The Influence of Temperature in the Ecology of the Intermediate Host Snails of Schistosoma and Fasciola (Trematoda) in Southern Rhodesia

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PREFACE.

The influence of temperature on the bionomics of *Bulinus (Physopsis) globosus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* has been studied both in the laboratory under controlled conditions and in the field under normal seasonal influences. Field studies were carried out in two different localities, one a semi-permanent pond and the other a temporary waterbody. For this purpose a sampling implement was developed. The results show the seasonal progression of these populations both with respect to estimated numbers and the size distribution of the snails. The rate of actual increase at different seasons was calculated for the three species where data were sufficient. In the laboratory the snails were maintained at various temperatures, other conditions being kept standard. Daily records of mortality and fecundity of various cohorts reared from the egg stage enabled the compilation of life tables for the species and from these data were calculated the intrinsic rate of natural increase and other parameters. Effects of crowding in aquaria were studied. From the data obtained in the laboratory it was possible to predict the distribution and population potential for each species of snail for various environmental conditions. These predictions were, in fact, confirmed by field observation.

I. INTRODUCTION.

The aquatic snail hosts of the blood fluke *Schistosoma* occur in a variety of waterbodies widespread throughout Rhodesia. These habitats are in a continual state of change and are subjected to both diurnal and seasonal variations in the physical factors affecting the environment. In summer they are heated by intense sunlight and periodically are flushed out as a result of heavy rainstorms. As the seasonal rains end conditions become stabilised for a short period but this is followed by a sharp drop in temperature with the onset of winter. The winter season is short, lasting two to three months, and the subsequent warm, dry spring period is characterised by rising temperatures and a high rate of evaporation which often results in the drying out of the waterbodies. This imposes a severe obstacle to the inhabitants of the biotope. After a period of varying duration the normal seasonal rains set in and the waterbodies are once more replenished.

The complex ecological sequences which occur in the biotopes are therefore dominated by a series of events such as dilution and flooding, concentration and desiccation, overcrowding, surfeit or scarcity of food, and great variations in temperature. These are best analysed individually and in stages. It is the purpose of this work to investigate the effects of temperature on the bionomics of the planorbid hosts of *Schistosoma*, *Bulinus* (*Physopsis*) *globosus* (Morelet) and *Biomphalaria* *pfeifferi* (Krauss), and then to attempt to validate the data obtained by field observations. This must involve a consideration of other aquatic flora and fauna, but for the purposes of this enquiry, only these other species of snails, *Bulinus* (*Bulinus*) *tropicus* (Krauss), *Bulinus* (*Bulinus*) *forskalii* (Ehrenberg) and *Lymnaea* *natalensis* (Krauss) have been included. This will not provide a complete ecological picture but if it helps to clarify one single aspect of the problem, the objective of this study will have been achieved.

When considering the relative importance of those physical factors which regulate the life of freshwater pulmonate snails, it would seem that temperature must rank among those most influential. However, it is seldom that temperature alone limits the numbers of a species, for such is the natural biotope that somewhere there will be a sheltered position where individuals can escape extreme conditions. Buxton (1932) has shown that even in deserts where there are great diurnal extremes of temperature and humidity in exposed locations, sheltered niches exist where conditions are buffered and are more tolerable to life.

In an aquatic environment, except when the habitat is drying out, it is seldom that maximum temperatures will have any direct limiting effects on the molluscan inhabitants (Gordon _et al_ 1934), and certainly in the highveld areas of Rhodesia it would be a most rare phenomenon if temperatures in waterbodies rose to extremes which would prove lethal to the creatures living there. The apparent ability of snails to withstand wide temperature variations has, however, been mentioned by many workers in this field. Gordon _et al_, (1934), van Someren, (1946), Watson, (1950, 1958), Abdel-Malek, (1958) and Gaud (1958) all draw attention to the wide temperature ranges which occur in snail habitats but all these authors quote water temperature recordings from one level only. Similarly, Hoffman and Zakhary, (1954), in a paper designed to indicate temperature ranges within a snail infested canal in Egypt, made all recordings at one depth. These measurements do not in fact reflect the overall condition within each habitat. While the surface waters become heated during the day, there can be marked thermal stratification, for convection is insufficient to allow for the distribution of this heat, so that on a very hot day water at a depth of 25 cm. will normally be 4 - 5°C. cooler than the surface water. Again Mosley, (1959), in discussing the importance of temperature, stresses the presence of microhabitats in which animals may seek refuge from overall conditions. It is thus highly probable that the apparently wide tolerance shown by these aquatic snails is not due to any abnormal physiological mechanisms, but to their ability to select the more suitable microhabitats. Watson, (1958) dealing with *Bulinus* (*Bulinus*) *truncatus* (Audoin) in the Middle East, states that this species is capable of breeding within the range of 18°C. to "near blood heat". However, results presented later will show that although they may survive such extremes of temperature, the capacity for increase of the species *B.* (*Ph.*) *globosus* and *B. pfeifferi* is greatly influenced by temperature and that this capacity for increase will be maximal only in much narrower temperature ranges.

It is clear that lethal temperatures are not important under these circumstances, thus it was felt that the most significant information could be obtained from a study of life tables which are a record of mortality and fecundity throughout the life span of a group of individuals. A prerequisite for the determination of life table data was to culture strains of the relevant snail species under controlled conditions in the laboratory and then to investigate the effects of temperature and also of crowding on growth and egg production. The data used to compile the life tables were obtained from *B.* (*Ph.*) *globosus*, *B. pfeifferi* and *L. natalensis*, keeping all conditions constant or similar, and varying only temperature and crowding. Daily records of egg production and mortality were made over a period of 30 months in order to determine these data with critical accuracy. Thus it was possible to calculate the intrinsic rate of natural increase, a measure of the reaction of the species to a set of conditions, optimal or otherwise. In conjunction with this, the rate of growth of *B.* (*Ph.*) *globosus*, *B. pfeifferi* and *L. natalensis* was measured under various conditions of temperature in order to be able to make an estimate of the rate of growth under field conditions. It was in the sphere of field observation and the application to this of the controlled laboratory data that the most exciting results were obtained. There proved to be a high degree of consistency in the two spheres of work. Quantitative sampling of naturally occurring snail populations over a period of time has enabled the estimation of actual numbers of snails existing within the habitats. By suitable techniques it has been possible to estimate the age structure of a population and thus, by watching the growth of a group within that population, to estimate its death rate and fecundity under natural conditions and to derive its rate of actual increase in the field.

II. SNAIL CULTURE.

Various methods of cultivating the intermediate host snails of Bilharziasis have been described. Cowper (1946) maintained *Bulinus* (=*Bulinus*) *truncatus*, *Planorbis* (=*Biomphalaria*) *boissyi* (Potiez and Michaud) and *Planorbis guadaloupensis* (=*Australorbis glabratus* (Say)) under conditions which required continual aeration. The snails were fed on young unboiled lettuce leaves. He mentioned the importance of boiling the water used in the aquaria to avoid the fungus *Catenaria* which attacked egg masses; however, the snails did not always survive well in the treated water. Stunkard (1946) recorded the successful culture of these species, the prosobranchiate hosts of *Schistosoma japonicum* (Mollendorf) and also *Physopsis africana* (Morelet) although he does not mention the actual method used. Standen (1949) describes very fully a method to maintain *B. boissyi* and *B. truncatus* using biologically balanced aquaria. These methods, slightly modified in regard to the preparation of the food, were applied successfully to the culture of *Australorbis glabratus* (Standen 1951).

