsules on smooth stone surfaces (i.e. 69.7% on the debris covered sample, 39.1% on the non-covered sample). The ratio of rough to smooth stones was approximately the same in each sample and represented ca. 50% of the total stone surfaces considered. The attractive value of the detritus accumulations on STATION 2 to P.contortus adults probably results primarily from the higher food supply which occurs there and avoidance of competition is probably a secondary outcome. A.fluviatilis is precluded from these sites by both the lack of food and the silty conditions.

Taking all the evidence together a number of general, and to some extent tentative statements can be formulated to account for the major distribution and regulation in populations of P.contortus and A.fluviatilis at Malham.

Firstly, the major distribution of the limpet and its density

in various parts of the Tarn appears to be governed by food supply. The algal food supply is apparently less on Ha Mire shore than at STATION 2 so that food supply may be involved in population regulation in the former case. Furthermore, this statement may apply to all the east shore stations which have been considered.

Secondly, the relationship between the major distribution of P.contortus and the bacterial food supply is less obvious. There is, however, a negative correlation between its abundance and that of A. fluviatilis and this has been interpreted in terms of interspecific competition for oviposition site which operates in such a way that competition is most intense when the density of A.fluviatilis is greatest. Coexistence between P.contortus and A.fluviatilis is allowed on Ha Mire shore because over most of the year other conditions are relatively unfavourable for A.fluviatilis, when compared with P.contortus (see PART V, SECTION 4. 4B). At STATION 2, however, where conditions favour the limpet, competition is more intense, and coexistence would be tenuous were it not for the refuges provided by the debris-covered stones. Thus the density of P.contortus at this location critically depends on, and may be regulated to some extent by the frequency of occurrence and extent of the debris-covered refuges. It would be interesting to note the effect of removal of these sites from all the north shore situations , on the density of P.contortus.

6. 3. The Phylogenetic, Physiological and Ecological Implications of Cellulase Distribution in the Freshwater Gastropoda

A. INTRODUCTION

A major conclusion which arose from Boycott's (1936) review was that what is good for one species of snail is good for them all and in favourable places one finds a large number of species. This implies a considerable degree of niche overlap in terms of the "n-dimensional hyperspace" concept of Hutchinson (1965; see also Wuenscher, 1969) and poses interesting problems with regards to competition and the so-called "Gause Hypothesis".

Although there is considerable morphological similarity between snail species with regards to their general body form and also radular construction (Hyman, 1967) differences in feeding behaviour do occur. Thus, in the present context P.contortus was found to be a detritophage apparently only being able to make use of the bacterial fraction of

its food supply and A.fluviatilis was found to be a microherbivore which prefers epilithic diatoms. Elsewhere, Calow (1970; PUBLICATIONS APPENDIX I) has shown that L.pereger obtusa , feeding on epiphytes, prefers and selectively ingests green algae. Furthermore, the preferred food materials are invariably digested more efficiently than the rest (see SECTION 5. 6, and Calow, Ibid.). The implications are that niche separation is dependent on physiological rather than morphological adaptations and that the former are possibly related to the quality and quantity of enzyme secretion. It is the purpose of this section to investigate this hypothesis innterms of cellulase secretion.

B. METHODS

i) Enzyme extraction : All snails for the study were obtained from both the weed bed and litoral situations at Malham Tarn. On collection individuals were starved for 2 days to effect gut clearance, killed in a freezing mixture and were subsequently stored,in-tact, (at - 20^0C) before extraction. Enzyme extracts were made either from whole animals or from various parts of the gut (i.e. the crop-gizzard apparatus and hepatopancreas) dependent on the size of the species involved. All dissection was carried out in iced 0.1M phosphate buffer (pH 5.5) and subsequent homogenisations were carried out in the same strength buffer solutions (1 volume tissue : 1 volume buffer). Cell debris was spun down (6000rpm. for 10 min.) and the supernatant dialysed in cellulose nitrate sacs for 24h. to remove sugars. After 24 hours dialysis the extracts were re-centrifuged to remove any precipitate and were stored (for no longer than 2 days) at 4^0C.

ii) Preparation of Substrate : The substrate employed was swollen cellulose. This was prepared by dissolving wet cotton wool in 65% H_2SO_4 at 0^0C and precipitating it after 2 min. in 15 times its own volume of water. The resulting milky suspension was neutralised with 1N NaOH and was washed 6 times with 5 volumes of water. This suspension was dialysed (method as above) for 72h. against tapwater and for another 72h. against distilled water. The cellulose obtained is of type II i.e. it is crystalline but completely hydrated (Koopmans, 1970).

Cellulose breakdown is a complex process involving several enzymic factors, and not all are necessarily present in a cellulose degrading organism (Siu, 1951; Cowling, 1963). Use of swollen cellulose in the current work takes no account of the presence of a swelling

factor in the molluscs considered (Koopman, Ibid.).

iii) Enzyme assay procedures : Activity measurements were made by estimating the reducing sugars (as glucose), liberated from the substrate, by the Nelson (1944) colorimetric method using the Somogyi (1952) alkaline copper reagent. 4ml. of enzyme extract were added to 50mg. of swollen cellulose in 1ml. of 0.1M phosphate buffer (pH 5.5) and all were incubated for 6h. at 4^0C. These conditions were optimum for cellulase activity in extracts derived from other molluscs (Koopman Ibid.). The reaction was stopped by adding 1ml. of 0.1N Na OH. Blank incubations were made using the enzyme extract without cellulose and corrections were subsequently applied to the actual determinations, for the small amount of reducing sugar present.. The protein concentration in the original extract was estimated on a separate subsample (4ml.) by the method of Lowry et. al. (1951).

iv) Estimations on the assimilation efficiencies of each snail species with respect to green algae : The efficiency by which snails digest green algae was used as an index of their ability to digest and assimilate cellulose. Scenedesmus was used as food supply because it was available in stock culture (see SECTION 3. 3A) and because it appears to have comparatively thick cellulose walls which increase its resistance to herbivorous grazing (Round, 1959). The assimilation efficiencies were estimated according to the technique of Calow and Fletcher (1972, see PUBLICATIONS APPENDIX III). All snails except A.fluviatilis were starved for 3 days at 10^0C prior to use and determinations were carried out at 10^0C. It was assumed that all snails absorb ca. 10% 51Cr as in P.contortus and A.fluviatilis. Data concerning the last species has been extracted from TABLE 52.

C. RESULTS

The results on both cellulase activity and digestive efficiency estimations are presented in TABLE 62. Enzyme activity has been expressed as :

$$\frac{\mu g. \text{ reducing sugar/ml. incubation mixture}}{\text{mg. protein/ml. extract}}$$

and assimilation efficiency as a percentage.

Stone and Morton (1958) have reviewed the cellulase activities

TABLE 62. Cellulase activity and assimilation efficiency (with respect to Scenedesmus) in various species of freshwater gastropod.

Species	Cellulase Activity[1] Whole Organism	in gut	in Hepato-pancreas	Assimilation Efficiency re. Scene-desmus %
Pulmonata				
L.stagnalis	-	275	270	76.0
L.pereger	-	246	210	71.5
P.fontinalis	-	104	96	39.1
A.fluviatilis	28	-	-	13.9
P.albus	40	-	-	26.0
P.contortus	32	-	-	7.7
P.planorbis	-	151	182	46.9
Prosobranchia				
B.tantaculata	-	281	284	89.0
H.jenkinsi	269	-	-	78.0
V.cristata	340	-	-	92.4

1. Defined in the text.

in the gut extracts taken from a variety of molluscs of which one was L.stagnalis. Their activities, for the latters species, expressed in the same units as defined above, were 272 and 263 in the crop-gizzard apparatus and hepatopancreas extracts respectively and these values are extremely similar to the ones presented in TABLE 62 for the same species. Their methods were almost exactly the same as those used here.

The gut extracts from the different snail species show differences in their cellulase activities. This reflects some underlying physiological variability in the species considered. Furthermore, there is a positive correlation between cellulase activity and the ability of a particular species to digest Scenedesmus. This is shown in FIG. 97. No line is drawn through the points in the figure because the theoretical relationship between enzyme activity and digestive efficiency is not known. A simple linear relationship is, however, suggested and a cause-effect association is implied.

D. DISCUSSION

Cellulases have been found in a wide range of the Gastropoda, although the freshwater representatives have generally been neglected (see review by Stone and Morton, Ibid.). The latter workers, for example, considered two freshwater species i.e. L.stagnalis (see C above for activities) and P.corneus in which digestive-gland extracts had a cellulase activity of 243 units. The ultimate source of cellulase i.e. from bacterial or snail tissue, however, remains conjectural even in the classical case of Helix pomatia and this difficult problem has not been pursued here. High cellulase activity in the hepatopancreatic extracts of the freshwater snails, from which this tissue could be isolated, is nevertheless suggestive of an endogenous origin.

The results presented in TABLE 62 and FIG. 97 conform to the previously reported findings on dietary preferences and on the fact that snails tend to prefer food-stuffs which are easiest to digest. Thus Calow (1970; PUBLICATIONS APPENDIX I) has shown that L.pereger obtusa seeks out, prefers, and is able to digest green algae better than other algal types. It was suggested that this trait may apply to the Lymnaeids in general, and TABLE 62 shows that this group has a high cellulase activity. A.fluviatilis, however, has a low cellulase activity and tends to prefer epilithic diatoms which do not have a

cellulose wall but do have a tough, protective siliceous shell. Casual observation has suggested that the gizzard musculature is better developed in this species so that the emphasis seems to have shifted from that of chemically digesting cellulose walls to that of mechanically rupturing diatom shells. Cellulase activity in the Planorbidae is more variable than in the other groups considered. The larger species e.g. P.planorbis and P.corneus have an active cellulase and assuming a detritophagous habit (see Boettger, 1944) may be able to make some use of the non-living organic detrital fraction (i.e.cellulose), whereas the smaller species, like P.contortus, have a low cellulase activity and this may result in (or be the result of) a bacterial feeding mode.

The original molluscan feeding habit was almost certainly of a generalised microherbivorous type (Graham, 1955; Morton, 1958) in which a cellulase would be necessary (Stone and Morton, Ibid.). The high cellulase activity of the prosobranchs given in TABLE 62 is not surprising, therefore, in view of the fact that these gilled species are nearer to the basal stock than the pulmonates. Using this reasoning the less specialised condition of the Lymnaeidae and the Physidae with regards to their cellulase activity makes them more primitive than the Ancylidae or the Planorbidae. The variability of cellulase activity in the Planorbidae conforms to the general heterogeneous nature of this family (Hubendick, 1955). The scheme of relationships which emerges (see FIG. 98), corresponds to the scheme proposed by Hunter (1956) on other grounds.

In summary the results presented tend to support the hypothesis (see A above) that in freshwater snails niche separation depends on a physiological rather than morphological radiation. It would appear that morphologically, snails have reached an adaptive peak and that subsequent divesification has occurred via physiological adaptations. The same situation applies in Drosophila (Dobzhansky, 1970) and possibly in the nematodes.

Although the physiological variations discussed here are limited to molluscan feeding behaviour, many ecologists feel that this dimension of the niche hypervolume is critical in determining the presence, absence and intensity of competition between species (Weatherly, 1963; DeBach, 1966; Miller, 1962). Furthermore,differences in food requirements may impose subtle differences on micro-dispersion patterns e.g. PART IV, SECTION 6 , which lead to corresponding spatial separation

in snail species involved. From this point of view it is interesting to note that Harman (1972) has found a convincing relationship between substrate diversity and species diversity in various freshwater snail "communities". Thus the problem posed by Boycott's (1936) observations (see A above) can be reconciled in terms of physiological variations which lead to distinctions in the food, and possibly also the living-space requirements of different taxonomic groups.

PART VIII

ENERGY LOSSES IN A.FLUVIATILIS AND P.CONTORTUS

1. INTRODUCTION

Energy losses form an important functional property of all natural populations. Energy may be lost in either a biologically useless state (e.g. as heat) or alternatively in a potentially useful form (e.g. as excretory material). In the first case energy is not only lost from the individual or population concerned, but also from the ecosystem in which it occurs and for that matter from the whole biosphere. In the second case the energy released in potential form is still available to decomposers.

Heat loss contributes to the entropy content of the universe and on the basis of the Second Law of Thermodynamics is to be expected at all levels of the biological hierarchy (i.e. from subcellular particles to individuals) since all living, organic entities are involved in energy transformations. Within living organisms, however, there is no one source of entropy production, since organismic metabolism consists of a conglomerate of energy transforming processes. Three major classes can, nevertheless, be distinguished, and these form useful operational divisions for considering metabolic heat release at the organismic level. Thus entropy production is associated with the metabolic transformations involved in maintaining living organisms at a fixed distance from the equilibrium point of maximum entropy (measured in resting metabolism - see Bertalanffy, 1952); it is associated with the metabolic transformations involved in the work of movement (measured in active metabolism), and it is also associated with the metabolic transformations involved in processing assimilated food (measured as specific dynamic action - see Brody, 1945). The latter has been identified with the entropy term $T \Delta S$, in Gibbs free energy equation, by Phillipson (1966) although this notion has been criticised by Mann (1967).

The biologically useful products lost from individual or population systems are usually in the form of excretory materials. These represent assimilated matter and energy which is in excess of metabolic requirements. Defaecatory materials are not included in this category since the gut merely represents an extension of the external environment into the body of the organism concerned, and although the passage of indigestible materials through the digestive tract may have profound and biologically important effects on the biochemical quality and physical structure of the matter involved,

the contained energy remains unchanged.

In snails a further significant source of energy loss occurs in the form of mucus. This is used in locomotion and also for binding and compacting faecal products. The latter prevents fouling of the head apparatus in the torted condition.

The various routes and rates of energy loss will be considered in the following sections. Heat loss is a function of respiration and will be considered as such in SECTION 2. Some attempt at partitioning of total energy output has been made in SECTION 2. 4 where the effects of food processing and movement on the respiratory processes have been considered. Excretory losses are considered in SECTION 3 and mucus losses in SECTION 4.

2. RESPIRATION IN P.CONTORTUS AND A.FLUVIATILIS

2. 1. Techniques

A. AIMS

The purpose of the work presented in this section was to discover that respirometric technique which would be most convenient for use with A.fluviatilis and P.contortus. Convenience used in this sense must be judged with respect to :

i) accuracy

ii) effort required to carry out a large number of observations

iii) artificiality in terms of the natural conditions under which snails exist.

Three techniques have been considered from these points of view i.e. the micro-Winkler (a chemical method), the Warburg (a gasometric method) and the oxygen electrode technique (a polarographic method).

B. METHODS

Suitability tests were carried out using snails collected in February, 1971. Three groups of 45 individuals (5.0mm. AL in A. fluviatilis and 3.0mm. MD in P.contortus)were acclimated at 10°C for 7 days in the presence of food (see PART VII, SECTION 5. 4 for methods) before respirometric determination. Snail shells were scrubbed before use to remove algal periphyton. All measurements were made through the day, and are expressed in terms of ul. of oxygen at S.T.P.

i) The micro- Winkler technique : Three snails were inserted into each of 15 pyrex vials (6 x 2cm.) filled to the brim with de-chlorinated, aerated tapwater at 10°C. Vials were sealed with polythene stoppers and vaseline and were left for 3h. in a thermostatically controlled bath at 10°C. Water samples were subsequently removed using syringes (Krogh, 1935) which were inserted directly through the thin-walled stoppers of the inverted vials. Two sets of controls were employed. One, consisting of 2 vials treated in the same way as the experimental group but containing no snails was sampled at the beginning of the experimental period, and the other, also consisting of 2 vials, was treated in the same way but was sampled at the end of the experiment. All vials were covered with tin foil so that experiments were effectively carried out in the dark. Titration methods were essentially those of Fox and Wingfield (1938) but included the sophistications of Carpenter

(1965 a and b) and Carrit and Carpenter (1966). Differences in oxygen concentrations in the control vials over the experimental period (which presumably derives from bacterial respiration) was less than 1% and was ignored. The difference between the oxygen concentration in the control and experimental vials was assumed equivalent to snail respiration.

ii) The Warburg technique : the methods used followed the classical techniques described by Umbreit et. al. (1946). The reaction flasks were 25ml. capacity and each was filled with 5ml. of dechlorinated, aerated tapwater at 10^0C. 20% KOH was used to remove CO_2 . Three snails were inserted into each of 15 reaction flasks and manometric measurements were made at 10 min. intervals over a 1 hour period. The oxygen uptake with respect to two thermobarometers was assumed equivalent to snail respiration. All the flasks were covered with tin foil to prevent the access of light.

iii) The oxygen electrode technique : Polarography measures dissolved oxygen from its rate of molecular transfer to an irreversible platinum electrode maintained at a negative potential to the solution. When this current is established under conditions of controlled stirring, the rate of molecular transfer, and thus the electrode current, becomes proportional to the concentration of dissolved oxygen. The amount of oxygen used up during the process is extremely small and can be ignored. This apparatus[1] operates at a fixed polarisation voltage of ca. 0.7v. (for circuit diagram of polarising unit, see FIG. 99). Oxygen diffuses through a thin (ca. 0.001cm.) teflon membrane which is permeable only to oxygen. The Pt/O_2 half cell of the electrode is joined to a reference Ag/AgCl half cell by an electrolyte bridge consisting of a layer of lens tissue soaked in saturated KCl. After setting up, the electrode becomes very stable within ca. 12h. A small flea with a metal core and glass surrounds was rotated within the reaction chamber to produce constant stirring. A platform consisting of a meshwork of platinum wire prevented the snails from falling onto the flea. The reaction chamber had a capacity of 5.0ml. and was filled with de-chlorinated, aerated tapwater at 10^0C. A water jacket surrounding the whole apparatus enabled temperature control.

The electrode current (I) is determined from the following equation (see Kay, 1964) :

1. A "Rank" oxygen electrode was used (Rank Bros., Bottisham, Cambridge.)

$$I = i + KC / FZ \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 1(8.2)$$

where i = current at zero oxygen content

C = oxygen concentration (g. moles/ litre)

F = Faraday's constant (charge/g. equivalent)

Z = The number of electrons involved in the reduction of 1 molecule of oxygen

K = A coefficient which depends on molecular transfer (g. moles/sec./unit conc.)

