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The ecology of ancylus fluviatilis (műller) in streams and rivers in parts of Northumberland and Durham

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The Ecology of <u>Ancylus fluviatilis</u> (Müller)

in streams and rivers in parts of

Northumberland and Durham

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the degree of Master of Science (Ecology) in the

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LIST OF CONTENTS

General introduction and project aims

The Basommatophora are those pulmonate molluscs which have colonised the freshwater habitat from the land. Hunter (1949) regards the primary adaptations of the Basommatophora allowing members of this air-breathing stock to live in freshwater as forming two divergent series. One line of development is cutaneous respiration and gas exchange through a bubble of air held in the pulmonary cavity. This method is used by _Lymnaea peregra_ (Müll) (Hunter 1949), the commonest freshwater gastropod in the British Isles (Conchological Society 1951). At higher temperatures (>12°C), however, this method becomes inefficient, and migrations to the water surface for air breathing, as described by Hunter (1953), become a necessity. The other line of adaptation is the development of gills. All the pulmonates, including the Basommatophora, form a stock which lost their original gills when they developed lungs. Thus the gill in the Basommatophora is not homologous to the gill of other gastropods, but is secondarily derived from a lobe of the anus. In the genus Planorbis and the family Ancylidae (the freshwater limpets _Ancylus fluviatilis_ (Müll) and _Acroloxus lacustris_ (Linn)) the 'lobe-gill' reaches a high degree of development, with complete afferent and efferent circulation. This very efficient primary adaptation of _Ancylus fluviatilis_ for respiration, coupled with the secondary adaptations of a muscular foot and specialised shell shape for life in the relatively hostile environment of fast flowing water, has given the species great success. Ellis (1951) says it is found all over Europe, with the exception of Iceland. The only places it has not been recorded in the British Isles are the Scilly Isles, Lundy, N. Aberdeen, and the Kildare and Longford districts of Ireland.

The earliest references to A.fluviatilis in the literature are mainly devoted to anatomy and physiology. (Bouchard-Chanteraux 1832; Moquin-Tandon 1852; Sharp 1883; Gain 1888; Andre 1893). The ecology of freshwater gastropods, and particularly A.fluviatilis , has been studied by Hunter (1952, 1953a, 1953b, 1957, 1961, 1962, 1964). A.fluviatilis was also the subject of a special study by Geldiay (1956). Hubendick (1960) has investigated speciation in the Ancylidae, and Bondeson (1950) carried out a detailed study of their reproduction. The respiration of the Ancylidae and its ecological significance has been studied by Berg et al. (Berg K. 1951, 1952, 1953; Berg, Lumbye & Ockelmann 1958; Berg & Ockelmann 1959). Reference to A.fluviatilis is often made in other general ecological investigations of stream fauna (e.g. Badcock 1940; Berg 1948; Carpenter 1927; Hynes 1961).

The growth and life cycle of A.fluviatilis has been fully described by Hunter (1953) and Geldiay (1956). One aim of the investigation was to follow the life cycle at two sites, one of average population density of A.fluviatilis (New Burn, Walbottle), and one where the population was at a very high density (Whitehouse Burn), and compare and contrast population changes at the two sites.

The second aim of the project was to obtain detailed information of the changes in numbers of adults, egg capsules and newly hatched individuals of A.fluviatilis throughout a breeding season, as no information of this type is available.

Bouchard-Chanteraux (1832), Moquin-Tandon (1855), Lehmann (1873), Wackenheim (1915), Percival & Whitehead (1929), Bondeson (1950), Hunter (1953) and Geldiay (1956) all give details of the number of egg capsules each Ancylus fluviatilis lays during a breeding season, and estimates of the average number of eggs per

egg capsule. The numbers quoted differ considerably, and hence
a third aim of the investigation was to determine the true
reproductive potential of A.fluviatilis and to compare this with
other freshwater gastropods.

Hunter (1961) has described the variation in population
density of A.fluviatilis in one stream over a number of years and
related this to the amount of incident sunlight in spring. There
is no data available, however, on the factors governing the variation
in A.fluviatilis population density from one stream to another, and
this was the primary aim of the project.

Part One - Life History

1. Introduction

Comfort (1957) quotes Francis Bacon - 'concerning the length or brevity of life in beasts, the knowledge which may be had thereof is slender, the observation negligent and the tradition fabulous.' Until recent years this statement was applicable to the freshwater gastropods, surprisingly few field studies on the growth and life cycles of even the commoner species being published. Because of the interests of parasitologists, the life cycles of the Lymnaeidae were among the first to be followed (e.g. *Lymnaea truncatula* (Müll) by Walton 1918 and Walton & Jones 1926; *Lymnaea brazieri* (Smith) by Ross & McKay 1929). Other investigations have given information on the life histories of *Lymnaea columella* Say (Bailey 1931), *Myxas glutinosa* Müll (Feliksiak 1939), *Lymnaea peregra* (Boycott 1936) and *Stagnicola catascopium* Say (McE.Kevan 1943). More recent studies are those of DeWit (1955) and Duncan (1959) on *Physa fortinalis* (Linn) and DeWitt (1954a, 1954b, 1955) on *Physa gyrina* Say. These detailed studies have discredited the assumption held by earlier authorities (e.g. Cooke 1895, Pelseneer 1906 and Baker 1911) that a biennial cycle is general in the pulmonates.

Berg (1948), looking at growth rings on the shells of *A.fluviatilis* from the River Sussa system, concluded that limpets may live for up to three years. However, the work of Hunter (1953) and Geldiay (1956) illustrated that a simple annual life cycle occurred in Britain. It is probable that Berg's growth rings were due to fluctuations in environmental conditions during the year, i.e. that they are 'disturbance rings' rather than annual rings.

In this investigation the growth and life history of
A.fluviatilis was followed at three localities : New Burn, Walbottle,
Whitehouse Burn, near Alnwick, Northumberland, and the river Tyne at
Wylam.

2. Methods

Compared to the commoner turbinate coiled form of the
shell in the majority of gastropods, the limpet shape is relatively
easy to measure, the greatest dimension of an ancylid limpet
occurring across the aperture of the shell along the antero-posterior
axis. This measurement ('shell length' - Figure 1) has been used
throughout the investigation and as there is no metamorphosis of the
shell during growth - 'growth along a turbinate spiral of low constant
angle persists in embryo, spat and adult' (Hunter 1953) - it is a
valid one. The shell length of specimens was measured using vernier
calipers for the larger animals. Spat were measured by binocular
microscope and slide micrometer. The outer periostracum of the shell
is lighter coloured in appearance and more flexible than the rest of
the shell, so allowing a close fit to any resting place on the substrate
despite irregularities. It is very easily damaged and great care was
needed when collecting A.fluviatilis for measurement.

Collections were made at regular intervals from New Burn
from 17 January until 5 August. Limpets from Whitehouse Burn were
collected at less regular intervals from 13 February until 1 August.
On each occasion the maximum number of limpets possible were collected
in the time available, the aim being to collect at least fifty
individuals. Due to a marked reduction in population density
throughout the investigation at New Burn this target became a difficult
one and collections were below this limit on two occasions.

FIG 1   THE   LIMPET   SHELL

Shell
Height

Shell   Length

Spat
Shell

Start of
Spring growth
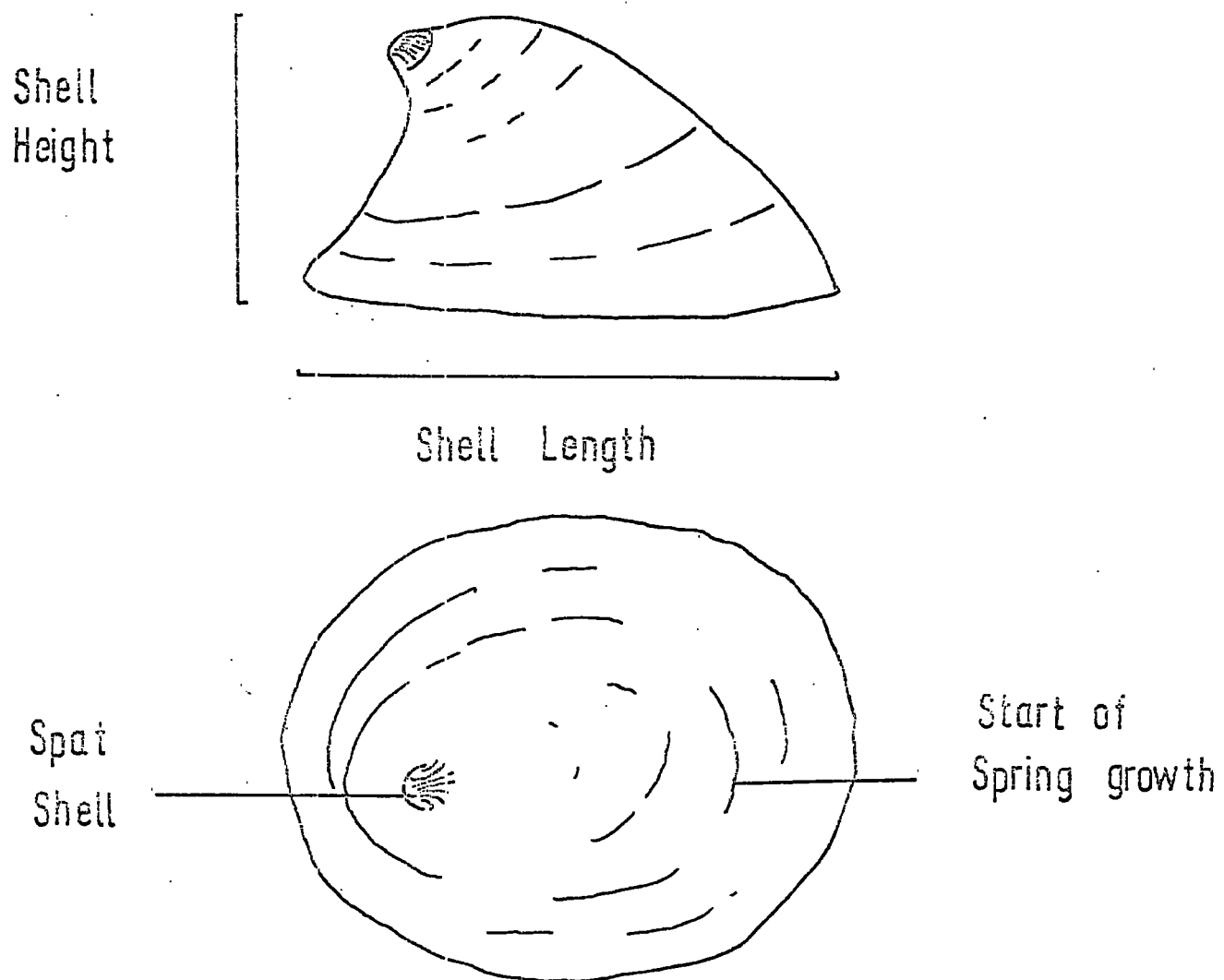
At each visit to the collection sites a ten minute count of _Ancylus_ numbers was made, always in the same part of the stream, to observe the changes in population density with time. To complement these observations, a more detailed study of this kind was carried out in the river Tyne at Wylam. A particular section of the river here is well known to the author and ten stones were selected which could be found with ease on any subsequent visit, and their position marked on a rough sketch map. At weekly intervals from 13 May until 15 July the number of adult limpets, spats and egg capsules were counted on these stones, giving a detailed picture of the population changes throughout the breeding season. Great care had to be taken not to expose egg capsules to the air for any length of time as they are extremely fragile. Young limpets are easily dislodged or crushed and are similarly averse to exposure. Hence care was needed when lifting and replacing the stones and they had to be repeatedly immersed during counting.

3. Results

These are given in tabular form in the Appendix (Tables 1 & 2). Graphical representation of the data is given in Figures 2 - 7. In Figures 2 and 3 the limpets have been placed in 0.5mm size groups and these figures expressed as percentages of the total number of limpets collected. Figure 6 illustrates changes in the mean shell length of the populations with time. Figures 4 and 5 record the decline of the population density of adult limpets at New Burn and Whitehouse Burn. Figure 7 illustrates the changes occurring in adult, spat and egg capsule numbers in the river Tyne at Wylam.