This latter species appears to adjust satisfactorily to laboratory conditions and has thus become the work horse of bilharziasis research. During the past few years much valuable work has been carried out on *A. glabratus* both in the laboratory and in the field. Perlowagora-Szumlewicz (1958) has reported in detail on the bionomics of the species under controlled laboratory conditions, describing fecundity, growth rates and survivorship in various combinations of crowding, temperature and feeding. Rowan (1958) has described a method of mass cultivation using large aquaria in which are suspended nylon mesh hammocks. The snails live and breed in these and can be removed en masse with ease. The effects of crowding on growth rate and fecundity under different temperature conditions were studied by Chernin and Michelson (1957a, b). Chemotaxis and the location of chemoreceptors has been investigated for this species, Michelson (1960), as have the effects of desiccation, Olivier (1956), Olivier and Barbosa (1956). As a final indication of the distribution of work done on the various species of snails, reference is made to the World Health Organization Bibliography on bilharziasis up to 1958. In this work *Australorbis* is indexed as the subject of 98 papers while *Biomphalaria* is reported 18 times and *Bulinus* (*Physopsis*) is mentioned only four times.

In comparison with all this information on *Australorbis glabratus* there is a veritable dearth of knowledge on the bionomics and ecology of the important host snails of *Schistosoma* in Southern Africa, *B.* (*Ph.*) *globosus* and *B. pfeifferi*. To this can probably be ascribed difficulties which have been encountered in the past when workers have attempted to rear these species under controlled laboratory conditions. The first really important work on this subject was published only recently by Claugher (1960) and describes a satisfactory method of rearing *Bulinus globosus*, *B. truncatus* and *B. forskalii* under laboratory conditions. The technique described here is based mainly on that of Claugher.

1. The culture of *Bulinus* (*Physopsis*) *globosus*.

The method of culture of this species is based on the techniques of several workers, Le Roux (personal communication), Mandahl-Barth (personal communication), and in the main that of Claugher (1960). Some minor additions have been included pertaining mainly to the accuracy of recording egg laying and fertility. Moulded glass aquaria are used as the breeding tanks; there should be no metal in contact with the water nor any obscured corners to hide the presence of eggs. The tanks are of two dimensions, 14 x 24 cm. x 15 cm. deep and 17 x 24 cm. x 18.5 cm. deep. The smaller tanks when containing three litres of water still retain sufficient air space under the cover, similarly with the larger tanks when filled with four litres of water. The covers used are sheets of glass and do admirably well for the recording of relevant data. Mature aquarium water is used in all the tanks and this is drawn from a large glass vessel of 50 litres capacity. Reservoir tanks have a sandy bottom planted with a sprig of *Vallisneria spiralis* and in them a community of guppies (*Lebistes sp.*) is maintained. The fish are fed daily with a small quantity of dry powdered dog meal. The tanks are filled with tap water of reasonably consistent salinity as supplied by the Salisbury Municipality. A series of water analyses during 1962-3 are given in Table II.,$_1$

When filled, the reservoir aquaria are allowed to stand for a period of five to seven days before any water is drawn for the snail aquaria. Furthermore, except for cleaning, these aquaria are never drained but are refilled when approximately two-thirds of the contents have been removed.

The parent snails, from which the whole experimental stock has derived, were collected in several batches from the Nyachivi River in the Chikwakwa Reserve (17° 53' S. : 31° 26' E.) and were kept in aquaria as described above. It was soon found that these snails readily deposited egg masses on the sides of the aquaria, favouring this situation to the sprigs of floating plants or to the bottom of the tank. They would also lay readily on one another. The eggs laid on the sides of the aquaria could easily be marked by means of a wax pencil, counted, the number of infertile eggs noted, and the data recorded on the glass cover of the tank.

At first the adults were left in the aquarium until 10 or 12 egg masses were laid and then they were removed to another. However, by this method it was impossible to know either the exact age of the F_1 snails or the accurate juvenile mortality rate and because of this it was decided to excise the egg masses as they neared maturity and to incubate them separately. This was done using a sharp scalpel to slice carefully between the egg mass and

TABLE II.1

Analyses of several samples of Hunyani treated water as supplied by the Salisbury Municipality to the Bilharziasis Research Laboratory during 1962 - 1963.

By courtesy of the City Chemist.

DATE	16.1.62	17.4.62	14.8.62	19.11.62	22.1.63	2.4.63
pH	8.3	8.1	8.1	8.0	8.5	7.8
TOTAL SOLIDS	98.0	82.0	110.0	108.0	88.0	84.0
DISSOLVED SOLIDS	98.0	82.0	-	108.0	87.8	84.0
ALKALINITY 'P' ($CaCO_3$)	2.0	1.0	2.0	Trace	4.0	Nil
ALKALINITY 'M' ($CaCO_3$)	32.0	32.0	36.0	30.0	36.0	28.0
TOTAL HARDNESS ($CaCO_3$)	42.0	38.0	42.0	38.0	42.0	34.0
PERM. HARDNESS ($CaCO_3$)	10.0	6.0	6.0	8.0	6.0	6.0
TEMP. HARDNESS ($CaCO_3$)	32.0	32.0	36.0	30.0	36.0	28.0
DISSOLVED OXYGEN	6.4	6.8	7.8	6.7	6.2	6.8
ALBUMINOID (N)	0.14	0.1	0.12	0.21	0.103	0.12
FREE NH_3 (N)	Trace	0.02	0.04	Trace	0.05	0.10
IRON (Fe)	Trace	Nil	Trace	Trace	Trace	Nil
ALUMINIUM (Al)	0.25	0.1	0.1	0.03	0.15	0.1
CALCIUM ($CaCO_3$)	30.0	26.0	28.0	26.0	32.0	24.0
MAGNESIUM ($CaCO_3$)	12.0	12.0	14.0	12.0	10.0	10.0
SULPHATE (SO_4)	23.2	16.9	16.9	18.6	17.9	16.2
CHLORIDE (Cl)	8.0	10.0	11.0	12.0	8.0	6.0
FLUORIDE (F)	0.15	0.1	0.1	0.1	0.25	Trace
PHOSPHATE (PO_4)	Trace	Trace	Trace	Trace	Trace	Trace
SILICATE (SiO_2)	14.7	14.2	15.8	13.3	13.6	12.5

the glass, and then transferring the egg mass to a smaller container. Either plastic 'jam pots' of 100 ml. capacity or 500 ml. glass crystallising basins were used.

The feeding of the young snails at this stage was most critical and if good survival rates were to be obtained, great care had to be exercised. An adequate food was faecal matter from adult snails. After approximately a week on this diet a thin slice of fresh carrot or some shreds of well boiled lettuce could be included. In the light of experience it is well to mention some points to which meticulous attention had to be paid. It was important that the eggs and faecal matter should come from unparasitised adults as the presence of turbellarians or a colony of Protozoa such as *Vorticella* or *Stentor* generally resulted in the extinction of the brood, particularly at the warmer temperatures.