In determining C, the parameters I, i and to a lesser extent Z are easily calculated but K is extremely intractable to exact computation so that electrode calibrations must be empirical.

Calibration was carried out at 10^0C using various known mixtures of air-saturated and nitrogen-saturated (de-oxygenated) tapwater solutions. Full scale deflection of the potentiometer was fixed at complete saturation and zero deflection was fixed at complete de-oxygenation. FIG. 100 shows a plot of the percentage deflection of the potentiometer versus the percentage saturation of the water samples used. The electrode response between the two fixed points was linear and this linearity has been assumed at other temperatures employed.

The oxygen consumption of acclimated snails was determined on groups of 3 individuals. Experiments were carried out over a 3h. interval and the reaction vessel was covered over with tin foil. Respiratory rates, in terms of oxygen consumed, were calculated from the potentiometer deflection and knowledge of the oxygen concentration of the original saturated tapwater solution which was added to the reaction vessel.

C. RESULTS AND DISCUSSION

Respiratory rates (expressed as μL./individual/h.) derived from each technique in both A.fluviatilis and P.contortus are presented together with their 95% confidence limits in TABLE 63. The variance ratios(F) were calculated on the assumption of a completely randomised experimental design and indicate that the results obtained from each technique are not significantly different at the 95% confidence level. Thus all the methods are equally suitable in the sense that they provide roughly the same results. In this event the effort required to operate the respirometers became an important criterion of suitability and from this point of view the semi-automatic nature of the oxygen electrode

TABLE 63. Comparison between the respiratory rates, obtained on standard individuals, from different respirometers.

Technique		Ave. Resp. Rate (µ L./ h./ind.)	± *	F	p
A.fluviatilis	Micro-Winkler	0.72	0.10	0.49	> 0.05
	Warburg	0.69	0.13		
	Oxygen electrode	0.71	0.09		
P.contortus	Micro-Winkler	0.35	0.05	0.72	> 0.05
	Warburg	0.37	0.04		
	Oxygen electrode	0.39	0.07		

* Confidence limits = t. S/√n where t = 2.145 for 14 degrees of freedom at the 95% level.

method meant that it was preferable to either the micro-Winkler or Warburg techniques.

The only disadvantage arising from use of the oxygen electrode was that measurements could not be made over long intervals of time so that allowance for possible diurnal rhythms becomes difficult. In the present context, however, this criticism is not serious because the results presented in SECTION 2. 6. indicate no significant difference in snail respiratory rates with time of day.

The above information can be considered as an extension of the conclusions of Lawton and Richards (1970), based on a comparison between the Cartesian diver, Gilson, Warburg and Winkler methods which suggested that the respiratory results obtained are independent of the techniques used, provided that sufficient care is exercised by the operator. The results presented here further support this statement and indicate comparability between gasometric, chemical, and polarographic methods. As Lawton and Richards (Ibid.) point out, however, comparability between the results obtained in various types of respirometric apparatus does not necessarily ensure comparability between these rates, and those which are operative under field conditions. Until the latter can be measured directly one must be content with using laboratory conditions which are as realistic as possible. Here, comparability of results by the rigid maintenance and specification of the conditions employed is extremely important.

The effect of environmental conditions on respiratory rates gives some insight into metabolism in the field and these are considered in the following sections. SECTION 2. 5 provides equations relating respiratory rates to body size and temperature and these corrected for seasonal variations (see SECTION 2. 6) will be used for the calculation of field rates.

2. 2. The Effect of Temperature Acclimation, and a Consideration of the Adaptive Significance of Reverse-acclimation

A. INTRODUCTION

Numerous reports have indicated that poikilotherms are able to exert a limited control over their metabolic rates in the face of temperature variations (see reviews of Bullock, 1955; Prosser, 1955; Fry, 1958; Precht, 1958; Prosser and Brown, 1961; Vernberg, 1962; Kinne, 1963). This has been called acclimation when observed under laboratory

conditions and acclimatization when applied to the more complex situation in nature (Hoar, 1966). Bullock (1955), however, considers such a separation trivial, and following his example, only the term acclimation will be used here.

Since eurythermal species (such as freshwater snails) are supposed to possess more efficient regulatory powers than their stenothermal equivalents (Bullock, 1955) and because acclimation has already been described for A.fluviatilis (Berg, 1953) the work presented in this section has been concerned with a detailed definition of the pattern and extent of this process in both A.fluviatilis and P.contortus.

B. METHODS

All snails used were collected from the shores adjacent to Ha Mire in March, 1970. The sample of each species was sorted into 5 cohorts of 30 snails and all individuals were of approximately the same size (i.e. 4.0mm. AL and 3.0mm. MD in A.fluviatilis and P.contortus respectively). Each of these cohorts was further sub-divided into groups of 3 individuals for purposes of determination and these were kept in strict association. Of the 5 cohorts 2 were acclimated at 4 or 18^{0}C and a single cohort was acclimated at 10^{0}C for 5 days in contact with food.

Following the acclimation period single cohorts were transferred from 4 and 18^{0}C directly to a 10^{0}C regimen, when their oxygen consumption was measured immediately using an oxygen electrode. Respiratory determinations were carried out group by group and the order of determination was noted and strictly maintained on subsequent occasions. Determinations were repeated at daily intervals. The cohorts maintained at constant temperature were used as controls and their rates were measured at less frequent intervals.

C. RESULTS AND DISCUSSION

FIGS. 101 and 102 show the respiratory responses of the experimental cohorts after an initial abrupt change in temperature and of control cohorts kept under constant conditions. Both species of snail show an acclimatory response but of opposite types. In A.fluviatilis the rates of the transferred, high and low temperature cohorts move at progressively reducing rates on to a target, plateau value, which is equivalent to the rates of the 10^{0}C control cohort. In P.contortus the rates of both the 4 and 18^{0}C cohorts initially over-

shoot the target level and then move at a progressively reducing rate on to it. The time course of complete acclimation (i.e. achievement of the target level) is shorter in P.contortus than A.fluviatilis, taking between 2-3 days in the former and 3-5 days in the latter species. The response of P.contortus, with an initial period of over-compensation followed by a decay to a target level, is typical for invertebrates in general (Bullock, 1955) and molluscs in particular (Segal, 1966). The response of A.fluviatilis, on the other hand, is atypical but has been recorded elsewhere for this species by Berg (1953) and seems to occur in the North American ancylid,F.rivularis (Burky, 1969). Berg (Ibid.) has called this phenomenon "reverse acclimation".

FIGS. 101 and 102 also indicate that under the laboratory conditions used the target level is not maintained indefinitely and after a short interval of time all rates decay. Most of the control cohorts also show this behaviour and it is probably due to some deleterious effect associated with laboratory culture. Berg et. al. (1958) have reported a similar response to laboratory conditions in A.fluviatilis, although in their case the effect was more gradual and was detectable after a shorter interval of time. Here the effect seems to be to some extent dependent on temperature (cf. decay at 18^0C with that at 4^0C in each species).

FIGS 103 and 104 show the respiratory rates (in logarithms) of cohorts of snails acclimated to either 4 or 18^0C, after an abrupt change in temperature to either 18, 10, or 4^0C (open circles). The 10^0C data was extracted from FIGS 101 and 102. The other data was obtained from separate experiments involved with the abrupt transference of 18^0C acclimated groups to 4^0C, and 4^0C acclimated groups to 18^0C. Apart from these differences in manipulation the techniques were essentially the same as those described in SECTION B above, and 30 snails were used in each determination. Also shown in FIGS. 103 and 104 are the respiratory rates of individuals completely acclimated to 4, 10, and 18^0C respectively (solid circles). Here data was extracted from controls in FIGS. 101 and 102.

The results indicate direct translation in the R-T curves of P.contortus (solid lines) and as would be expected from their acclimatory response, reverse translation in A.fluviatilis (for terminology see Prosser and Brown, 1961). Within the temperature range considered there is no evidence of rotation (Prosser, 1958), although this phenomenon cannot be discounted because it has been

demonstrated outside the above range in the freshwater pulmonate Physa hawnii (Lea.) by Daniels and Armitage (1969).

Q_{10} values based on FIGS. 103 and 104 are presented in TABLE 64. From this information it can be seen that Q_{10} falls with an increase in temperature in P.contortus but rises with temperature in A.fluviatilis. The former response is more usual than the latter (Krogh, 1916; Rao and Bullock, 1954) and this difference means that A.fluviatilis is better adapted for life at low temperatures whereas P.contortus shows the reverse property. Similarly Q_{10} rises in the acclimated state in A.fluviatilis and is higher than in the non-acclimated condition, whereas Q_{10} falls in acclimation in P.contortus and is lower than in the non-acclimated condition. This can be interpreted to mean that A.fluviatilis is better adapted to rapid temperature fluctuation, whereas P.contortus is better adapted for life in situations where fluctuations are more gradual. All these differences in adaptation essentially result from differences in the pattern of acclimation (i.e. reverse v. normal) shown by these two species and help to explain their ecological requirements.

Both species are highly cosmopolitan but A.fluviatilis is more characteristic of shallow, fast-flowing (or wave swept) habitats and P.contortus is more typical of still, even stagnant, lentic situations (Moquin-Tandon, 1855; Ellis,1926; Boycott, 1936; Boettger, 1944; Baker, 1945). The distribution of P.contortus in the littoral region at Malham is, therefore, somewhat unusual and may be facilitated by the suitability of the food material present (see PART VI, SECTIONS 4 and 6) and the ability of this species to avoid wave action by living in the crevices on the undersides of rocks (see PART IV, SECTION 4). The temperature characteristics of lotic (or shallow littoral) habitats are usually lower and subject to more abrupt (often diurnal) changes than deeper lentic situations. In this sense the compensatory behaviour shown by A.fluviatilis and P.contortus correspond to their more usual habitat requirements and may suggest yet another reason for the success of A.fluviatilis on north shores at Malham (see also PART V, SECTION 6).

There has been considerable controversy over the adaptive significance of reverse acclimation. It was considered unusual by Fry (1958) and non-adaptive (even paradoxical) by Prosser (1967). Burky (1971) has challenged this last statement on the grounds that selection could not allow the retention of a non-adaptive metabolic pattern that

TABLE 64. Q_{10} values for the respiratory rates in A.fluviatilis and P.contortus between 4-10°C and 10-18°C using animals with different thermal histories.

Temperature Range	Physiological State	A.fluviatilis	P.contortus
4 - 10°C	Acclimated at 4°C	1.706	3.720
	Acclimated at 18°C	1.766	2.871
	Acclimated at both 4 and 10°C	2.642	2.188
10 - 18°C	Acclimated at 4°C	2.109	2.510
	Acclimated at 18°C	1.972	2.564
	Acclimated at both 4 and 10°C	2.704	1.930

has such a profound effect on the biology of an organism. He explains reverse acclimation in the Ancylidae in terms of winter food shortage when reduced metabolism would be important. All these workers (including Berg, 1958), however, have only considered the immediate effects of the phenomenon i.e. in terms of the immediate response after an abrupt temperature change. A consideration of the time-course of acclimation processes and their consequent effects on the R-T curves and Q_{10} values is critical to a realistic interpretation of reverse acclimation in terms of its adaptive significance. This analysis of the response of A.fluviatilis as presented above, in comparison with that of a normal regulator (i.e. P.contortus) has provided some insight into the relationship between the pattern of acclimation and its adaptive value in terms of the ecological distribution of the organism concerned.

As well as their theoretical implications the above results are also important from a practical point of view. Ideally the respiratory rates should be measured in conditions of temperature fluctuations approximating to those which occur in the field. The rates and extent of these fluctuations, however, are extremely intractable to estimation and computation, so that for the sake of replicability constant conditions must be used. In this event the fully acclimated state is most easily defined and will be used in furture estimation. The inaccuracies involved in extrapolation of such measurements into the field make all estimates of energy losses based on them extremely tentative and crude. Widdows and Bayne (1971) have discussed the effect of temperature acclimation on the energy budget of Mytilus edulis. The results presented above also indicate that animals should not be kept in the laboratory over extended periods of time prior to use. Consequently most of the snails considered in future sections had been kept in the laboratory for no longer than 5 days.

2. 3. The Effect of Environmental Oxygen Concentration

A. INTRODUCTION

In conditions of reduced environmental oxygen tension many animals are able to maintain a fixed respiratory rate at least down to some critical tension (i.e. regulators), whereas in other species respiratory rate faithfully tracks the environmental oxygen levels (i.e. conformers). Here the terminology follows Prosser and Brown

(1961) who provide numerous examples of each type of response. The distinction between regulation and conformity is not necessarily absolute and may depend on other factors e.g. population density (Tang, 1933).

The respiratory response to environmental oxygen in snails is variable and has been considered extensively but not exhaustively by Berg and Ockelman (1959). In general the smaller species seem to be capable of better regulation than the larger species. A.fluviatilis was found to be a regulator by these workers. Less work has been carried out on the Planorbidae than most other groups and no information exists with regard to the respiratory response of P.contortus to environmental oxygen tension. The presence of haemoglobin throughout the whole planorbid family, however, has led numerous workers to postulate tolerance to de-oxygenated conditions in this group (Leitch, 1916; Maćela and Seliskār, 1925; Borden, 1931; Wolvekamp, 1932; Fox, 1944; Zaaijer and Wolvekamp, 1958; Jones, 1961). Von Brand et. al. (1948) have demonstrated regulation in Australorbis glabratus.

In this section the observations of Berg (1952) will be repeated, and the behaviour of P.contortus will be considered. Some information regarding the survival of these two species under anaerobic conditions will also be presented.

B. METHODS

All experiments involved groups of snails, of approximately the same size (4.0mm. AL for A.fluviatilis and 3.0mm MD for P.contortus) each consisting of 30 individuals (in groups of 3) which were satiated and which had previously been acclimated to the test temperature. Determinations were carried out using the oxygen electrode technique. An experimental temperature of 16^0C was employed to facilitate direct comparison with the results of Berg (1952).

The respiratory rates were measured in a range of solutions (tapwater) of varying oxygen concentrations and these were prepared by mixing various quantities of de-oxygenated and oxygen-saturated water. De-oxygenation was achieved by bubbling nitrogen through the water for 12h. and oxygen-saturated water was prepared by bubbling air through the water for a similar period of time. The saturated solution at 16^0C thus contained 7.01ml. oxygen/l. (S.T.P.).

All determinations were carried out on non-restrained animals,

so that active metabolism was monitored. Fry (1957) has suggested that any restriction in active metabolism due to the oxygen content of the environment is likely to be deleterious to the species. The critical concentration at which restrictions in metabolism occur is known as the "incipient limiting level" (Fry, Ibid.).

Other experiments have been undertaken on the survival of both P.contortus and A.fluviatilis under anaerobic conditions. Groups of 25 individuals of each species were placed, separately, in two 1 litre containers filled with de-oxygenated tapwater (for methods of de-oxygenation, see above) and the number of individuals remaining alive was noted at daily intervals.

C. RESULTS AND DISCUSSION

FIG. 105 shows the respiratory response of A.fluviatilis and P.contortus to various conditions of environmental oxygen concentration. The respiratory rate is expressed as the average uptake of each experimental group, expressed as a percentage of the inspiration (μL./individual/h.) which occurred at maximum saturation. The operative level of oxygen concentration, applicable throughout the period of determination, is represented as the median level, between introduction and removal of snails, expressed as a percentage of the maximum saturation condition at 16^0C.

The results show that both species are capable of compensation but that P.contortus is a better regulator than A.fluviatilis. The incipient limiting level occurs at approximately 30% saturation (ca. 2.0ml./L.) in the former species and at approximately 50% saturation (ca. 3.5ml./L.) in the latter species. The results for A.fluviatilis are equivalent to those reported by Berg (1952) for this species.

FIG. 106 shows the survival of cohorts of snails under complete anaerobiosis and indicates that both species are able to survive for a limited amount of time in the absence of oxygen. The form of this survivorship curve for A.fluviatilis in the present instance is similar to that reported by Berg (Ibid.) for this species (Berg's data are also plotted in FIG. 106).

Tolerance of freshwater snails to anaerobic conditions has been recognised for a long time. André (1893), for example, reports keeping ancylids (species not specified) in boiled water for 4-5 days and this

level of tolerance appears to be of general occurrence in the Pulmonata (Alsterberg, 1930; Raffy and Fisher, 1933). Von Brand et. al. (1950) have shown that the Planorbidae can survive anaerobic conditions, and are generally more resistant than other pulmonate species. These workers suggest that resistance is a function of ability to excrete lactic acid, whereas in a comparison between the resistance of A. fluviatilis and A.lacustris Berg (Ibid.) found that the latter, more resistant, species contained a greater quantity of glycogen and suggested that this feature enabled greater survival under anaerobic conditions since glycogen is the major substrate source of fermentative catabolism. Both factors are probably important.

The lower incipient limiting level of P.contortus, and its greater ability to resist anaerobic conditions indicates yet another physiological feature which contributes to the success of this species in still, lentic environments (see SECTION 2. 4). Although A.fluviatilis has the ability to regulate, its restricted ability to survive under anaerobic conditions may be one of the factors which limits its distribution to fast flowing lotic or wave swept, lentic situations (Berg, 1952).

From a practical point of view the above results suggest that determinations should be carried out under conditions of oxygen concentration which are never allowed to fall below the incipient limiting level, and this has been ensured in the experiments which are reported in the following sections. It should be noted that implicit to this manipulation is the assumption that oxygen is never limiting under the wave-swept conditions which pertain on Ha Mire.

D. A NOTE ON THE MECHANISMS OF RESPIRATION IN FRESHWATER PULMONATES

At this juncture it is pertinent to discuss the respiratory structures employed by A.fluviatilis and P.contortus. In the pulmonates the anteriorly situated mantle cavity is modified into a "lung" and the ctenidia are absent (Morton, 1958). The pulmonary cavity is, however, absent in the Ancylidae although a secondary, vascularised, branchial flap, which overlies the anal aperture, may be of respiratory significance (Andrē, 1893). In the Planorbidae the pulmonary cavity is retained and this group also possess a dorso-anal branchial flap (Baker, 1945).