FIG 2 NEW BURN, POPULATION GROWTH
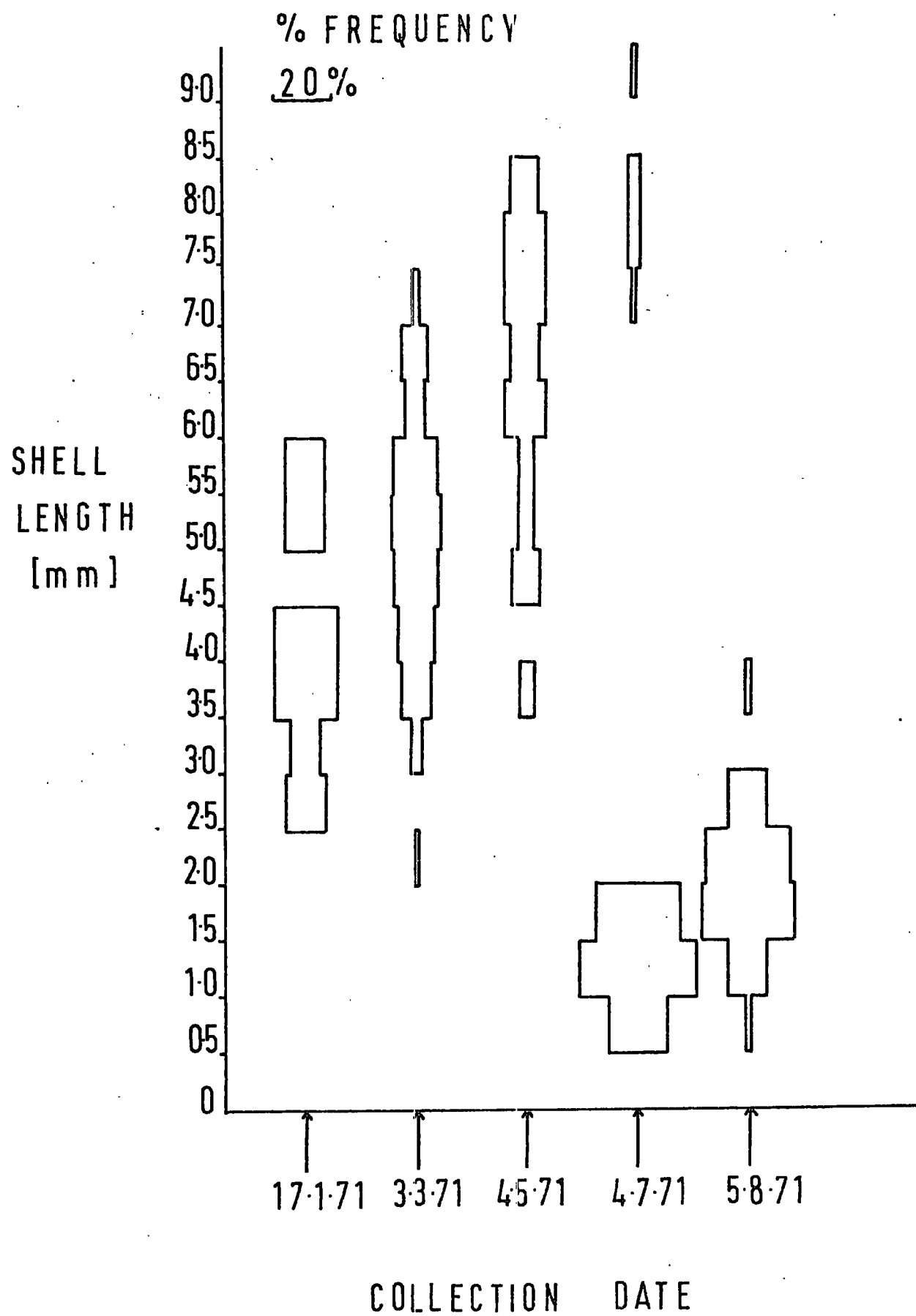
FIG 3 WHITEHOUSE BURN, POPULATION GROWTH
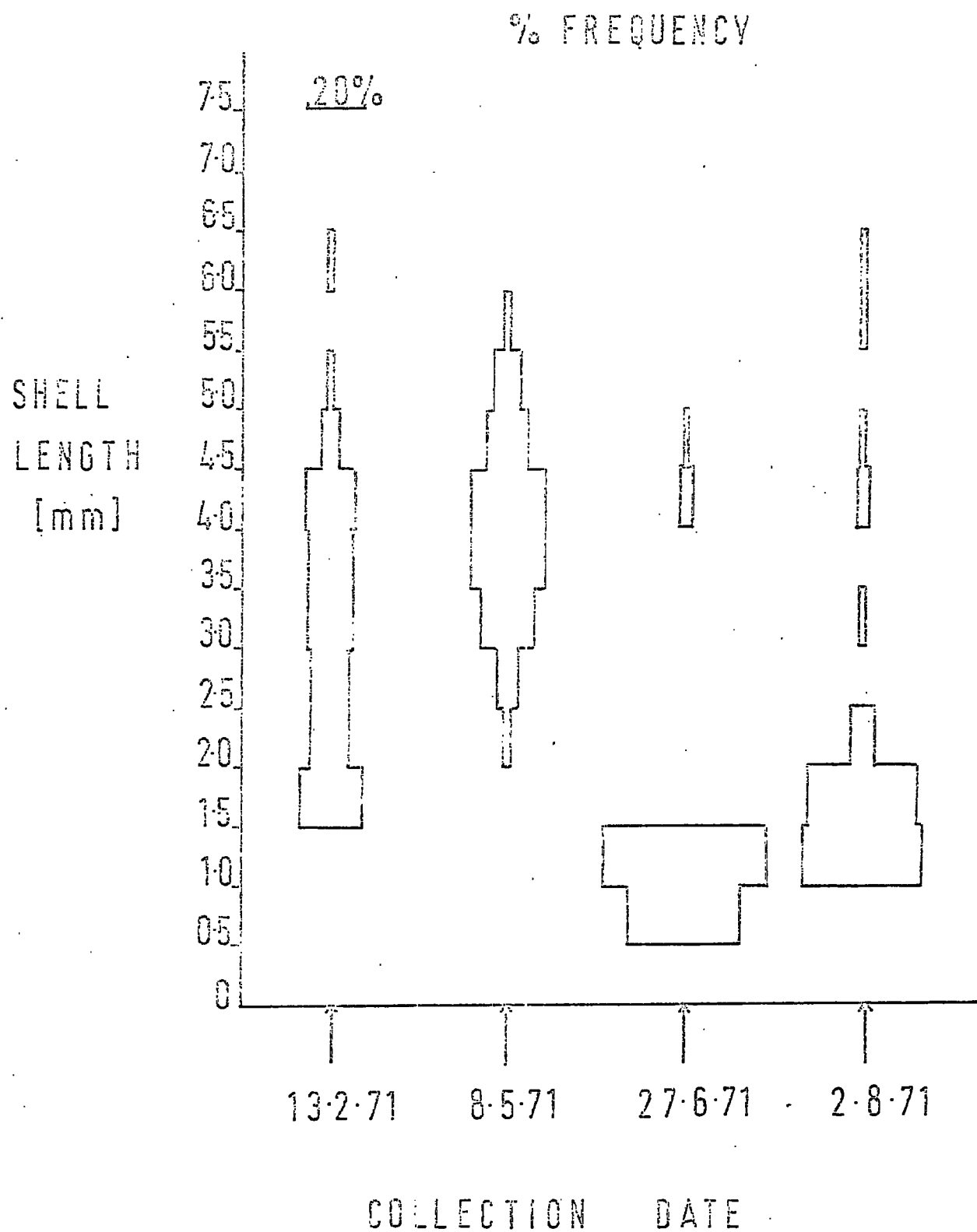
FIG 4   CHANGE IN POPULATION   DENSITY   OF   ADULT ANCYLUS,
WHITEHOUSE   BURN
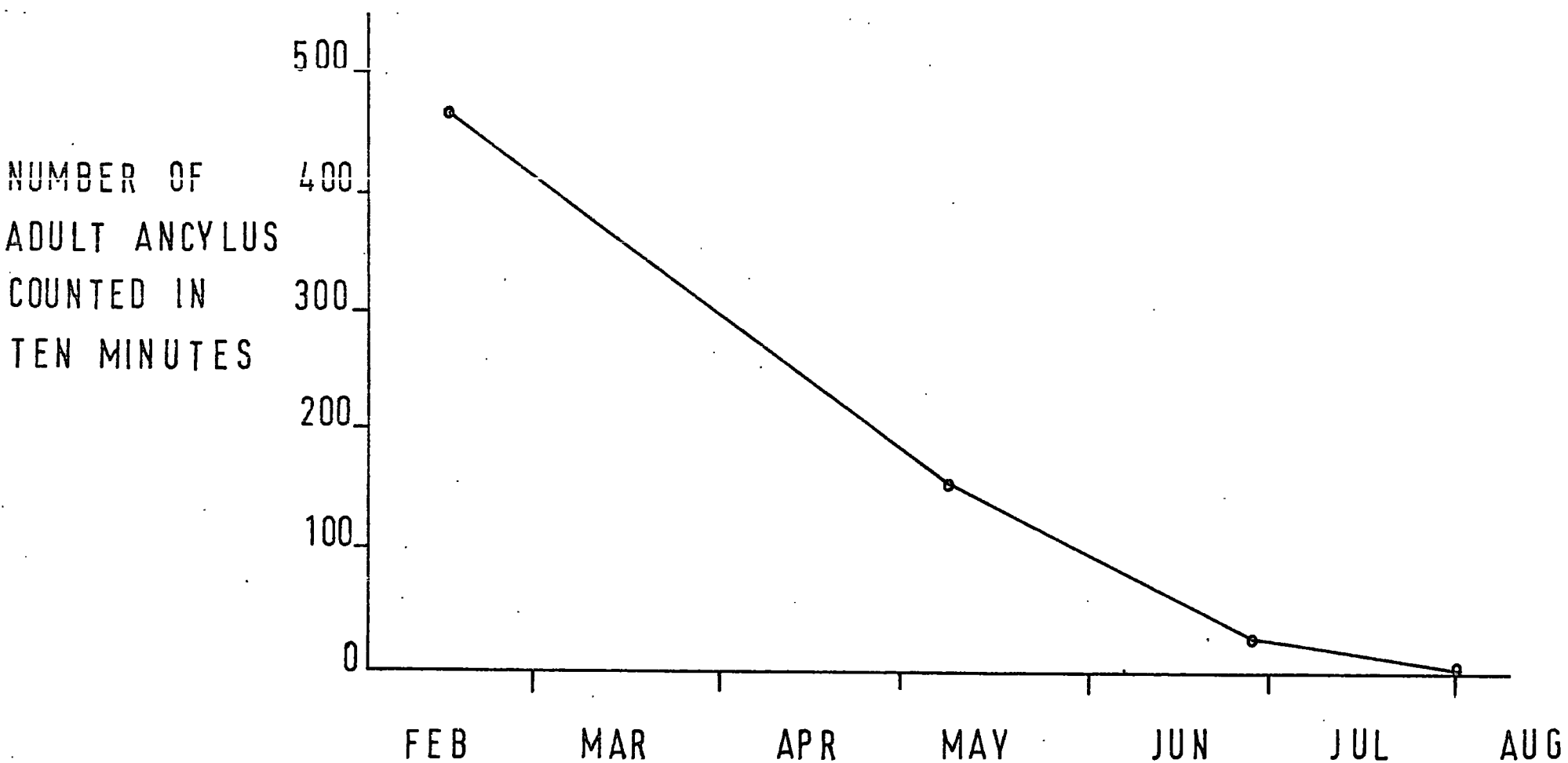
FIG 5   CHANGE IN POPULATION   DENSITY   OF   ADULT   ANCYLUS,
NEW   BURN .
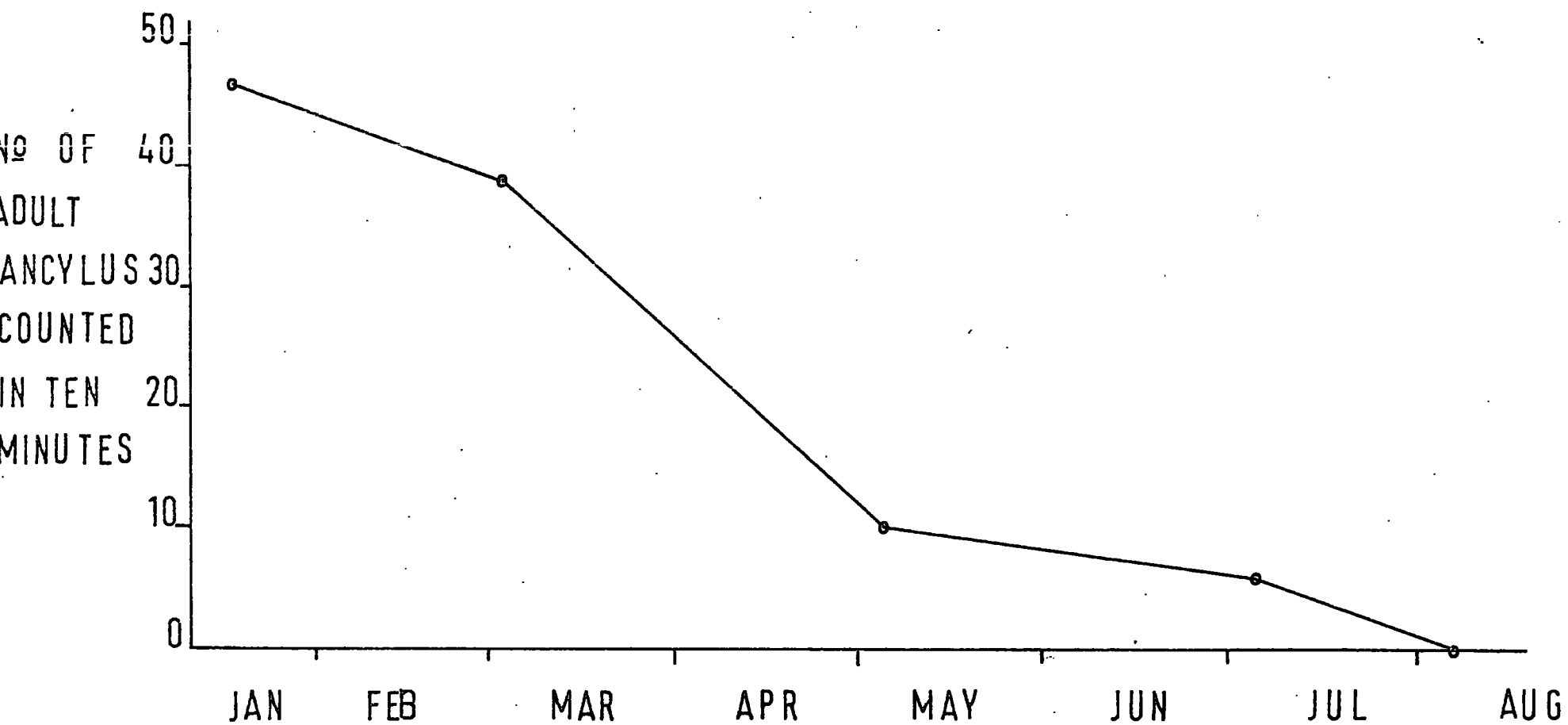
FIG 6 CHANGE IN MEAN SHELL LENGTH WITH TIME
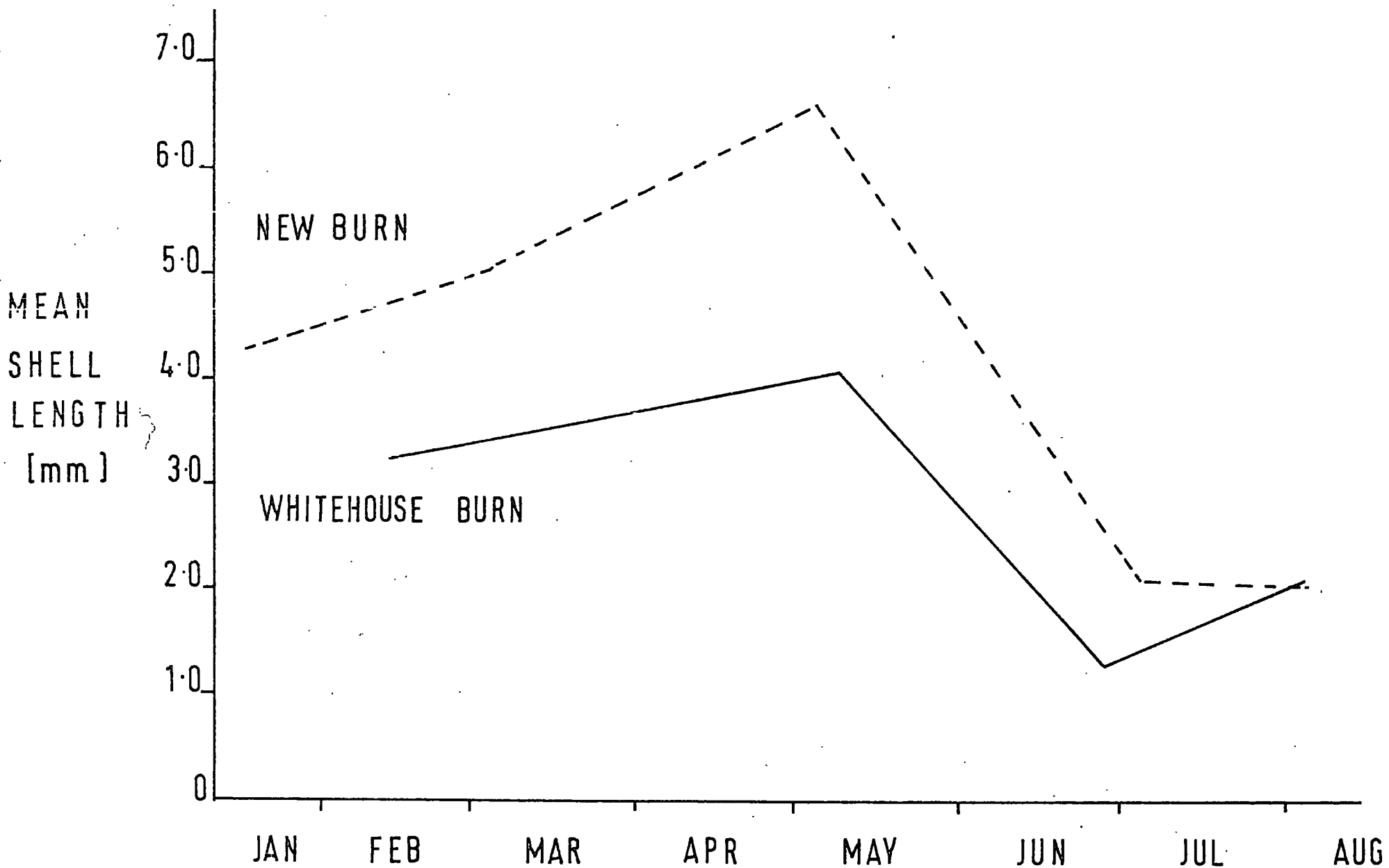
FIG 7   RIVER TYNE, WYLAM, POPULATION   CHANGES   DURING   THE   BREEDING
SEASON
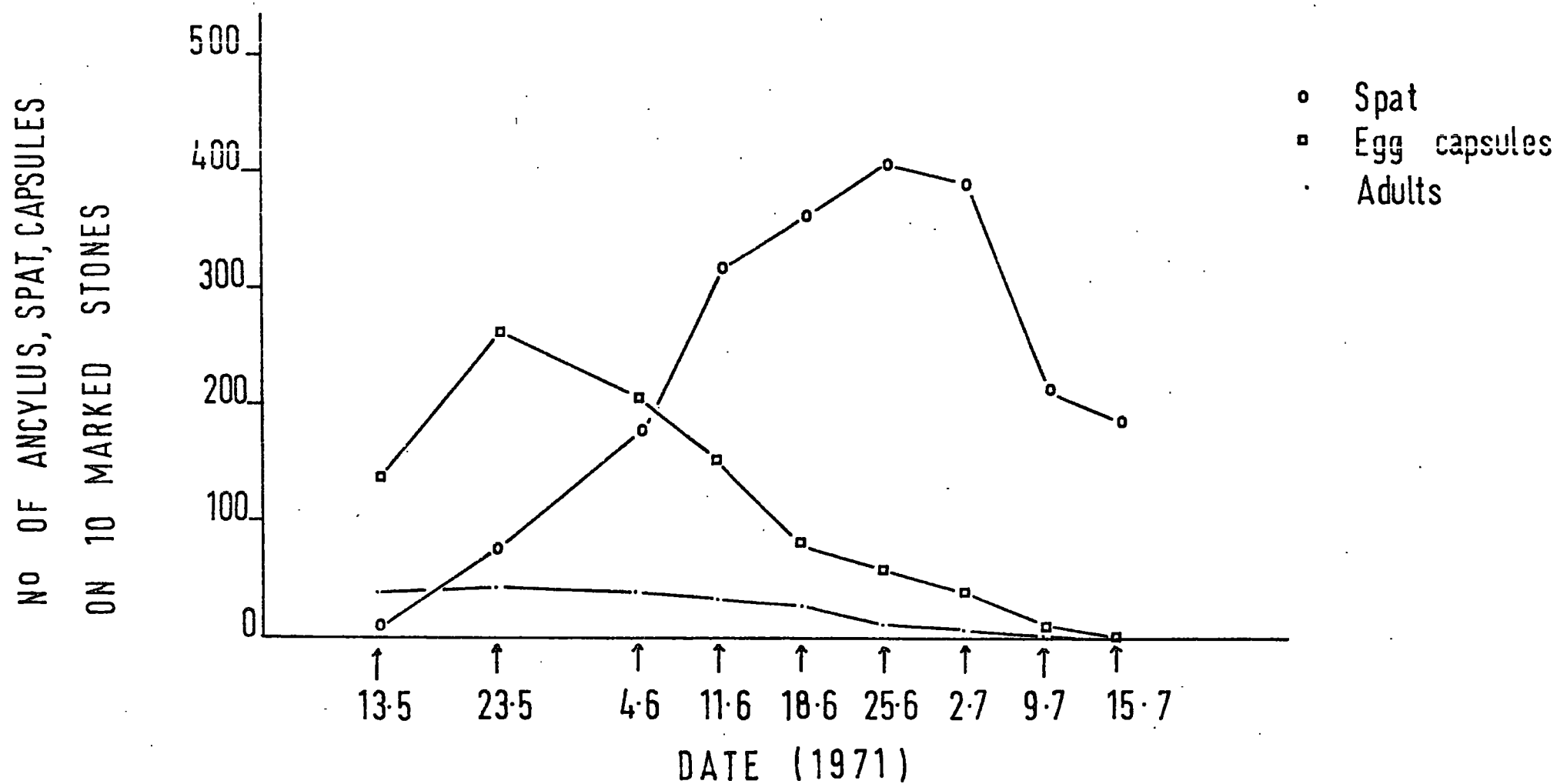
4. Discussion

(i) New Burn

This highly eutrophic, slightly alkaline (pH 7.6) stream with high calcium content (77ppm), which runs into the river Tyne, supports a great variety of fauna, and an average population density of Ancylus fluviatilis. Figures 2 and 6 show that the life history of limpets in this stream follows the typical annual cycle as described by Hunter (1953) and Geldiay (1956). The first three collections show the gradual increase in size of individuals in the population, from a mean size of 4.25mm to 6.6mm, an average growth rate of 0.107mm/week. Rising temperature is the environmental trigger for the breeding season (Bondeson 1950) which begins in early May. Copulation and egg laying reach their peak in the middle of the month. The population of New Burn illustrates a point which is common to all breeding populations of Ancylus, which is the great variation in shell length of individuals, in this case 3.5 - 8.5mm. The collection of 4 July shows the influx of the new generation, the majority of the population being in the 0.5 - 2.0mm shell length range. After egg laying the adults begin to die off, and this, plus a dilution effect due to the large number of spat, results in the decreased number of adult limpets in this collection. By 5 August all the adult limpets have died out, while the spat have grown considerably.

Geldiay (1956) reports that he found little change in the population densities of the limpet populations he studied throughout the winter. He presumed that the factors controlling population density acted on the spat, and that once the limpets

had reached a certain size, these factors were relaxed and the
population then remained at a stable level. However, Figure 5
illustrates a marked decrease in _Ancylus_ population density with
time (on the basis of ten minute counts) in the New Burn even before
breeding begins and the limpets begin to die, perhaps due to the
physiological stresses of egg laying. Many factors could contribute
to this pre-reproductive decline, but among the most important must
be winter flooding. The effect of flooding could be threefold :
(i) to change the course of the river, so exposing stones (and
limpets) in the previous watercourse; (ii) the increased speed of
water flow may be enough to dislodge limpets from the stones; and
(iii) physical movement of the substrate, the grinding and rolling
motion of stones, must exert an effect. However, to verify these
theories the population density immediately before the flood must
be known and this is not possible unless checks on the population
density are performed at very short intervals. The New Burn did,
however, on a number of occasions change its course, and the author
found limpets exposed due to this.

Predation, notably by the mollusc eating leech (_Glossiphonia_
complanata, may also contribute to the decline of _Ancylus_ numbers.
It is difficult to imagine intraspecific competition exerting any
effect where the population density is fairly low as in the New
Burn. As _Ancylus_ always lives in the faster flowing parts of the
river, there is little overlap between it and the other common
gastropod in the New Burn, _Lymnaea peregra_, which inhabits the
slower reaches, hence interspecific competition is probably minimal.

(ii) Whitehouse Burn

This stream is less eutrophic than New Burn, is less alkaline
(pH 7.45) and has a lower calcium concentration (49ppm), yet supports
one of the highest Ancylus population densities found by the author.
Figures 3 and 6 show that the limpets in this stream conform to the
typical annual life cycle.

In a population of such a high density as Whitehouse Burn,
it is possible that growth and size will be reduced, as Forbes &
Crampton (1942) found for Lymnaea palustris. Certainly the mean
size of limpets at the start of the breeding season (4.08mm) was
smaller than for New Burn (6.6mm). Also the rate of growth
(0.07mm/week) is slower than New Burn (0.19mm/week), again indicative
of competition.

The timing of the annual cycle of the Whitehouse population
is slightly behind that of New Burn, and this is the other main
difference between the two populations. This effect is due to the
temperature of the New Burn being slightly higher than Whitehouse.
The decrease in population density of adult Ancylus is even more
spectacular at Whitehouse Burn than at New Burn (Figure 4, Table 1).
The first ten minute count in February yielded 466 individuals,
but by August this was down to 5. Although winter flooding must
be important as at New Burn, it is probable that intraspecific
competition is also important at this site in reducing the population
density. Indeed, a smaller breeding size and slower growth rate as
previously mentioned indicates that competition is occurring. Which
of the two factors is more important it is impossible to say. No
other molluscs are present in Whitehouse Burn, thus there is no
interspecific competition at this site.

(iii) <u>River Tyne at Wylam</u>

Figure 7 gives the details of changes occurring in the population during the breeding season and is self-explanatory. The main point coming from this study is that the reproductive potential of the original 41 adult <u>Ancylus</u> is never realised. Hunter (1953) states the average number of eggs laid by an adult limpet is 46 in 12 capsules. Thus in theory the adults should produce about 1886 spat. Even taking account of the facts that (i) the adults can move considerably and not all the eggs will be laid on the marked stones; (ii) malformed eggs are sometimes laid (a rare phenomenon according to Bondeson (1950)); (iii) spat may move off the stones (although spat move little when first hatched), it seems that spat mortality is high. Up until 15 July, when 180 spat still survived, spat mortality was approximately 90%.

(iv) <u>Temperature and the life cycle</u>

It is convenient at this point to discuss certain factors concerning the life cycle of <u>Ancylus</u> noticed in the visits to sampling sites carried out to obtain information for Part III of the project.

In theory, the higher the average water temperature, the faster will be the growth rate of limpets, they will have a higher average size, and reach maturity faster. The original breeding season will be advanced, so leading to the possibility of a second. Geldiay (1956) was the first person to record this phenomenon for <u>Ancylus fluviatilis</u>, for a population in Lake Windermere. In general, the larger the river, the higher its average temperature, and hence it was expected that if a second generation would be found, it would be in the river Wear or river Tyne.

A preliminary visit to the river Wear in December 1970 produced five newly hatched spat (average size 0.18mm) along with 41 adults, which was the first suggestion of a second generation. The same locality, the river Wear at Durham Sands, was visited on 12 May when the river temperature was 16.25°C. Only one adult was found, a specimen of 8.2mm shell length, suggesting that the original generation had already bred and were already dying out. The Wear at Sunderland Bridge, visited on 14 July, produced specimens of the 'spat' from the first breeding season of average shell length 4.34mm. Many of these were forming copulating pairs and numerous egg capsules were present. Thus in the lower reaches of the Wear it seems that two generations of Ancylus/year do occur.

The river Tyne at Corbridge, visited on 21 May, when the water temperature was 17.25°C, showed that here the breeding season was well under way, with a large number of spat already hatched. A very fast growth of spat was noticed during the visits to the Tyne at Wylam. 'Spat' from the first breeding season had reached an average size of 3.8mm in the Tyne near Stocksfield on 13 July, and copulation was witnessed again, although no egg capsules had been laid.

No evidence of a possible second generation was found in any of the smaller streams visited, and it is only in the larger rivers where a second generation is possible. Boycott (1928) mentionts that in particularly favourable conditions Lymnaea peregra can also have two generations per year, and this is commonly found when this snail is kept in laboratory conditions.

Geldiay (1956) states that the offspring and parents from the second breeding season grow up together through the winter.

It is not difficult to imagine the younger breeding animals being
able to survive breeding stresses better than adults of the first
generation. Unfortunately time did not allow collection of data
on the survival of these animals.

5. Conclusions

    (i)   <u>Ancylus fluviatilis</u> has a simple annual life cycle at
          the sites investigated. There were fairly typical
          limpet habitats and it is probable that in the majority
          of sites where <u>Ancylus</u> is present, a similar cycle is
          followed.