Apart from removing oxygen and food, the foreign organisms, especially the Turbellaria, actually consumed the newly hatched snails (Claugher, 1960). A second important detail was to ensure that the aquaria were examined daily and that decaying food material was removed. In these small dishes the oxygen balance could be easily upset by the presence of an excess of decomposing organic material. A few Cladocera, *Ceriodaphnia sp.*, introduced into these aquaria were beneficial in that they would reduce the bacterial flora and thus reduce the protozoans which appeared to impede the snails. A flourishing community of *Ceriodaphnia* resulted in beautifully clear water and healthy snails.

When the snails were approximately two mm. long they could be removed from the small aquaria and transferred to one litre crystallising basins. At this stage great care had to be exercised in handling the young snails. Fine camel-hair paintbrushes were satisfactory and it was important to equate the water temperature in the two aquaria before transfer.

Optimum conditions existed with a volume of the order of one litre per adult snail at the warmer temperatures, while at lower temperatures approximately 500 ml. per adult snail was sufficient. If conditions were more crowded egg production appeared to be reduced and rate of growth was affected. Apart from crowding, water temperature was most important. Ideal conditions appeared to be at a constant temperature of 25°C. but the snails survived well between 20 and 27°C. whether the temperature was constant or subject to normal daily and seasonal fluctuations. Average egg production for a group of 32 snails kept at 25°C. over a six week period was 83.4 eggs per snail per week, while for a batch of 25 snails kept for a similar period at room temperature (19 - 22°C.) average production was 20.4 eggs per snail per week.

Maintenance and feeding.

The aquaria were cleaned out daily, faeces and uneaten food being removed by means of pipettes fitted with rubber teats, after which fresh food was added. The main food material was lettuce prepared according to Claugher (1960). Fresh green lettuce leaves were boiled for two minutes and then immersed in cold water for a further few minutes. The leaves were then spread out on glass sheets and allowed to dry after which the thin tissues of lettuce leaf could be peeled off the glass and kept for long periods of time. In addition to this, thin slices of raw carrot were fed to the snails once a week. This food was taken particularly well by the younger snails but in warm conditions it decomposed rapidly and had to be removed from the aquaria within 48 hours.

The aquarium water was chemically conditioned by the addition once a week of a few drops of a 5% suspension of calcium carbonate. Without this the shells became extremely soft and often badly eroded. The water was completely changed from time to time when it became discoloured, cloudy or when the algal growth was too dense. Healthiest conditions obtained with the water crystal clear and supporting a colony of Cladocera.

2. The culture of Biomphalaria pfeifferi.

Biomphalaria pfeifferi, apart from minor exceptions, was cultured similarly to Bulinus (Physopsis) globosus. Glass aquarium tanks were used and were filled with mature aquarium water. Of choice, the snails did not lay eggs on the glass walls of the aquaria but preferred sprigs of plant floating near the surface. This fact was noted by Standen (1949) when culturing B. boissyi. However, a few egg masses were deposited on the glass walls of the tanks and these could be excised and used to establish colonies of known age. Sprigs of the aquatic plant Vallisneria spiralis taken from outdoor ponds were used in the aquaria. Prior to their introduction they were soaked in a 2% solution of Urethane (ethyl carbamate) for 30 minutes and then washed for several hours in tap water to remove foreign organisms.

The snails were fed with the same food as B. (Ph.) globosus and the aquaria were cared for in an identical manner. The treatment of the young snails was different in that they did not require faecal matter from adults but readily took freshly boiled or powdered lettuce. As can be seen from the life table data (Ch. VII) high survival rates have been recorded both at room temperature and at 25°C. All the B. pfeifferi used in this series of experiments were derived from a single batch collected from the same locality as the B. (Ph.) globosus mentioned above.

A peculiarity which has been noticed during the laboratory culture of this species was that some snails became inclined to crawl out of the water and adhere to the glass sides or lid of the aquarium. Unless replaced they would remain out of the water until finally they succumbed. Once the snails in an aquarium exhibited this tendency to leave the water they would continue persistently no matter how frequently they were returned and during this period, which could last for several weeks, they would not feed at all and growth became negligible. After a period of time the urge to wander would decrease and the snails would remain longer in the water and once more commence feeding and normal growth.

There was no apparent reason for this behaviour. It has been observed to occur with *Lymnaea cailliaudi* (van Someren, 1946) but he too failed to ascribe any reason for it. It has been observed under all temperature conditions used in laboratory experimentation, particularly when temperature was constant, starting and ceasing without any particular reason or pattern. The only consistent fact noted was that the snails most likely to be affected were those within the 4 - 6 mm. diameter size group.

B. pfeifferi appeared to be less sensitive to crowding than *B.* (*Bh.*) *globosus* and could tolerate densities of up to four snails per litre without serious impairment of egg production and with no effect upon the normal rate of growth.

3. The culture of *Lymnaea natalensis*.

Lymnaea natalensis was cultured successfully by a method similar to that used for the other species. The only alteration necessary was in the rearing of the newly hatched snails. The young snails would not eat prepared foods but required a diet of green algal encrustation thus it was necessary to prepare a brood aquarium before a batch of snails could be reared. When an algal encrustation had formed on the sides of the dish, a selected egg mass could be removed from the parent aquarium and placed in the brood dish. The young snails would take no supplementary food until 2 - 3 mm. long, after which they would feed entirely on carrot or prepared lettuce.

Growth was rapid and the snails would commence egg laying when between 9 and 10 mm. long. Floating plants were prepared as egg laying sites although in the absence of these the walls of the aquarium tanks would be used. As with the other species, all aquaria were conditioned by the weekly addition of a few drops of a 5% suspension of calcium carbonate which helped promote healthy shell growth.

The species appeared to be very susceptible to overcrowding. Egg production declined when snails were maintained in tanks at a density of two or more snails per litre.

III. DESCRIPTION OF HABITATS.

1. FOYLE.

Description of the site.

Foyle Farm lies some five miles to the north-west of Mazoe, 17° 31'S. : 30° 58'E., and is in the drainage system of the Little Mazoe River. In general, soil drainage on the farm is poor and there are large tracts of practically flat land which tend to be marshy during the rainy season. These damp regions are known colloquially as "vleis", and in a large vlei near the Little Mazoe river a series of two depressions in close proximity to each other have been excavated. Originally, clay for the manufacture of bricks was removed but for several years the holes have been neglected and have become temporary waterbodies holding water from the onset of the rains, usually in November until the warm dry weather of August. Aquatic and semi-aquatic plants have become established in the ponds which now form a satisfactory habitat for _Bulinus_ (_Physopsis_) _globosus_ and _B._ (_Bulinus_) _forskalii_.

The upper pond is long and narrow (Fig. III.$_1$) with steep sides and is between 50 and 80 cm. deep when full. The bottom is soft and muddy with a few broken fragments of bricks scattered around. The lower pond is roughly triangular in shape with the apex towards the upper pond and the base formed at a road crossing below the pond. Here too the sides are steep and the bottom is muddy, while the depth, as before, varies between 50 and 80 cm. when full. The ponds lie in the natural drainage line of the vlei, and throughout the rainy season there is a constant flow of water into the upper pond and thence, through a series of grassy runnels, to the lower pond and out across the road.