It has been assumed by many earlier workers that those freshwater pulmonates which retain a pulmonary cavity, use it as a lung

and are obliged to surface periodically for air (Taylor, 1895). Other workers have, however, suggested that this process may not be obligatory (Rozkowski, 1914; Cheatum, 1934; Noland and Reichel, 1943). Here the pulmonary cavity apparently remains filled with water throughout life and merely provides an extension of the body surface for cutaneous respiration by diffusion. More recently Hunter (1953c) has demonstrated that most species of freshwater pulmonate in Loch Lomond have water-filled cavities, even in the littoral region, and only surface for air when the dissolved oxygen becomes depleted (e.g. at high summer temperatures). There may also be differences between adults and spat with respect to this behaviour.

At Malham casual observation has indicated that the pulmonary cavity of P.contortus on Ha Mire is filled with water throughout the year. A random sample of this species (30 individuals) taken in December, 1970 and August, 1971 failed to reveal any air-filled lungs. Furthermore surfacing has never been observed under field conditions although individuals brought into the laboratory at room temperature quickly fill their pulmonary cavities and make irregular excursions to the surface. The use of aerial oxygen can be considered as an emergency response to low oxygen concentrations within the aquatic environment. The total exposed body surface is the most important site for respiration, which probably occurs via aqueous diffusion.

2. 4. The Effect of Movement and Starvation

A. INTRODUCTION

As already noted (see SECTION 1) the total heat loss and thus the respiratory metabolism of organisms may consist of three major components, i.e. one due to the work of movement, one due to the processing of assimilated food (S.D.A.), and one associated with complete rest. The latter has been called basal metabolism in homeotherms (Brody, 1945) but due to difficulties in its definition, standard metabolism in the poikilotherms (Krogh, 1941). The sum of all three components will be defined as routine metabolism in the present work.

Most researchers, in considering the respiration of freshwater snails, have measured routine metabolism e.g. Berg (1953, 1958, and 1961), Berg et. al. (1958), Berg and Ockelman (1958), Lumbye (1958), Lumbye and Lumbye (1965), Von Brand et. al. (1948, 1950). Berg (1952, 1961) has assumed that routine metabolism in the sluggish

Ancylidae closely approximates to standard metabolism. All the above mentioned workers have considered the effects of starvation on respiratory metabolism but the results obtained by them have been variable.

In some species respiration falls almost immediately with starvation (e.g. A.fluviatilis) whereas in other species respiration appears to be unaffected by food deprivation at least up to some critical point (e.g. M.glutinosa, B.tentaculata, V.piscinalis and L. auricularia) and in yet others there may be an initial rise in oxygen consumption associated with starvation (e.g. P.jenkinsi). Von Brand et. al. (1950), however, have shown that 4 species of pulmonate considered by them (i.e. A.glabratus, H.duryi, Physa spp. and Physa gyrina) followed the same time course of a continuous, but progessively decelerating, reduction in respiratory rate with starvation time, and pointed out that this type of response also appears to be typical of the homeotherm condition (Krogh, 1916).

The following section will be concerned with a consideration of the effects of movement and starvation on respiration in both A. fluviatilis and P.contortus. Some attempt will be made to reconcile the above observations in terms of the relationship between these two variables.

B. METHODS

The snails used in the following experiments were collected in March, 1971 and were acclimated (to 10^0C) and fed prior to use. Within each species 2 groups of 30 individuals of approximately the same size (5.0mm. AL in A.fluviatilis, 4.0mm. MD in P.contortus) were considered. The respiratory rate of subgroups of 3 individuals in each major group was measured immediately after their removal from food (time 0) and determinations were repeated at various intervals after this time. All subgroups were marked so that a strict time sequence could be maintained during experimentation. Respirometric determinations were carried out at 10^0C using the oxygen electrode technique.

During the experiments individuals in one of the two groups within each species were allowed complete freedom of movement, both within the respirometer and also during the intervening periods. Individuals within the other group, however, were constrained within small platinum cages which prevented movement and which could be sus-

pended within the electrode chamber of the respirometer. Between determinations these snails were retained within their cages. The experiment was continued over a 96h. starvation period during which time and between determinations, the subgroup of snails were kept individually in pyrex vials (3 x 1cm.) sealed over with gauze and suspended in a larger tank (capacity 5 litres) containing aerated tapwater at 10^0C.

C. RESULTS AND DISCUSSION

FIGS. 107 and 108 show the effect of increasing starvation on the respiratory rate of mobile and non-mobile individuals of A. fluviatilis and P.contortus respectively. The condition of constraint will be assumed approximately equivalent to a resting (standard) state, although in reality both species showed an initial period of struggle (ca. 30 min.-1h.) within the platinum cage before becoming quiescent. Most individuals recovered after release, and the data from those that did not have been discarded together with that derived from snails which died during the course of the experiments. Also included within FIGS. 107 and 108 are curves representing the time course of gut emptying during food deprivation (data derived from FIGS. 86 and 87).

The results show that the pattern of change in respiratory metabolism during starvation differ in the active and pacified individuals. In the pacified snails respiratory metabolism falls, at a progressively reducing rate, with starvation time and closely follows the time-course of gut emptying. Hubbell (1969, 1971) has reported the same type of response in the terrestrial isopod Armadillium vulgare and has indicated that there are two major additive components to this process, i.e. a fast phase due to reductions in S.D.A. (as the amount of material assimilated becomes reduced) and a slow component due to a gradual reduction in endogenous body stores. This interpretation can also be applied to the snails, although here the fast phase can further be divided into two other components, one associated with emptying of the gizzard, the other with emptying the hepatopancreas (see PART VII, SECTION 5. 5.).

The results presented suggest that between 40-50% of routine metabolism may be concerned with S.D.A.. Rubner (cited in Brody, 1945) has shown that between 15-40% of the total respiratory output may arise from S.D.A. in homeotherms and Hubbell's (Ibid.) data suggest a value of 60% in woodlice, so that the results obtained from A.

fluviatilis and P.contortus are not unusual. The interpretation of S.D.A. has been varied. Brody (1945) discounts the fact that it is solely due to the work of digestion and follows Rubner (Ibid.) in believing it to be associated with the post-absorptive processing of food, particularly proteins. In snails, however, there are two gut regions endowed with considerable musculature i.e. the buccal mass, which operates the radula and the gizzard which is concerned with trituration. Both these structures only operate in the presence of food and presumably consume a considerable amount of energy. In consequence they probably contribute a significant amount to the S.D.A. and the fact that reduction in respiration with starvation tracks both the emptying of the hepatopancreas and also the gizzard supports this hypothesis.

The pattern of changes in respiratory rates with starvation differs in the non-constrained individuals of P.contortus and A. fluviatilis. With regard to the initial state of starvation (i.e. time 0), the fiducial limits suggest that the respiratory rates of the constrained and non-constrained individuals are significantly different in P.contortus but not in A.fluviatilis. This difference is probably associated with the fact that the limpet is far more sluggish than P.contortus. The latter moves at approximately twice the rate of the former species (see FIGS. 113 and 114) and here the difference between active and pacified metabolism may provide a rough index of the proportion of total respiratory metabolism involved in locomotion, i.e. ca. 21%. In the limpet a negligible amount of energy is used in movement.

After the initial respiratory determination the respiratory rates of non-constrained individuals in both species maintain a higher level and initially reduce at a lower rate than those of constrained snails. There is an initial period of divergence between curves followed by convergence. This probably derives from the fact that snails become more mobile as starvation time increases at least up to some critical point after which mobility becomes reduced, presumably as a result of depletion in endogenous energy stores (see SECTION 4. 2).

A realisation that activity can modify the patterns of change in respiratory rate with respect to starvation may help to explain the differences in those patterns which have been recorded by other workers (see A above). As already noted, these previous workers have measured routine metabolism. Recognising that different species of

snail are likely to vary in both their characteristic mobility and their movement response to starvation, then different patterns of change in routine metabolism with starvation must also be expected. The pattern of change in non-active respiration is probably constant both in snails in particular and other animals in general (Krogh, 1916; Hubbell, 1969, 1971). It is significant from this point of view that the curves relating respiration to starvation time presented by Berg et. al. (1958) for A.fluviatilis and Von Brand et. al. (1950) for four other pulmonate species are most similar to the ones presented here for constrained individuals and were measured under conditions which closely approximated to a resting state.

From a practical point of view, the effect of starvation on respiratory rates means that some assumption must be made regarding the nutritive conditions of snails in the field if laboratory data are going to be extrapolated. In the absence of a quantitative expression of the natural food supply of snails on Ha Mire, satiation has been assumed even though this may not be absolutely true (see PART VII, SECTION 6).

2. 5. The Effect of Snail Size and a Further Consideration of the Effect of Temperature

A. INTRODUCTION

In this section the relationship between respiration, body size and temperature will be considered from the point of view of predicting the respiratory rate of individuals under field (Ha Mire) conditions. The information presented in previous sections has been used to provide conditions of measurement which were relevant in field terms. Selection of these conditions may be of critical importance in accurately describing the respiratory functioning of natural populations so that it is unfortunate that a number of assumptions had to be made in this respect. These assumptions have been discussed in the previous sections but will be re-stated here for the sake of clarity. The assumptions are :

i) that animals under field conditions are acclimated to the temperature conditions of their existence.

ii) that the waters of the littoral region at Malham are completely saturated with oxygen.

iii) that snails in the field are completely and continuously satiated.

iv) that snails under field conditions are continually moving.

B. METHODS

Animals for the study were collected haphazardly from the shores adjacent to Ha Mire in March, 1971, and were acclimated to the desired temperature (i.e. 4, 10, or 18°C) for 4 days prior to use, in the presence of food. All measurements were on routine metabolism and were determined using the oxygen electrode technique.

The experiments were carried out during the day i.e. from 9 a.m. to 6 p.m. and three individuals (of the same linear size) were used for each determination. Aperture lengths and maximum diameters of the snails used were transformed first to dry weight using equations 3(6. 2) and 4(6. 2), and then to ash-free dry weight assuming that 10% of the body dry weight is ash. Between 20-25 determinations were considered at each temperature (i.e. 4, 10, and 18°C) for both species and all determinations lasted 3h. In no case was the incipient limiting level exceeded.

C. RESULTS AND DISCUSSION

The relationship between body size (mg. ash-free dry weight) and respiratory rate (μL./individual/h.) when plotted on logarithmic co-ordinates is linear (see FIG. 109). The equations describing these relationships at each of the temperatures considered are :

for A.fluviatilis

$$\text{at } 4^\circ\text{C} \quad \text{Log } y = \underset{a}{0.147} + \underset{b}{0.659} (\pm 0.081)x \quad n = 24 \quad \ldots 2(8.\ 2)$$

$$\text{at } 10^\circ\text{C} \quad \text{Log } y = 0.415 + 0.693 (\pm 0.051)x \quad n = 23 \quad \ldots 3(8.\ 2)$$

$$\text{at } 18^\circ\text{C} \quad \text{Log } y = 0.841 + 0.677 (\pm 0.090)x \quad n = 22 \quad \ldots 4(8.\ 2)$$

for P.contortus

$$\text{at } 4^\circ\text{C} \quad \text{Log } y = 0.200 + 0.675 (\pm 0.110)x \quad n = 20 \quad \ldots 5(8.\ 2)$$

$$\text{at } 10^\circ\text{C} \quad \text{Log } y = 0.453 + 0.658 (\pm 0.101)x \quad n = 25 \quad \ldots 6(8.\ 2)$$

$$\text{at } 18^\circ\text{C} \quad \text{Log } y = 0.672 + 0.664 (\pm 0.131)x \quad n = 25 \quad \ldots 7(8.\ 2)$$

where

y = 100 x respiratory rate (μL/individual/h.)

x = 100 x ash-free dry weight (mg.)

n = number of observations involved

All the regression coefficients (b) are significantly different from zero (b > 2 confidence limits in all cases), but none of them is significantly different from a hypothetical value of 0.67. A t-test was used in the latter instance since all the regression coefficients

are based on samples which consist of less than 30 individuals. TABLE 65 presents the t-values for the regression coefficient of each species at each temperature together with the associated level of significance.

TABLE 65. t-values based on a comparison between the regression coefficients presented in equations 2(8.2)-7(8.2)and a hypothetical value of 0.67

	A.fluviatilis			P.contortus		
	t.	p	df.	t.	p	df.
4°	0.14	> 0.10	22	0.05	> 0.10	18
10°	0.45	> 0.10	21	0.12	> 0.10	23
18°	0.08	> 0.10	20	0.05	> 0.10	23

Because of this lack of significance all the regression coefficients given in equations 2(8. 2)-7(8. 2) have been assumed equivalent to 0.67 and their a-coefficients have been suitably modified to provido the following equations :

for A.fluviatilis

$$\text{at } 4^{\circ}C \quad \text{Log } y = \underset{a}{0.138} + \underset{b}{0.67} \log x \quad \ldots\ldots\ldots\ldots 8(8.2)$$

$$\text{at } 10^{\circ}C \quad \text{Log } y = 0.438 + 0.67 \log x \quad \ldots\ldots\ldots\ldots 9(8.2)$$

$$\text{at } 18^{\circ}C \quad \text{Log } y = 0.848 + 0.67 \log x \quad \ldots\ldots\ldots\ldots 10(8.2)$$

for P.contortus

$$\text{at } 4^{\circ}C \quad \text{Log } y = 0.205 + 0.67 \log x \quad \ldots\ldots\ldots\ldots 11(8.2)$$

$$\text{at } 10^{\circ}C \quad \text{Log } y = 0.430 + 0.67 \log x \quad \ldots\ldots\ldots\ldots 12(8.2)$$

$$\text{at } 18^{\circ}C \quad \text{Log } y = 0.666 + 0.67 \log x \quad \ldots\ldots\ldots\ldots 13(8.2)$$

Taking antilogs of these equations provides statements which are of the general and familiar allometric form i.e. :

$$Y = a X^{b} \quad \ldots\ldots\ldots\ldots 14(8.2)$$

and this type of relationship seems to be applicable throughout the whole of the living world (see reviews by Brody, 1945; Kleiber, 1947; Zeuthen, 1953; Hemmingsen, 1960) although in some instances a tendency to isometry (b = 1) has also been noted (e.g. in certain insect larvae, Bertalanffy, 1949, 1951). When b tends to 0.67, as above, a functional relationship between the respiratory rate and body surface area is implied (see also PART VII, SECTION 5. 8). This

may, perhaps airse from the fact that pulmonates use their body and lung surfaces for obtaining oxygen by gaseous diffusion (see SECTION 2. 3B) although there may not be such a simple relationship between the value of b and the size parameters of in-tact organisms (Newell and Pye, 1971). In fact there appears to be a considerable amount of interspecific variability in the value of coefficient b found in various species of freshwater gastropod (see DATA APPENDIX XIV). On theoretical grounds, i.e. with regard to the shape of the growth curve, Bertalanffy (1949, 1951) predicted that b should take a value of between 0.67 and 1.00 in the pulmonates. The actual range reported, however, is far wider than this i.e. from 0-1.00. Similarly, Krywienczyk (1952) proposed that coefficient b should tend to 0.67 in the operculates since they depend on gill surfaces for their oxygen supply. Datapresented in DATA APPENDIX XIV do not support this hypothesis.

Although the coefficient b reported here for P.contortus and A.fluviatilis falls within the range given in DATA APPENDIX XIV, the value obtained for the limpet does not fall into the range of values previously obtained for this species (0.70 - 0.80). It should, however, be noted that the latter values were determined with respect to snail wet, not dry, weight and that the units in which mass is expressed may have some influence on the value of b. If, for example, it is assumed that larger individuals contain proportionately less water than smaller individuals a reduction in b can automatically be expected when the allometric relationship is considered with regard to organismic dry weight. That this state of affairs may apply in the snails is suggested by the data presented in FIG. 110 for L. stagnalis. Furthermore Reichle (1968) has noted in woodland diplopods that coefficient b is reduced and tends closer to 0.67 in the allometric expressions concerned both with the ingestion of food and inspiration of oxygen when diplopod weight is given in dry, rather than wet terms. The above explanation may, therefore, be more generally applicable. Obviously more work is required on the relationship between the units in which weight is expressed and coefficient b in the allometric term.

It should be noted that all composite curves based on data from a large number of species (i.e. of snails in particular; see DATA APPENDIX XIV, or living organisms in general; see Hemmingsen, 1960) are based on wet weight formulations, and tend approximately to 0.75.

Even if this value is accepted, however, variations from 0.75 in individual species determinations can still be expected since the composite expression absorbs these as deviations around the common regression line. Thus the results presented here do not necessarily oppose the value of coefficient b derived from a consideration of a large number of species.

TABLE 66 presents estimates on the respiratory rates of standard snails (1.0mg. ash-free dry weight) at 18°C derived from equations 10(8. 2) and 13(8. 2) and also comparative information on the respiratory rates of A.fluviatilis derived from the data of Berg and Ockelman (1959), i.e. from their FIG. 4, by assuming that dry weight represents ca. 25% of snail wet weight and that ash constitutes 10% of the dry weight. As can be seen, my data correspond extremely closely to that of Berg and Ockelman (Ibid.). There are no comparable data available in the literature with regard to P.contortus and the information on the Planorbidae in general, is sparse. The respiratory rate of a standard P.contortus individual is lower than for the standard limpets. Recalculation of Borden's (1931) data for P.corneus (making the same assumptions as in Berg and Ockelman's work), however, suggests that a standard individual (1mg. ash-free dry weight) in this species also has a relatively low respiratory rate i.e. between 0.5 - 0.8 µL./individual/h. Perhaps the presence of a red blood pigment enables more efficient utilisation of inspired oxygen and thus a reduction in the respiratory rates of the Planorbidae in general.