    (ii) There is great variation in shell length of breeding
          individuals, both within a population, and from one
          population to another. In rivers where high average
          water temperatures are found, a second breeding season
          is possible, resulting in two generations per year.
          This phenomenon is rare and confined to larger rivers.

    (iii) At New Burn and Whitehouse Burn there was a gradual
          decline in <u>Ancylus</u> population density throughout the
          investigation. It is proposed that at New Burn the
          major factor contributing to this decline is winter
          flooding, whereas at Whitehouse Burn the same factor,
          coupled with the effects of intraspecific competition,
          is responsible.

    (iv) At higher population densities the growth rate and shell
          length of limpets are markedly reduced.

    (v)   Mortality of newly hatched spat and young limpets is very
          high, but the factors causing this are not known.

Part Two - Reproduction

1. Introduction

Ancylus fluviatilis is hermaphrodite, but according to Bondeson (1950) it 'shows a marked instinct for copulation.' He found that the Ancylidae will not reproduce in an isolated state, thus confirming the view that the most specialised families of gastropods are the ones most dependent on copulation.

It was stated in Part I that rising temperature is the environmental trigger for the breeding season and Bondeson (1950) puts the limit at $7^{o}C$. Variation in temperature from one stream to another will lead to a corresponding variation in limpet size and breeding season.

Bondeson (1950) stated 'that theoretically there should be nothing to prevent chain copulation in Ancylus fluviatilis, but such a phenomenon has never been observed and would no doubt be a daring experiment in rapidly flowing water.' However, Geldiay (1956) published an account of chain copulation, and stated that this was the general rule in the Lake District. Similarly Crabb (1927) has reported chain copulation in Lymnaea stagnalis.

Eggs are laid ('on the underside of stones', Bondeson 1950) by an individual over a period of approximately one month. There is a noticeable decrease in the number of egg capsules laid, and the number of eggs per egg capsule towards the end of the breeding season (Bondeson 1950; Clapp 1921). A similar reduction has been noted in the Planorbidae (Bondeson 1950; Cole 1935), Lymnaeidae (Bailey 1939; Noland & Caniter 1946; Taki 1931) and Physidae (DeWitt 1954).

The egg capsule, according to Moquin-Tandon (1885) is 'like amber' or, according to Wackenheim (1915), 'has a milk white tinge.' Percival & Whitehead (1929) describe the egg capsule as

'having a greyish appearance.' The most detailed description of

the Ancylus egg capsule is given by Bondeson (1950) - 'small, circular,

with a long entirely adnate terminal tail. The operculate suture

is seen as a broad double contoured line which lies outside the

edge of the tertiary envelope. The foot envelope often forms a

broadly scalloped margin. Posteriorly this margin may attain a

breadth of over 1mm. The foot gland may sometimes leave a mark

which is seen as a tongue about 4mm broad, usually pointing forward

in the direction in which the eggs are laid. The extremely regular,

large eggs are almost circular in the isolated state but in capsules

with several eggs they are of polygonal shape. They are always

arranged in one row with quite regular overlapping.' A typical

egg capsule is illustrated in Figure 12.

The average size of egg capsules according to Bondeson (1950)

is 3.3 x 2.8mm, with the largest he recorded measuring 4.5 x 4.2mm.

Geldiay (1956) found the average size of capsules to be 3.42 x 2.7mm.

Perhaps the greatest difference of opinion reigning over

the reproduction of Ancylus concerns the number of egg capsules laid

per individual, and the average number of eggs per egg capsule.

Bouchard Chanteraux (1832) claimed each Ancylus laid 7-10 capsules

and the number of eggs varied from 4 - 6 per capsule. Moquin-Tandon

(1885) thought Ancylus could lay up to 12 capsules, Lehmann (1873),

however, gave the much lower figure of 5 - 7. Percival & Whitehead

(1929) said there was usually 7 eggs per capsule. More recent studies

by Bondeson (1950) carried out in the laboratory put the number of

egg capsules laid at ten, with a very low figure, 2 - 3 eggs per

capsule. Hunter (1953) stated that Ancylus lays an average of

46 eggs in 12 capsules. Geldiay (1956) counted 200 egg capsules

in nature which had an average of 3.99 eggs/capsule. A total of

55 capsules counted in the laboratory had an average of 4.27 eggs/

capsule. He came to the vague conclusion that 'a limpet therefore

probably lays between ten and twenty capsules, the number being more likely nearer the lower figure .... the total number of eggs is perhaps about 50.' Much confusion here probably arises due to the confrontation of laboratory counts and those made in natural conditions. There is also bound to be a bias in the latter case depending on the state of progress of the breeding season when the counts were made.

The aims of Part II of the project were as follows :
(i) to look at the variation in breeding populations due to temperature; (ii) to elucidate the evidence for, and the incidence of, chain copulation in nature and the laboratory; (iii) to examine the position of egg capsules laid in nature; and (iv) to determine the reproductive potential of Ancylus in nature and the laboratory.

2. Methods

Information on egg capsules laid in nature was obtained during the visits made to localities for Part III of the investigation. At each site the number of adults, egg capsules and spat per quarter of a square metre of stream bed was counted, giving information on the progress of the breeding season at that locality. This was complemented by ten minute counts of adults, capsules and spat. When excavating the $\frac{1}{4}m^2$ of stream bed, the position of each egg capsule on the stones was noted. Water temperature was also determined at each locality.

The number of eggs in an egg capsule cannot be counted when the egg capsule is newly laid. The spat must be considerably developed before this is possible, and a hand lens is needed even then. A light coloured substrate and bright sunshine also make counting easier.

In the laboratory two main experiments were carried out. A stock of _Ancylus_ was kept in a large water-filled jar, with algae covered stones provided for food and adequate aeration. These limpets were kept simply to obtain a large number of egg capsules for counting. Limpets kept in the laboratory in other experimental tanks also laid egg capsules which were counted. Where the eggs are laid on glass surfaces, they can be counted easily, even when fresh laid. The possibility of counting capsules twice was avoided by marking each one after counting, either by using a felt tipped pen if laid on glass, or by making a scratch mark if laid on stone.

To determine the number of egg capsules laid per snail, twelve 250ml beakers containing pond water and algae covered stones were utilised. Two limpets were placed in each beaker and the number of egg capsules laid recorded, each capsule being marked as before to avoid confusion. The water in the beakers was changed each day. The limpets were collected from the river Tyne at Wylam on 23 May when the breeding season had already begun, and it is possible that some of the individuals had already laid capsules prior to the experiment.

Results

These are given in tabular form in the Appendix (Tables 3 & 4). Figures 8 and 9 are histograms illustrating the frequency of eggs per egg capsule laid in the laboratory and in nature. Figure 11 illustrates the decrease in rate of capsule laying with time by limpets kept in the laboratory; Figure 10 illustrates the cumulative total of egg capsules laid.

FIG 8 FREQUENCY OF EGGS PER CAPSULE LAID IN THE LABORATORY
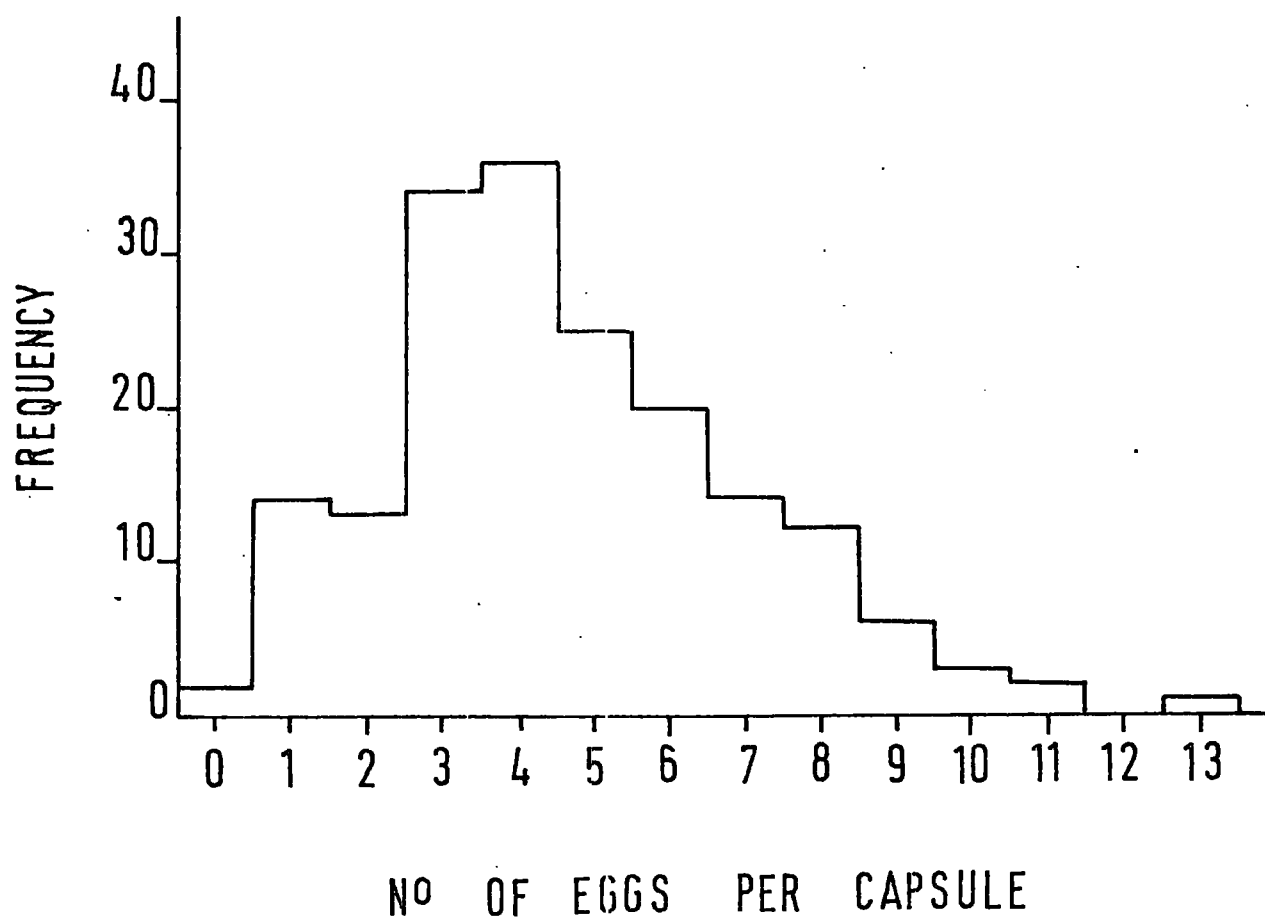
FIG 9   FREQUENCY   OF   EGGS   PER   CAPSULE
LAID   IN   NATURE

Nº OF EGGS PER CAPSULE
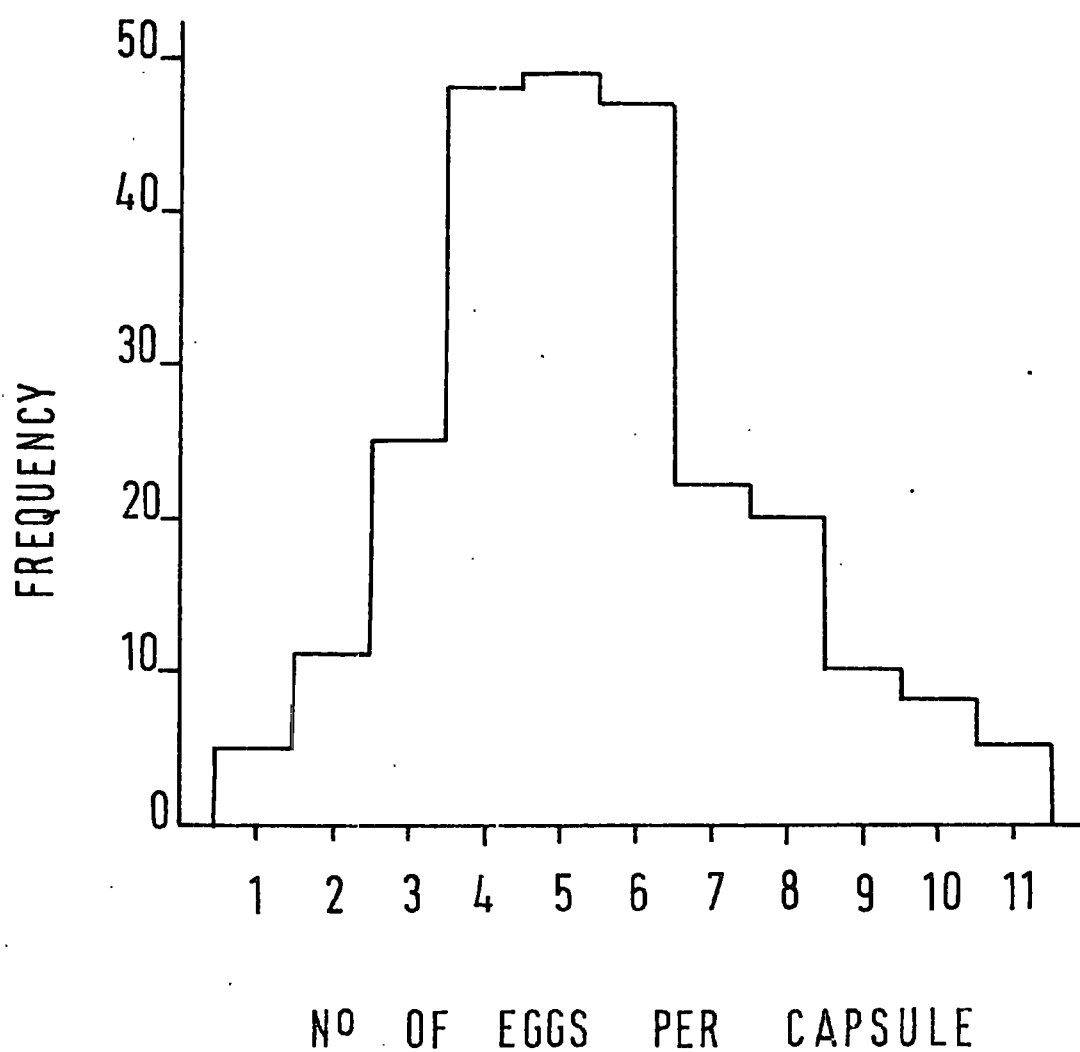
FIG 10 BUILD UP IN THE TOTAL NUMBER OF EGG CAPSULES LAID
BY 24 ANCYLUS IN THE LABORATORY

CUMULATIVE TOTAL
OF EGG CAPSULES
LAID BY
24 ANCYLUS

DATE (1971)
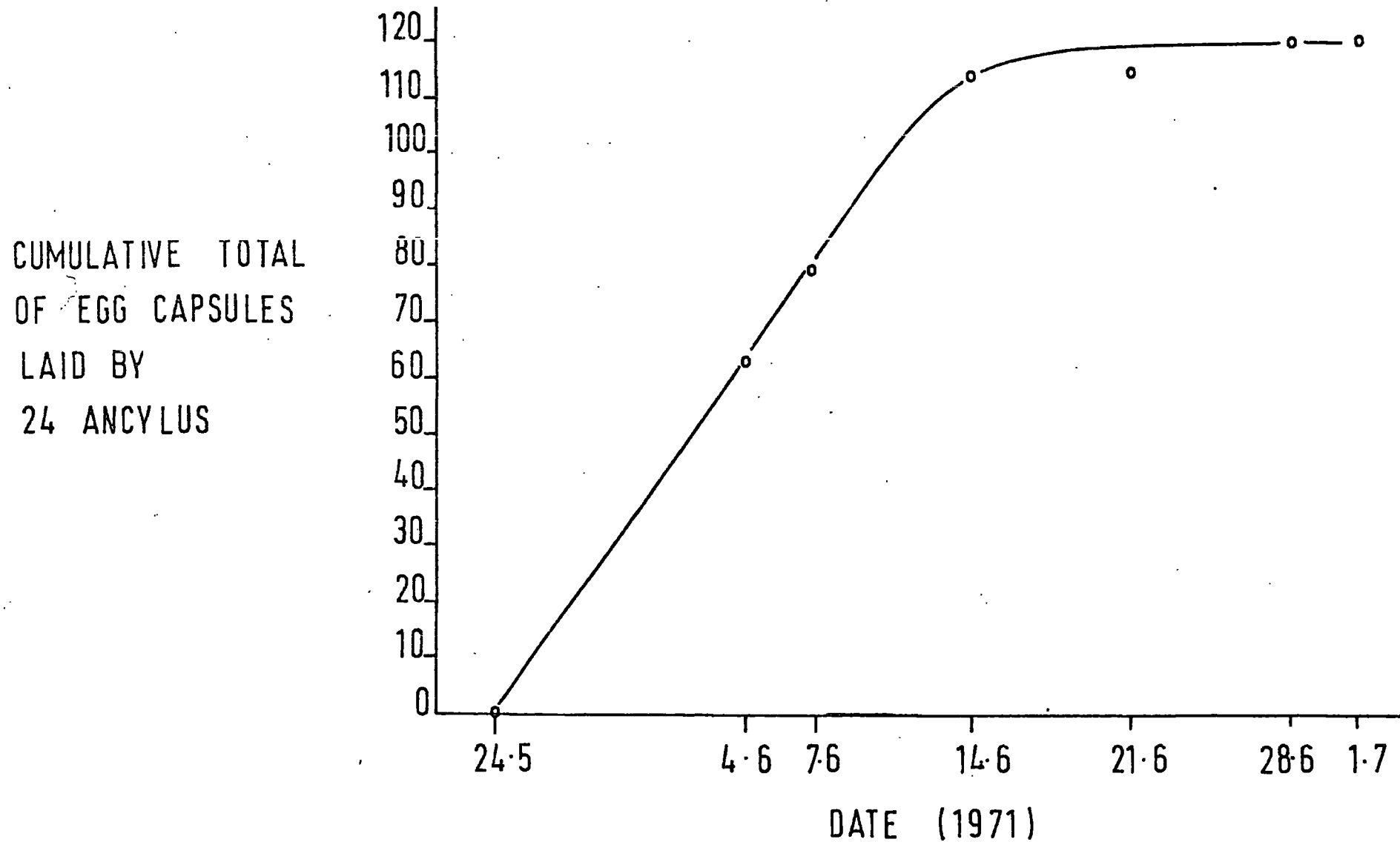
FIG 11   THE DECLINE IN EGG CAPSULE PRODUCTION
IN   THE   LABORATORY

MEAN
N⁰ OF EGG
CAPSULES LAID
PER DAY
SINCE PREVIOUS
COUNT

DATE (1971)
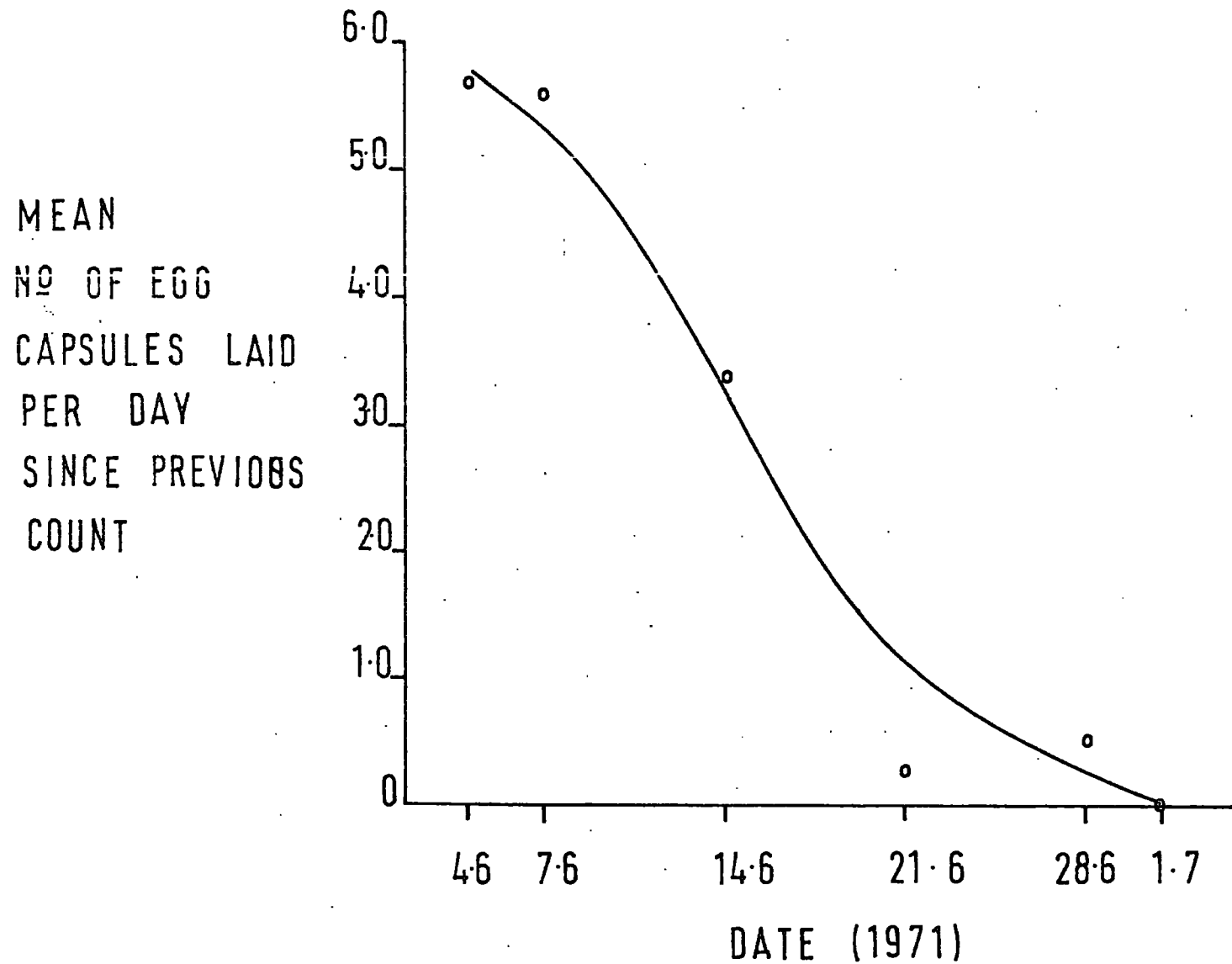
4. <u>Discussion</u>

The timing of the breeding season is dependent entirely upon temperature. This was discussed with reference to the life cycle and the possibility of a second generation in a year in Part I. One example is sufficient here to illustrate the importance of temperature. On 13 July the river Tyne at Stocksfield (site 44) and Stocksfield Burn (site 45) were visited. In the river Tyne the spat from the breeding season had reached a mean shell length of 3.8mm and were copulating, indicating the start of a second generation. In Stocksfield Burn the spat had an average size of 2.4mm and egg capsules from the breeding season were still present, although the adult generation had died off. The water temperatures at these two sites were 20^{c}C (river Tyne) and 14°C (Stocksfield Burn).