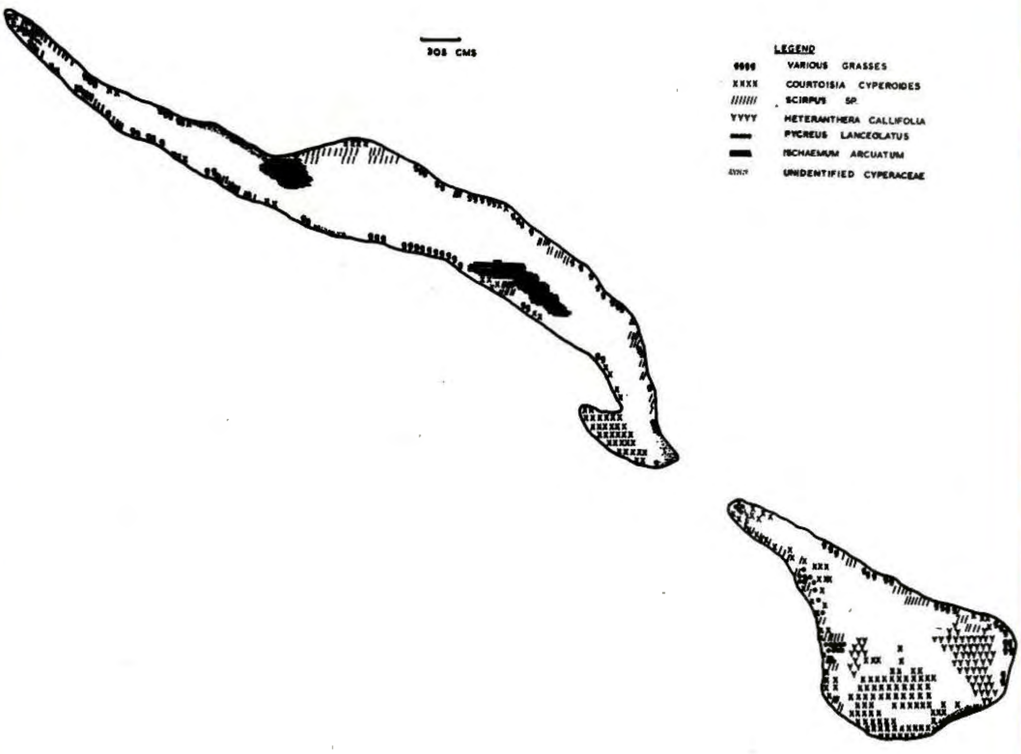


FIG. III.1 A sketch-map, in spacial arrangement, of the two ponds which comprise the Foyle habitat. The distribution of vegetation is representative of that when the ponds are full.

As the vlei has a large catchment area, heavy rains result in flooding of the waterbodies but as the discharge end is unrestricted the flooding is temporary and the normal full level is very consistent. As the ponds are interconnected for much of the year (November - April), they are treated in this work as an integral whole and have been sampled as one waterbody. The area of the combined ponds when full is 433 sq. metres and during the period under consideration the pond was full from March to May, 1962, and from December to March, 1963. The water level dropped in June and July and by early August only 43 sq. metres of water 10 - 12 cm. deep was left. This soon dried up and the habitat remained dry until the 22nd November when the ponds began filling up. Both ponds were completely full early in December.

The dominant snail in the habitat was *B.* (*Ph.*) *globosus* with *B.* (*B*) *forskalii* present in small numbers early in the rainy season. A few specimens of the planorbid snail, *Gyraulus sp.*, were found throughout the year and occasionally *Lymnaea natalensis* was taken. For the purposes of the experiment and to exclude stray cattle from entering the waterbody a fence was constructed around the ponds.

Vegetation.

The distribution of the vegetation in the ponds can best be described with reference to the map, Fig. III.$_1$. Grasses and sedges comprisedthe greater part of the vegetation associated with the waterbody. The grasses were mainly on the banks and in the shallows and therefore submerged only when the pond was full: for the most part the grasses, once submerged, began to decompose and often became encrusted with filamentous algae. Any floating fragments of grass, whether living or decaying, are an important constituent of the ecosystem. They provide a substrate frequented by snails. The sedge *Scirpus sp.* occurred on the banks of the waterbody and in shallows where the depth did not normally exceed 15 cm. It was not particularly favoured by the snails and was of little importance. This was not the case with the hard stemmed *Courtoisia cyperoides* (Roxb.) Nees which dominated the lower pool and was well established in the upper pond. The flat sides of the triangular stems were favoured by *B.* (*Ph.*) *globosus* as egg laying sites and consequently were the 'nurseries' for this species. They also provided some shelter from the scouring action of flood waters, thus protecting some snails from being washed away. The lower pond was fairly broad and no grasses could colonise the central regions; there was, however, a broad-leafed floating plant, *Heteranthera callifolia* Rchb. ex Kunth, which provided a resting place similar to the fragments of grass nearer the bank. Snails were often taken on this plant and the broad leaves were used occasionally for egg laying.

Temperature.

A constant recording thermometer was set up in the waterbody, the bulb, which was sheltered from incident sunlight, was adjusted to float five cm. below the surface. The records have been converted to daily maxima and minima and weekly averages are given in Fig.III.$_2$. In this habitat temperature records were made at one level only. It is assumed that conditions were comparable with those recorded at Marlborough and Derbyshire and that temperatures at a depth of 25 cm. would be somewhat lower than those near the surface.

Seasonal trends similar to those recorded in the other waterbodies were recorded in this pond. Although they are not reflected in the figure, maximum temperatures exceeded 30°C. on two occasions during the year. Nevertheless, temperatures remained high until early May when the weather became cold. In June a sequence of warm sunny days kept the maximum temperatures above 20°C. but during the cold nights temperatures dropped as low as 7°C. In early August day temperatures started to rise but by the 12th August the waterbody became dry and no further records were made until the last week in November when the ponds filled up once more. The temperature during