TABLE 66.The Respiratory Rates of Standard Sized (1mg. ash-free dry weight), Non-breeding Snails at 18°C

Species	Rate (µL./individual/h.)	Source of Information
A.fluviatilis	1.50 - 1.60	Berg and Ockelman (1959)
A.fluviatilis	1.55	equation
P.contortus	1.00	equation
P.corneus	0.50 - 0.80	Borden (1931)

The relationship between temperature and respiratory rate has already been discussed in SECTION 2. 2. Lack of a linear response between respiratory rate (expressed in logarithms) and temperature, shown in FIGS. 103 and 104,requires separate expressions for changes

in respiratory rate over the 4-10 and 10-18°C intervals which have been considered. This necessarily assumes linearity of response along these shorter segments of the R-T curves. Lawton (1971) used the same technique when considering the respiratory response of dragonfly larvae with respect to temperature. The changes in $\log_{10}$ respiratory/°C rise in temperature derived from FIGS. 103 and 104 are :

for A.fluviatilis

between 4-10°C; change in $\log_{10}$ respiratory rate/°C = 0.041 µL./h.
" 10-18°C; " " " " " /°C = 0.050 µL./h.

for P.contortus

between 4-10°C; change in $\log_{10}$ respiratory rate/°C = 0.034 µL./h.
" 10-18°C; " " " " " /°C = 0.026 µL./h.

This information together with equations 8(8. 2)-13(8. 2) will be used to specify the respiratory rates of snails under various conditions of field temperature.

2. 6. A Consideration of Seasonal and Diurnal Variations in Respiratory Rates

A. AIMS

The purpose of the work discussed in this section was to compare the results obtained from equations 8(8. 2)-13(8. 2) (which were derived from determinations carried out during the day and at one time of the year) with observations made at other times of the day and year. Both Edmondson (1961) and Phillipson (1962 and 1963) have noted the possibility of introducing considerable inaccuracies by not taking into account seasonal and diurnal variations in respiratory determinations.

B. METHODS

The methods used were essentially similar to those described in the previous sections except that determinations were carried out at various times of the year, between March 1971 and February 1972 (actual dates are specified in FIGS. 111 and 112) and a single determination was made during the night (i.e. 10 p.m.-4 a.m.) in March 1971. On each occasion of determination 10 replicates (each consisting of 3 individual snails) were considered. All snails in each monthly

group were of the same size and a conscious attempt was made to pick snails approximating to the mean monthly size characteristic derived from the preceding year (see FIGS. 29 and 30). All determinations were carried out on acclimated and satiated snails at 10°C, and routine metabolism was determined.

C. RESULTS AND DISCUSSION

FIGS. 111 and 112 show the relationship between the mean respiratory rates obtained at various times of the day and year with values predicted by equations 9(8. 2) and 12(8. 2). The 95% confidence limits of the standard regression curves are also plotted as dotted lines and the 95% confidence limits (2.262 $S/\sqrt{n}$, for 9 df.) of the point estimates are represented as horizontal bars.

The results indicate no significant difference between day-time and night-time respiratory estimates in both species. It will be assumed, therefore, that there is no diurnal respiratory effect. There is, however, a clear seasonal effect. Thus from November to April in P.contortus and from November to March in A.fluviatilis equations 9(8. 2) and 12(8. 2) provide a relatively good description of the respiratory processes. Between May and July in P.contortus and April and July in A.fluviatilis, however, the observed rates are significantly higher than those predicted from the March data. Furthermore in the August adults of both species the observed respiratory rates are significantly lower than the predicted values.

The months during which the respiratory metabolism rises are associated with egg production and there may be a functional relationship between these two processes. Berg et. al. (1958), for example, found a similar rise in the respiratory rate of A.fluviatilis during breeding. The fact that my data indicate a rise in the respiration of A.fluviatilis prior to P.contortus, and in fact prior to actual egg deposition, may indicate some preparatory procedure in this species, perhaps associated with the production of its large yolky eggs. The August fall in the metabolism of both species occurs in post-ovipositional adults. Burky (1971) has observed the same phenomenon in F.rivularis and has suggested that it may be associated with senescence.

TABLE 67 shows the relationship between the observed respiratory rates, and those predicted from the March estimates, (i.e. by equations 9(8. 2) and 12(8. 2)) in those months when there was a significant difference. During breeding the metabolism is elevated by ca. 1.5

times in A.fluviatilis and by ca. 2.5 times in P.contortus.

TABLE 67. The Relationship Between Observed and Predicted Respiratory Rates in P.contortus and A.fluviatilis

Date	A.fluviatilis (Mean observed respiratory rate/predicted respiratory rate)	P.contortus (Mean observed respiratory rate/predicted respiratory rate)
April	1.518	-
May	1.540	2.468
June	1.541	2.520
July	1.518	2.491
August	0.561	0.514

The biological significance of the difference is not known. During senescence the metabolism is depressed by approximately the same amount (i.e. ca. 0.5 times) in both species. These approximations will be used as correction factors in future estimations of respiratory rates during reproductive and post-reproductive intervals (e.g. in PART IX).

It should be noted that the latter procedure assumes constancy in the proportional rise of respiration with respect to different snail size classes. This may not be exactly correct because Berg and Ockelman (1959) and Berg (1961) have shown that the slope of regression line relating respiratory rate to body size may also alter during the breeding condition. Nevertheless, the self-conscious selection of snails with sizes approximating to the mean monthly level reduces the errors associated with this assumption of constant proportionality.

3. EXCRETION IN P.CONTORTUS AND A.FLUVIATILIS

3. 1. Introduction

Problems of nitrogen excretion in the pulmonates have been extensively studied since the classical work of Baldwin and Needham (1934), Baldwin, (1935a) and Needham (1935). Modern reviews on the subject are given in Florkin (1966) and Potts (1967, 1968) and Campbell and Bishop (1970). Despite the vast amount of information available, however, the picture, particularly with regard to the freshwater species, is far from clear and has been complicated by a general lack of controlled experimental technique (Florkin, 1966; Potts, 1967). The major source of error has arisen from a failure to take account of microbial products of metabolism. Nevertheless, most of the previous workers have been in agreement that freshwater species only lose a small proportion of their excreta in the form of ammonia. This is contrary to the usual state of affairs in aquatic species (Potts,1967).

The last finding has considerable implications with regard to an energetics study since although energy losses due to the excretion of ammonia can safely be ignored (e.g. Lawton, 1971), the energy losses via other more complex excretory materials cannot. This section will be concerned with both the qualitative and quantitative aspects of these excretory losses in both P,contortus and A.fluviatilis.

In freshwater snails excretory losses may occur via routes other than in the urine. Thus amino acids may be lost over the whole body surface (Potts, 1967, 1968), and excretory particles may occur in the liver string fraction of the faeces (Carriker, 1946; Calow,1970; see PUBLICATIONS APPENDIX I). Possible energy losses in these materials will also be discussed.

3. 2. Estimates of Excretory Products Lost in the Urine and Retained in the Body Tissues

A. METHODS

Fifty snails of both species were kept in each of two closed containers with 1L. of tapwater over a 24h. period. Penicillin (1000 units/25ml.) was added to the water to prevent microbial metabolism. After 24h. the ammonia present within this medium was estimated according to the method of Sutton (1972, p.118) slightly

modified for freshwater organisms. Three 5ml. aliquots of solution were removed from the containers and to each was added 0.5ml. Nesslers reagent. A brownish-yellow colour indicates that ammonia is present and this can be determined quantitatively from a series of standard solutions of graded strengths prepared from dilute $(NH_4)_2SO_4$. An initial subsample (3 aliquots of 5ml.) taken from the experimental chambers prior to insertion of snails was used as a control.

The above solution, from the closed containers, was also used to test for the excretion of urea. The latter was determined by initially converting it to ammonia with urease (i.e. B.D.H. tablet form). One tablet was added to 100ml. of the medium and this was left for 3h. at room temperature before estimating the amount of ammonia produced using the methods described above.

No free uric acid deposits were observed in either the medium used in the present experiments or in media surrounding other snails which had been kept in captivity. Consequently the faeces produced during the experiment were tested for the presence of uric acid as were the body tissues of post-reproductive adults, spat and snail egg capsules. Both freshly laid capsules and those on the point of eclosion were considered separately. Each determination involved 20-30mg. shell-free dry weight of adult tissue, 5.0mg. shell-free dry weight of spat, and 10mg. of egg capsules.

All samples were dried and powdered before being transferred to a solid watch glass (heated to 80°C). For each 10mg. of sample 0.1ml. of Li_2CO_3 was added and the resultant concentrate was diluted to 50ml. with distilled water, filtered and cooled. 2.5ml. NaCN and 0.5ml. Benedict's solution were added to each of three, 5ml. subsamples from the diluted solution. A pink colour develops if uric acid is present and its intensity is proportional to the quantity of uric acid in solution. The latter was determined with respect to standard solutions prepared from Folin's reagent (2ml./100ml. distilled water which contains 20 μg./ml. of uric acid).

The presence of amino acids in the solution derived from closed containers, described above, has only been investigated in a qualitative sense. Single, 5ml. aliquots were prefiltered through membrane filters (0.8μ pore size) to remove any possible microbial and mucus contamination, and then treated with 10 drops of Ninhydrin solution (0.04g/20ml. distilled water). A blue colour develops if amino acids are present.

B. RESULTS.

The tests for ammonia, urea and amino acids in the snail water yielded negative results. No uric acid was found in the faecal material derived from other species. Whole-body and egg capsules analyses did, however, indicate its presence. TABLE 68 presents the results in terms of mg. uric acid/g. adult dry weight and % mg. uric acid/mg. of egg capsule dry weight.

TABLE 68. The uric acid content of snail tissues.

	P.contortus	A.fluviatilis
Spat	0.005mg./g.	0.002mg./g.
Post-reproductive adults	0.097mg./g.	0.110mg./g.
Freshly laid eggs	0.09%	0.14%
Pre-emergent eggs	0.53%	3.78%

C. DISCUSSION OF THE RESULTS WITH A NOTE ON THEIR PHYLOGENETIC IMPLICATIONS

Failure to demonstrate the presence of excretory products in antibiotically treated water which had surrounded snails (for a 24h. period) together with the apparent rise in tissue concentration of uric acid throughout life (cf. spat and senescent adults in TABLE 68) suggests that excretory products may not be lost in the urine of P.contortus and A.fluviatilis but stored within the body tissues. Some loss of excretory material (other than mucus which has a functional role)does, however, occur in the faeces since excretory particles are clearly visible. The nature of this material is unknown although the particles are vacuolar, stain with neutral red and methylene blue, and are insoluble in conc. HCl (Carriker, 1946). They arise from cells in the hepatopancreas.

Duerr (1966, 1967) also failed to demonstrate direct excretory losses in the urine from L.stagnalis but was able to demonstrate an endogenous rise in the uric acid content of this and several other species of snail (i.e. Lymnaea palustris, Planorbis corneus and Physa pakeri). On this basis he suggested that pulmonates may only void excretory products infrequently or not at all. This is in contrast to earlier workers' findings (e.g. Delaunay, 1931; Spitzer, 1937). They demonstrated the loss of ammonia and urea. It is perhaps notable,

however, that in the latter cases antibiotically treated water was not used. Badman (1970) has observed a similar retention behaviour in the terrestrial pulmonate Mesomphix vulgatus (Baker), although Bayne and Friedl (1967) have found a low but measurable release of ammonia and urea from L.stagnalis even in the presence of antibiotic. The results presented here support Duerr's (Ibid.) interpretation.

Within the animal kingdom 3 major types of excretory products are used, i.e. ammonia, urea, and uric acid. These are written in order of decreasing toxicity and solubility but increasing potential energy contents. Thus organisms excreting ammonia lose least free energy but require most water for the process, whereas the reverse applies to organisms excreting uric acid. Ammoniotelism is consequently a feature of aquatic forms whereas uricotelism (or purinotelism) is a feature of terrestrial existence. On this basis Needham (1935, 1938) saw purinotelism in freshwater pulmonates as evidence for a terrestrial origin. Anatomical and embryonic evidence, however, suggest an aquatic origin (Morton, 1955; Bondesen, 1950) and as Needham (Ibid.) himself has pointed out the type of excretory end product employed may be better correlated with embryonic environment than with phylogenetic history. Thus organisms which produce cleidoic eggs (closed against water loss) require to excrete inert, non-toxic products (e.g. purines) in-embryo and this is often retained to adulthood (e.g. birds, insects, saurian reptiles). On the other hand, animals whose embryos can excrete freely into a watery surrounding, and this includes the mammals, can afford to excrete more soluble and toxic substances (e.g. ammonia, urea).

The eggs of freshwater snails in general and pulmonates in particular tend to be of a cleidoic nature. The quaternary envelope of the Ancylidae and the foot secretions of the Planorbidae (see PART V, SECTION 4. 2) make this statement particularly pertinent to these groups. TABLE 68 indicates that embryonic excretion is essentially uricotelic in P.contortus and A.fluviatilis and suggests that the uric acid is retained in-embryo. Baldwin (1935a) has similarly demonstrated uric acid accumulation in the egg capsules of L.stagnalis though Sloan (1964) detected ammonia release from the egg capsules of Marisa cornuaricties (L.). Perhaps the relative extent of uricotelism and ammoniotelism is directly related to the permeability of the egg capsule membranes. Further work is obviously required on this problem.

Accepting that some species of pulmonate are sufficiently cleidoic to depend on uricotelism and following Needham's (1935, 1938) logic

that excretion in the adult reflects the embryonic state, an explanation of uricotelism in adult pulmonates can be given without reference to their phylogenetic origins. Furthermore, uricotelism in some egg producing prosobranchs e.g. Viviparous (Needham, 1938) may also be explained in these terms. It is possible, therefore, that rather than being derived from a terrestrial ancestor, uricotelism may provide a necessary pre-adaptation for the conquest of land.

In summary the results have suggested a uricotelis mode in P. contortus and A.fluviatilis and also that this material is not voided as such but is retained within the body tissues. In theoretical terms the endogenous neutralisation of potential energy in this way is tantamount to its loss from the system. In practical terms, however, its partitioning from the available components of snail biomass would be difficult so that in future calculations it will be considered as part of the latter. Retention of excretory material (presumably within the kidney) is only possible in short-lived species, and presumably is advantageous in reducing the energy cost of the excretory processes. The failure to demonstrate amino acid secretion over the whole body surfaces of snails conforms to Spitzer's (1937) generalisation that this behaviour is limited to marine species.

3.3. An Estimate of the Amounts of Energy Lost as Excretory and Mucus Materials Within the Faeces

As already noted the faecal materials of freshwater pulmonates consist of excretory particles and a mucus binding material as well as true egesta. The excretory mucus material represents a source of metabolic energy loss. Unfortunately, it has not been possible to separate these faecal components and thus directly estimate the extent of the loss of faecal metabolic secretions and excretions in absolute gravimetric or calorimetric terms.

A crude radiotracer method, however, has enabled some estimation of the proportion of total faecal material which is derived from snails' metabolism rather than from the ingested food material (see PART VII, SECTION 5. 9). This was found to be in the order of 5% for A.fluviatilis and 15% for P.contortus. It is possible that the higher value in the latter species may be associated with its bacterial feeding mode. Here the prevention of the fouling of head apparatus by the faecal components may be extremely important and require a thicker

mucus coat than in the algal feeding species. Furthermore, the bacterial diet will be highly proteinaceous and the catabolic end products of excess proteins may contribute to a greater output of faecal excretory particles.

The two coefficients given above for P.contortus and A.fluviatilis allow a crude estimation of the proportion of absorbed energy devoted to the production of the mucus-excretory faecal complex. If it is assumed that the caloric density of this complex is approximately equivalent to the caloric density of the food ingested, then the amount lost in calorific terms is ca. 5.25 and 17.25% of the food energy egested and thus represents ca. 3.5 and 5.5% of the food energy absorbed in A.fluviatilis and P.contortus respectively. Since, however, the caloric density of the mucus-excretory complex is likely to be less than that of the food material (see Brody, 1945 for list of calorific values of excretory products) these values probably represent overestimates. Furthermore, it is likely that the above ratios alter with changes in both external and internal conditions. Nevertheless, they provide an indication as to the extent of excretory and mucus losses in the faeces and indicate that this route of energy output may not be trivial. This assumption was implicit to use of the 14C - 51Cr method for estimating assimilation efficiencies (see PUBLICATIONS APPENDIX III).

4. MOVEMENT IN P.CONTORTUS AND A.FLUVIATILIS IN TERMS OF PATTERN, SPEED AND INVOLVEMENT OF MUCUS

4. 1. Introduction

In the Pulmonata locomotion involves muscles, mucus and cilia (Hyman, 1967). Main articles on the locomotion of the freshwater group are those of Kaiser (1959) and Elves (1961). Both authors declare that muscular waves are absent and ascribe the typical gliding locomotion to the beating of cilia which cover the sole of the foot. The cilia obtain leverage on the mucus trail and locomotion cannot be accomplished without a mucus secretion. Thus although mucus may represent a considerable source of energy loss its secretion is indispensible for existence.

Most authors have, however, ignored mucus production as an element of energy loss in computing energy budgets. Of notable exception is the work of Teal (1957) who estimated that ca. 57% of assimilated energy in aquatic flatworms may eventually appear as mucus. Paine (1965, 1971) estimated that 7% of the ingested energy may be lost as mucus in the marine gastropods, Navanax inermis and Tegula funebralis and Carefoot (1967) working with 3 species of Opisthobranch, assumed the summed loss of excreta and mucus to represent 15% of assimilated energy. All these estimates are based on indirect reasoning (i.e. computation by difference) but indicate that mucus in both molluscs and flatworms may contribute significantly to the energy budget and cannot be ignored (Paine, 1971).

It is the aim of this section to consider the pattern and rate of movement in A.fluviatilis and P.contortus particularly with regard to the feeding condition of the animals concerned (SECTION 4. 2) and to provide a direct estimate of the energy lost as mucus in these two species (SECTION 4. 3). Some consideration will also be given to the suitability of mucus as a medium for bacterial growth (SECTION 4. 4).

4. 2. The Pattern and Rate of Movement Under Various Conditions of Starvation

A. METHODS

The patterns and rates of movement in P.contortus and A. fluviatilis were assessed by inserting individuals in small perspex

pots (3 x 3 x 2cm. i.e. coverslip containers) full of tapwater and sealed over with plankton net. These were suspended in a larger tank (5L.) containing aerated tapwater where they were left over a 6h. period. Following this time and after removal of the snails, ca. 10mg. of carmine particles was added to each pot. The carmine particles adhered to the mucus track so that on removal, the latter were clearly visible as red bands. Consequently the distance moved over the time allowed could simply be assessed from the length of snail trails produced.