Chain copulation seems to be a relatively rare phenomenon. Out of thirty five sites where <u>Ancylus</u> was present, it was witnessed at only five of these, and always where the population density was high (e.g. river Tyne at Corbridge, river Wear at Stanhope). In the majority of streams where <u>Ancylus</u> is present, the population density is usually low, thus reducing the incidence of multiple encounters. Indeed, in many of the streams, <u>Ancylus</u> has such a low population density that copulation may not be possible, and self fertilisation must occur. So although multiple copulation does occur, it is certainly not the 'general rule' as Geldiay (1956) found in the Lake District. Certainly he seemed to be dealing with populations which had very high densities, recording variations in ten minute counts of 6000 - 100 individuals. Also many of Geldiay's sites were in still waters of lakes and tarns where multiple copulation becomes a more feasible proposition.

The positions of 1,293 egg capsules laid in nature on stones have been recorded. The majority of capsules were laid on the sides (51.9%) and the bottom (44.2%) of stones. Only 3.9% of the capsules were laid on the more exposed upper surfaces. Laying capsules in the more sheltered positions must certainly improve the chances of survival of both the egg and newly hatched spat.

The decrease in number of egg capsules laid with time was seen at Wylam (Figure 7). As the later visits were paid to sampling sites there was a marked decrease in the number of egg capsules recorded. The number of eggs per capsule also decreased in nature as the breeding season progressed. In the river Tyne, for example, the mean number of eggs per capsule at Corbridge on 21 May was 7.04. At Bellingham, on 3 June, the mean value had dropped to 4.2, and at Wylam on 2 July had reached 3.7.

A total of 250 egg capsules were examined in nature and the number of eggs each contained recorded. They were counted from many different sites (Table 3) at different times and conditions of breeding season, and it was hoped that in this way a time assessment of egg production could be obtained. The total number of eggs recorded was 1388 giving a mean value of eggs per capsule of 5.5. This is a higher figure than those quoted by Bondeson (1950), Hunter (1953) and Geldiay (1956).

In the laboratory reasonable numbers of egg capsules were obtained. In spite of using sophisticated flow tanks for his limpets, Bondeson (1950) remarked that 'usually it was only possible to make each individual lay 2 - 4 capsules in the laboratory' and came to the conclusion that 'a fully reliable value for the egg production of the individual it will scarcely be possible to give'. Geldiay (1956) also mentions the work of Diver, who, when experimenting on snail genetics, found that the number of eggs a snail laid was

influenced by the size of its container and the frequency of water changing. Incidentally, egg capsules laid in the laboratory verified both Moquin-Tandon's (1885) and Wackenheim's (1915) description of egg capsule colour. When laid on glass, the egg capsule appears amber coloured, when laid on stone, white.

The twelve pairs of limpets kept in the 250ml beakers laid a total of 120 egg capsules over a period of four weeks, giving a mean value of only 5 capsules per limpet. During this experiment a number of the animals died, due either to breeding stress or the experimental conditions. This decline in the numbers of adult limpets (from 24 -> 11 by the end of the experiment) parallels the results found in nature (Wylam, Figure 7). There was a great deal of variation in the number of egg capsules laid in each jar, the maximum being 22, the minimum 1. Considering that (i) the experimental conditions were far from optimal for a theophilous animal; (ii) it is possible that some had laid eggs before being brought into the laboratory; and (iii) a number of limpets died before laying any capsules, the small average figure for the number of capsules per limpet is understandable. It is probable then that the largest figures for egg capsule production in the laboratory are the more reliable, which is in the order of 10 - 11 capsules per limpet. Observations in nature reinforce this view, When isolated limpets have been found laying capsules, and surrounded by nine or more of them. In the river Tyne at Corbridge, visited at the height of egg laying, the numbers of Ancylus and egg capsules per $\frac{1}{4}m^2$ quadrat result in a mean figure of capsules/Ancylus of 12.38.

One hundred and eighty two egg capsules were counted in the laboratory, containing 844 eggs, with a mean value of 4.63 eggs/ capsule. This figure is slightly higher than the one given by

Geldiay (1956) from laboratory laid capsules of 4.27. It is expectedly lower than the figure for capsules counted in nature.

A decrease in the number of eggs per capsule with time was also noticed in the laboratory. For example, the first 30 egg capsules laid in laboratory conditions had an average of eight eggs/capsule, the last 30 only three eggs/capsule.

From the combined observations of laboratory and field experiments, the average number of eggs laid by an individual of Ancylus fluviatilis in nature is in the order of 60, in approximately eleven capsules. This is higher than the figures quoted by Hunter (1953) of 46 eggs, and Bondeson (1950) of 30 eggs. However, the latter author reached his conclusion via a three year laboratory study, and the former does not specify where or when he obtained his information. In fact, sixty eggs is still a very low number for a freshwater pulmonate. The large eggs of Ancylus, however, compensate for the low number produced. The considerable egg size (1.42 x 1.20mm), Bondeson 1950) can be interpreted as an adaptation to life in rapidly flowing water, which is a comparatively hostile environment for a gastropod. The young are thus able to develop to a large size (= 1.5mm) before hatching, and are able to survive in strong water currents. Thus for Ancylus to maintain a stable population density the annual selection ratio is about 60 : 1, which is considerably less than for other freshwater molluscs (e.g. Lymnaea peregra 1400:1, Planorbarius corneus 100:1, Anodonta 1,000,000:1).

The reproductive potential of Ancylus is modified by a number of factors. Hunter (1961) found that the population density of Ancylus in a small stream varied by up to seven times from year to year, and was able to correlate this with variation in incident

FIG 12 EGG CAPSULE DEVELOPMENT
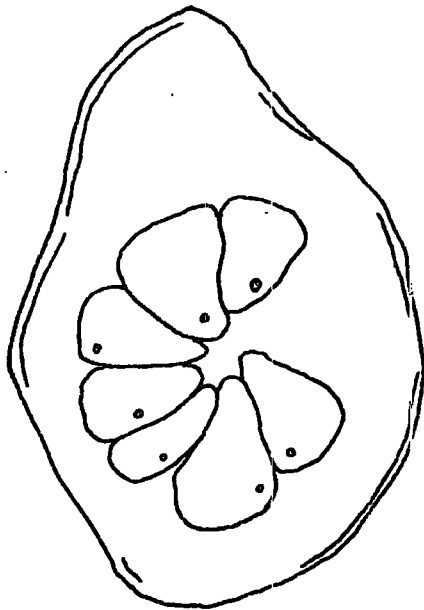
DAY 1
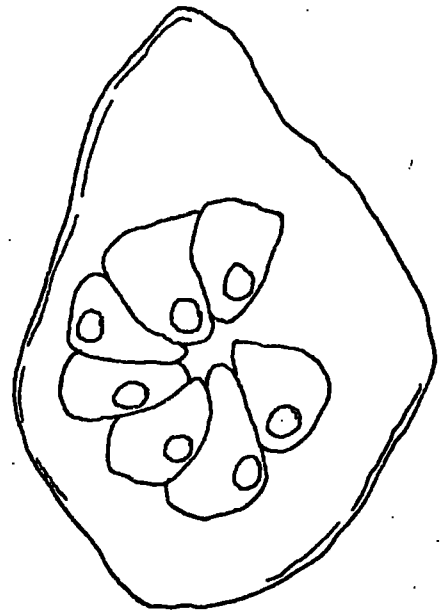
DAY 4
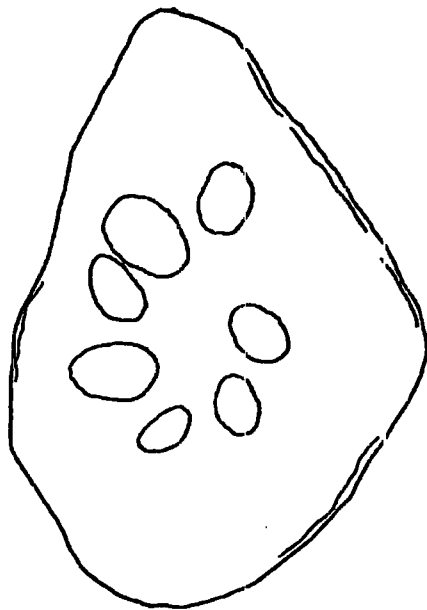
DAY 7
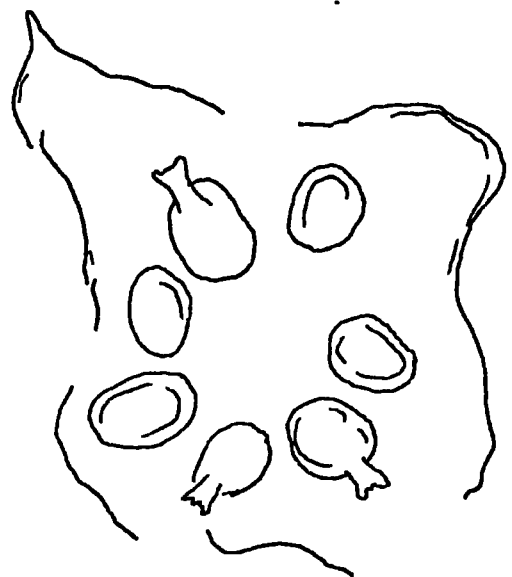
DAY 14

sunlight. Presumably this results in more algae for food and hence more energy can be channeled into reproduction.

A correlation between the average number of eggs per capsule and shell height has been reported for _Physa fontinalis_ (DeWit 1955) and _Planorbis corneus_ (Precht 1936). DeWitt (1954) found a correlation between total egg production and size in _Physa gyrina_. No work of this kind has been done for _Ancylus_. It is possible that the size factor (if it exists) could be responsible to some extent for the variation in figures quoted for egg production, in _Ancylus_. Population density may also affect egg production. Eisenberg (1966) found that in _Lymnaea elodes_ the number of eggs/ capsule decreased as population density increased. Hunter (1961) showed that if the number of _Ancylus_ and egg capsules on a number of stones are counted, then the figures obtained are directly proportional. At population densities of 100 - 400 per m^2, then the number of egg capsules = 7.5 x the number of adults. If population densities were higher than this, then the egg capsule/ adult ratio decreased.

Once egg capsules have been laid, egg development is quite fast. In the laboratory, where the water temperature averaged $16^{o}C$, eggs hatched within 14 days of being laid. It is probable that in nature the time taken is approximately the same, any variation dependent on water temperature. The typical stages of a developing capsule are shown in Figure 12.

Non-development of eggs was rare. Only once in the laboratory was an egg of this type seen, and that was at the close of the breeding season when the eggs laid become smaller, the number of eggs/capsule is low, and the capsules themselves are

defective. Bondeson (1950) discusses the frequency of a number of egg abnormalities, e.g. eggs without egg cell (5.12%), dwarf eggs (6.77%), giant eggs (0.18%), twins (0.73%), and egg cell only, no albumen (1.64%). However, in the present investigation it has been found that the majority of eggs hatch, leading to high density spat populations, the decrease of which was discussed in Part I.

One very interesting point made by Bondeson (1950) is a comparison of the eggs of Ancylus fluviatilis and Acroloxus lacustris. On the basis of morphological grounds he concludes that the family Ancylidae is of diphyletic origins, and that Ancylus and Acroloxus have no true connections.

5. Conclusions

(i) There is great variation from one stream to another in the state of progress of the breeding season, due entirely to temperature.

(ii) Chain copulation was found to be a rare phenomenon, only occurring in sites where population density was high. In the majority of streams, low population density will decrease the incidence of multiple encounters. In streams of very low population density self fertilisation may occur.

(iii) The majority of egg capsules are laid in sheltered positions on the sides and bottoms of stones. Eggs hatch approximately 14 days after laying. Although abnormalities occur, their incidence is low. The majority of eggs laid are viable and few eggs laid fail to hatch.

(iv) The average number of eggs/capsule laid in nature was 5.5. In the laboratory the lower figure of 4.6 was found. Each limpet lays approximately eleven capsules, containing sixty eggs. The number of eggs/capsule decreased in the later stages of the breeding season, both in nature and in the laboratory.

Part Three - The distribution and abundance of Ancylus fluviatilis

1. Introduction

Hunter (1961, 1962) has described the variation in Ancylus
population density in one stream over a number of years and correlated
this with the weather conditions during the spring of the previous
year. Geldiay (1956) looked at variation in population density
from one stream to another but commented that 'the factors governing
the density were not discovered.' This part of the investigation
was concerned with this problem.

2. Methods

The problems of quantative sampling on stony bottoms as
mentioned by Macan (1958) and Britt (1955) do not apply when an animal
has a mode of life similar to Ancylus. Carpenter (1927) classified
Ancylus as a 'stone clinger' in her Lithophilous Association. This
description is very apt, and limpets are not easily dislodged when
stones are lifted. Thus, to obtain a quantitative estimate at each
site, a $\frac{1}{4}m^2$ quadrat frame was placed on the stream bed. The stones
within this were removed and the number and position on the stones of
limpets, egg capsules and spat recorded. A further quantitative
estimate, in the form of a 'ten minute count' was carried out to
complement the quadrat counts. Figure 13 compares numbers of adults
counted by each method. There is good correlation between them,
especially at lower densities. At higher densities, time is spent
actually counting the animals, causing a plateau effect.

The actual siting of the quadrat was subjective. Many
authorities (e.g. Berg 1948, Carpenter 1927) point to the theophilous

FIG 13 A COMPARISON OF THE TWO SAMPLING METHODS

NO OF ANCYLUS COUNTED IN TEN MINUTES

NO OF ANCYLUS PER $\frac{1}{4}M^2$
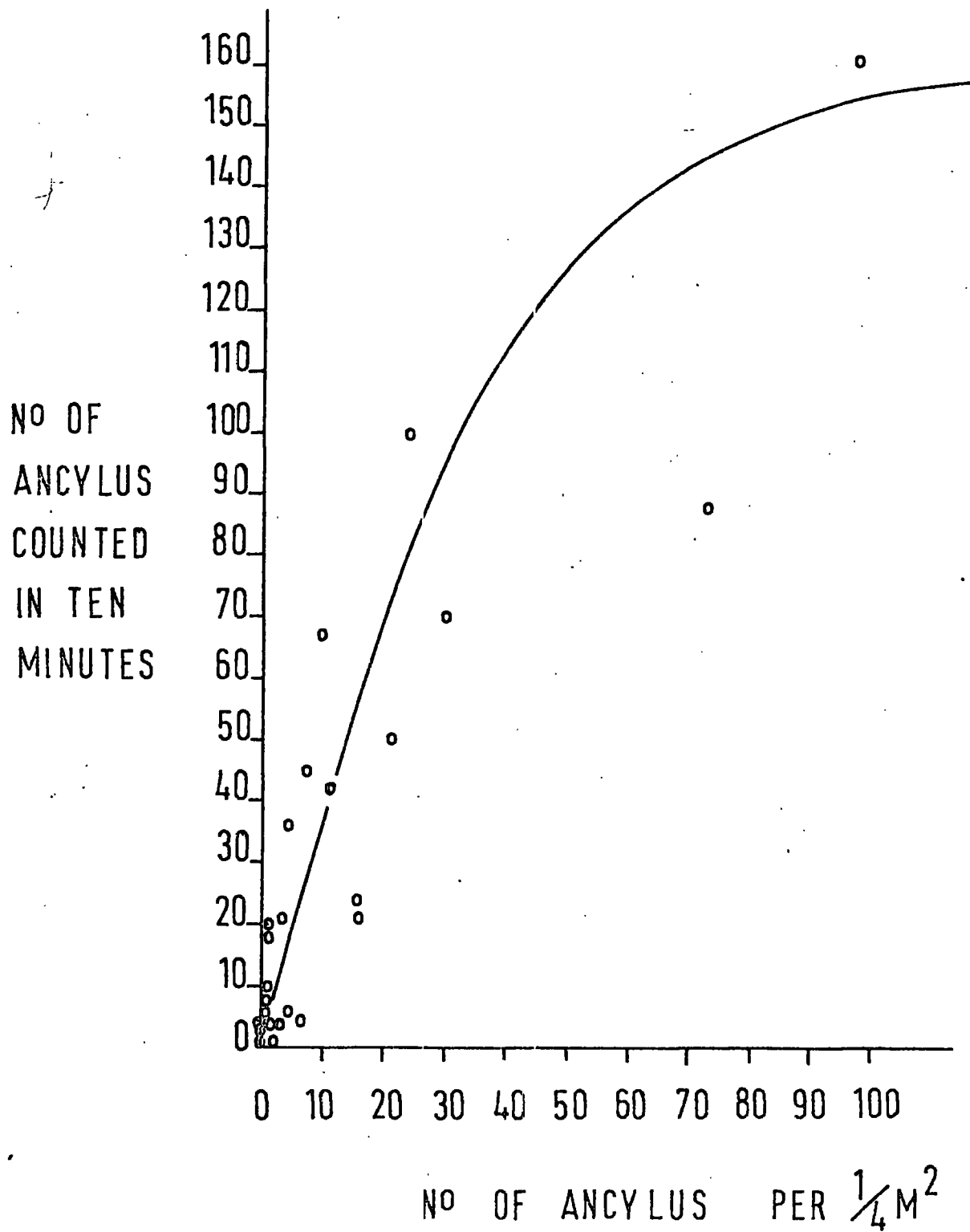
nature of <u>Ancylus</u>, and hence the quadrat was always placed in a fast running stretch. Although subjective, this method gives good comparative results.

The sampling sites were visited over a period of nine weeks from 7 May until 14 July. Because of this, different stages of the breeding season were encountered and hence the difference in numbers of limpets, their egg capsules and spat from one site to another were to some considerable extent due to this. However, the figures obtained at each site still give a good indication of the degree of success of the species at the particular site.

The area of stones within the quadrat were measured following Muller's method (1953) of finding the two longest dimensions measured in a straight line and multiplying them together. This gives an estimate of available living space, and indicates any stone size preference of the limpets. A substrate sample was also collected for identification.

Also within the quadrat the depth of water was recorded and stream flow measured at the surface and at the maximum depth, using a Pitot tube. A subjective assessment of algal and moss cover was made within the quadrat for the top, sides and bottom of stones using the following scale : 0 - no algae; 1 - algal slime; 2 - covering of algal slime + some filamentous algae; 3 - increase in filamentous algae; 4 - algal slime + patchy cover of algae and mosses; 5 - a complete thick cover. A sample was collected of the covering algae and mosses for later identification and a note made of any other vegetation.

The river temperature and width were also measured, and a water sample collected for pH measurement and calcium analysis.

A number of _Ancylus_ were collected and taken back to the laboratory for measurement of shell length and weighing. Any other molluscs were collected for identification. Notes were made of any other relevant factors, e.g. predators and amount of shade.

3. Results

(a) Occurrence

Geldiay (1956) found _Ancylus_ in every beck he examined except for the very small ones, and also in Wastwater and Ennerdale, two of the most unproductive lakes in the area. _Ancylus_ is often mentioned in ecological studies of stream fauna (e.g. Percival & Whitehead 1930; Badcock 1940). Ellis (1951) commented on its widespread geographical distribution. Berg (1948) mentions its high percentage occurrence in the R. susaa system. In this investigation, out of 50 randomly chosen sampling sites, _Ancylus_ was present at 35 of them, a seventy percent occurrence. All these reports support Geldiay's view that '_Ancylus fluviatilis_ is a remarkably ubiquitous snail.'