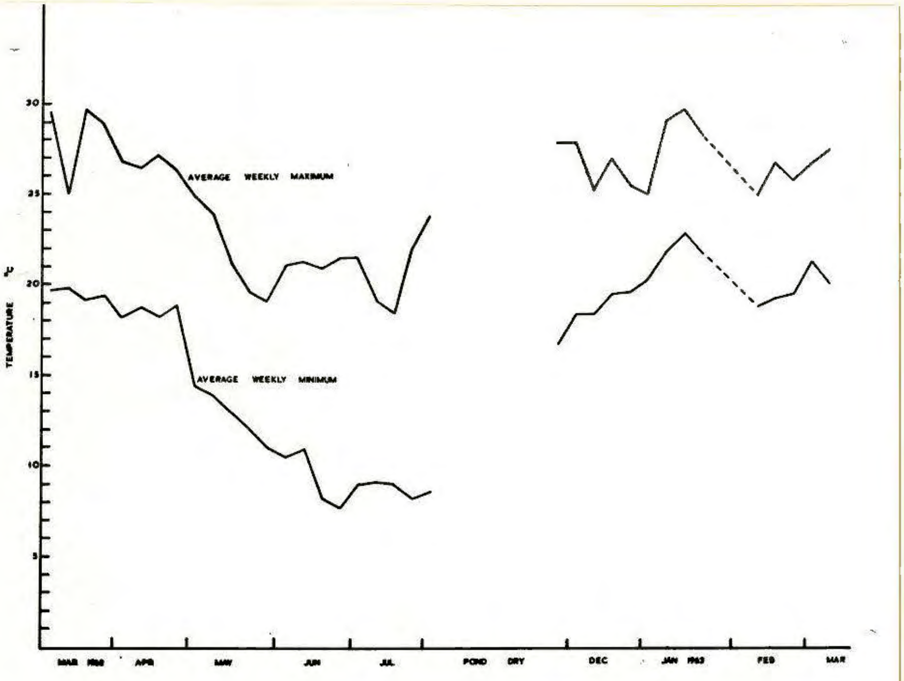


FIG. III.$_2$ Temperature records in the Foyle habitat during 1962 - 1963. Records made by a constant recording thermometer at a depth of 5 cm.

December, January, February and March remained fairly warm, maxima fluctuating between 25 and 30°C. and minima between 18 and 23°C. This picture was similar to that recorded during March and April of the previous year.

2. MARLBOROUGH.

Description of the site.

The Marlborough pond is situated just north of Salisbury 31° 18' 30" E. : 17° 44' 20" S., and is in the headwater system of the Gwebi River. The pond is, however, independent of any watercourse and is in an old borrow pit from which clay was removed for the manufacture of bricks. Apart from seepage, the waterbody is replenished only by that rain which falls in the immediate vicinity. As the general slope of the land is away from the pit, very little run-off water finds its way in. The actual pit is almost rectangular, being some 60 m. long and 40 m. wide. The bank is steep on the southern side of the pit but on the other sides numerous shelves jut out into the waterbody, and at the western end are shallows which become inundated only when the pond is well filled.

For the period under consideration, namely June, 1961 - June, 1962, the pond was at greatest depth during February, March and April, and during these months there was no apparent change in the surface area of the waterbody which was found to be 1640 sq.m. At this time the average depth of the pond was approximately 1.5 m. with a maximal depth of 2.5 m. in a channel extending some 25 m. across the pond near the eastern bank. The greatest change in surface area of the waterbody took place during the months August, September and October when temperatures were high and evaporation at its maximum. During this period the area of the pond diminished from 1296 sq.m. to 807 sq.m. with the average depth dropping from approximately 1.0 m. in August to approximately 0.4 m. in October.

The bottom was composed mainly of organic sediments and a heavy clay of the type suitable for making bricks. As is common in this type of pit, there was a considerable amount of brick rubble scattered throughout the pond, and this was frequently taken in the dredge samples.

Three species of aquatic pulmonate snails abound in the waterbody. Apart from the latter two months of the period under consideration the dominant species was *Lymnaea natalensis* with *Bulinus* (*Bulinus*) *tropicus* next and *Biomphalaria pfeifferi* a small but fairly consistent segment of the population. The limpet, *Ferissia* *sp*. also occurred in the pond.

Vegetation.

The dominant emergent vegetation was a species of *Typha* which originally occurred in belts scattered throughout the waterbody, but, as can be seen on the vegetation maps (Figs. III.$_3$, III.$_4$ and III.$_5$) these belts expanded considerably towards the end of the period. Apart from the *Typha* a dense stand of *Phragmites mauritianus* Kunth occurred on the north-eastern end of the pond. The fairly shallow western end was covered with a mixture of a stoloniferus grass and the broad leafed *Polygonum salicifolium* Brouss ex Willd. Both these plants extended through the surface in the shallow water. Of the purely aquatic plants, the dominant feature of the deep water was *Potamogeton schweinfurthii* A. Benn which, when the water level was rising grew upwards in long filaments, and when the water was dropping lay in dense mats tangled on the surface. In the shallower water (approximately 0.7 m.) *P*. *salicifolium* dominated, and interspersed with it was *Nitella*, while sometimes in these regions small quantities of *Spirogyra* were recorded. Both these algae became more evident as the water level in the pond fell, and they reached peak incidence during October and November.

The three sketch maps illustrate the vegetational areas and topography of the pond. The map for July (Fig. III.$_3$) shows the situation early in the period when the pond was full, October (Fig.III.$_4$) when the water level was at a minimum, and February (Fig. III.$_5$) when

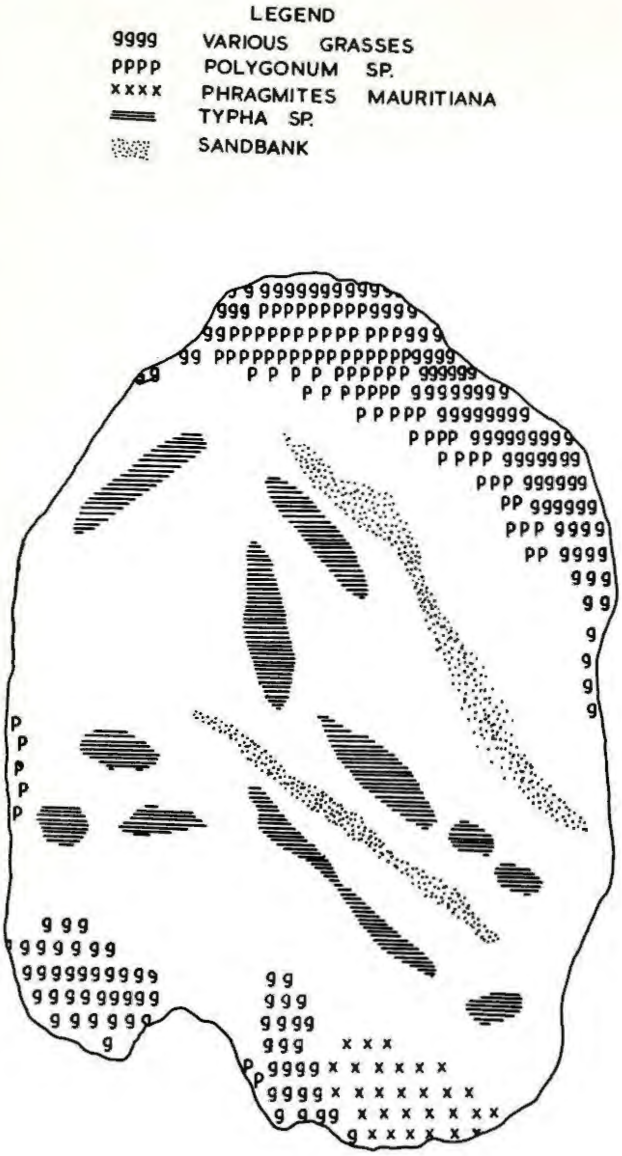


FIG. III.3 Marlborough pond showing outline of water level and distribution of vegetation in July, 1961.