Two factors in the above technique could result in an underestimation of the actual distance moved. These are:
i) the dissolution of mucus during the experimental period
ii) the movement of the snails over the plankton net.
With respect to the first source of error it has been noted that carmine coloured trails, immersed in water, retain their integrity for up to 3 days although they become progressively indistinct, presumably as a result of microbial activity. The likelihood of the loss of snail trails over the 6h. experimental period is not, therefore very serious. With respect to the second source of error it should be noted that P.contortus and A.fluviatilis appear to be either negatively geotropic and/or phototropic and were rarely, if ever, found on the plankton nets which were always positioned facing upwards in the larger experimental tank.

The determinations were carried out at 10°C under a continuous light regimen. The snails used were acclimated to 10°C for 4 days prior to use and were considered in various states of starvation. In most of the experiments food was not present although in one group food was made available by suspending the whole pots in cultures of Navicula and Bacterium D for 7 days prior to use. The algal-conditioned pots were used for A.fluviatilis and the bacterium-conditioned pots were used for P.contortus. A clearly visible algal or bacterial film developed on the walls of the conditioned pots. The snails involved in this experiment were satiated.

Another experiment was designed to investigate the effects of violent water movements on the rate of snail movement. Under usual circumstances air was bubbled through the large containing tank to provide little,if any, water movement, whereas in the latter instance several air inputs were used to provide violent agitation.

Fifteen snails were considered in each experimental regimen. All the individuals used were of approximately the same size i.e. 4.0 mm. AL in A.fluviatilis and 3.0mm. MD in P.contortus.

B. RESULTS AND DISCUSSION

FIGS. 113 and 114 show the effects of starvation time, the presence of food, and violent water movement on the rates of movement (cm./day) in P.contortus and A.fluviatilis respectively. Also included in the figure are typical tracings made from the snail-trails produced in the pots under the above conditions.

The confidence limits on the histograms indicate no significant differences in the distances moved by satiated snails in the presence and absence of food. The patterns of movement do, however, change. When food is present movement is systematic whereas when there is no food available the movement becomes more random and haphazard. In the presence of food systematic movement will provide for efficient grazing (i.e. little food will be overlooked) and random movement, in the absence of food, may represent an adaptation for more efficient searching.

The results also indicate a rise in the rate of movement as the snails become more starved. This occurs up to some optimum level after which the rate of movement again falls presumably in response to a reduction in endogenous energy stores. Both these phenomena have implications regarding the difference between the response of routine and resting metabolism to starvation (see SECTION 2. 4). The rise in the rate of movement of snails during starvation and the change in pattern of movement presumably reflect an increased effort being made by the snails to find food. In nature local depletion of food may occur through overgrazing when these two behavioural responses may be of considerable value in returning snails to regions of food abundance. The random movements of the limpet become more directed when they come into contact with food whereas the random movements in P.contortus probably become more directed when they are able to sense the chemical exudates arising from their preferred bacterial food source (see PART VII, SECTION 2).

Violent water movement appears to have little effect on the rate of movement of A.fluviatilis whereas it significantly reduces the rate of movement in P.contortus. This may be connected with the more streamlined nature of the limpet's shell. It has already been noted that

P.contortus, on Ha Mire, attempts to escape wave action by living in the cracks and crevices of submerged stones.

Under still conditions P.contortus is more active than A.fluviatilis. The rates presented here for both species are generally lower than the laboratory estimates made by other workers on other species of freshwater and terrestrial molluscs (see DATA APPENDIX XV). It should be noted, however, that most of the latter values were obtained on results from a limited observational period (i.e. < 1h.) and that the movement of snails measured under field conditions are generally much slower, e.g. in nature P.jenkinsi moves at between 20-60cms/day (Haywood and Edwards, 1962) and Lymnaea bulimoides Lea moves at between 300-900cm./day (Foster, 1971). Furthermore various environmental factors can affect the rate of movement e.g. texture of the substratum (Heywood and Edwards, Ibid.), current speed (Doner and Vaillant, 1954), light and temperature (Hutcheson, 1947).

4. 3. An Estimate of Energy Lost in the Mucus Produced for Locomotion

A. METHODS

It was not possible to collect sufficient mucus from either A.fluviatilis or P.contortus for calorimetric determination. Consequently a larger species of snail was used for this purpose, i.e. L.stagnalis. The mucus was collected according to the method of Wilson (1968), in which removal was effected by stroking each snail's foot with a glass rod. The mucus adhered to the glass rod and was scraped off into distilled water. Approximately 50 snails were treated in this way and these yielded ca. 5mg. dry weight of mucus material. This was subsequently subjected to bomb calorimetry using cellulose acetate as filler (see also PART VII, SECTION 5. 2). The major assumption implicit in this procedure is that the composition of mucus, derived from different species of snail, is the same.

Determination of the weight of mucus produced by P.contortus and A.fluviatilis was effected by enclosing 50 satiated snails of each species in 2 two litre beakers containing aerated tapwater at 10°C. Individuals in each group of snails were all of approximately the same size (i.e. 5.0mm. AL in A.fluviatilis and 3.0mm. MD in P.contortus) and were both acclimated to 10°C prior to use. The experiments were carried out at 10°C for 24h. after which the snails were removed and the faecal material was decanted away. The mucus trails coating

the sides of the vessels were subsequently scraped off into distilled water. The use of warm water facilitated this process and showed up the trails as opaque strands. A spatula was used for the purpose of scraping. The mucus-water solution was ultimately filtered through a pre-weighed membrane filter (pore size = 0.8 μm). This procedure was repeated 4 times on the same group of snails in order to obtain sufficient mucus material for weighing. On alternate days, between determinations, the snails were fed.

B. RESULTS AND DISCUSSION

The calorimetric determination of the mucus derived from L. stagnalis yielded a calorific density of 5.708 kcal./g. dry weight. Only one determination was possible so that fiducial limits cannot be associated with this estimate. Mucus is a complex chemical which contains proteins, carbohydrates and lipids. Proteins, however, seem to form the largest single component (Wilson, 1968) and the calorific value cited above fits in with this characteristic.

The results on mucus production in P.contortus and A.fluviatilis indicate that 50 individuals produce 0.21 and 0.18mg. dry weight/day in these two species respectively. Associating these results with the calorific value given above suggests that 50 individuals lose 1.199 and 1.027 cals./day in A.fluviatilis and P.contortus respectively. By equations 3(6. 2) and 4(6. 2) (and assuming 10% ash) the average weight of individuals in each experimental group was 1.947 mg. ash-free dry weight in A.fluviatilis and 0.38mg. ash-free dry weight in P.contortus. Using equations 13(7. 5) and 16(7. 5) and assuming the calorific value of algal food is 5.126 kcal./g. (i.e. the average caloric density of natural epilitha - see TABLE 51) and bacterial food is 5.33 kcal./g. (see PART VII, SECTION 5. 2) it is possible to predict that each group of 50 individuals at 10°C, assimilate ca. 13cal./day in A. fluviatilis and ca. 4.0 cal./day in P.contortus. Thus energy losses via the mucus in the groups considered here and under the defined experimental conditions represent approximately 7.69% of the food input in the limpet and 25.68% of the input in P.contortus. These levels are not trivial and must be considered within the energy budget. It is recognised that the above estimates are crude and variations in the ratios given could occur both with changes in external and internal conditions. The higher percentage energy loss in P.contortus as opposed to A.fluviatilis probably reflects its more active state (see

also SECTION 4. 2).

4. 4. A Note on Mucus as a Medium for Microbial Growth

Casual laboratory observations have indicated that the sides of mucus coated glassware quickly become colonised with bacteria. Within ca. 48h. the mucus becomes extremely slimy and develops from a clear, more or less invisible state into a white or opaque colour. Smears from this material have been subjected to Gram stain and have indicated that the majority of the bacteria present were Gram positive Micrococci, similar in form to bacterium D. Thus energy losses via mucus, particularly in P.contortus, may not be lost entirely from the system but may act in some provendering role to provide suitable bacteria. Furthermore the relatively unusual dominance of Gram positive Micrococci within the epilithic, heterotrophic microflora on the shores of Malham Tarn (see PART VII, SECTION 4. 4.) may derive, in part, from the mucus secretions of the snails.

4. 5. General Discussion and Summary Regarding the Excretory and Mucus Losses

P.contortus and A.fluviatilis are uricotelic. It has been suggested that this adult excretory mode may derive from the cleidoic nature of the embryonic environment. The uric acid produced, however, is not lost from the bodies of the snails but accumulates within them. In an absolute sense such tying up of potential energy is tantamount to loss and should theoretically be treated as such. Practically, however, it would be difficult to effect the necessary partitioning so that this potential energy,bound up within stored uric acid,will be treated as part of the snails'biomass.

Some excretory material is lost within the faeces of freshwater snails and this, together with energy losses associated with the mucus coat of the faecal pellets and the mucus produced for purposes of movement may contribute up to 11.19% and 31.18% of the amount of food energy absorbed in A.fluviatilis and P.contortus respectively. It has repeatedly been emphasised that these values represent only crude approximations. Nevertheless, they account reasonably well for the energy imbalances which occur in the energy budget statements of the two species concerned when the mucus and excretory losses are not included (see PART IX).

PART IX

THE DETAILED DYNAMIC FUNCTIONAL ASPECTS OF POPULATIONS OF PLANORBIS CONTORTUS AND ANCYLUS FLUVIATILIS ON HA MIRE SHORE

1. INTRODUCTION

PARTS III to V considered the structural aspects of snail populations, and particularly those of A.fluviatilis and P.contortus on Ha Mire shore. PARTS VI to VIII have sought to extend this structural description into functional terms and particularly into a consideration of energy fluxes. Food energy inputs were considered in PART VII, heat and excretory energy outputs in PART VIII and growth in PART VI. It is the purpose of the following sections to integrate this functional information into a coherent, meaningful whole within the framework of an energy budget statement.

There is a paucity of information regarding the functional ecology of freshwater snails, epilithobionta and freshwater detritus/bacterial feeders. A consideration of the energy budgets of A. fluviatilis and P.contortus makes some contribution to all these areas and provides partial justification for the work.

In its reductionist formulation the energy budget is in no sense predictive (see also PART 1). It provides a convenient decriptive summary of the functional dynamics of populations over a short period of time and under specified conditions. It does not allow extrapolation beyond the time interval or the conditions implicit to its original construction because it fails to account for interactions which occur between its parts and for the resultant emergence of control. In the following sections the functional ecology of P.contortus and A.fluviatilis will be treated in this classical descriptive sense. The extraction of various ratios of efficiency will be emphasised since, within the constraints of the conditions of their measurement these enable a comparison with other populations in other habitat situations.

One part of the aim of ecology is an understanding of the function and functioning of natural populations (see also PART I). The ultimate expression of this aim would be a sound predictive theory, which would provide an objective means of assessing a-priori postulates. Prediction also provides the necessary challenge and stimulus for future research efforts and, therefore, acts as a directing influence. In this scheme comparative studies are essentially correlational and rely on a-posteriori interpretation. They suggest causal relationships but, like any historical approach, do not provide absolute verification since they rely heavily on subjective judgement. They, therefore represent a first-stage attempt at understanding and ordering

observations. The comparative methodology has been used to advantage in the fields of anatomy and physiology when emphasis has been on demonstrating a unity of origin (Waterman, 1961). At the other end of the scale, however, comparison underlines the structural and functional diversity of living systems and suggests the adaptive significance of particular functional strategies, and structural forms. The latter has more relevance to the ecologist who is concerned, at least in the first instance, with understanding the structure and function of present-day ecosystems. At all levels, however, the comparative approach has the advantage of shifting the emphasis from a consideration of specific types to a consideration of the general case..

It is in the above spirit that the following sections are written. The energy budget has provided a convenient system for summarising the results obtained in previous parts of the thesis, and for extracting the necessary efficiencies for comparison(N.B. in this sense the energy budget provides an operational device similar to that of the life-table in structural ecology - see Deevey, 1947 and Morris and Miller, 1954). A conscious effort will be made to compare the functional properties of snail populations (in terms of their metabolic efficiencies with those of other similar and dissimilar populations in an effort to extract some, albeit tentative, generalisations.

Throughout PARTS VI, VII, and VIII due regard was given to metabolic homeostasis. A consideration of the relevance of these results to the energy budget expression and to the erection of an ultimate predictive theory of ecological energetics will be postponed until PART X.

2. TERMINOLOGY

The usual equation will be used to define the energy budget of freshwater snails, viz. :

$$C - F = D = P + R + U + Sh \quad \ldots\ldots\ldots\ldots 1(9.\ 2)$$

Here the notation follows Petrusewicz (1967) with the exception of Sh which represents energy losses into the periostracum. The latter is, to some extent, analogous with energy losses as exuviae (Ev - see Lawton, 1971) in the arthropods. Here it is tacitly assumed that the energy diverted to the organic fraction of the shell cannot be re-used. The term for production (P) has been partitioned further into a component due to growth (Pg) and a component due to reproduction (Pr). Since there is no excretion in the sense of urinary potential energy losses, it has been taken to represent mucus losses (M) in locomotion and with the faeces, together with the loss of faecal excretory particles (E). Thus $U = E + M$. The term D can be calculated from both sides of equation 1(9. 2). When derived from terms on the right-hand side of the equation it will be called D(calc.) and when derived from terms on the left-hand side of the equation, D(obs.).

In P.contortus D and F can either be expressed in terms of the true-food material i.e. bacteria, or true-food plus inert food-carrier i.e. lignin, (see PART VII, SECTION 4). In the former case consumption and defaecation will be defined as C(b) and F(b) whereas in the latter case the same parameters will be defined as C(b+L) and F(b+L) respectively.

Equation 1(9. 2) will be denoted in lower case when referring to individual organisms and higher case when referring to the whole population.

The energy budgets of eggs will also be considered (see SECTION 4). Here the following equation will be used :

$$C(e + m) - C(m) + R(e) + U(e) = C(spat - calc.) \ldots 2(9.\ 2)$$

where $C(e + m) = C(e) + C(m)$

$C(e)$ = the energy content of an individual egg

$C(m)$ = energy content of the capsule membrane associated with an individual egg =

$$\frac{\text{Av. total calorific value of whole capsule membrane}}{\text{Av. no. of eggs/capsule}}$$

R(e) = energy losses through embryonic respiration

U(e) = energy losses through embryonic excretion

C(spat-calc) = energy content of emergent spat

Notice also that :

C(spat-calc) = C(spat-obs) ..... 3(9. 2)

where C(spat-obs) = the calorific content of actual, freshly emerged spat.

3. THE ENERGY BUDGETS OF INDIVIDUAL SNAILS

3. 1. Definition of Terms and Methods of Calculation

The energy budgets for both species have been calculated over a single generation (i.e. no. 2, see DATA APPENDIX 1) beginning in July (J 7) for P.contortus and August (A 8) for A.fluviatilis (see PART V, SECTION 5). The completion of GENERATION 2 was taken to be in the middle of August (i.e. midway between J20 and A21) for both species. This assumption was based on the fact that sampling interval J20 represented the last date on which adults of GENERATION 2 were observed (see FIGS 27 - 30). It was, therefore assumed that these adults died midway between sampling occasions J20 and A21.

The values of the terms given in equation 1(9. 2) were calculated over 28 day intervals spanning successive sampling occasions, except in the final interval when only 14 days were involved. The temperatures operating over each interval were assumed to be equivalent to the mean field temperatures summarised in FIG. 4. The value for each term in equation 1(9. 2) was calculated as follows :

i) d(OBS.) - was obtained from equations 12(7. 5) - 17(7. 5) corrected to mean field temperatures by equations 18(7. 5) - 19(7. 5) and converted to calories using the average field estimate of epilithic algae (i.e. 5.126 k.cal./g. ash-free dry weight) for A.fluviatilis and the average bacterial caloric density of 5.33 k.cal./g. ash-free dry weight) for P.contortus.

ii) c - was obtained by back-calculating from d(OBS.) using the assimilation efficiency (AE) i.e. :

$$c = \frac{d(OBS.)}{AE} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 1(9.\ 3)$$

The logic behind this method of calculation was discussed in PART VII, SECTION 5. 9. In A.fluviatilis AE was assumed equivalent to 60% except in the first month when a value intermediate between that of adults (60%) and spat (65%) i.e. 62.5% was used (see PART VII, SECTION 5. 9). In P.contortus the mean of all observed adult values of AE (i.e. from TABLES 53, 54, and 56) which was 76.3% was employed in all except the first months. In the latter instance a value intermediate between the average AE for adults (76.3%) and that for spat (94.0%, see TABLE 55) i.e. 85.2% was employed. It should be noted that

assimilation efficiencies were initially calculated with reference to the ash-free dry weight of food. Since, however, the ash-free dry weight of algae and bacteria are assumed functionally related to their calorific contents by the appropriate caloric densities, no modification of the AE estimates is required.

iii) $c(b + L)$ in P.contortus - Accepting the results given in TABLE 56 as indicative of the ratio between true food and food carrier taken by P.contortus under field conditions, it is possible to say that approximately equal amounts of lignin and bacteria are eaten by this species in terms of mass. Assuming further, that the calorific equivalent of the food carrier approximates to the caloric density of natural epilithic detritus it is possible to use the average value of the latter, derived from FIG. 81 and TABLE 42, i.e. 4.055 ($\pm$ 0.32), to provide an estimate of $c(L)$ in terms of energy by :

$$c(L) = \left(\frac{c(b)}{5.33}\right) 4.055 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 2(9.3)$$

This probably represents a slight overestimate since natural epilithic detritus contains a bacterial fraction. Nevertheless, ignoring this possible source of error :

$$c(b + L) = c(b) + c(L) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 3(9.3)$$

iv) f - was obtained by difference from :

$$f = c - d \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 4(9.3)$$

where in P.contortus

$$f = f(b) \text{ when } c = c(b) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 5(9.3)$$

and $f = f(b+L)$ when $c = c(b+L)$ ..... 6(9. 3)

v) r - in terms of μL. of oxygen, was derived from equations 8(8. 2) to 13(8. 2) corrected to the average monthly field temperatures by reference to FIGS 103 - 104 (see also PART VIII, SECTION 2. 5) and modified with respect to seasonal variability by the factors presented in PART VIII, SECTION 2. 6. The RQ value of 0.812, calculated by Burky (1971) from the biochemical constitution of the tissue of an "average" freshwater snail given by Hunter et. al. (1968), with a consequent oxycalorific equivalent of 4.813 calories/ml. inspired oxygen (Brody, 1945) has been used to convert the respiration data to energy units.

vi) OPERATORS IN THE METABOLIC EQUATIONS - The ash-free dry weight operators for equations 12(7. 5)-17(7. 5) and 8(8. 2)-13(8. 2) used in i) and v) above, were derived from a knowledge of mean snail lengths

(i.e. MD or AL, see FIGS. 68 and 69) on each sampling occasion, the relationship between lengths and tissue dry weights given by equations 3(6. 2) and 4(6. 2) and an assumption of 10% ash. The dry weights of spat are taken from TABLE 22 and 20% ash was assumed. The actual ash-free dry weight operators used over a particular interval were taken as the average between the snail mass calculated at the beginning and end of the interval concerned. In P.contortus, however, MD values vary haphazardly above and below an average of 2.706 mm. MD between sampling occasions N11 - M18. Since these fluctuations are not significant, see FIG. 29, they have been considered as arising from sampling error and the average value of 2.706mm. MD has been used throughout the interval. A similar assumption has been made for A. fluviatilis between D12 and F14 when an average value of 3.327mm. AL was used. The lower temperature limit for laboratory determination of assimilation and respiration was 4°C (see PARTS VI and VIII and SECTIONS 5. 8 and 2. 2 respectively). Reference to FIG. 4 indicates that in certain months some extrapolation below this temperature was necessary.

vii) sh - was calculated from the difference between the energy content of periostraca on successive sampling occasions. These were derived from a knowledge of the mean shell lengths at various times of the year (see FIGS. 68 and 69), equations 5(6. 2)-6(6. 2) relating shell length to shell weight, an estimate that 5% of the shell dry weight is organic (see PART VI, SECTION 2) and a periostracal calorific equivalent of ca. 5 k.cal./g. ash-free dry weight (see TABLE 25).

viii) pg - was calculated from the difference between the energy contents of soft body tissues on successive sampling occasions. These were obtained from a knowledge of mean shell lengths at various times of the year, length-dry weight relationships (given in equations 3(6. 2) and 4(6. 2), the percentage ash (i.e. 10% in adults and 20% in the spat) and the caloric densities given in TABLE 25.