No quantitative estimates have been given for the position where _Ancylus_ is usually found on stones. There are many vague references to _Ancylus_ being particularly common on upper surfaces of stones (e.g. Carpenter 1927). Berg (1948) comments that 'large individuals are found on the upper sides of stones with a rich coating of algae, smaller individuals are found on the sides.' In this investigation the position of 387 adult _Ancylus_ was plotted. Of these, 52.4% occurred on the tops, 36.9% on the sides, and the remaining 10.7% on the undersurfaces of stones. Of 441 spat recorded, 35.6% were found on the tops, 54.4% on the sides, and 10% on the

undersurfaces of stones.   These figures seem to verify Berg's statement.

The numerical density of adult <u>Ancylus</u> varied from very low (e.g. 1 per 10 minutes or < 1 per $\frac{1}{4}m^2$ at Horsley Burn, Stanhope) to high (e.g. 160 per 10 minutes or 99 per $\frac{1}{4}m^2$ at Whitehouse Burn). These densities, however, cannot compare to those that Geldiay (1956) and Moon (1936a,b) quoted for their highest density populations of <u>Ancylus</u> in the Lake District of 6000/10 minutes and 80/sq.foot respectively.   In the majority of sites where <u>Ancylus</u> was found, it was present in low densities.   High population densities were usually only found in the larger, more eutrophic rivers, e.g. river Tyne and river Wear. although occasionally high numbers were recorded from smaller streams (e.g. Whitehouse Burn (2) and Sandyfords Burn (39)).

(b)   Substrate

Berg (1948), Macan. (1950, 1960) and Hunter (1957) have all referred to <u>Ancylus</u> being limited to a hard, clean substrate.

Substrate size and stability is determined by stream speed, and its nature is determined by the geology of the surrounding area. There was a great deal of variation in substrate size in any one stream, but very little difference from one stream to another. In fact, the majority of the larger streams conform to Percival & Whiteheads (1929) type 4 substrate, which is defined as 'stones of variable size and shape set in a matrix, stable, and covered with <u>Cladophora</u>.'   They state that <u>Ancylus fluviatilis</u> was most numerous on this type of substrate.   Some of the smaller, unproductive and usually higher altitude streams had more similarity with their type I substrate - 'loose round stones more than 5cm in diameter forming an unstable bottom and carrying no vegetation visible to the naked eye.'

Percival & Whitehead also collected Ancylus from this type of
substrate, but not in as great a number. Certainly the field
observations of the author agree with the findings of Percival &
Whitehead. No hard conclusions can be reached concerning the effect
of substrate on Ancylus distribution, simply that a 'type 4' substrate
is more suitable than a 'type 1'. Also, in any one stream, the
larger stones seem to be preferred, probably because of their
greater stability. The most important fact is that stones be clear
of any thick covering vegetation which excludes the mollusc, and
this is determined by stream speed.

   (c) Algal growth

      Ancylus is a grazer on the algal felt covering the stones.
It is hard to imagine that this sort of feeding could be selective,
but specimens observed by Schmidt (1932) had a preference for
submerged lichens. Geldiay (1956) concluded that limpets browse
indiscriminately on the algal felt. Badcock (1949) examined five
Ancylus guts, the contents of which were 'mineral particles, diatoms,
desmids and other encrusting algae.' Thus, a thin algal film
provides all the food a limpet needs, and this requirement is very
rarely absent in any river or stream. Food is therefore not likely
to be a limiting factor, except in oligotrophic streams, or in a
very high density population. An example of the first type was
seen at Bollihope Burn which, although not particularly oligotrophic,
had no algal growth at all, and an extremely low Ancylus population.

      Algal growth has a more important effect on populations
when it begins to reduce the amount of available living space.
As already mentioned, the preferred areas of grazing are on the
upper surfaces of stones. However, once the top becomes colonised

by the larger filamentous algae (e.g. <u>Cladophora</u>) and the aquatic
mosses, exclusion of <u>Ancylus</u> must occur and they are forced into
sub optimal habitats on the stone sides. <u>Ancylus</u> cannot graze
the filamentous algae or mosses, which also restrict the amount of
thin algal film available to the limpet. The overall effect is then
a marked decrease in living space and available food which could
result in intraspecific competition, especially in streams of high
population density. The effect must also intensify during spring
as the algal cover becomes more dense, perhaps resulting in a
continuing drop in population numbers. It is possible that this
effect occurred at Whitehouse Burn (see Figure 4 and text page 7).

The reduction in available living space caused by algal
and moss growth could be one of the factors causing variation in
population density of <u>Ancylus</u>. At Whittle Burn (site 9), for
example, the tops and sides of stones had a thick cover of <u>Ulothrix</u>,
<u>Batrachospermum</u>, <u>Spirogyra</u> and <u>Cladophora</u>. Few stones were without
this algal cover, leaving little clean substrate, and this must be
the cause of the exclusion of <u>Ancylus</u> from this stream. The nearby
Horsley Wood Burn (No.8) had little algal growth, but apart from this
was similar in all respects. Here an average population density of
<u>Ancylus</u> was found. Preliminary observations in the river Wear at
Durham Sands carried out in December first indicated an exclusion
effect. The tops and sides of the stones were covered in a thick
growth of filamentous algae, and of 46 <u>Ancylus</u> collected, 25 (54%)
were found on the undersides of stones, and 19 on the sides, Only
2 specimens were found on the upper surfaces.

Thus, with a reduction in living space and possible
intraspecific competition, a dense growth of algae should result in
a reduced population. However, some of the highest population

densities found by the author occur in the more eutrophic streams and rivers where algal cover is high (e.g. river Wear at Wolsingham and Stanhope, river Tyne at Corbridge). Perhaps in these sites, although living space is reduced, the production of the algal film is enough to compensate for this.

Figures for the algal cover for each site are given in the Appendix.

(d) Water velocity

The speed of the water current determines the size of the substrate, and the amount of algal growth on stones. Velocity of the water also acts directly on the fauna.

Many authors (e.g. Berg 1948) have indicated the rheophilous nature of Ancylus fluviatilis. The limpet is ideally adapted for life in rapidly flowing water, the shell shape giving streamlining and improved attachment. The shell is kept closely drawn down to the level of the stone to which the animal adheres by its flattened sole-like foot, the intimate contact of the two moist surfaces effectively resisting forces of dislodgement. In nature Dorier & Vaillant (1954) found that Ancylus was limited to streams with a maximum current speed of 24cm/sec. This is a particularly low figure and does not agree with the observations of the author. The average speed of flow at the water surface in a typical limpet habitat is approximately 20cm/second. The highest stream speed recorded where Ancylus was present was 35cm/second, at the river Tyne, Bellingham.

As mentioned previously, Ancylus needs a stony substrate. Hence, velocity restricts its geographical distribution by determining substrate size, as it is never found on sandy or silty substrates.

The effects of current velocity within a river are best described by reference to a specific example. In the river Wear at Wolsingham (site 15) on 20 May three $\frac{1}{4}m^2$ quadrats were taken in three sites which had different stream speeds. The first quadrat site was in a current of 19.0cm/second at the water surface. There was a heavy growth of Cladophora, Ulothrix and Hormidium on the tops and sides of stones, and trailing masses of Ranunculus aquatilis were also present. This heavy vegetation growth had reduced the amount of clean substrate to practically nil, and no Ancylus were recorded. A second quadrat was taken in a very rapidly flowing area, of water surface speed 44.3cm/second. All the stones were clean, no algae being able to establish themselves in such a current. However, this velocity was also too great for Ancylus, as none were found. The third quadrat was intermediate between these two extremes, with a surface speed of 31.3cm/second. This allowed an algal growth which was quite dense to grow, but not to the extent of excluding limpets, sixteen of which were found in the quadrat.

Thus, within a river, the distribution of Ancylus is patchy, corresponding to the effects of current speed. Lymnaea peregra is often found in the slower reaches from which Ancylus is excluded, and the two species rarely co-exist.

(e) Temperature

Hunter (1964) remarked that the temperature range within which some freshwater molluscs can live practically corresponds to the absolute limits for metabolism in metazoan tissues. This great plasticity in tolerating a wide range of temperatures makes it highly doubtful that temperature is limiting for Ancylus in a natural habitat. Certainly in the localities where the highest temperatures ($\simeq 20^{\circ}C$) were recorded (the river Tyne), the Ancylus population thrived.

(f) Altitude

Boycott (1936) found Ancylus at an altitude of 2300' in
a stream on Brandon Mountain, Kerry, and Geldiay (1956) and Macan (1950)
found Ancylus in high altitude tarns in the Lake District. I have
recorded Ancylus from high altitude streams (e.g. Horsley Burn,
Stanhope), but found it to be absent in high altitude acid moorland
streams (e.g. Rookhope Burn).

(g) River size and eutrophy

A large river tends to be warmer, have a higher calcium
concentration, and be more eutrophic than a small stream. In these
conditions, the majority of snail species usually occur in greater
abundance. Ancylus is no exception to this rule, the greatest
population densities almost always being found in the large rivers
(e.g. river Tyne at Corbridge, river Wear at Stanhope). Certain
exceptions to this rule did occur (e.g. Sandyfords Burn, Whitehouse
Burn), but in the majority of streams, Ancylus was present in low
population density.

(h) Hydrogen ion concentration

The majority of streams visited had a pH in the region of
6.5 - 7.5. Only one really acid stream was encountered, Rookhope
Burn, pH 4.2, and here no Ancylus were found. Of the sites with
alkaline readings, Croxdale Hall river had the highest figure of
pH 8.4. Here again Ancylus was absent, although a large number of
other molluscs (Lymnaea peregra) were present. Thus it is possible
that extremes of pH can be limiting. In the majority of habitats
in which Ancylus is found, however, pH has a negligible effect on
population density.

(i) Parasitism and commersalism

Volz & Fromming (1936) have described the parasites of Acroloxus lacustris, but I was unable to find any reference to Ancylus fluviatilis. Trematode parasites may cause mortalities in some species (Sewell 1922, Rankin 1939) or have a negligible effect (Rankin 1939, Pratt & Barton 1941). It seems unlikely that Ancylus is limited in this way. The presence of Chaetogaster limnei Baer, a commensal oligochaete, seen on a number of occasions, is immaterial.

(j) Depth

The majority of streams visited were shallow and rapid running. The greatest depth at which Ancylus was found was 70cm in the river Pont, Stamfordham, the slowest running locality visited. In general, deeper water meant that a thicker algal growth occurred, along with silting, and an unsuitable substrate resulted. Geldiay (1956) found high limpet populations living at 5 metres throughout the year in Lake Windermere.

(k) Oxygen

The work of Berg (1951, 1952, 1953), Berg, Lumbye & Ockelmann (1958), and Berg & Ockelmann (1959) has indicated that the oxygen consumption of the two species of Ancylidae is very similar, remaining stable for most of the year with an increased consumption during the breeding season. Berg (1952) showed that oxygen consumption of Ancylus remains constant independent of the oxygen concentration of the water. However, Ancylus has not the capacity to survive anaerobic conditions, and this was noticed in the laboratory where Ancylus kept in stagnant water tended to migrate to the water surface.

Berg concluded that the distribution of <u>Ancylus</u> cannot be explained in terms of oxygen requirements. Macan (1963) considers Berg's 'ecological premise' – that <u>Ancylus</u> is essentially a stream-living animal – to be at fault, having found the limpet in the comparatively calm waters of lakes and tarns in the Lake District. On the basis of these findings, it is very unlikely that oxygen is a limiting factor in the distribution of <u>Ancylus</u>. The rheophilous nature of <u>Ancylus</u> in fact does not concern the need for a high concentration of oxygen, but for the need of a clean hard substrate.

(1) <u>Competition</u>

Eisenberg (1966) has studied density regulation in the pond snail <u>Lymnaea elodes</u>. He stated that regulation is mediated through food limitation as expressed in fecundity. He concluded that 'it seems reasonable to propose that the type of food limitation found in the pond snail may be common among animals of similar trophic classification in aquatic environments.'

The information obtained during this investigation would seem to support this view. However, it is probable that in the majority of sites where <u>Ancylus</u> is present, competition between adult snails is low, simply because the low population densities reduce interaction between individuals. In the more eutrophic rivers, where population densities are high, competition is far more likely to occur. The results from Whitehouse Burn (see Part One) seem to confirm this, a decline in population density and a low growth rate being recorded.

Even in moderate density <u>Ancylus</u> populations, the competition occurring among spat must be very high. Certainly spat mortality is very high (see Part One, page /0) in natural conditions. High spat densities must result in competition both

for food and living space, and this must be responsible in part for the decline in the spat populations, as recorded, for example, at Wylam (see Figure 7). Evidence for competition between spat was also obtained in the laboratory. A large number of egg capsules laid by stock animals in a large bowl were allowed to hatch, resulting in a high spat population of 250+ individuals. Algal covered stones were placed in the bowl for food, and algae were also present on the glass sides. The water was kept constantly aerated. However, after four weeks, only ten spat survived.

Hunter (1961) also produced evidence of intraspecific competition in Ancylus. He found that during the breeding season, if the number of Ancylus and the number of egg capsules were counted on stones, the figures were directly proportional. When adult limpet densities of between 100 - 400/sq.metre were recorded, then the number of egg capsules = 7.5 x the number of adults. At higher densities, a lower figure is found. Hunter postulated from this that overcrowding results in decreased egg production, which agrees with Eisenberg's theories. However, I feel the reliability of this type of figure is suspect, as a variation in the egg capsule/adult ratio will occur dependent on the progress of the breeding season. Thus it is difficult to compare two sites of different population density unless their breeding seasons are perfectly synchronised.

If the phenomenon found in Physa fortinalis by DeWit (1955), i.e. a reduction in the number of eggs laid with decreasing size of the snail, also occurs in Ancylus, then the reduced growth of individuals due to density effects will also reduce egg production.

Thus the role of intraspecific competition in determining the population density of Ancylus populations is certainly important.

FIG 14   CALCIUM AND ANCYLUS
POPULATION   DENSITY
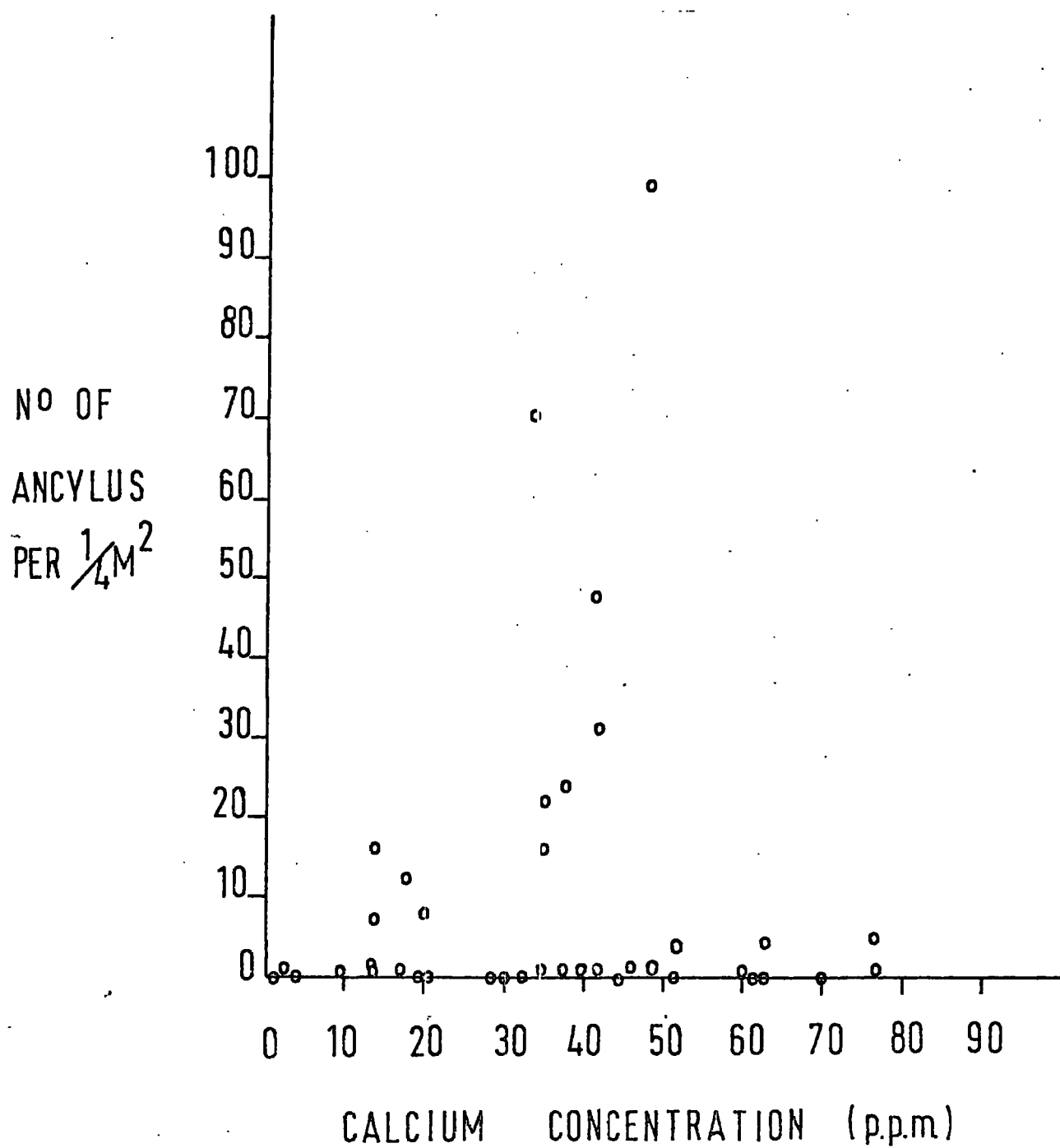
Boycott (1936) states that the ideal habitat for a mollusc is 'a large, slow flow of clean hard water, warm, and fair, but not excessive, weed growth.' By this definition Ancylus is a very aberrant mollusc, and because of this does not come into contact to any great extent with other snails, and so interspecific competition plays little part in determining population density. The only mollusc which is found to any extent in the same streams as Ancylus is Lymnaea peregra, and even then this species is found in the quieter stretches, and little overlap occurs.

The intraspecific competition among Ancylus spat has already been mentioned. In the river Tyne at Wylam, in slower running areas, stones have been found with large populations of both Ancylus and L.peregra spat, and interspecific competition must be occurring. This situation was only noticed at this one site however.

(m) Calcium

Boycott's (1936) 'ideal mollusc habitat' requires hard water, calcium being needed for shell growth and to precipitate clay particles, so producing clear water. The majority of freshwater snails are calciphiles and require at least 20mg/l of calcium (Hunter 1964). Ancylus, however, is one of the few molluscs that can tolerate low calcium concentrations and this was demonstrated during the investigation, limpets being found in reasonable number in the river Breamish (42) which had a calcium concentration of only 3ppm.

The correlation coefficient for calcium concentration and limpet numbers is not significant, and Figure 14 demonstrates the wide scatter of points obtained. This indicates that calcium concentration alone does not determine limpet success and that other factors must be of equal or greater importance.

5. <u>Conclusions</u>

    (i)   The distribution and abundance of <u>Ancylus fluviatilis</u>

          is determined by a large number of interacting factors.

    (ii) The importance of any one of these factors varies from

          one stream to another.

    (iii) The most important limiting factors are substrate,

          algal growth, water velocity and intraspecific competition.

    (iv) Temperature, altitude, pH, parasitism, oxygen concentration

          and calcium concentration are unlikely to be limiting in

          natural conditions.

Part Four - The effects of natural catastrophes on populations

of Ancylus fluviatilis

1. Introduction

In Part III the majority of factors affecting limpet populations were discussed. Because natural catastrophes are sporadic and occur in varying intensity, they are treated separately in this section. In any river system, flood and drought are important catastrophic factors and may have marked effects on the flora and fauna.

2. Discussion

(a) Flood

The effect of flooding on Ancylus populations has been discussed to some extent in Part I. Flooding may have three effects : (i) to alter the course of the stream, exposing animals in the previous watercourse; (ii) an increased water speed could wash away animals; and (iii) the grinding and crushing movements of the substrate in strong currents may also result in high mortalities. The intensity of these effects on any stream animal will depend on the frequency and intensity of flooding, the stability of the substrate and the adaptations of the animal itself for resisting water pressure.

Ancylus fluviatilis is admirably adapted to life in rapidly flowing water, having a streamlined shell shape and a strong muscular foot. Although Dorier & Vaillant (1954) found in nature that the maximum stream speed where Ancylus was present was 24cm/second, I have found the species in currents of 35cm/second in some localities.

The same authors found in laboratory experiments, however, that
Ancylus could move into a current of 109cm/second and was washed
away at 240cm/second. Thus, where a stable substrate occurs,
the effect of flooding on Ancylus populations is probably less
than on other less well adapted species. The results found at
New Burn, however, which were discussed in Part I (see page 8),
suggest that where the substrate is less stable, flooding can reduce
limpet population densities. If flooding occurs during the breeding
season, then it could contribute to the destruction of the very
fragile egg capsules if the substrate is unstable, and may wash
away newly hatched spat, as their powers of adhesion are not very
great.