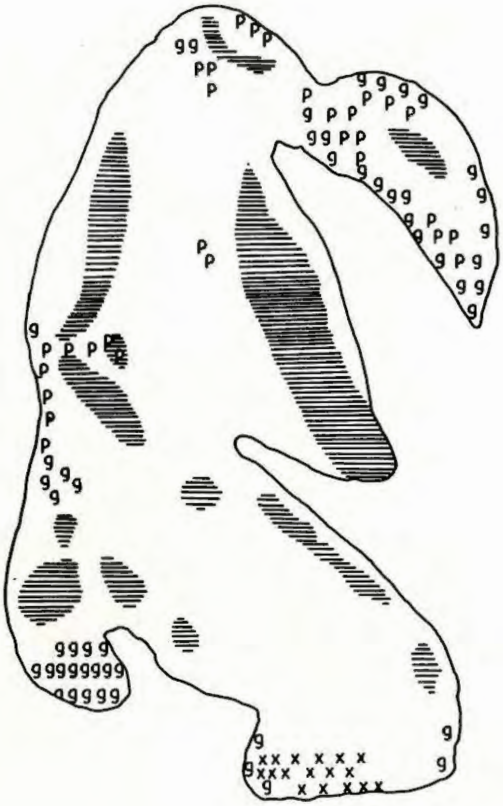


FIG. III.$_4$ Marlborough pond showing outline of water level and distribution of vegetation in October, 1961. Symbols as for Fig. III.$_3$

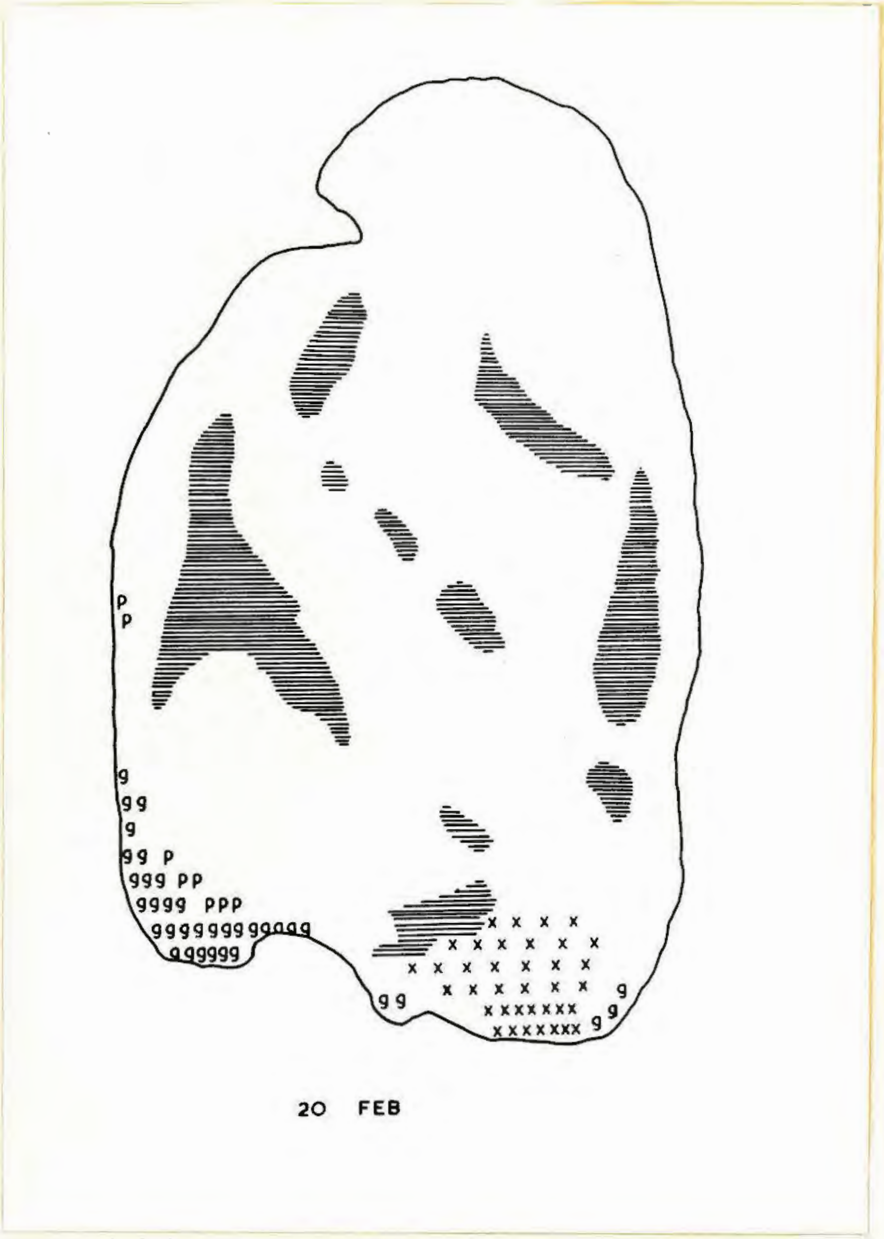


FIG. III.5 Marlborough pond showing outline of water level and distribution of vegetation in February, 1962. Symbols as for Fig. III.3

the pond was again full.

Temperature.

Weekly minimum and maximum temperatures were recorded from three levels in the pond for a complete annual cycle. Three 'Sixes' thermometers were suspended from a float standing in a region of clear open water, the thermometers were adjusted to remain horizontal at a depth of 5, 25 and 90 cm. with the bulbs shielded from incident sunlight. Readings were made at weekly intervals throughout the period and the results are shown graphically in Fig. III.$_6$. The wide difference between minima and maxima in the surface levels was a reflection of the normal diurnal variations, high in this part of Africa because of the intense daily insolation. At the deep level (90 cm.) the difference between minima and maxima was greatest towards the end of summer and during early winter. It was at this time that minima at all three levels were very similar, but as winter progressed into early summer, the coldest conditions were recorded in the deep water at which level even the maximum temperatures were several degrees lower than at either of the shallower levels.

It is possible to arrive at certain definite conclusions with the help of this series of temperature recordings.

(a). During a hot period with intense insolation surface maxima rose above 26°C., and although temperatures at the 25 cm. level followed the same general pattern as that recorded at the 5 cm. level, maximum temperatures were never in excess of 25°C. and even during the hottest period were mainly in the region of 22 - 23°C.

(b). Although temperatures in the surface levels were subject to wide variation, at a depth of 25 cm. extreme conditions were considerably buffered while at a depth of 90 cm. maximum temperatures were even lower.

(c). Except for the winter period when surface maxima fell there would normally be a wide range of temperatures available to any aquatic animal capable of diving to a depth of 25 cm.