(N.B. the calculation of terms in vii) and viii) above embody the same assumptions with regard to the mean length of P.contortus over the period N8-M18 and of A.fluviatilis over the period D12-F4 as contained in vi) above).

ix) pr - was derived from a knowledge of average number of egg capsules laid by a standard individual over the 1971 breeding period (see TABLE 19), converted to energy equivalents using the information contained in TABLE 25. Partitioning between months was achieved by reference to information on standard oviposition activity given in FIGS. 35 A

and D .

Due to the crudity of estimates made on the energy associated with mucus and faecal excretory particle loss (see PART VIII, SECTION 4. 5) these have not been incorporated directly into the energy budget statement. The sum of all terms calculated, therefore, provides an estimate of assimilation, less the energy involved in u.

3. 2. Results

The total utilisation and partitioning of energy over the whole generation interval (i.e. 13.5 months for P.contortus and 12.5 months for A.fluviatilis), expressed in terms of the parameters on the right-hand side of equation 1(9. 2), is given in TABLE 69. A detailed breakdown of the variation in each energy budget.parameter from month to

TABLE 69. The total utilisation and partitioning of assimilated energy by individuals of P.contortus and A.fluviatilis over a 13.5 and 12.5 month interval respectively. The units are expressed in calories per individual and S.I. equivalents are contained in parentheses.

	P.contortus		A.fluviatilis	
	cals.	(Joules)	cals.	(Joules)
pg	2.237	(9.364)	17.622	(73.766)
pr	2.955	(12.370)	8.634	(36.142)
sh	1.131	(4.734)	1.485	(6.216)
r	15.446	(22.797)	38.848	(162.618)
d(calc.)-u	21.769	(91.125)	66.589	(278.475)
d(obs.)	28.874	(120.867)	72.091	(301.773)

month is given in DATA APPENDICES XVI and XVII for P.contortus and A.fluviatilis respectively.

The difference between (d(calc.)-u) and d(obs.) represents the elements of the budget not accounted for in the former expression (i.e. u) and also errors of estimation. The extent of agreement between these two estimates expressed as :

$$\frac{d(calc.) - u}{d(obs.)} \times \frac{100}{1} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 7(9.\ 3)$$

for the totals given in TABLE 69 are 92.4% for A.fluviatilis and 76.4% for P.contortus. This, however, obscures a considerable degree

of, to some extent, haphazard monthly variation in the expression given by equation 1(9. 2) (see DATA APPENDICES XVIII and XIX). The range of variation in A.fluviatilis for example is between 240.1-49.5%. Nevertheless for 9 out of the 13 intervals d(calc.)-u and d(obs.) are within 25% of each other and the periods of maximum imbalance in favour of d(obs.) (i.e. D12-F14) coincide with winter months when blue-green algae, of lower caloric densities (see PART VII, SECTION 5. 2) dominated the food taken (see FIG. 79). Here the calorific value of food actually ingested may be lower than the mean annual estimate of 5.126 k.cal./g. ash-free dry weight which has been used. The two months in which there are excessive imbalances in favour of d(calc.)-u (i.e. O10 - N11 and F14 - M15) cannot be accounted for in these terms and may result from experimental errors. It should be noted, however, that the considerations given in PART VII, SECTION 5. 9, suggesting that the food energy absorbed may be (by virtue of controlling mechanisms) to some extent independent of the quality of food ingested, possibly makes utilisation of the caloric density of Navicula more pertinent for application (i.e. 5.473 k.cal./g. ash-free dry weight). This would have the effect of reducing imbalances in favour of d(calc.)-u but would magnify the imbalances in favour of d(obs.).

In P.contortus the imbalances expressed by equation 7(9.3)range from 43-141%. Most of the imbalances in favour of d(calc.) occur during the winter months when it is possible that some energy is extracted from the non-living fraction of the detritus.

Neglecting the monthly variations between d(obs.) and d(calc.)-u the values based on the totals given in TABLE 69 are in the same order of magnitude as would be expected to occur from excluding u(=m+e) in the construction of the energy budget. Thus information given in PART VIII, SECTION 4. 5 suggests that u may account for 11.19% and 31.18% of the total energy absorbed in A.fluviatilis and P.contortus respectively. The close agreement between these two independent estimates suggests that much of the monthly variation discussed above is spurious and results from errors of estimation. More confidence should, therefore, be placed in the summed estimates which, like all summations and averagings, absorb some of the underlying variation in the component data.

The energy utilisation and partitioning in terms of the parameters present on the left-hand side of equation 1(9. 2) are given in TABLE 70 for both A.fluviatilis and P.contortus. The data are in terms of

the whole generation interval. Monthly variations in and methods of calculating each of the parameters presented are given in DATA APPENDICES XX and XXI.

TABLE 70. Ingestion, absorption and defaecation of energy by typical individuals of A.fluviatilis and P.contortus over GENERATION 2. The data are expressed in calories per individual and S.I. equivalents are given in parentheses.

	A.fluviatilis		P.contortus	
	cals.	(Joules)	cals.	(Joules)
d(obs.)	72.09	(301.769)	28.874	(120.867)
c *	120.052	(502.538)	37.663	(157.657)
f *	47.961	(200.765)	8.789	(36.791)
c(b +)	-		66.312	(277.582)
f(b +)	-		37.437	(156.711)
c(e)	-		28.649	(119.925)

* c = c(b) and f = f(b) for P.contortus

Various efficiencies of energy transformation, extracted from the information given in TABLES 69 and 70, and representing typical individuals in GENERATION 2 in Ha Mire populations of A.fluviatilis and P.contortus are given in TABLE 71. These are not exhaustive but are sufficient for future discussion.

TABLE 71. Various efficiencies of energy conversion in typical individuals of A.fluviatilis and P.contortus. The results apply to GENERATION 2 in Ha Mire populations.

Efficiency	A.fluviatilis	P.contortus
1. Assimilation Efficiency		
$\frac{d(obs.)}{C_{++}} \times \frac{100}{1}$	59.82	76.70
$\frac{d(obs.)}{C(b+L)} \times \frac{100}{1}$	-	44.14
2. Proportion of absorbed energy which was respired.		
$\frac{r}{d.obs.} \times \frac{100}{1}$	53.89	53.46
3. Proportion of absorbed energy used in pg.		
Gross growth efficiency (K_1) $= \frac{pg}{C_{++}} \times \frac{100}{1}$	14.70	6.21
$\frac{pg}{C(b+L)} \times \frac{100}{1}$	-	3.57
Net (K_2) $\frac{pg}{d.obs.} \times \frac{100}{1}$	26.46	7.75
4. Proportion of energy absorbed which was "excreted"		
$\frac{sh + u}{d(obs.)} \times \frac{100}{1}$	9.69	28.5
$\frac{sh}{d(obs.)} \times \frac{100}{1}$	2.05	3.92
	** ***	** ***
$\frac{u}{d(obs.)} \times \frac{100}{1}$	7.60 (11.19)	24.60 (31.18)
5. Proportion of absorbed energy used in reproduction.		
$\frac{pr}{d(obs.)} \times \frac{100}{1}$	11.98	10.23
6. Proportion of non-respired absorbed energy used in reproduction.		
$\frac{pr}{d(obs.)-r}$	26.00	22.00
7. The ratio of energy use in growth to that used in reproduction. ?		
$\frac{pr}{pg}$	49.00	10.23

++ $c=c_b$ for P.contortus ** calculated *** experimentally observed

4. ENERGY BUDGETS OF THE EGGS

4. 1. Definition of Terms and Methods of Calculation

The terms used in equations 2(9. 2) and 3(9. 2) were calculated as follows :

i) Ce - was derived from the information given in DATA APPENDIX VI

ii) Cm - represents the average amount of membrane energy associated with each egg contained within a capsule. It is obtained from the total calorific value of the capsule membrane (see DATA APPENDIX VI) divided by the average capsule size (i.e. 2.56 and 3.49 for A.fluviatilis and P.contortus respectively i.e. the averages of the values given in TABLE 13)

iii) Re - no direct estimations on egg respiration have been made. Baldwin (1935b), however, has considered the respiratory rates and RQ values for individual eggs of L.stagnalis and his results have been assumed applicable to freshwater snails in general. From his TABLE 1 it is possible to compute an average respiratory rate which can be applied over the whole embryonic period. This was found to be 34.2μL./g./h. It should be noted, however, that the respiratory rate is not constant throughout embryogenesis but increases, at a reducing rate, as development procedes. RQ values also change within the embryonic period being slightly greater than unity (i.e. 1.05) in the initial phases, but falling below unity (i.e. to 0.99) prior to eclosion. An average value of 1.00 with an associated oxycalorific equivalent of 5.047 cals./ml. oxygen inspired (Brody, 1945) has been used here. Knowing the average length of the developmental period between laying and hatching i.e. 13.3 days for P.contortus and 25.8 days for A. fluviatilis (see PART V, SECTION 4. 2A) it is possible, on the basis of the above information, to calculate the caloric loss due to respiration over this interval.

iv) Ue - in terms of uric acid production, was calculated from the information contained in TABLE 68 together with that concerning the average weight of individual eggs (see TABLE 68). Uric acid was taken to have a caloric density of 2.74 cal./mg. ash-free dry weight (Brody, 1945). Although this material is not lost from the egg capsule during embryogenesis it is assumed to be left behind on eclosion.

v) C(spat-obs.) - was derived from a knowledge of the average dry weight

of spat (see TABLE 22), the calorific values given in TABLE 25 and on the assumption that 20% of the spat dry weight is ash.

4. 2. Results

The values of the terms contained in equations 2(9. 2) and 3(9. 2) are presented for both species in TABLE 72.

TABLE 72. The values of terms contained in equations 2(9. 2) and 3(9. 2). These are expressed in terms of calories although S.I. equivalents are given in parentheses.

	P.contortus		A.fluviatilis	
	cals.	(Joules)	cals	(Joules)
Ce	0.056	(0.234)	0.197	(0.825)
Cm	0.031	(0.130)	0.081	(0.339)
Ce + m	0.087	(0.364)	0.278	(1.164)
Re	2.5 * x 10^{-4}	(10.5 x 10^{-4})	0.008	(0.034)
Ue	0.002	(0.008)	0.003	(0.013)

* ignored

A check on the assumptions implicit to the calculations embodied in SECTION 4. 1 is obtained by a comparison of C(spat-calc.) and C(spat-obs.) as given in equation 3(9. 2). The information presented in TABLE 72 enables evaluation of equation 2(9. 2) and provides estimates of C(spat-calc.) i.e. ca. 0.050 and 0.181 cals. in P.contortus and A.fluviatilis respectively. This value in P.contortus is identical to c(spat-obs.) i.e. 0.050 cals. and the value of c(spat-calc.) is within 3% of c(spat-obs.) in A.fluviatilis i.e. 0.179 cals.

The efficiencies derived from these considerations are contained in TABLE 73 in which terms 1 and 2 can be considered as net and gross efficiencies respectively.

TABLE 73. Efficiencies of energy transformation within the eggs of P.contortus and A.fluviatilis

Efficiency	P.contortus	A.fluviatilis
1 $\frac{C(spat-obs.)}{Ce}$	96.4%	91.9%
2 $\frac{C(spat-obs.)}{C(e + m)}$	62.0%	66.9%

5. POPULATION ENERGY FLOW

5. 1. Definition of Terms and Methods of Calculation

The terms necessary for describing energy flow through Ha Mire populations of A.fluviatilis and P.contortus were calculated as follows :

i) MEAN MONTHLY DENSITIES ($\bar{N}$) - Estimates of snail population densities over GENERATION 2 are given in FIGS. 46-50. Equations 2(5. 5), 3(5. 5) and 6(5. 5) describe the reduction in density with time, and using initial densities derived from TABLE 20, column 1,were used to predict density levels (i.e. as no./10,000LP) at 28 day intervals from the first day of GENERATION 2 (see SECTION 3. 1). The density reductions within each interval can be taken as arising from mortality since emigration (and immigration) is not likely to be significant within the study area (see PART IV). $\bar{N}$ for a particular month was obtained from the sum of the mean density level at the beginning and end of the period divided by 2.0. This assumes that the individuals dying within the interval can live for 14 days. All mean density estimates were expressed in terms of stone surface area (m^2) by dividing each density estimate in terms of 10, 000LP by a factor of 2.2 (see Calow 1972; see PUBLICATIONS APPENDIX II)

ii) THE ENERGY BUDGET PARAMETERS - The values for parameters given in equation 1(9. 2) for a typical individual were corrected to the population level by multiplying by $\bar{N}$ for each month e.g.

$$\bar{N}r = R$$

Population assimilation over the whole of GENERATION 2 was calculated from :

$$\frac{\Sigma Pg + \Sigma Pr + \Sigma Sh + \Sigma R}{1 - x} = D \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 1(9.\ 5)$$

where Σ indicates summation of each parameter over the whole of GENERATION 2 and x = 0.076 and 0.250 for A.fluviatilis and P.contortus respectively and represents the calculated minimum imbalance between d(obs.) and d(calc.)-u. Parameter x, therefore, takes account of the proportion of total absorbed energy diverted to the production of faecal excretory particles and mucus. This formulation was also used to provide an estimate of D for each monthly period and the latter has been used as an index of population energy flow.

Total population ingestion (C) was calculated from :

$$\frac{D}{AE} = C \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 2(9.5)$$

where AE = 59.82 for A.fluviatilis and 76.70 (when C = C(b)) or 44.14 (when C = C(b + L)) in P.contortus (see TABLE 71).

The population energy loss as faeces (F) was calculated from :

$$F = C - D \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 3(9.5)$$

remembering that F = F(b) when C = C(b) and F = F(b + L) when C = C(b+L) in P.contortus.

iii) Biomass ($\bar{B}$) - this parameter was taken to represent the mean population standing crop (in calories) over a 28 day interval. It was calculated from the mean caloric size of individual organisms over the period concerned (i.e. the results from the calculations described in SECTION 3. 1 iv) corrected to calories by the information presented in TABLE 25) multiplied by $\bar{N}$.

iv) PRODUCTION (P) - is considered to represent the growth increments of all individuals existing at the beginning of GENERATION 2 and surviving to its end plus the growth of individuals which die during the interval. This follows the classical definition of Thienemann (1931) advocated by Winberg (1971). Monthly population production is, therefore, calculated from :

$$Pg = \bar{N}pg \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 4(9.5)$$

and total generation production from :

$$P = \sum_{j=1}^{x} \bar{N}pg \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 5(9.5)$$

where x = 12.5 in A.fluviatilis and 13.5 in P.contortus.

v) Yield (Y) - This term can be considered in a number of different ways. It can either be used to denote the total amount of energy transferred to all other trophic levels i.e. that produced which has continuing biological significance (c.f. heat production) or it can be construed to represent the biologically useful energy transferred from the population in question to some particular, usually predatory, trophic group. It will be used in both senses in the following sections. Total yield Yi will be considered as the energy content of all the metabolic products produced by GENERATION 2 i.e. :

$$Yi = \sum_{j=1}^{x} D - R \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 6(9.5)$$

where x is defined above.

There is some doubt as to whether faeces should be included in this estimate (Slobodkin, 1962b), but since they are not produced in the true sense of the word they will not be included here. It should be noted, however, that the structural modifications effected on indigestible materials as they pass through the gut may have profound biological importance (Edwards and Heath, 1963; Mason, 1970b).

The egg capsule membranes which are discarded on hatching, egg excretory losses and the mortality of both eggs and the young which die immediately on hatching form the yield from the reproducta (Yr) and can be considered as contributing to a new form of the total yield (Yii). This is defined as :

$$Yii = Yi + Yr \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 7(9.5)$$

Total yield in this sense probably allows closest approximation to the staedy state condition demanded of the energy budget statement (Odum, 1957, 1960; Slobodkin, 1960, 1962b).