(b) Drought

Hynes (1958) has described the effects of drought on the
fauna of a small mountain stream in Wales. Unfortunately no molluscs
were present at this locality, but the consequences of prolonged
drought had a marked deleterious effect on the fauna that was present,
and in particular on insect nymphs and larvae. Boycott (1928)
discussed the significance of periods of drought on the molluscan
fauna of ponds in the parish of Aldenham, and found a marked reduction
in the distribution of some species. For example, Lymnaea peregra,
Planorbis fontanus, Acroloxus lacustris and Sphaerium corneum,
which were present in twenty three ponds in 1915, were only present
in ten in 1925 after the drought. He concluded, however, that 'a
drought has little effect on the (species composition of) molluscan
fauna of a pond, unless it is sufficient to dry it up fairly completely.'

Observations in the field and the laboratory indicated that
drought could be responsible for a decline in limpet population density.
It was noticed that in the laboratory limpets moved to the water surface,

FIG 15   EXPOSURE TOLERANCE   OF ANCYLUS
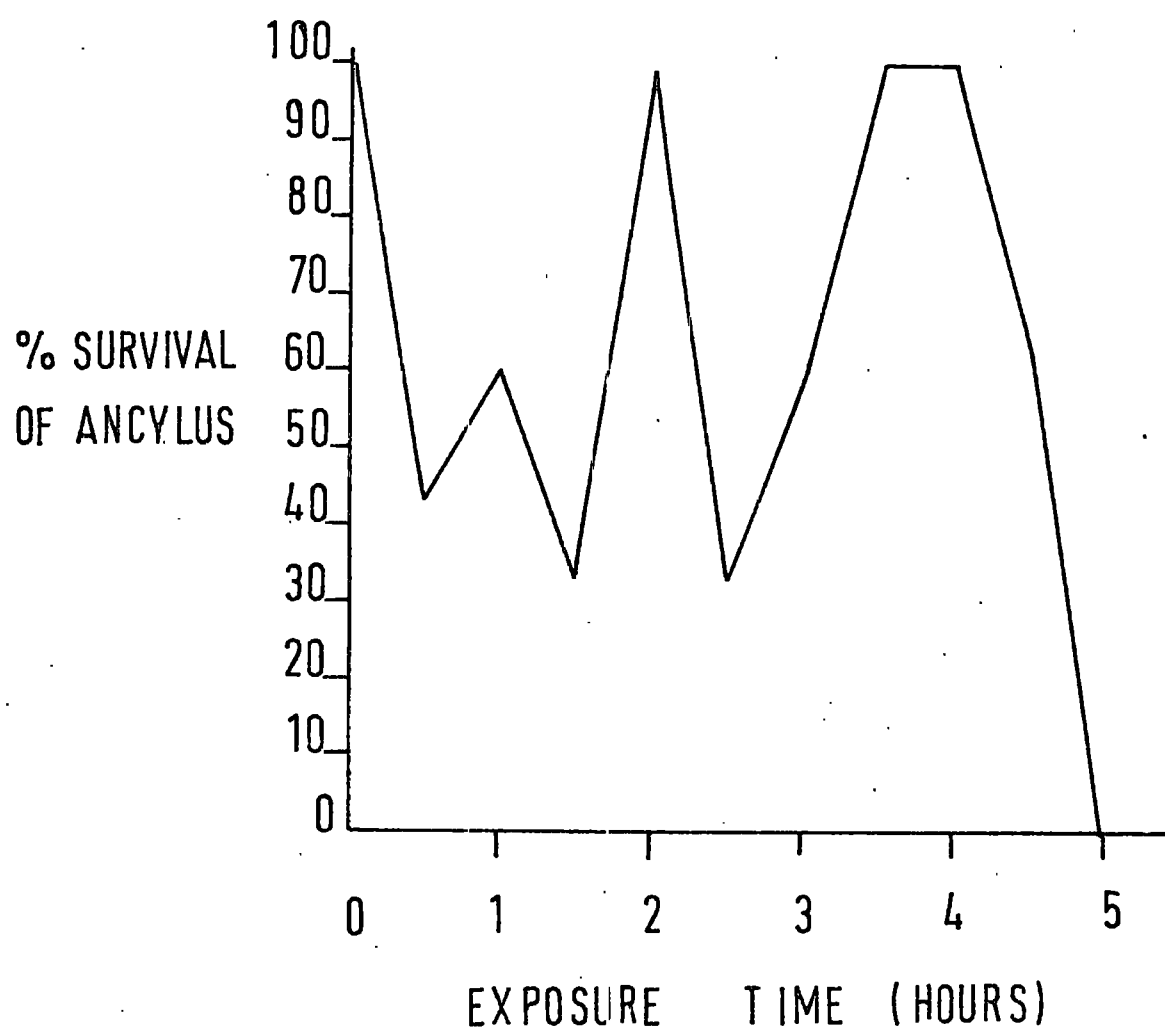
and as water evaporated from the container, so the snails were
stranded, and did not move down with the water level. Spat were
particularly susceptible to this form of mortality. When following
the population changes on marked stones in the river Tyne at Wylam,
a similar effect was found. At this locality, on 15 July, the
water level was very low, following a period of prolonged dry
weather, and a number of the marked stones were exposed to the air.
On these stones large numbers of dried up egg capsules and spat
shells were present, and a marked decline in the limpet population
was the result (see Figure 7). These observations contrast with
those that Geldiay (1956) made in Lake Windermere, where a falling
lake level concentrated the population. He does not record exposure
of Ancylus.

Experiments were carried out on the exposure tolerance of
Ancylus, the results of which are given in the Appendix, Table 15.
The tolerance of spat was very low, sixty percent surviving after
thirty minutes exposure. Spat exposed for an hour or more did not
survive. Larger limpets (mean size 4.5mm) show a very varied
exposure tolerance, as shown in Figure 15, but the maximum survival
time recorded was four and a half hours.

3. Conclusions

(i) Flooding may cause a reduction in limpet population
density. The intensity of flooding, and substrate
stability, will affect the survival of individuals.

(ii) Drought can cause limpet mortality, and, in particular,
mortality of spat. Egg capsules are particularly
sensitive to exposure.

(iii) The tolerance of spat to exposure is very low.
Adults can survive for approximately four and a half
hours.

Part Five - The effect of predation on Ancylus fluviatilis

Introduction

Wild & Lawson (1937), Berg (1953), Boycott (1936) and Michelson (1957) have reviewed the predators of freshwater molluscs. The list of molluscan enemies is a long one, including representatives from all the major phyla of animals. Obviously not all the possible predators on Ancylus could be studied, and attention was focussed on the most common ones encountered, the freshwater leeches and fish.

Methods

Three main methods have been used to study predation : (i) examination of gut contents of larger predators; (ii) predation experiments in the laboratory; and (iii) serological techniques.

Gut analyses of the fish present were not carried out by the author, due to lack of time available. However, Gee (1971, unpublished) in his work on the fish populations of rivers in the Durham area has supplied details of gut analyses which he undertook.

Predation experiments were carried out, however, by supplying the predators in question with limpets, and observing the animals over a number of days. The details of these experiments are given in the Appendix, Tables 16a and 16b.

Discussion

Erpobdella octoculata (Linn.) was the most common leech found in the rivers visited. When kept in the laboratory with Ancylus it did not prey on the snail. Mann (1955, 1964) has found its diet to consist of chironomid, trichoptera and simuliid larvae, ostracods, copepods and cladocera.

Mann (1955) found <u>Glossiphonia complanata</u> in 82% of all his running water stations, and it was commonly found in the streams and rivers visited during this investigation. <u>Glossiphonia heteroclita</u> was also found in the river Wear.

In the laboratory <u>G.complanata</u> was found to be the only significant predator on <u>Ancylus</u>, and specimens eventually ate all the limpets supplied to them. When species of <u>Lymnaea peregra</u> and <u>A.fluviatilis</u> were supplied together, there was no preference for either species.

The method by which <u>Glossiphonia</u> attacks <u>Ancylus</u> is shown in Figure 16. The leech attaches its posterior sucker to the shell of the limpet and arches over, pushing its proboscis under the shell into the mantle cavity. A similar method was adopted when attacking <u>L.peregra</u>. No 'leech avoidance reaction', as Frieswijk (1957) described for <u>Physa fortinalis</u> and <u>P.acuta</u> when attacked by <u>Glossiphonia</u>, was evident in <u>Ancylus</u>.

Bennicke (1943) also reported <u>Glossiphonia</u> feeding on <u>Ancylus</u> - 'in aquaria the species has been observed sucking <u>Planorbis corneus</u>, <u>P.vortex</u>, <u>Physa fortinalis</u>, <u>Ancylus fluviatilis</u> and <u>Bithynia tentaculata</u>.'

Minnows (<u>Phoxinus phoxinus</u>) were present in a large number of the sites visited, and often in very large shoals, particularly in the river Wear. In the predation experiments, this species was used on a number of occasions, but only one adult limpet and five spat were eaten. In food preference experiments carried out in the laboratory, minnows took almost everything offered except molluscs. Gee's (1971, unpublished) analyses of 276 minnow guts only produced one specimen of <u>Ancylus</u>, the dominant foods being insect larvae and algae. These findings complement those of Frost's (1943) on the food of minnows.

Sticklebacks (Gasterosteus aculeatus) were also very commonly found during the investigation. Gee (pers.comm.) has also examined the gut contents of this species and found the food to be very similar to that of the minnow, and found no Ancylus. Sticklebacks kept in the laboratory did not feed on limpets, either adult or spat. Hynes (1950) found that molluscs only form a maximum of 5% of the food composition of the gut contents of this species, and it is usually less than this.

Loach (Nemachilus barbatula) were also present at a number of sampling stations. In the laboratory they did not feed on Ancylus. Hartley (1948) found their main foods to be insect larvae and crustacea.

Brown Trout (Salmo trutta) are common predators in most streams visited. Unfortunately I was unable to obtain any live specimens of this species for predation experiments. Frost (1938, 1950) found that molluscs are never a dominant food organism, and usually the average number of molluscs per trout is less than one. Ancylus formed only 0.3% of the total food eaten.

Small specimens of eels (Anguilla anguilla) were very common in the river Tyne during the summer months. Frost (1946) found that molluscs formed 53.7% of the food organisms, but Ancylus itself formed only 0.4%.

Various authors (Badcock 1949, Frost & Went 1940, Frost 1950, Allan 1941) have recorded Ancylus being eaten by salmon parr, but usually forming a very low (<1%) proportion of the food eaten.

Predation by fish appears to be of little significance to populations of Ancylus. In fact it is probable that predation generally is of little significance unless the habitat supports a large population of Glossiphonia complanata.

FIG 16 GLOSSIPHONIA   COMPLANATA
        FEEDING   ON   ANCYLUS
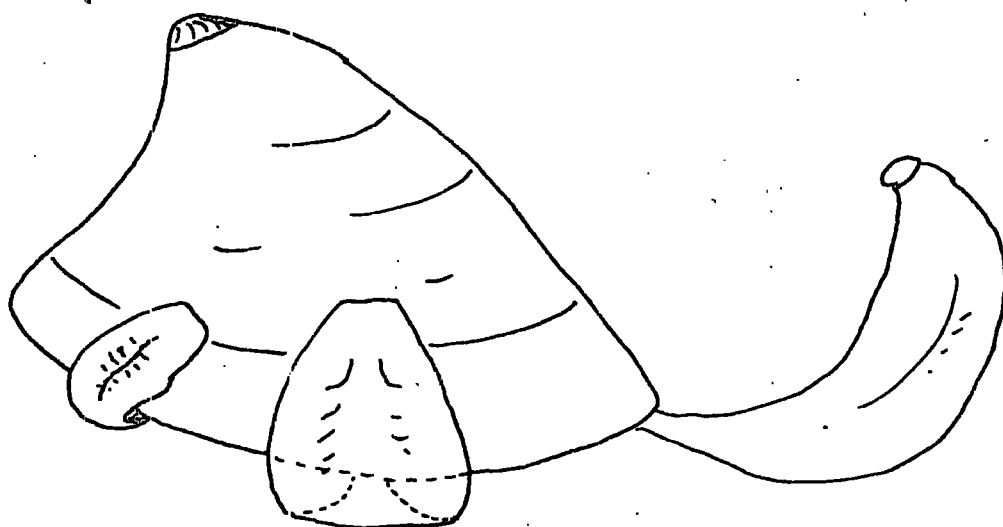
Conclusions

1. *Glossiphonia complanata* is the only significant predator of *Ancylus*.

2. Predation of limpets by the common freshwater fish is very low.

3. Predation can only have a significant effect where large numbers of *Glossiphonia complanata* are present. In the majority of habitats where *Ancylus* is present, predation is unlikely to be a limiting factor.

PART SIX -- MOVEMENT OF ANCYLUS FLUVIATILIS

1. Introduction

Fraenkel & Gunn (1940) stated that 'rheotactic behaviour occurs in all the active inhabitants of streams.' Bovbjerg (1952) found orientation to stream flow in the snail _Campeloma_, which resulted in a net upstream movement. The homing behaviour of gastropods has been recorded by many authors (e.g. Hewatt 1940, Edalstam & Palmer 1950, Newell 1958 and Frank 1964) for a variety of species. Movement, orientation and homing in _Ancylus_ were studied by a number of laboratory experiments.

2. Methods

Two large circular tanks with central paddles driven by electric motors were utilised for the experiments. The paddle depth and speed of revolution were adjustable. Large algal covered stones were placed in the tanks and a number of limpets were placed on them. Information on rate of movement and orientation was obtained by simply observing the limpets. The possibility of homing was investigated after limpets had been in the tanks for some time, the limpet shells being marked with cellulose paint as were their 'homes' - i.e. their position when marked.

3. Discussion

Hunter (1953) found that _Ancylus_ moved at a speed of 6 - 12cm/hour whilst feeding. This is probably a fair estimate, the fastest progression rate for an adult limpet I recorded being 14cm/hour. Adult limpets are often inactive for long periods however, which has probably given rise to the suggestions that the

animals live a more or less sessile existence (Bondeson 1950).
These rates of movement then would enable the limpets to move
upstream at an appreciable speed for colonisation, providing they
show rheotactic behaviour. It is hard to imagine that any stream
living animal would not respond to current direction, and yet in
the laboratory no such response was found. This may have been due
to the swirling action of the water in the tanks. However, it is
interesting to note that Elliott (1971) recorded no upstream
movement in Ancylus.

In nature, aggregations of Ancylus were frequently
recorded, often on one particular side of a stone. It was thought
that this may be due to orientation to current flow. A large number
of different sized stones were present in the tanks and the flow
patterns around these were very varied. Although limpets moved
from one stone to another, no aggregation was recorded.

Marked Ancylus showed that no homing behaviour occurs in
this species, but that individual animals can travel long distances.

4. Conclusions

(i)   Adult limpets are often inactive, but when feeding
      move at speeds of 4 - 14cm/hour.

(ii) Rheotactic behaviour was not recorded in the
      laboratory.

(iii) Ancylus shows no homing behaviour.

PART SEVEN - SHELL SHAPE AND GROWTH

During this investigation shell height and shell length, as in Figure 1, were measured for a number of Ancylus individuals from different locations. Also, the total weight and shell weight ~~and shell weight~~ of individuals was investigated.

The results of these measurements are shown in Figures 17 - 20. Figures 17 & 18 show that there is no significant difference in shell shape from one locality to another.

The relationships between shell length and weight, and shell length and shell weight are shown in Figures 19 & 20. To obtain the full range of shell lengths, data from a number of localities have been combined.