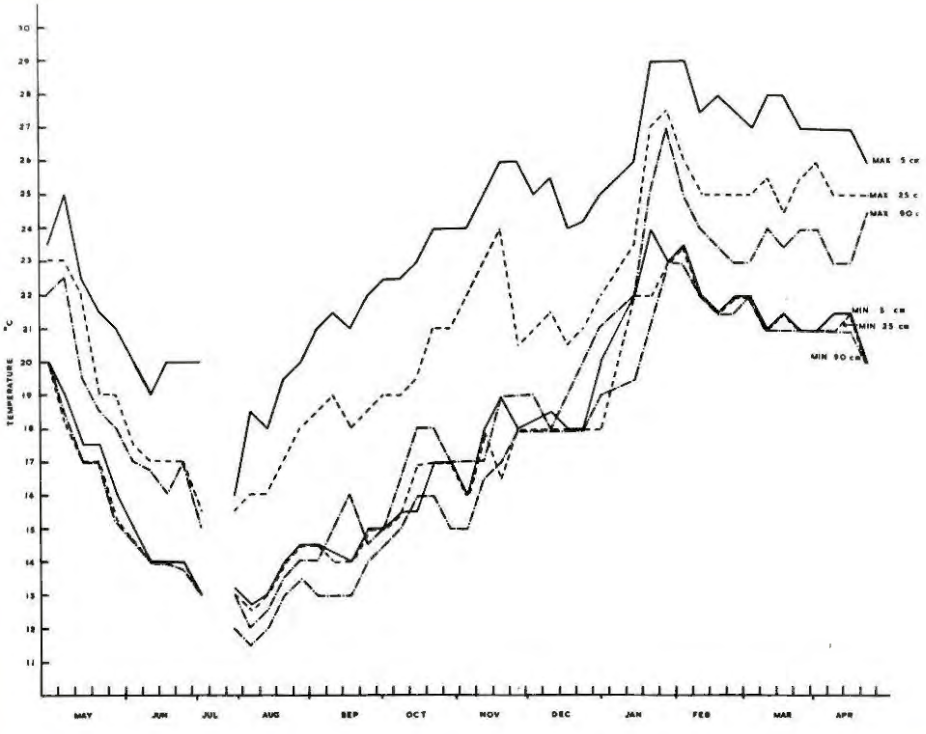


FIG. III.6 Temperature recordings made in the Marlborough pond during 1962 - 1963. Figures represent weekly recordings of absolute maxima and absolute minima taken from 5 cm., 25 cm. and 90 cm. deep.

(d). The temperature records made at the 90 cm. level seem to reflect the amount of heat within the main body of water, a point which is brought out when considering the winter - spring series. There was very little difference between minima and maxima during this period and both extremes follow the general pattern exhibited by the minimum temperature records made at the other levels.

Finally, it must be emphasised that even a depth of 90 cm. is well within the range of most aquatic fauna which indicates the varied choice of temperature conditions available within the body of the habitat.

3. DERBYSHIRE.

The Derbyshire sand quarries lie some four miles south-east of Salisbury and draw water supplies from a pond formed by a concrete weir across a small stream. Originally it was decided to use the waterbody for snail sampling but as the population of all species was meagre the site was discarded. Temperature records were taken in the waterbody for one complete year and are cited here for comparison with those measured at Marlborough and at Foyle.

Weekly minimum and maximum temperatures were recorded from two levels in the pond. Two 'Sixes' thermometers were suspended from a float among a dense stand of waterlilies (*Nymphaea sp.*). The thermometers were adjusted to remain horizontal with the bulbs shielded from incident sunlight at a depth of 5 cm. and 25 cm. below the surface. The records are shown in Fig. III.7. Although these records were for a different season from those made at Marlborough and in spite of the dense vegetation cover in the Derbyshire pond, there was a remarkable similarity between seasonal trends and temperature gradients in the two localities. It can therefore be inferred that heat dissipation and convection are not normally hindered by surface vegetation, and it is probable that similar patterns of temperature change occur in all smaller waterbodies in this region of Africa.

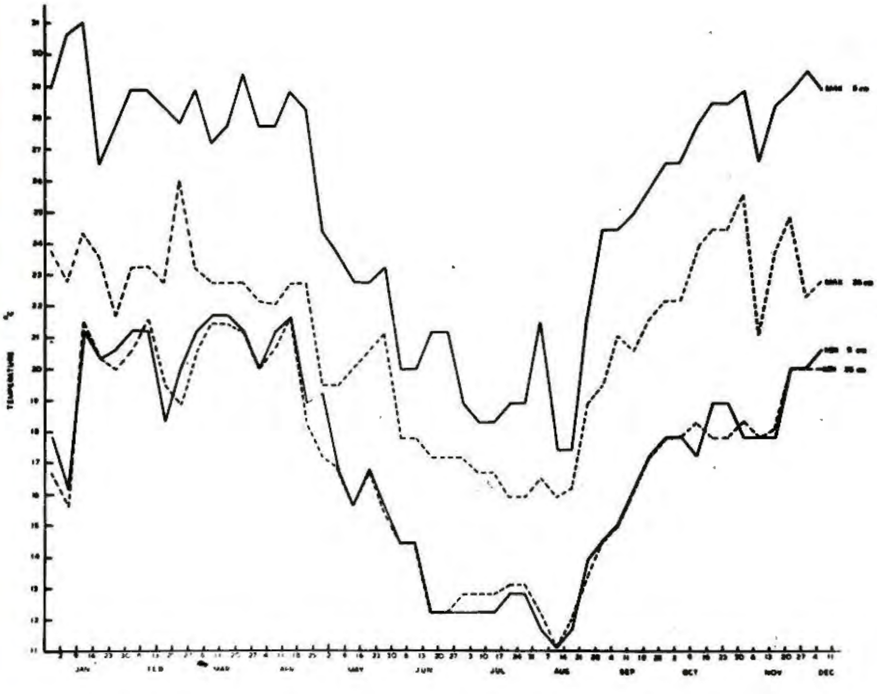


FIG. III.7 Temperature recordings made in Derbyshire pond during 1961 - 1962. Figures represent weekly recordings of absolute maxima and absolute minima taken from 5 cm. and 25 cm. deep.

IV. DISCUSSION OF THE VARIOUS PARAMETERS TO BE MEASURED.

Any study which attempts to seek explanations of the bionomics of a particular species within its environment, must rely on certain population parameters or measurements calculated mainly from experimental data, and these should indicate the potentialities of that species to exist within prescribed conditions. From this study it must be possible to gauge the age structure of the population and thus to outline the life pattern of the species. Natural conditions, however, are most difficult to define because even though measurements of the gross physical features of the habitat may be easily carried out, the subtle conditions of the microhabitat in which the individual actually exists are often too fine for normal recording techniques. The ensuing study of aquatic pulmonate snails has been based on field observations made regularly at definite localities. These will be compared with series of laboratory experiments which attempt to cover all aspects of life and growth in relation to one of the more influential physical conditions of nature, namely temperature.

Three parameters will be discussed, first, the intrinsic rate of natural increase which includes the infinitesimal and the finite values of the innate capacity for increase, and the actual or observed rate of increase which can be calculated from field data; second is the mean generation time which is a corollary of the intrinsic rate of natural increase and can be calculated from the same data, and the third is the average rate of growth under various temperature conditions. The last named is a necessary tool for the estimation of age distribution within a population.

1. The intrinsic rate of natural increase.

It is a feature of animal life that organisms tend towards unlimited increase but under natural conditions this increase becomes restricted. For any particular set of environmental circumstances an animal will live according to a life pattern. It will exist for a period of time during which it may produce a number of offspring. It will probably live longer and produce more offspring under favourable conditions than when circumstances are adverse. However, this pattern is not completely dependent on environmental factors but is also affected by an inborn attribute of the animal itself. The whole pattern forms the basis of the concept of the intrinsic rate of natural increase which is normally designated by 'r_m' and defined as "the maximal rate of increase attained at any particular combination of temperature, moisture, quality of food and so on, when the quality of food, space and other animals of the same kind are kept at an optimum, and other organisms of different kinds are excluded from the experiment". (Andrewartha and Birch, 1954).