In the snail species considered here, it is likely that only a small proportion of either Yi or Yii is transferred to predators (see PART V, SECTION 5. 2.). It will be assumed that only spat dying over the first month of life, plus all the eggs lost during the breeding season (see PART V, SECTION 4. 6) together with the loss of spat immediately on hatching from the egg crop of GENERATION 2 (see PART V, SECTION 4. 7B) are used by predators. Thus, ignoring the egg phase and subsequent spat production by GENERATION 2, yield to predators (Yiii) becomes :

$$Yiii = \left(\frac{n_1 - n_2}{2} \right) pg \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 8(9.5)$$

where n_1 and n_2 = snail densities on the first and second sampling occasions of GENERATION 2

pg = individual growth over the interval between the first two sampling occasions

Including the egg phase and subsequent spat production the yield to predators (Yiv) becomes :

$$Yiv = \left(\frac{n_1 - n_2}{2} \right) pg + C_e M_e + C(\text{spat-obs.}).\, M(\text{spat}) \ldots\ldots\ldots\ldots\ldots\ldots \quad 9(9.5)$$

where M_e and M(spat) represent the proportion of eggs and spat respectively which are lost from the total egg crop produced by GENERATION 2. C_e and C(spat-obs.) have been defined earlier (see

SECTION 4. 1). It is assumed that egg capsule membranes are not eaten by predators (see PART V, SECTION 4. 6C) and that spat shells are also rejected (see PART V, SECTION 5. 2). The latter may not always be the case (e.g. with the predator E.octoculata) and the picture may be complicated since the predators seem to reject snail feet. Some predation probably occurs in adulthood so that both Yiii and Yiv represent minimum estimates.

Yield to detritovores which includes individuals dying naturally (or at least not via predatory action), periostraca, mucus, excreta, and egg case membranes can be defined either exclusive of the egg phase :

$$Yv = Yi - Yiii \quad \ldots\ldots 10(9.5)$$

or inclusive of the egg phase :

$$Yvi = Yii - Yiv \quad \ldots\ldots 11(9.5)$$

5. 2 Results

The total utilisation and partitioning of energy by Ha Mire populations of A.fluviatilis and P.contortus over GENERATION 2 is summarised in TABLE 74. The seasonal fluctuations in tissue production

TABLE 74. Total utilisation and partitioning of energy by GENERATION 2 population. The units are expressed in calories/m^2 and S.I. equivalents are given in parentheses.

	A.fluviatilis		P.contortus	
	cals./m^2	(Joules)	cals./m^2	(Joules)
Pg	81.745	(342.185)	110.178	(461.205)
Pr	11.040	(46.213)	14.360	(60.111)
Sh	11.381	(47.641)	45.105	(188.810)
R	90.835	(380.235)	150.072	(628.201)
Σ	195.001	(816.274)	319.715	(1338.327)
D	208.651	(873.413)	399.644	(1672.910)
*C (D/AE)	348.799	(1460.073)	521.048	(2181.107)
*F (I - A)	140.148	(586.660)	121.404	(508.197)
C (b + L)			905.401	(3790.009)
F (b + L)			505.757	(2117.099)

* C = C(b) and F = F(b) in P.contortus

(Pg), energy flow (of which the monthly amounts of energy assimilated were used as an index), population biomass ($\bar{B}$) and numbers (per $m.^2$ of stone surface), together with fluctuations in temperature are given in FIGS. 115 and 116 for A.fluviatilis and P.contortus respectively.

TABLE 75 contains various ecological efficiencies (E) defined generally as :

$$E = \frac{\text{YIELD}}{\text{FOOD ENERGY INPUT}} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 12(9.5)$$

(Slobodkin, 1959, 1960, and 1964) and extracted from the information contained in TABLE 74. Within this formulation the terms, "FOOD ENERGY INPUT", and "YIELD", are ambiguous. Food input can either be used to denote the energy ingested (apparent input) when a gross efficiency (Eg) is defined or food energy assimilated (actual input) when a net efficiency (En) is defined. The efficiencies given by Slobodkin (1959, 1960 and 1964) are in terms of Eg. In P.contortus further complications arise from the fact that food input with respect to ingested materials may be expressed in terms of either true food (bacteria) or this material plus the inert carrier. These two possibilities will be distinguished as follows :

$$En, b = \frac{Y}{C(b)} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 13(9.5)$$

$$En, b+L = \frac{Y}{C(b+L)} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 14(9.5)$$

Ambiguities in using the term "YIELD" have already been discussed (see SECTION 5. 1). The term E can be defined in terms of either Yi or Yii or Yiii or Yiv or Yv or Yvi, and each related efficiency will be denoted by the appropriate subscript e.g. :

$$Eni = \frac{Yi}{A} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 15(9.5)$$

As Kozlovsky (1968) has noted the number of ecological efficiencies which can be defined is almost unlimited. This is particularly the case if specific peculiarities of population energy flow are taken into account (see En, b and En, b+L , of P.contortus above). The efficiencies which have been defined here are not exhaustive but are relevant to future discussion.

Finally it should be realised that an ecological efficiency,

TABLE 75. Various ecological efficiencies (in percentages) for Ha Mire populataions of P.contortus and A.fluviatilis over GENERATION 2. For further explanation, see text.

Efficiency		Definition	A.fluviatilis	P.contortus
	E,g,i	Yi/c *	30.61	45.14
Ei	Eg,b+L,i	Yi/c(b+L)	-	25.98
	E,n,i	Yi/D	51.17	58.86
	E,g,ii	Yii/c *	33.22	53.83
Eii	Eg,b+L,ii	Yii/c(b+L)	-	31.01
	E,n,ii	Yii/D	55.69	70.17
	E,g,iii	Yiii/c *	0.75	7.06
Eiii	Eg,b+L,iii	Yiii/c(b+L)	-	4.07
	E,n,iii	Yiii/D	1.25	9.21
	E,g,iv	Yiv/c *	2.41	7.93
Eiv	Eg,b+L,iv	Yiv/c(b+L)	-	4.60
	E,n,iv	Yiv/D	4.17	10.33
	E,g,v	Yv/c *	29.86	38.08
Ev	Eg,b+L,v	Yv/c(b+L)	-	21.91
	E,n,v	Yv/D	49.92	49.65
	E,g,vi	Yvi/c *	30.82	45.90
Evi	Eg,b+L,vi	Yvi/c(b+L)	-	26.41
	E,n,vi	Yvi/D	51.52	59.80

* c = c(b) in P.contortus

being a ratio, is dimensionless (Slobodkin, 1962b). All the efficiencies presented in TABLE 75 are expressed as percentages.

6. DISCUSSION

Appendices XVI - XXI show that the pattern of energy utilisation by individual snails for growth, respiration, etc. varied widely throughout development. In general, most energy was assimilated during the reproductive phases of the life cycle and this was involved mainly in the formation of reproducta. In P.contortus and to a lesser extent A.fluviatilis assimilation was reduced during winter months, growth ceased and most of the energy input was involved in maintenance. In this instance the latter includes mucus and excretory losses as well as respiration.

The assimilation efficiencies have already been discussed in PART VII, SECTION 5. 6. It should be noted, however, that the e efficiencies presented in TABLE 71 taking into account the food-carrier in P.contortus, fall close to the efficiencies reported by Mason (1970a) for various species of terrestrial pulmonate (i.e. 50-60%). As already discussed, the assimilation efficiency of P.contortus is high considering its detritophagous habit. This seems to result from some active selection of the digestible (bacterial) component of the epilithic detritus, separation of the true-food from the food-carrier prior to its reaching the hepatopancreas, and a greater consumption of food in the presence of the diluent. Some other aquatic detritophages have lower assimilation efficiencies than P.contortus e.g. the chydorid Eurycercus lamellatus - 20% (Smirnov, 1962), and the plecopteran larva, Pleuronercys scottii 8.5 - 15.9% (Mc Diffet, 1970) and Hyalella azteca - 6 - 22% when feeding on pure detritus (Hargrave, 1970a). Yet Tubifex tubifex has a relatively high efficiency of ca. 50% (Ivlev, 1939) and it may be significant that this species feeds on bacteria (Brinkhurst and Chua, 1969; Wavre and Brinkhurst, 1971). A statement on the relationship between high assimilation efficiencies and a bacterial feeding mode requires more information than is at present available. Certainly benthic bacterial feeders, when offered pure bacterial cultures as food, have high assimilation efficiencies although their planktonic counterparts have lower efficiencies (see Calow and Fletcher, 1972; PUBLICATIONS APPENDIX III). Healey (1967) has reported high assimilation efficiencies in collembola feeding on fungi (i.e. 40-70%) which is, in some respects, similar to the bacterial feeding habit.

Welch (1968) analysed the relationship between individual growth

and food assimilation efficiencies in aquatic consumers. Actual gross and net growth efficiencies are considerably lower than the values predicted on the basis of a 60% assimilation efficiency in A.fluviatilis and a 44% efficiency for P.contortus. The predicted values are k_1 = 50 and 58% and k_2 = 26 and 25% in the microherbivore and the detritophage respectively (c.f. TABLE 75). Lawton (1971) has already called question to Welch's analysis. Nevertheless ignoring excretion and reproduction Welch's relationship predicts an r/d value (i.e. assuming r = d - pg) of ca. 50-60% and this compares well with the r/d efficiencies presented in TABLE 75. Divergence from the predicted pg/d value, therefore, seems to arise from a large production of "excreta" (sh + u) which represents ca. 10% of the assimilated energy in A.fluviatilis and ca. 30% in P.contortus.

These excretory energy losses are vital to the well-being of the snails. Some are used in the production of periostracum but most in producing mucus. The latter is necessary for compacting faeces in order to prevent the fouling of the head apparatus in the torted condition and is also essential for movement. The higher mucus production in P.contortus has already been discussed (see PART VIII, SECTION 4. 3).

Reproductive losses are also involved in the inconsistencies between actual and predicted net and gross efficiencies of growth. The pr/pg values are extremely high in both P.contortus and A.fluviatilis (see TABLE 75) but are not inconsistent with other values reported in the literature, e.g. the isopods Oniscus ascellus and Porcellio scaber have pr/pg ratios of 196.0 and 345.45% respectively (Watson, 1966). Hunter (1970) has indicated that freshwater snails may divert as much as 87% of their non-respired, assimilated energy to reproducta during breeding. This behaviour may be expected in semelparous organisms where there is a considerable premium on replacement. Calow (1972 , see PUBLICATIONS APPENDIX IV) has suggested that in these cases reproduction may occur at the expense of the parental metabolic requirements.

The lower pr/pg values in A.fluviatilis with respect to P. contortus may result from the emergent spat of the former species being larger and thus having a better chance of survival than the smaller spat of P.contortus. This follows from the greater albuminous content of limpet eggs and probably means that P.contortus requires to exert a greater reproductive effort (in terms of energy) to replace itself.

Thus the greater energy content of A.fluviatilis eggs means that it requires to expend less energy (in terms of the energy used for parental growth) in replacement and survival.

Eggs receive their total energy requirements for embryogenesis from their parents. This includes the potential energy needed for structural developments as well as that required for powering the latter. If Baldwin's (1935b) data are accepted, little energy is lost as a result of embryonic respiration and most energy losses occur at eclosion when the egg membranes are discarded and insoluble excretory products are left behind. The last statement is assumed, not proved, although good balance in equation 3(9. 2) (see TABLE 72) lends support to this assumption. Brody (1945) cites examples for chick, silkworm, frog and sea urchin eggs in which 63, 63, 51, and 59% respectively of the eggs initial energy content (i.e. on laying) appeared in the newly hatched young. The net efficiencies quoted in TABLE 73 are far higher than this although the gross efficiencies, in which the egg membranes are accounted for, correspond to Brody's results. High net egg efficiencies may represent a response to the large amounts of energy required for incorporation into the egg membranes. The adaptive significance of these structures has already been discussed (see PART V, SECTION 4. 6).

The population energy flow characteristics and conversion efficiencies are the product of the energetic behaviour of the component individuals, but are complicated by the emergent, determining characteristics which are unique to the population. These include immigration, emigration, age structure, sex ratio, mortality, and natality. The population is not an aggregate of its parts but represents a system in the true sense of the word in which the reductionist concept of additivity is irrelevant

Immigration and emigration can be important components of the population energetics (Wiegert, 1964), but are probably of little consequence in the two populations being considered here since they can be considered as ecologically isolated (see PART IV). Furthermore age structures and sex ratios are not applicable since both P.contortus and A.fluviatilis are annual, with a single fixed breeding season followed by parental death and both species are hermaphrodite. The effect of the single fixed breeding period is to limit rising population changes to one, fairly limited period, so that all other density changes are falling and are due to mortality. This probably

represents the simplest possible natural case.

A comparison between population density (nos./$m.^2$), biomass (standing crop in cals./$m.^2$), energy flow (cals,/28 days/$m.^2_1$), and tissue production (cals./28 days/$m.^2_1$) has been presented in FIGS. 115 and 116. The fluctuations in mean monthly temperature are also included within these figures. Assimilation rather than consumption has been used as the index of population energy flow since difficulties in interpreting the consumption of P.contortus (i.e. because it consists of true-food and food-carrier) would have made comparison with A. fluviatilis impossible.

In P.contortus the hyperbolic nature of the mortality curve impresses itself on the other population characteristics considered. This is particularly the case with respect to energy flow and production. An end of season rise in energy flow is correlated with the resumption of tissue growth, but more importantly with reproduction. In A. fluviatilis energy flow and production are better correlated with biomass than with changes in population density. Again there is an end of season peak in energy flow associated with reproduction and a short, sharp peak before this related to a pre-ovipositional resumption of growth and possibly to preparation for reproduction.

The seasonal temperature fluctuations are correlated with the seasonal fluctuations in the functional characteristics of both species. This is to be expected since temperature is an important determining characteristic in all elements of poikilotherm energy budgets, see PARTS VII and VIII and SECTIONS 5. 8 and 2. 2 respectively. Nevertheless, the ability to regulate, acclimate (see the above PARTS and SECTIONS) means that the relationship between temperature and population functioning will not be a simple one (see also Widdows and Bayne, 1971). Thus the dramatic early reductions of Pg and energy flow in P.contortus together with an extended winter period when Pg and energy flow is negligible are probably related to reducing or reduced temperature conditions since this species is poorly adapted to low temperature (see PARTS VI and VII and SECTIONS 4. 2 and 2. 2 respectively). In contrast Pg and energy flow is not so sensitive to temperature in A.fluviatilis since this species is better adapted to low than high temperatures (see the above PARTS and SECTIONS).

1-in the last interval of GENERATION 2 these parameters are expressed in terms of a 14 day interval.

Throughout the thesis great emphasis has been placed on the fact that the density of P.contortus on Ha Mire is greater than that of A.fluviatilis. FIGS. 115 and 116, however, show that apart from the first 2 months of GENERATION 2 the biomass of A.fluviatilis is at least equivalent to and indeed may be greater than that of P.contortus. Similarly the energy flow in the limpet may be greater than that of P.contortus. These differences result from the larger size (in terms of mass and energy) of A.fluviatilis with respect to P.contortus. This underlines the view proposed by other workers that various modes of expression and methods of measuring the ecological importance of particular populations can give different results (Odum, 1962; Macfadyen, 1964; Vickers, 1969; Wilhm, 1970). As Slobodkin (1962b) has remarked, " no one (population) parameter is intrinsically important", (my terminology is given in parentheses). Which parameter is considered will depend on the types of question being asked. Thus in the present instance, questions concerning functional importance or competition (if it occurred for food) must be answered in terms of biomass, production, or energy flow. A discussion of competition in terms of space (see PART V, SECTION 4. 4B) in which the numbers of individuals present will be the critical parameter, must be framed in terms of density.

Because of the high levels of mucus production total net and gross production efficiencies for P.contortus and A.fluviatilis, inclusive and exclusive of the reproducta (i.e. efficiencies Ei and Eii in TABLE 75; N.B. total yield is equivalent to total production in annual populations) are higher than most other reported figures (see Engelmann, 1961, 1966; Golley, 1960; Mann, 1965; Qasrawi, 1966; Schroeder, 1969; Wiegert, 1964). They are not, however, inconsistent with the value of ca. 88% quoted by Teal (1957) for the freshwater planarian Phagocota group where mucus production is also high. Here Teal (Ibid.) ascribes the reduced metabolic cost as being a specific adaptation to compensate for the high costs of mucus production. Tilly's (1968) results on Physa integra are the only others available for a freshwater snail population and the production efficiency quoted (i.e. 27.9%) is lower than the ones given above for P.contortus and A.fluviatilis. Tilly (Ibid.), however, took no account of mucus and excretory losses in the energy budget of P.integra so that the production efficiency reported is probably under-estimated.

The production efficiencies for marine Gastropoda are generally

lower than the ones quoted here for freshwater species e.g. :

Littorina irrorata	-	14% (Odum and Smalley, 1959).
Tegula funebralis	-	19.8-22.9% (Paine, 1971)
Fissurella barbadensis	-	26.7% (Hughes, 1971)
Nucella lapillus	-	26-27% (Hughes, 1972)

Only Paines (1971) results, however, take direct account of mucus losses although even his results are low. Each of these marine species is littoral and is subject to reduced locomotion between tides so that mucus losses due to locomotion are unlikely to account for as great a proportion of total energy flow as in the continuously mobile freshwater species. Furthermore, littoral existence and the tidal phenomenon may produce metabolic stress and result in greater metabolic costs than in continuously submerged species. Information on terrestrial snails is generally lacking.

The dominance of mucus secretions in the metabolism of P.contortus and A.fluviatilis precludes use of the equations of McNeill and Lawton (1970) relating production to respiration and vice-versa. These workers specifically excluded mucus producing organisms from their considerations and as expected the P/D values derived from their equations representing the general invertebrate case and the short life-cycle species underestimate the values of Ei and Eii obtained here. Using total respiration (R) the values obtained are 22.60 and 26.84%[1] for A.fluviatilis and 19.9 and 25.9%[1] for P.contortus.

The equations of Mathias (in Mann, 1969) relating biomass to production in animals provide estimates of production which are lower than total production (i.e. including Pr, Sh, and U) in P.contortus and A.fluviatilis. The results obtained were 81.28 cals./m.^{2} /GEN.2 for the former species and 102.00 cals./m.^{2} /GEN.2 for the latter species. These values, however, show close correspondance with Pg. The equations of Mathias (Ibid.) for organisms with a life cycle longer than 1 year were completely inapplicable.