FIG 17   RELATIONSHIP BETWEEN SHELL HEIGHT AND SHELL LENGTH IN ANCYLUS
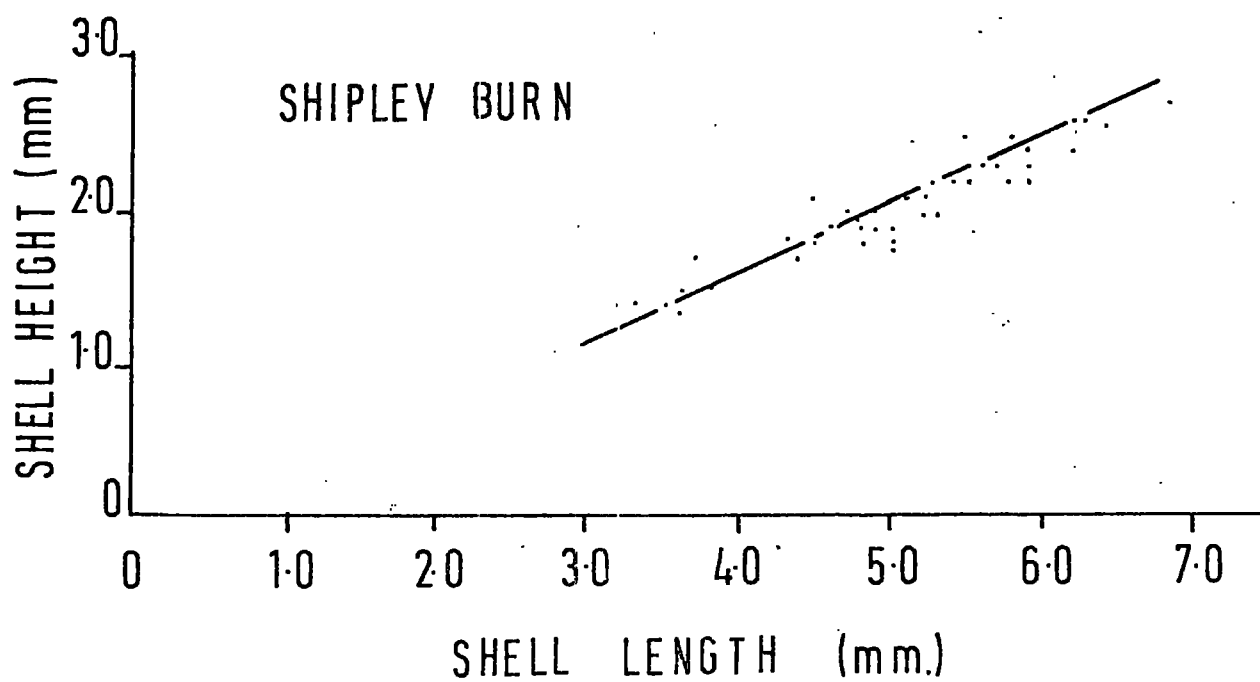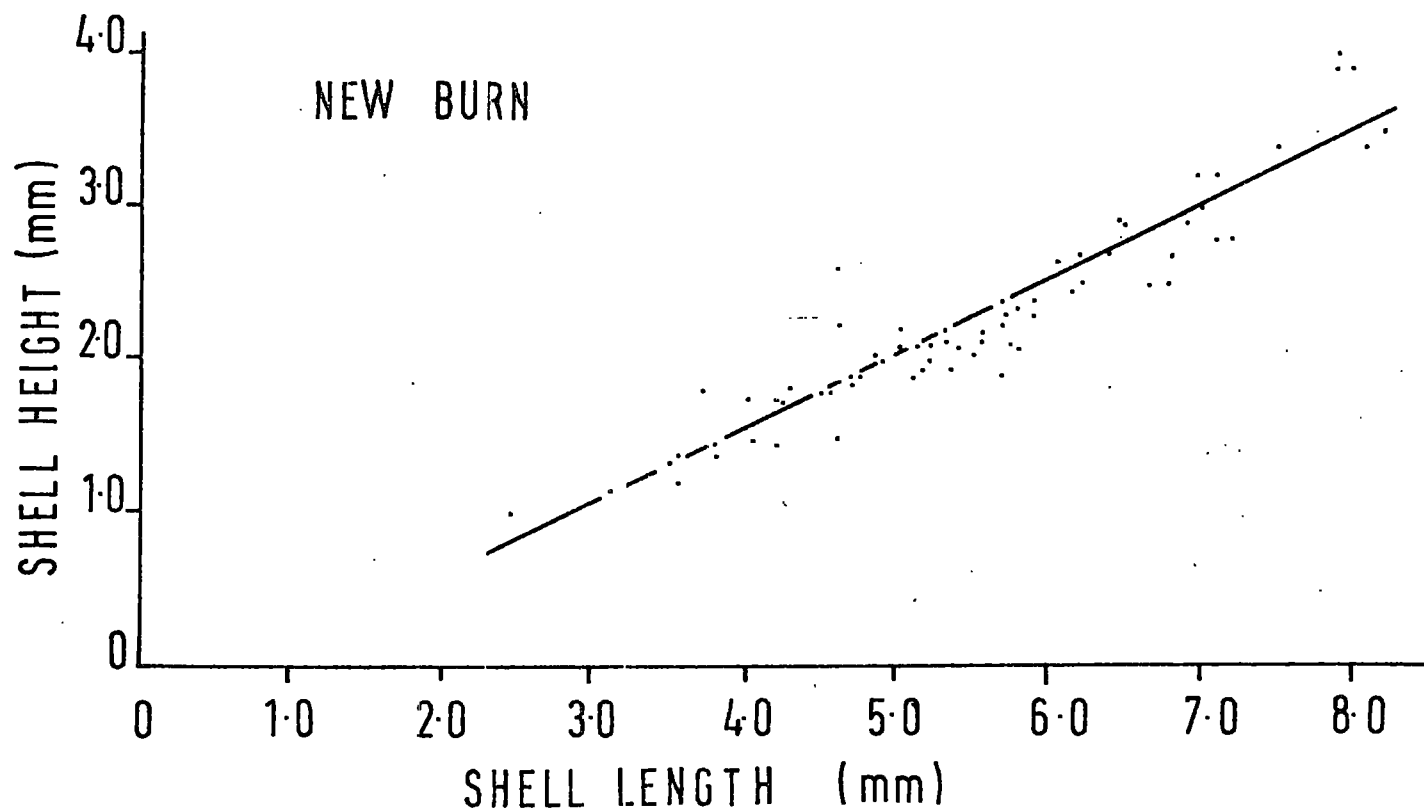
FIG 18 RELATIONSHIP BETWEEN SHELL HEIGHT AND SHELL LENGTH
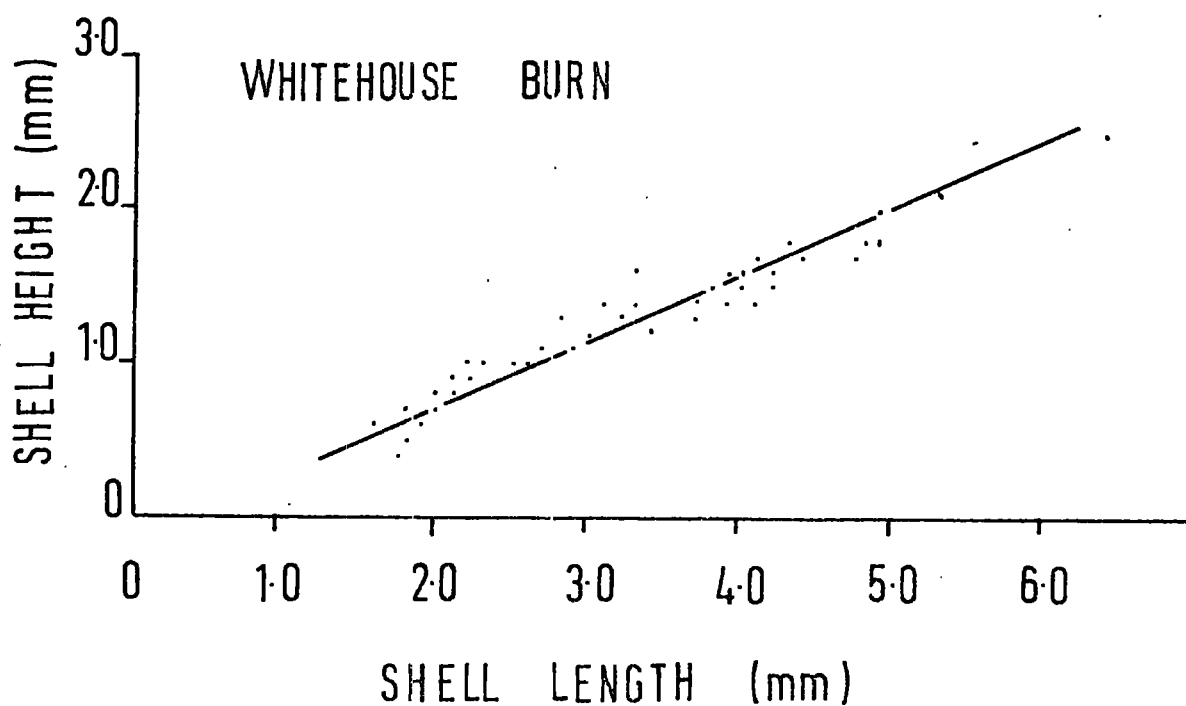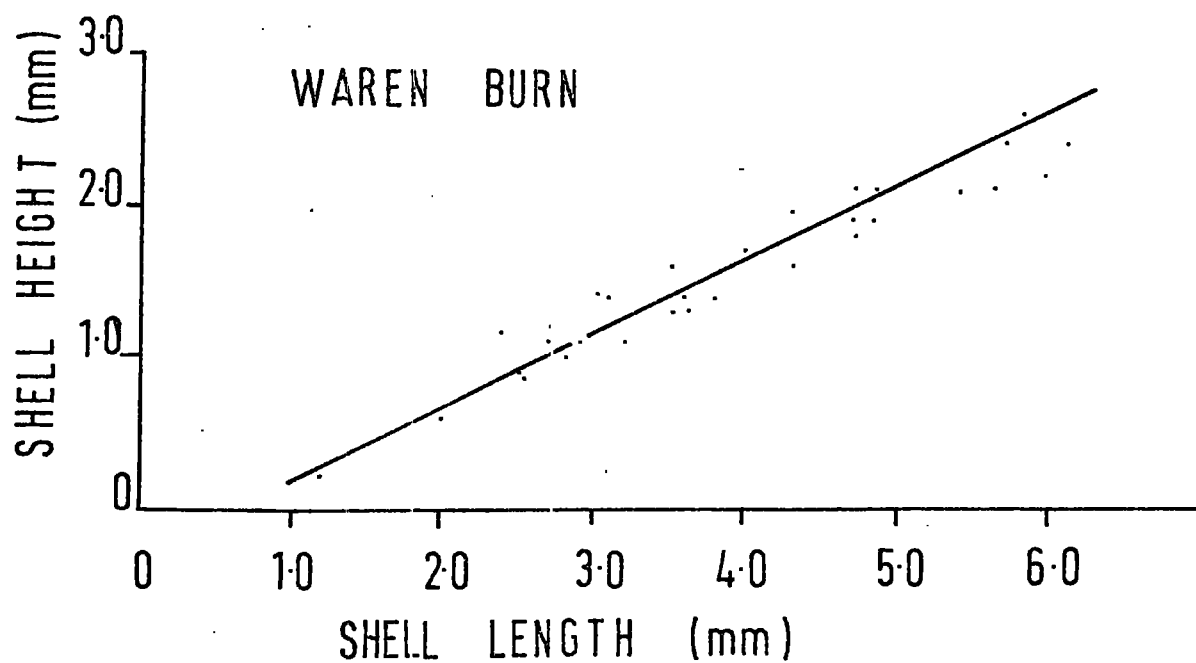
FIG 19   RELATIONSHIP   BETWEEN   WEIGHT
AND   SHELL   LENGTH
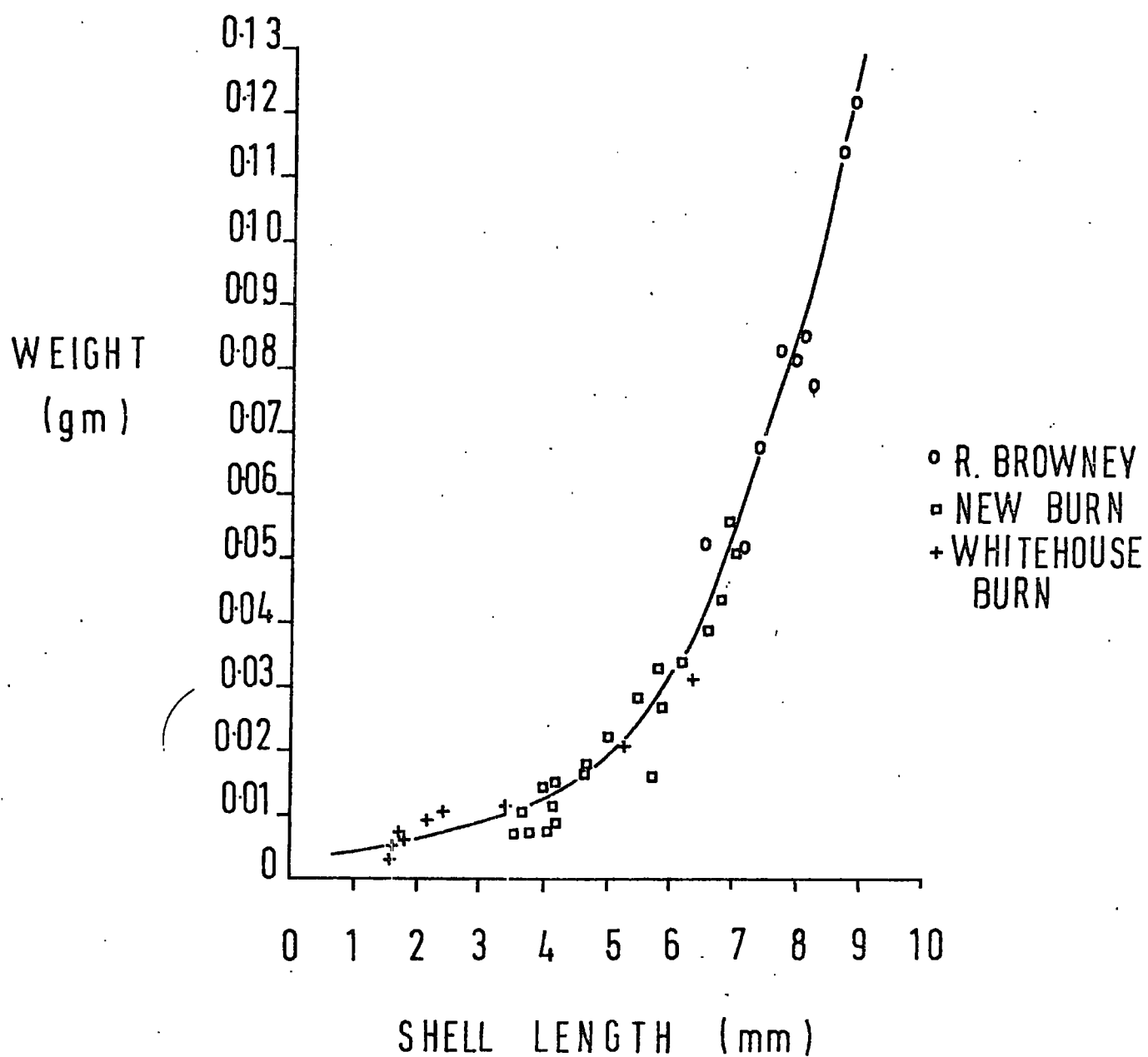
FIG 20   RELATIONSHIP   BETWEEN   SHELL   WEIGHT
AND   SHELL   LENGTH
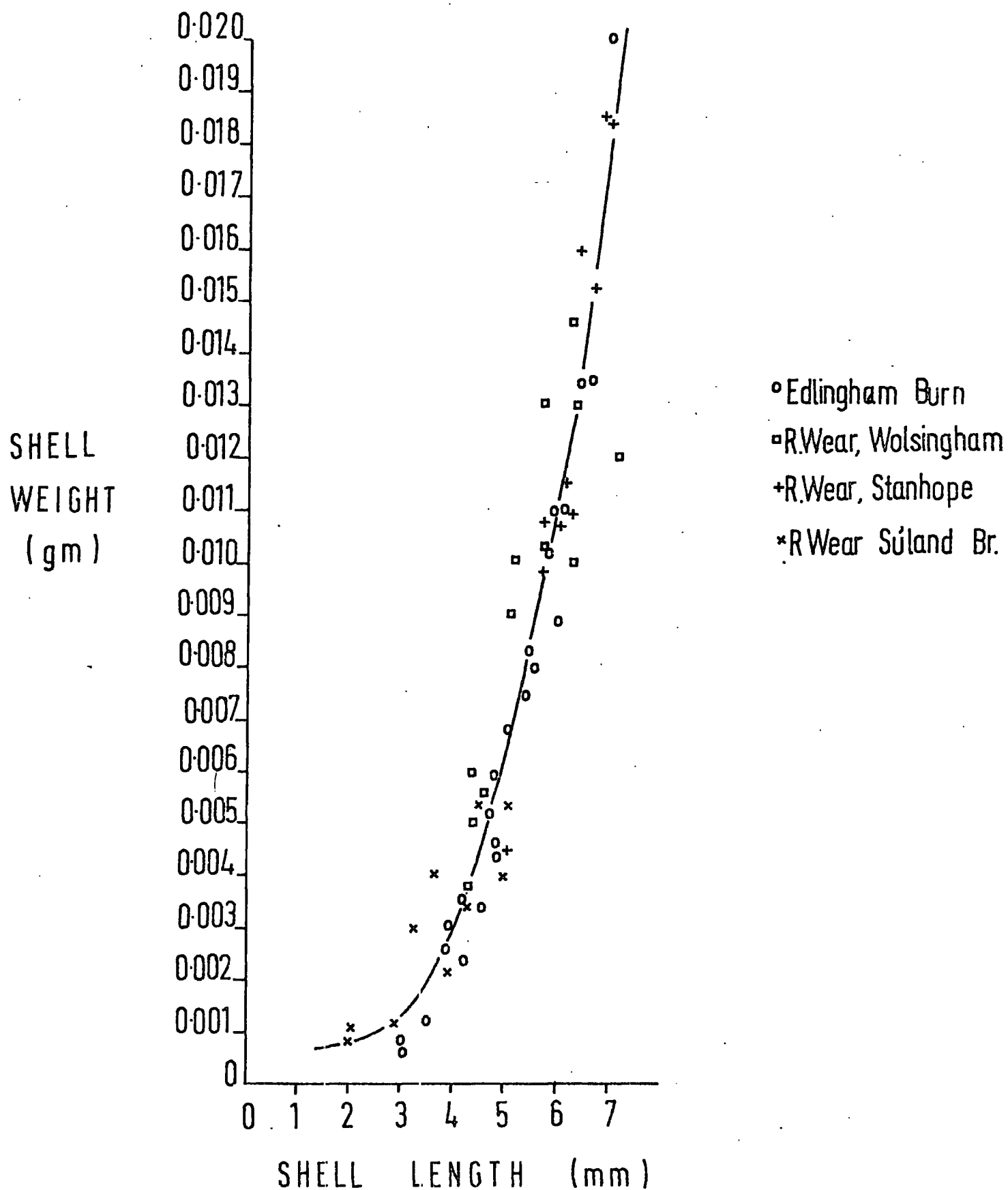
SUMMARY

(i) Investigations into the life history of _Ancylus fluviatilis_
(Müller) have shown that this species has a simple annual
life cycle.   This may be modified in rivers having a higher
average temperature, when two generations a year are possible.

(ii) A gradual decline in population density of _Ancylus fluviatilis_
was found in the streams studied.   It is proposed that the
factors causing this decline are flooding and intraspecific
competition.

(iii) Investigations in the laboratory and in nature indicate that
Ancylus lays approximately sixty eggs in eleven capsules.
In nature an average of 5.5 eggs/capsule was found.   The
corresponding figure in the laboratory was 4.63 eggs/capsule.
Nearer the end of the breeding season the number of eggs per
capsule decreases.

(iv) Factors influencing the distribution and abundance of
Ancylus fluviatilis were investigated.   The most important
of these are substrate, algal growth, current speed, intra-
specific competition and flooding.

(v) The only significant predator of _Ancylus_ is the leech
Glossiphonia complanata.

(vi) Rheotactic behaviour was not shown by _Ancylus_ in the
laboratory.   Homing does not occur in the freshwater limpet.

(vii) The shell shape of _Ancylus_ does not vary significantly from
one locality to another.

ACKNOWLEDGMENTS

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APPENDIX

Table 1. Growth of _Ancylus_ at New Burn and Whitehouse Burn

Date of Collection	No. of _Ancylus_ collected	Minimum shell length (mm)	Maximum shell length (mm)	Mean shell length (mm)	No. adults _Ancylus_ counted in 10 mins
New Burn :					
17.1.71	27	2.8	5.8	4.25	47
3.3.71	54	2.45	7.1	5.08	39
4.5.71	18	3.7	8.2	6.6	10
4.7.71	54	0.8	9.3	2.1	6
5.8.71	45	1.0	3.6	2.05	0
Whitehouse Burn :					
13.2.71	49	1.6	6.4	3.24	466
8.5.71	45	2.3	5.5	4.08	160
27.6.71	52	0.8	4.9	1.28	32
2.8.71	40	1.2	4.6	2.07	5

Table 2.   Population changes on marked stones at Wylam

| | No. counted on 10 marked stones | | |
Date	Adults	Egg capsules	Spat
13.5.71	40	140	10
23.5.71	45	265	73
4.6.71	41	210	181
11.6.71	34	155	320
18.6.71	32	83	367
25.6.71	13	6	410
2.7.71	9	41	392
9.7.71	4	10	215
15.7.71	0	2	185

Table 3. Details of egg capsules counted in nature

Location	Date	Total no. of egg capsules	Total no. of eggs	Mean no. of eggs per capsule
Corbridge, R.Tyne	21.5.71	75	528	7.04
Wylam, R.Tyne	23.5.71	18	87	4.83
Blackheddon Burn	2.6.71	15	89	5.93
R.Blyth	2.6.71	15	79	5.26
Hart Burn	2.6.71	8	50	6.25
R.Tyne, Bellingham	3.6.71	8	34	4.2
Tanters Burn	3.6.71	2	10	5
R.Wear, Stanhope	10.6.71	30	147	4.9
Wark Burn	19.6.71	2	7	3.5
Wylam, R.Tyne	2.7.71	56	210	3.7
New Burn	4.7.71	3	22	7.3
Stocksfield Burn	13.7.71	5	27	5.4
Stockley Beck	14.7.71	10	53	5.3
R.Wear, Sunderland Bridge	14.7.71	3	25	8.3

Table 4.   Details of egg capsules laid by 24 _Ancylus_

Jar No.	CUMULATIVE TOTAL OF EGG CAPSULES LAID ON :					
	4.6.71	7.6.71	14.6.71	21.6.71	28.6.71	1.7.71
I	5	5	9	9	9	9
II	3	3	3	3	3	3
III	5	5	5	5	5	5
IV	4	7	9	9	9	9
V	1	1	9	10	11	11
VI	9	15	21	22	22	22
VII	11	12	20	20	20	20
VIII	7	8	8	8	8	8
IX	7	8	11	11	11	11
X	0	1	1	1	1	1
XI	5	7	11	11	13	13
XII	6	8	8	8	9	9
Cumulative total of egg capsules	63	80	114	116	120	120
No. of surviving adults	19	18	16	11	11	11

Table 5a - Location of sampling sites

Sample Number	Location	Date of collection	ORdnance Survey reference	Altitude (feet)
1	BOLLIHOPE BURN	7.5.71	Sh.84.005349	750
2	WHITEHOUSE BURN	8.5.71	Sh.71.166168	350
3	PITMAN'S BURN	8.5.71	Sh.71.127187	250
4	EDLINGHAM BURN	8.5.71	Sh.71.115089	280
5	R. WEAR, DURHAM SANDS	12.5.71	Sh.85.278432	100
6	STANLEY BURN, WYLAM	13.5.71	Sh.77.121642	100
7	R. TYNE, WYLAM	13.5.71	Sh.77.121647	100
8	HORSLEY WOOD BURN	14.5.71	Sh.77.104649	200
9	WHITTLE BURN, OVINGHAM	14.5.71	Sh.77.083637	50
10	HOLYWELL BECK	18.5.71	Sh.85.253374	150
11	R. BROWNEY, BRANDON	19.5.71	Sh.85.258415	250
12	R. DEERNESS	19.5.71	Sh.85.244413	250
13	UNTHANK STREAM	19.5.71	Sh.85.237414	300
14	TRIBUTARY OF DEERNESS, NEW BRANCEPETH	19.5.71	Sh.85.224419	300
15	R. WEAR, WOLSINGHAM	20.5.71	Sh.84.073368	500
16	WASKERLEY BECK	20.5.71	Sh.84.075376	500
17	THORNHOPE BECK	20.5.71	Sh.84.069378	500
18	R. TYNE, CORBRIDGE	21.5.71	Sh.77.992641	100
19	R. BRUN, HURSTWOOD	29.5.71	Sh.95.882312	650
20	TRIB. OF PENDLE WATER	30.5.71	Sh.95.849416	650
21	R. PONT, STAMFORDHAM	2.6.71	Sh.77.075719	350
22	BLACKHEDDON BURN	2.6.71	Sh.77.083748	475
23	R. BLYTH	2.6.71	Sh.77.095799	340
24	UPPER WANSBECK	2.6.71	Sh.77.093843	260
25	HART BURN	2.6.71	Sh.77.089861	375

Table 5b - Location of sampling sites

Sample number	Location	Date of collection	Ordnance Survey reference	Altitude (feet)
26	R. FONT, NETHERWITTON	2.6.71	Sh.77.098908	350
27	R. TYNE, CHOLLERFORD	3.6.71	Sh.77.918707	230
28	R. TYNE, BELLINGHAM	3.6.71	Sh.77.818841	380
29	TARSET BURN	3.6.71	Sh.77.791882	490
30	TARSET BURN TRIBUTARY	3.6.71	Sh.77.772898	540
31	STREAM, HIGH HOUGHALL	9.6.71	Sh.85.274397	150
32	CROXDALE HALL RIVER	9.6.71	Sh.85.272378	150
33	HORSLEY BURN, STANHOPE	10.6.71	Sh.84.974383	800
34	R. WEAR, STANHOPE	10.6.71	Sh.84.989393	700
35	STANHOPE BURN	10.6.71	Sh.84.988398	750
36	ROOKHOPE BURN	17.6.71	Sh.84.905432	1300
37	R. WEAR, WEARHEAD	17.6.71	Sh.84.858395	1100
38	WARK BURN	19.6.71	Sh.77.838768	400
39	SANDYFORDS (1)	26.6.71	Sh.71.108258	600
40	SANDYFORDS (2)	26.6.71	Sh.71.107256	600
41	REAVELEY BURN	26.6.71	Sh.71.029169	350
42	BREAMISH	26.6.71	Sh.71.995165	550
43	NEW BURN, WALBOTTLE	4.7.71	Sh.78.167651	100
44	R. TYNE, STOCKSFIELD	13.7.71	Sh.77.062625	50
45	STOCKSFIELD BURN	13.7.71	Sh.77.053618	100
46	STICKLEY BECK, BRANCEPETH	14.7.71	Sh.85.222378	200
47	OLD HOUSE BECK, PAGE BANK	14.7.71	Sh.85.230355	175
48	R. WEAR, PAGE BANK	14.7.71	Sh.85.235355	175
49	R. WEAR, SUNDERLAND BRIDGE	14.7.71	Sh.85.267378	150
50	R. BROWNEY	14.7.71	Sh.85.267388	150