At this juncture it is pertinent to make some comment on the so called, "short cut techniques" (e.g. Welch, 1968; Engelman, 1966; Mathias, cited in Mann, 1969; McNeill and Lawton, 1970) as contributions to the general framework of ecological theory. These methods are essentially correlational. A fit between two parameters is found,

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1 - These values were obtained from McNeill and Lawtons' (1970) equation representing invertebrates with a short life cycle.

accepted and used, and provided the fit is significant the method is quite acceptable. Short cut methods, then, provide the facility for predicting one parameter from another and lessen the tedium of ecological research (e.g. Hughes, 1972). We have seen in the present instance, however, that none of these methods is directly relevant to the particular, albeit extreme, cases under consideration. This calls question to their generality. Furthermore, it goes without saying that correlation does not necessarily imply causal relationship and may not even assist in causal interpretation. This criticism can be leveled at all multivariate methods. Thus, "short cut" methods have their place in producing answers quickly and inexpensively, but it is questionable whether they can contribute to ecological understanding in the true sense of the word.

Of all the efficiencies presented in TABLE 75 those presented under Eiv, in the approximate steady state situation, are most closely related to the ecological efficiency as conceived by Slobodkin (1959, 1960, and 1962b). Because Slobodkin (Ibid.) considered energy input in terms of ingestion efficiencies Egiv and Eg, b +L , iv are probably particularly relevent. The ecological efficiencies obtained by Slobodkin for laboratory populations of Hydrida and Daphnia ranged between 4-13%. The values presented in TABLE 75 for P.contortus fall within this range whereas that for A.fluviatilis, judged in terms of consumed energy, falls below the lower limit of 4% given above. This is probably due to the low susceptibility to predation both in the egg, spat and adult stages (see PART V, SECTIONS 4. 6, 4.7B, 5. 2 respectively) of this species. It should also be noted that the estimates made on energy losses to predators are minimum in the sense that possible predatory losses during adulthood have been ignored. Furthermore, if one accepts the possibility of metabolic control there is no a-priori reason for believing that the ecological efficiencies considered in the above sense, or for that matter any contained in TABLE 75 should remain constant either within or between species. Thus an environmental perturbation in terms of a reduction in food input, within limits, will not be expected to produce a proportional reduction in protoplasmic production (yield to predators) since the organisms concerned may be able to regulate the latter with respect to the former (see PART VI, SECTION 4. 3). In this situation Slobodkin's ecological efficiency would rise.

In summary, if one accepts the crude estimations on "excretory"

energy losses given in PART VIII, SECTION 4. 5 it is clear that the energy budgets of the two species of snail which have been considered are dominated both at the individual and population levels by mucus production. This makes interpretation of the individual and population energy conversion efficiencies difficult from the point of view of previously reported results and syntheses. Indeed the latter are not directly applicable in the present case. As already noted mucus production is essential to the existence of freshwater snails. Furthermore, the energy lost in association with it may not be completely lost from the snail systems, since it apparently stimulates the growth of the bacteria which P.contortus eats. Recent work has also shown that algae may be involved in considerable heterotrophic activities during darkness (Monheimer, 1972) so that the breakdown products of mucus may be utilised by epilithic algae.

The efficiencies presented in TABLE 71 and TABLE 75 indicate that both A.fluviatilis and P.contortus divert most of their biologically useful energy to detritus food chains. This, together with the trophic requirements of the snails,therefore specifies their trophic position and functional role within the epilithobionta in particular and freshwater ecosystems in general. The P.contortus population probably acts as a "closed loop" system within the detritus level, using detrital products (i.e. bacteria) as food and recirculating energy to the detritus. The A.fluviatilis population effectively speeds the passage of energy from the epilithic primary producers to the detritus chains without allowing transmission through a predatory system.

PART X

GENERAL DISCUSSION

Freshwater pulmonate snails are extremely convenient for ecological research because they have a simple, annual life-cycle with relatively distinct generations, provide few taxonomic difficulties, and are easily manipulated under laboratory conditions. The dearth of quantitative ecological information on this group is, therefore, surprising but seems to have arisen from sampling difficulties associated with the complex (weed-bed and stony littoral) habitats in which freshwater snails live (see PART V, SECTION I). The sampling technique developed in PUBLICATIONS APPENDIX II, and used in PART V has partially overcome these difficulties with regard to stony littoral situations and has provided quantitative information on the structural ecology of freshwater snail populations in Malham Tarn.

Within Malham Tarn snail populations are aggregated at all levels of the distribution hierarchy ranging from the whole Tarn to micro-levels. Wind and wave action seem to be the ultimate determining agents (see PART IV) although these may operate via resultant food supply and sedimentation heterogeneities (see PART VI SECTION 6). Inter-specific competition may also be involved (see PART VI SECTION 6).

A detailed consideration of the phenologies of isolated populations of A.fluviatilis and P.contortus in quantitative terms has confirmed previous qualitative findings (see Hunter, 1956, 1957, 1961 a and b). Both species have a simple annual life-cycle, but may show seasonal variation in phenological detail which depend on external conditions (see PART V, SECTION 3). Apart from the early life-history stages, i.e. eggs and spat, predators seem to have little effect and adult mortality probably results from adverse physical conditions and possibly food shortages. Indirect evidence has suggested that the latter applies to the population of A.fluviatilis on Ha Mire (see PART VI SECTION 6). The recruitment of spat from the previous adult generation is under density dependent control (see PART VI SECTION 4. 8). This phase of the life-cycle involves four distinct processes, i.e. egg production, oviposition, egg survival, and the survival of spat on hatching. Each may be sugject to density dependent constraints (see PART V, SECTIONS 4. 6–4. 8) though which, if any, is the most important process from this point of view is not yet known.

The functional aspects of the ecology of populations of P. contortus and A.fluviatilis on Ha Mire shore have been considered in the framework of the mechano-reductionist, energy budget statement. Taken at face value, the results have indicated that energy loss

through mucus secretions dominate the functioning of these two snail populations and that, in consequence, much of their production is diverted to detritus food chains. Since A.fluviatilis is a herbivore feeding on epilithic algae and P.contortus is a detritovore which makes use of the bacterial fraction of its food supply the functional role of the former species can be specified as that of speeding the flow of matter and energy from primary to detritus and intermediary (see PART VII, SECTION 6. 2A) trophic levels whereas the functional role of the latter species seems to be to create a closed loop within the detritus system. The recirculation of energy through the snails themselves is also feasible since bacteria and possibly the epilithic algae, make use of the potential energy contained within the secreted snail mucus.

These conclusions provide useful descriptive statements but are inadequate in a predictive sense since they derive from observations made on particular populations at a particular time and under particular conditions. A-posteriori interpretation of previously collected data (historicism) retains an element of subjectivity which stands without formal justification. More confidence can be placed in ideas formulated before a relevant event and found to hold afterwards, than in explanations conceived as an after-thought. This is why predictive statements and empiricism are of central importance in scientific endeavour. The role of the empiricist is not just in the sense of Galileo's dictum to make measurable what cannot be measured, but also to make objective (or at least as objective as possible within the limitations of human psychology and technology) that which is essentially subjective.

Much of ecological research remains in a historical frame. This applies both to the structural and functional fields and also to most of the content of this thesis. With the advent of functional ecology, and particularly the adoption of energy as a unit of ecological currency, it became possible to describe diverse ecological (and in fact biological) entities in common terms, so that generalisation became at least feasible. Predictive statements have still been slow to arise and this probably derives from the inadequacy of our current theoretical framework embodied in the energy budget statement.

We have already noted that the energy budget equation and its more complex derivative, the Pütter growth equation, are reductionist statements (see PART I, PART VI SECTION 4 and PART IX SECTION I).

They reduce the complex phenomenon of metabolism into the simpler subcomponents of anabolism and catabolism and on the basis of information obtained on these parts attempt to re-simulate the behaviour of the whole process. This approach is quite justified in simple, physical machine terms since the energy budget is based on accepted physical theory (the first and second laws of thermodynamics) and the parameters within the equation have both physical and biological meaning. Yet living organisms do not behave as simple physical machines. Their growth processes, which contribute to population production, are not analogous to the passive growth of physical and chemical systems (e.g. crystals - Oparin, 1953) but are subject to active endogenous control. This is illustrated quite categorically in FIG. 64, and is to be expected since growth represents an ordering process within a universe where disorder appears to be the natural state. The fact that most species tend to some recognisably characteristic size bears witness to the operation and potency of regulation and modification of the parameter values in the Pütter equation with respect to experimentally imposed perturbations (see Armitage, 1962; Clark, 1955; Norris et. al., 1963; Vernberg, 1959) probably represents an outward manifestation of organismic control.

Throughout the body of this thesis and particularly in PARTS VII and VIII due regard has been given to the behavioural and physiological mechanisms which contribute to the phenomenon of metabolic homeostasis. The regulatory response involved in counteracting two common perturbing agencies i.e. temperature and food supply have been considered in greatest detail since these agents have a direct impact on the functioning of populations and are probably the most commonly encountered in nature. Others e.g. pollutants may also be involved.

Much has been written about metabolic homeostasis with respect to temperature. It is operative even in the poikilotherms where it has been called acclimation (Bullock, 1955; Prosser, 1955; Fry, 1958; Precht, 1958; Prosser and Brown, 1961; Vernberg, 1962; Kinne, 1963); Stated simply it consists of a release of metabolism, through active control, from the temperature dependency of simple physico-chemical systems summarised in the van't Hoff and Arrhenius equations. The Q_{10} of whole-organism-systems rarely correspond to the classical value of 2.0 which is characteristic of physical and chemical reactions. The phenomenon of acclimation has been observed here in <u>A.fluviatilis</u>

and P.contortus except that in the former instance a peculiar type of reverse process was recorded (see PART VIII, SECTION 2. 2). This means that A.fluviatilis is best adapted to life at low temperatures where rapid temperature fluctuations occur, whereas P.contortus is better adapted to gradual temperature changes and higher ambient levels. These adaptive differences can be correlated with differences in the usual habitat requirements of these two snail species.

Various regulatory processes have been noted in both P.contortus and A.fluviatilis in terms of food supply perturbations and these also appear to have more general applicability. A starving snail increases its efforts to find food (see PART VIII, SECTION 4. 2), reduces its rate of gut emptying thereby increasing its chances of extracting nutrients from the remaining gut contents (see PART VII, SECTION 5. 5) and when it comes into contact with new food, feeds more voraciously than normal and increases its efficiency of digestion (see PART VII, SECTION 5. 4). Under conditions of starvation snails are also less discerning in what they eat (see FIGS. 75 and 83). Similar starvation responses with respect to searching have been noted in fish, by Ivlev (1961), with respect to gut emptying in woodlice by Hubbell (1969 and 1971), and with respect to appetite and assimilation by Holling (1966 a and b), Hubbell (Ibid.) and Beukema (1968) for mantids, woodlice and fish respectively. Emlen (1966) has shown,on theoretical grounds, that the ability to accept and use those foodstuffs during starvation which are normally rejected, represents an optimal food strategy and Ivlev (1961) has found the electivityof various fish species to alter in this way during starvation.

Respiration also becomes reduced with starvation (see FIGS. 107 and 108) and follows the same time course of reduction as gut emptying. This implies that the fall in metabolism is associated with reductions in S.D.A. Hubbell (Ibid.) has noted the same phenomenon in woodlice. In these cases the metabolic control involved is probably passive and results from a reduction in assimilated food materials. They, nevertheless, contribute to metabolic homeostasis by reducing the "cost of living" under conditions when food is in short supply.

It should also be noted that food perturbations may occur via quality as well as quantity. Animals may experience starvation effects even when food supply is apparently super-abundant since food of poor quality may predominate. Furthermore this situation may be more common than originally anticipated in herbivorous populations (see

PART VI, SECTION 3. 6). Snails generally prefer foods which provide most calories per mouthful or alternatively per unit effort of collection and processing (see PART VII, SECTION 5. 6). The latter parameter is determined both by the food material's own caloric density and, more importantly, by the snail's digestive abilities. If, however, snails are forced to feed on less preferred, and consequently less well assimilated , food-stuffs they increase their ingestion rate (see FIG. 90). Schindler (1971) has found the same response in various crustacean zooplankters, and it obviously represents a homeostatic mechanism geared to maintaining a constant transfer of energy across the gut wall when the ingested material is of poor quality. The feeding response of P.contortus in terms of dilution of its "true-food" (bacteria) with a lignacious "food-carrier" can be considered as an extension of this homeostatic mechanism (see PART VII, SECTION 5. 7). Digestive interference from the food diluent is probably circumvented by strict separation of the digestible from the non-digestible components of the ingesta prior to their transmission to the actual digestive site (i.e. the hepatopancreas). The extent to which these mechanisms are used in bacterial feeding detritivores in general cannot be assessed until more information is available on this poorly considered trophic group.

A further mechanism which may be involved in the regulation of assimilation in terms of qualitative changes in the diet is intra-specific enzyme adaptations. The overall adaptation of an animal's gut secretions towards its normal,(in terms of the types and relative amounts of enzyme produced) food is not always immutable and the emphasis upon a particular type of enzyme can shift to another if the dominant component of its diet changes (Jennings, 1955). Thus, in theoretical terms at least, animals can become more adept at extracting nutrients from otherwise infrequently taken food materials by an active modification of their gut secretions. Whilst there is no direct evidence for this phenomenon in freshwater snails, inter-specific variations in cellulase secretions have been observed (see PART VII, SECTION 6. 2).

Clearly animals in general and snails in particular have a wide range of behavioural and physiological mechanisms involved in regulating their growth processes in the face of environmental perturbations. This capacity for control is, however, limited in the sense that prolonged starvation, or even prolonged existence under an unfavourable

temperature regimen, would ultimately result in system degeneration and death. It is likely that the effectiveness of control rises with level of organisation and probably reaches its ultimate adaptation in homeotherms. The parameter k_{corr} (see PART VI, SECTION 4) provides a convenient means of assessing and summarising an organisms ability to regulate. It should also be noted that, although plants are unable to turn the sun on and off, they can effect a high degree of control over the rate at which they fix radiant energy in photosynthesis. This is exerted on a short-term basis through a variety of biochemical mechanisms and phototropic responses, and on a long-term basis through vegetative growth plasticity.

Like other physiological processes growth is under active endogenous control. Indeed, homeostasis is a basic feature of all living systems and processes at all levels of the biological hierarchy from subcellular particles to ecosystems. In this sense the energy budget statement, and for that matter the Pütter growth equation, is inadequate both in philosophical and operational terms. The functioning of individual organisms and whole populations cannot be considered solely in terms of the metabolic parts involved since the emergent's of interaction and regulation which ultimately lead to homeostatic control are either relegated in importance or are simply overlooked.

Added to these criticisms is the fact that the energy budget is subject to some considerable circularity of application. It is employed to predict individual growth or production (perhaps not intentionally, but certainly implicitly because a comparison between the budgets growth predictions with actual observations is often used as a test of its accuracy) by using observed growth data as operators for the anabolic and catabolic terms within the equation. This almost certainly introduces a self-correcting effect which could mask or dilute significant errors. Nobody, as far as I am aware, has attempted to use the budget as an autonomous system without recourse to external inputs as equation operators. In these terms the results derived from the above procedures can only be viewed as a form of quantitative description (see also PART IX, SECTION I).

There is a basic need in functional ecology, therefore, for a predictive model of whole organism growth which is realistic and general but which forfeits some physiological detail and precision because of the essential lumping of lower level systems' dynamics. To be realistic the model must provide a wholistic representation with

energy regulation as a central feature. In this sense, it seems logical to shift attention from the simple machine analogy in the energy budget statement to a more complex machine analogy in which regulation by feedback is the order of the day. This necessitates moving into the realms of Systems Theory, cybernetics, transfer functions and electrical analogues.

Recently Hubbell (1969 and 1971) has proposed a cybernetic model of whole organism metabolism. This is discussed and elaborated in PUBLICATIONS APPENDIX IV. His analysis, however, is mainly on theoretical grounds and probably goes too far in physiological detail for ecological purposes. Working in a hierarchically structured universe we must accept that research at a particular stratum necessarily requires that certain "black-boxes" remain closed. Hubbell's model, however, provides a valuable contribution to functional ecology and the simplified version summarised in FIG. 65 may find some practical ecological application.

A central feature of this cybernetic model is the desired growth rate subsystem (KDG). This provides some criterion of "ideal" performance (DG(S)), the reference input, which is compared with the actual performance of the basic metabolic loop (AG(S)). If these two parameters differ, an error correcting feedback signal (E(S)) is generated to compute the appropriate "control effort" necessary to force the output from basic metabolism closer to the desired level, thereby reducing the performance error. Error correction is rarely complete, however, because of the systems' inherent control limitations. This is expressed by the correction constant (k_{corr}) which can take a value between 0 - 1 dependent on the system's controlling abilities. In reality k_{corr} consists of two components, one associated with the control limitations involved in energy input (KAE) and the other associated with the control limitations of energy output (KRE). As already noted in PART VI, SECTION 4.3, the desired growth rate generating subsystem is sensitive to organismic size.

Given, then, some expression for KDG, k_{corr}, and the basic metabolic loop it becomes possible to erect a realistic, albeit superficial, predictive model of whole organism growth which could be operated on either digital or analogue computers. Hubbell (Ibid.) has outlined two methods for estimating KDG i.e. the optimal environment and perturbation methods. The former measures growth under assumed optimal conditions, the latter determines how the system reacts to precisely controlled disturbance inputs and deduces the nature of

the controller from the dynamics of recovery of the system. A crude method for estimating k_{corr} has been outlined in PART VI, SECTION 4 where other applications of this parameter have also been considered. This leaves the basic metabolic loop which is most profitably considered and determined from the relationship between organismic size (AG(S)/S) and both assimilation (KAP) and respiration (KRP) under assumed optimum or at least constant, near-optimum, conditions.

Determination of the parameters within the systems model is at least theoretically feasible. The resultant expression would be crude. It would ignore a considerable amount of physiological detail and, as a first stage, the non-linearities which are characteristic of biological systems (Milsum, 1966). Used in an ecological context, however, this level of approximation and simplification may not be intolerable, and in terms of functional ecology it would provide a theoretical framework of considerable generality and predictive power.

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