Table 6a - Stream data

Sample Number	River width (m)	River temperature (°C)	Depth at sampling point (cm)	Water velocity at surface (cm/sec)	Water velocity at max depth (cm/sec)	Substrate type
1	8	10	15	27.2	19.8	COARSE SANDSTONE & LIMESTONE
2	3	10.25	12	22.1	9.9	FINE GRAIN SANDSTONE
3	2	13	9	24.2	19.8	MEDIUM/FINE SANDSTONE
4	1	9	13	15.6	9.9	MED/FINE SANDSTONE & SHALE
5	30	16.25	6	22.1	7.0	MED.SANDSTONE & LIMESTONE
6	3	15.5	7	18.5	14.0	MED/COARSE SANDSTONE
7	40	17	14	15.6	9.9	FINE SANDSTONE & LIMESTONE
8	4	10.25	12	21.0	14.0	SHALE & MEDIUM SANDSTONE
9	8	14	12	17.1	12.1	FINE/MEDIUM SANDSTONE
10	2	15.25	4	17.1	9.9	MEDIUM SANDSTONE
11	15	11.5	15	24.2	17.1	MEDIUM SANDSTONE
12	8	11.75	12	31.3	22.1	MEDIUM SANDSTONE
13	½	9.25	10	17.1	12.1	FINE SANDSTONE
14	2	12	7	19.8	19.8	TIP RESIDUE
15	25	12	10	31.3	22.1	MED/SANDSTONE & LIMESTONE
16	5	11	10	22.1	15.6	MED/SANDSTONE & LIMESTONE
17	3	12.25	11	22.1	14.0	MEDIUM SANDSTONE
18	60+	17.25	18	27.2	15.6	FINE SANDSTONE
19	6	13.5	7	19.8	9.9	FINE SANDSTONE
20	6	10.75	10	24.7	19.8	MED/SANDSTONE & LIMESTONE
21	2	13.5	70	7.0	0	FINE MUDSTONE & SANDSTONE
22	1	15.75	12	17.1	9.9	FINE/MEDIUM SANDSTONE
23	5	18	9	22.1	15.6	FINE SANDSTONE
24	10	18	21	27.2	22.1	FINE SANDSTONE
25	20	17.5	10	27.2	15.6	MED. SANDSTONE

Table 6b - Stream data

Sample Number	River width (m)	River temperature (ºC)	Depth at sampling point (cm)	Water velocity at surface (cm/sec)	Water velocity at max depth (cm/sec)	Substrate type
26	17	14.75	10	27.2	19.2	FINE SANDSTONE & LIMESTONE
27	80	16.5	9	27.2	19.8	FINE SANDSTONE & LIMESTONE
28	50	16.75	16	35.0	22.1	FINE SANDSTONE
29	15	16.5	26	22.1	15.6	MEDIUM SANDSTONE
30	5	16.75	9	22.1	14.0	FINE SANDSTONE
31	2	10.75	6	22.1	9.9	MEDIUM SANDSTONE
32	5	11	12	31.3	22.1	MEDIUM/FINE SANDSTONE
33	3	7.5	8	19.8	9.9	SHALE, MUDSTONE & SANDSTONE
34	30	9.25	15	22.1	14.0	FINE SANDSTONE
35	4	8.5	7	27.2	22.1	MED/COARSE SANDSTONE, LIMESTONE
36	2	10	10	38.4	27.2	COARSE SANDSTONE
37	10	11	11	15.6	9.9	MEDIUM SANDSTONE & LIMESTONE
38	4	10.75	10	22.1	15.6	FINE SANDSTONE & SHALE
39	1	12	6	22.1	15.6	VERY FINE SANDSTONE & MUDSTONE
40	1	12.25	5	19.8	14.0	MEDIUM SANDSTONE
41	2	11.5	25	15.6	9.9	MEDIUM/FINE SANDSTONE
42	2	12.25	15	22.1	14.0	MEDIUM FINE SANDSTONE
43	2	13.75	9	19.8	12.1	FINE SANDSTONE
44	30	20	11	15.6	12.1	VERY FINE SANDSTONE
45	3	14	15	14.0	12.1	MEDIUM FINE SANDSTONE
46	3	12.5	11	9.9	9.9	MEDIUM FINE SANDSTONE
47	½	14	10	19.8	14.0	MEDIUM FINE SANDSTONE
48	25-30	17.5	13	27.2	22.1	MEDIUM SANDSTONE
49	20	19	10	24.2	19.8	FINE SANDSTONE
50	7	18.5	10	15.6	9.9	MEDIUM SANDSTONE

Table 7.   Chemical data

Sample Number	pH	Calcium concentration p.p.m.	Sample Number	pH	Calcium concentration p.p.m.
1	7.1	10	26	7.8	38
2	7.45	49	27	7.3	17
3	7.2	77	28	7.15	14
4	7.4	20	29	7.3	10
5	6.95	42	30	8.0	21
6	7.3	61	31	7.2	32
7	6.75	35	32	8.4	70
8	7.0	52	33	7.5	20
9	7.3	52	34	7.8	38
10	6.8	49	35	7.5	30
11	7.45	49	36	4.2	1
12	7.5	63	37	7.15	14
13	7.4	52	38	7.6	40
14	7.15	45	39	7.8	34
15	8.0	35	40	6.3	3
16	7.2	14	41	7.5	14
17	7.35	14	42	7.1	3
18	6.9	42	43	7.6	77
19	7.3	17	44	7.65	42
20	7.4	28	45	7.4	42
21	7.8	63	46	7.1	45
22	7.8	49	47	7.5	98
23	7.95	61	48	7.5	77
24	7.55	46	49	7.45	52
25	7.5	36	50	7.75	38

Table 8a.   Data on algal and moss cover

Sample Number	Moss & Algal growth on stones			Sample Number	Moss & Algal growth on stones		
	top	sides	bottom		top	sides	bottom
1	1	0	0	26	4	3	1
2	4	3	0	27	2	2	1
3	3	1	0	28	3	2	1
4	2	1	0	29	2	2	0
5	3	2	1	30	5	4	1
6	5	1	0	31	1	1	0
7	4	3	0	32	3	2	1
8	1	1	0	33	1	1	0
9	5	3	0	34	3	2	1
10	5	5	1	35	1	1	0
11	4	3	0	36	1	0	0
12	2	2	0	37	3	3	1
13	4	4	0	38	2	2	0
14	0	0	0	39	1	1	0
15	4	3	1	40	2	1	0
16	3	2	0	41	5	5	1
17	3	2	0	42	3	3	0
18	4	3	0	43	3	3	1
19	2	1	0	44	3	2	1
20	1	1	0	45	1	1	0
21	5	4	0	46	1	1	0
22	4	4	1	47	1	1	0
23	4	4	1	48	4	4	1
24	5	5	1	49	3	2	1
25	5	4	1	50	5	5	1

Table 8b.   Identification of covering vegetation

Sample Number	Algae	Mosses	Others	Sample Number	Algae	Mosses	Others
1	Un			26	C		R.aq.
2	C			27	C		
3	C			28	C	Sph.F.	R.aq.
4	Un	F.Sph.	N	29	C	Sph.	
5	C			30	B		
6	C			31	Un	Sph.	
7	C	Sph.	R.aq.	32	C	Sph.	
8	Un			33	C	Sph.	
9	Ul.B.C.			34	C		
10	C.Un			35	St.		
11	C			36	St.		
12	C			37	Ul.		
13	C			38	C	F.Sph.	
14				39	Un	Sph.	
15	C.Ul.H			40	Un	Eur.Sph.	
16	C.Ul			41	Ul.S		N
17	Ul			42	C.Rh.	Sph.	
18	C	Sph.	R.aq.	43	C		
19	Un	Sph.		44	C		
20	C			45	C		
21	C.Ul.		E.L.N.I.	46	C		
22	C.S.			47	Ul.		
23	C	F		48	C.St.	Eur.	
24	C	F.Sph.	R.aq.	49	C	Eur.Sph.	
25	C	Sph.		50	C.Rh.m?		

Key :

Un	–	Unicellular algae	Rh	–	Rhizoclonium		
C	–	Cladophora	M	–	Microspora	L	–	Lemna
Ul	–	Ulothrix	F	–	Fontinalis	N	–	Nasturtium
B	–	Batrachospermum	Sph	–	Sphagnum			officionale
H	–	Hormidium	Eur	–	Eurhynchium	I	–	Iris
S	–	Spirogyra	E	–	Elodea			pseudacorus
St	–	Stigeoclomium	R.aq.	–	Ranunculus aquatilis			

Table 9a. Quadrat data

Sample Number	Number of mature Ancylus/ $\frac{1}{4}m^2$ quadrat	Number of egg capsules/ $\frac{1}{4}m^2$ quadrat	Number of newly hatched Ancylus/ $\frac{1}{4}m^2$ quadrat	Number of other molluscs/ $\frac{1}{4}m^2$ quadrat
1	θ	θ	θ	θ
2	99	0	0	0
3	5	0	0	0
4	8	0	0	0
5	1	0	0	0
6	0	0	0	1
7	22	114	0	3
8	4	0	0	0
9	0	0	0	0
10	0	0	0	1
11	1	11	0	0
12	0	8	0	0
13	0	0	0	0
14	0	0	0	0
15	16	46	0	0
16	7	7	0	0
17	0	0	0	0
18	31	384	72	0
19	12	31	0	0
20	0	0	0	0
21	4	17	0	0
22	2	53	14	0
23	0	5	0	0
24	0	0	0	0
25	1	7	0	0

Table 9b. Quadrat data

Sample Number	Number of mature Ancylus/ ½m2 quadrat	Number of Ancylus egg capsules/ ½m² quadrat	Number of newly hatched Ancylus/ ¼m² quadrat	No. of other molluscs/ ¼m² quadrat
26	1	0	0	0
27	1	2	0	0
28	16	53	0	0
29	0	2	0	0
30	0	0	0	0
31	0	0	0	0
32	0	0	0	12
33	0	0	0	0
34	24	211	4	0
35	0	0	0	0
36	0	0	0	0
37	0	0	0	0
38	1	0	0	0
39	73	361	78	0
40	0	0	0	0
41	1	1	8	0
42	0	5	16	0
43	1	11	6	0
44	(47)	0	1	0
45	0	28	289	7
46	1	40	26	1
47	0	0	0	0
48	0	0	0	0
49	10	11	0	0
50	0	0	0	0

Table 10a.   Data from ten minute counts

Sample Number	Number of _Ancylus_ (mature) counted in ten minutes	Number of _Ancylus_ egg capsules counted in 10min	Number of newly hatched _Ancylus_ counted in 10min	Number of other molluscs counted in ten minutes
1	1	0	0	0
2	160	0	0	0
3	36	0	0	0
4	45	0	0	0
5	0	0	0	0
6	2	2	0	1
7	50	0	0	7
8	21	3	0	1
9	0	0	0	0
10	0	0	0	2
11	7	56	0	1
12	1	6	0	0
13	0	0	0	0
14	0	0	0	1
15	21	60	0	0
16	5	16	0	0
17	1	0	0	0
18	70	1050	0	5
19	42	209	0	0
20	0	0	0	0
21	6	0	0	0
22	2	90	26	0
23	2	44	6	0
24	1	2	0	0
25	2	48	0	0

Table 10b. Data from ten minute counts

Sample Number	Number of mature Ancylus counted in 10mins	Number of Ancylus egg capsules counted in 10mins	Number of newly hatched Ancylus counted in 10mins	Number of other molluscs counted in 10mins
26	10	2	0	0
27	20	10	0	0
28	24	56	32	0
29	0	0	0	0
30	0	0	0	0
31	0	0	0	0
32	0	0	0	92
33	1	8	0	0
34	100	1010	50	0
35	0	0	0	0
36	0	0	0	0
37	0	0	0	0
38	5	13	0	0
39	88	310	30	0
40	0	0	0	0
41	4	6	10	0
42	2	86	84	0
43	2	6	5	1
44	(253)	0	6	0
45	0	30	1010	20
46	18	110	50	10
47	0	0	0	0
48	0	0	0	1
49	67	50	6	0
50	0	0	0	0

Table 11a. Position of adults, egg capsules and spat of _Ancylus_

Sample Number	Position of adult _Ancylus_ on stones			Position of egg capsules on stones			Position of newly hatched _Ancylus_ on stones		
	top	side	bottom	top	side	bottom	top	side	bottom
1	0	1	0	0	0	0	0	0	0
2	69	29	1	0	1	0	0	0	0
3	2	3	0	0	0	0	0	0	0
4	4	4	0	0	0	0	0	0	0
5	0	0	1	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	13	8	1	0	4	0	0	0	0
8	1	3	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0
11	0	1	0	0	6	5	0	0	0
12	0	0	0	0	8	0	0	0	0
13	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0
15	1	7	8	1	15	30	0	0	0
16	5	1	1	0	4	3	0	0	0
17	0	0	0	0	0	0	0	0	0
18	5	20	6	0	202	182	–	–	–
19	8	4	0	8	6	17	0	0	0
20	0	0	0	0	0	0	0	0	0
21	2	1	5	4	8	5	0	0	0
22	0	2	0	0	15	38	0	7	7
23	0	0	0	0	2	3	0	0	0
24	0	0	0	0	0	0	0	0	0
25	0	0	1	0	0	7	0	0	0

Table 11b. Position of adults, egg capsules and spat of _Ancylus_

Sample Number	Position of adult Ancylus on stones			Position of egg capsules on stones			Position of newly hatched Ancylus on stones		
	top	side	bottom	top	side	bottom	top	side	bottom
26	1	0	0	0	0	0	0	0	0
27	0	1	0	0	0	2	0	0	0
28	2	12	2	13	33	7	0	0	0
29	0	0	0	0	0	2	0	0	0
30	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0
34	11	8	5	4	169	38	0	4	0
35	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0
38	1	0	0	0	0	0	0	0	0
39	33	27	13	15	164	182	6	53	19
40	0	0	0	0	0	0	0	0	0
41	0	1	0	0	0	0	0	7	1
42	0	0	0	0	1	4	0	12	4
43	0	1	0	1	3	7	0	5	0
44	39	8	0	0	0	0	1	0	0
45	0	0	0	2	22	4	144	145	0
46	1	0	0	4	9	27	6	7	13
47	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0
49	6	2	2	0	11	0	0	0	0
50	0	0	0	0	0	0	0	0	0

Table 12a.   Shell length measurements

Sample number	No. of Ancylus collected	Maximum shell length (mm)	Minimum shell length (mm)	Mean shell length (mm)	Standard Deviation
1	1	5.5	–	–	–
2	45	5.7	2.3	4.08	0.443
3	30	7.6	3.8	5.83	0.930
4	39	7.0	3.1	4.96	1.923
5	1	8.2	–	–	–
6	2	5.0	4.5	4.75	–
7	42	6.8	3.7	5.28	0.344
8	24	7.2	3.5	4.97	0.340
9	0	–	–	–	–
10	0	–	–	–	–
11	9	8.9	6.6	7.87	–
12	0	–	–	–	–
13	0	–	–	–	–
14	0	–	–	–	–
15	33	7.2	4.1	5.31	1.493
16	11	7.0	2.8	4.93	–
17	1	6.6	–	–	–
18	34	8.2	0.7	5.1	2.58
19	45	7.3	3.8	5.77	0.881
20	0	–	–	–	–
21	9	6.2	4.2	5.18	–
22	3	7.0	5.3	6.4	–
23	1	6.7	–	–	–
24	1	4.2	–	–	–
25	4	7.4	6.2	6.82	–

Table 12b. Shell length measurements

Sample Number	No. of Ancylus collected	Maximum shell length (mm)	Minimum shell length (mm)	Mean shell length (mm)	Standard Deviation
26	5	5.2	3.9	4.36	-
27	24	7.9	3.8	5.66	0.930
28	25	8.3	4.5	6.03	0.850
29	0	-	-	-	-
30	0	-	-	-	-
31	0	-	-	-	-
32	0	-	-	-	-
33	1	5.0	-	-	-
34	45	7.1	3.1	5.78	0.426
35	0	-	-	-	-
36	0	-	-	-	-
37	0	-	-	-	-
38	6	6.2	2.9	5.16	-
39	52	5.0	3.4	4.77	0.37
40	0	-	-	-	-
41	1	4.3	-	-	-
42	1	7.2	-	-	-
43	54	9.3	0.8	2.1	2.144
44	35	4.4	3.0	3.8	0.545
45	29	3.0	1.5	2.4	0.354
46	2	6.9	6.7	6.8	-
47	0	-	-	-	-
48	0	-	-	-	-
49	26	6.1	2.0	4.34	0.517
50	0	-	-	-	-

Table 13.   Weight measurements

Sample Number	No. of mature _Ancylus_ weighed	Maximum weight (gm)	Minimum weight (gm)	Mean weight (gm)
2	45	0.0352	0.0031	0.0123
3	30	0.0679	0.0115	0.0386
4	39	0.0536	0.0035	0.0211
11	9	0.1221	0.0521	0.0818
15	33	0.0539	0.0147	0.0282
16	11	0.0523	0.0030	0.0235
34	45	0.0487	0.0047	0.0290
49	26	0.0259	0.0013	0.0126

Table 14.   Predators and other molluscs

Sample Number	Predators	Other Molluscs	Sample Number	Predators	Other Molluscs
1	-	-	26	S	-
2	G	-	27	G	-
3	-	-	28	SG	-
4	-	-	29	-	-
5	G.S.Ga.Ph.N	L	30	-	-
6	-	L	31	-	-
7	G.S.A	L	32	S	.L
8	-	L	33	-	-
9	S	-	34	S	-
10	G	L	35	S	-
11	G	L	36	-	-
12	-	-	37	-	-
13	-	-	38	S	-
14	-	L	39	-	-
15	S	L	40	-	-
16	-	-	41	S	-
17	-	-	42	G S	-
18	S.A.	L	43	G Ph.	L
19	-	-	44	S	-
20	S	-	45	S	L
21	-	L	46	-	L
22	Ph. G	-	47	-	-
23	S.Ph.	-	48	-	-
24	Ph. S	L.Lt.Sp.Pl.	49	-	-
25	S	-	50	-	-

Key :

G -	Glossiphonia complanata	A -	Anguilla anguilla
S -	Salmo trutta	L -	Lymnaea peregra
Ga -	Gasterosteus aculeatus	Lt -	Lymnaea truncatula
Ph -	Phoxinus phoxinus	Sp -	Sphaerium
N -	Nemachilus barbatula	Pl -	Planorbis planorbis

Table 15. Results of laboratory exposure experiments

Exposure time (hours)	Number alive at time 0		Number alive 48 hrs after exposure		Percent survival	
	Spat	Adults	Spat	Adults	Spat	Adults
0.5	9	7	6	3	66.6	42.8
1.0	3	5	0	3	0	60.0
1.5	4	3	0	1	0	33.3
2.0	3	3	0	3	0	100.0
2.5	3	3	0	1	0	33.3
3.0	40	5	0	3	0	60.0
3.5	3	3	0	3	0.	100.0
4.0	6	5	0	5	0	100.0
4.5	16	3	0	2	0	66.6
5.0	6	2	0	0	0	0

Table 16.   Results of predation experiments

Expt. No.	Prey Species	Number	Prey Species	Number	No. of days of contact	No. of prey eaten
1	Ancylus(adult)	3	Glossiphonia complanata	4	1	3
2	Ancylus (ad.)	2	"	7	5	2
	Lymnaea peregra	2	"			2
3	Ancylus (ad.)	2	"	3	3	2
	" (spat)	2				2
4	Ancylus (ad.)	2	"			2
	" (spat)	2		6	7	
5	Ancylus (sp.)	7	"	1	6	7
6	" "	10	"	1	9	5
7	" "	3	"	1	9	2
8	Ancylus(adult)	3	Erpobdella octoculata	7	12	0
9	" (spat)	2	"	6	7	0
10	Ancylus(adult)	2	Gasterosteus aculeatus	1	12	0
11	" "	2	"	1	12	0
12	" "	1	"	1	7	0
	" (spat)	1				
13	" "	8	"	1	9	0
14	Ancylus(adult)	2	Nemachilus barbatura	1	12	0
15	" "	2	"	1	12	0
16	" "	2	"	1	7	0
	" (spat)	2				
17	" "	7	"	1	9	0
18	" "	3	"	1	9	0
19	Ancylus(adult)	2	Phoxinus phoxinus	1	12	0
20	" "	1	"	1	.7	1
	" (spat)	1				0
21	" "	4	"	1	9	0
22	" "	5	"	1	9	5