In the past, many workers have concerned themselves with population growth. The Malthusian concept of an expanding population in a restricted environment was expressed by Chapman (1930) in terms of biotic potential and environmental resistance. These are treated as independent and opposed entities but it is not really possible to separate environmental conditions on the one hand and rate of development, longevity and fecundity on the part of the organism on the other hand. Lotka (1925), working in the field of human demography has related, in mathematical terms, birth, death and fertility to a parameter describing the 'true' or 'inherent' or 'intrinsic' rate of natural increase. This is similar to Volterra's (1928) coefficient of increase. The intrinsic rate of natural increase was first applied in the field of animal ecology by Leslie and Ranson (1940) working with the vole, _Microtus agrestis_. Birch (1948, 1953a, b), Howe (1953) and Andrewartha and Birch (1954) elaborated and stressed the importance of this principle and applied it to various species of insects.

As indicated by the definition, the intrinsic rate of natural increase reflects an intimate interdependence of the potential for increase of an individual with certain features of its environment, both biotic and physical. It does not attempt to disassociate interrelated factors but combines a specified environment with its effects on such vital statistics as longevity and fecundity of the individual. In this way it is superior to the 'biotic potential-environmental resistance' concept.

Unless an animal is producing offspring at the same rate throughout its life and is exposed to a constant risk of dying as it grows older, the rate of increase cannot really be defined without considering the age of the animal. In point of fact, for any particular set of circumstances, a population will exhibit a definite pattern of death rates and fecundity for each age group. These can be measured and are termed 'age specific life schedules'. Lotka (1925) has shown that a population increasing in an unlimited environment, whose birth and death rates for each age group remain constant, will assume a 'stable age distribution' and its rate of increase will be constant. This is the intrinsic rate of natural increase and it can be measured for various sets of circumstances as long as there is no crowding effect.

The rate of increase of a population of stable age distribution existing in unlimited space is given by

$$\frac{dN}{dt} = (b - d)N$$

Where b and d are constants representing the infinitesimal birth and death rates, t is time and N is the number of individuals.

Now the birth rate minus the death rate is the rate of increase, 'r_m'. Thus

$$\frac{dN_t}{dt} = r_m N$$

so integrating

$$N_t = N_o e^{r_m t}$$

N_o = number of animals at time zero
N_t = number of animals at time t
r_m = intrinsic rate of natural increase
e = base of nat. logs.

As this increase is geometric, the relationship between $\log_e N$ and t is a straight line the slope of which gives the value of r_m. This is the infinitesimal rate of increase and from this can be derived the finite rate of increase R. This is the actual number of individuals by which a population increases per head per unit time, and it is given in the following relationship:-

$$\frac{N_t}{N_o} = R = e^{r_m}$$

so $\quad R = \text{antilog}_e\, r_m$.

A numerical example may help to clarify. Consider a population of stable age distribution which multiplies ten times in two weeks.

$$N_t = N_o e^{r_m t}$$

or

$$\frac{N_t}{N_o} = e^{r_m t}$$

thus

$$r_m = \frac{\log_e N_t/N_o}{t} = \frac{\log_e 10}{2} = 1.1513$$

thus 1.1513 is the infinitesimal rate of increase per head per week

but $\quad R = \text{antilog}_e\, r_m = 3.16$

therefore the population would increase 1.1513 times per head per week, but the actual number of individuals arising from one female each week would be 3.16 (Andrewartha and Birch, 1954).

Calculation of the intrinsic rate of natural increase.

For the calculation of these parameters it is necessary to construct life tables based on direct observation of a cohort of individuals reared under carefully defined conditions. These tables give an age specific schedule for survivorship and fecundity. The time interval between measurements is arbitrary and is designated by x; successive periods are indicated by 1x, 2x, 3x .... nx, while birth or the time the egg was laid is taken as zero age. The choice of the unit of time is guided by the rate of maturation of the animal in question for it should not be too long lest the immature period and its relevant data be obscured, nor should it be too short otherwise the calculations may miss the most productive portions of the animal's life. This is because with prolific animals, the most significant information for the calculation of the intrinsic rate of natural increase will be available when the animals have been bred under standard conditions for a period which is long enough to enable the contribution of the product of survivorship and fecundity for each successive age group to 'r_m' to become insignificant.

(a). Survivorship (l_x).

The offspring of a parent generation die at different ages. From a record of this 'schedule of deaths' the number remaining expressed as a fraction of 1.0000 (100% survival) represents the survivorship of the experimental population. For the purposes of calculating r_m, this is required for the female population only, but when dealing with hermaphrodite animals, every individual is capable of egg production and therefore the whole population has to be considered for the collection of data.

(b). Fecundity (m_x).

This is given by a 'schedule of births' or eggs laid per unit time by a female of age 'x'. For the purposes of calculating r_m only female births per female are required. As before when dealing with hermaphrodites, the whole population is considered.

For each age group the survivorship fraction is multiplied by the female egg production per female and this is entered in the l_xm_x column. A summation of this l_xm_x gives the multiplication per generation or the nett reproductive rate which is designated by R_o. This nett reproductive rate is necessary for the calculation of r_m through the relationship

$$r_m = \frac{\log_e R_o}{T}$$

where T is the mean generation time.
Now T may be defined approximately as

$$T = \frac{\sum x l_x m_x}{\sum l_x m_x}$$

However, these calculations lead to only a rough estimate of r_m because they assume that all the births for each generation took place at one moment. This, of course, is not so and it is necessary to introduce the concept of the stable age distribution to the calculation. As a population living under certain conditions tends to approach a stable age distribution, its rate of increase tends towards a constant, and this is the intrinsic rate of natural increase for those conditions.

According to Andrewartha and Birch, (1954) the precise value for r_m is derived from the following equation:

$$\int_o^{\alpha} e^{-r_m x} l_x m_x \, dx = 1$$

where o - α is the life span of the reproductive individuals.

Certain simplifications of this formula have been suggested by Birch (1948) and Howe (1958). The essence of these is to substitute summation for the integral. Because of this the data for mortality and fecundity are assumed to apply to the mid-point of each time interval and are recorded at 0.5x, 1.5x, 2.5x ..... etc. They state that this approximation is justifiable because the extent of experimental error occurring within the observations does not warrant such intricate manipulation as the process of integration. A further simplification can be introduced which reduces tedious calculation to simple arithmetic and obviates the necessity for using natural logarithms.

e^{r_m} = R, the finite rate of natural increase; substituting this in the modified integral formula we get

$$\sum \frac{l_x m_x}{R^x} = 1$$

A value for R is obtained by trial and error and the infinitesimal value, r_ml is the natural logarithm of R. (Dr. N. Hairston, personal communication.)

<u>The biological significance of the intrinsic rate of natural increase.</u>

The intrinsic rate of natural increase applies to a population with a stable age distribution and is therefore an abstraction from nature. No natural population has ever been demonstrated to have attained a stable age distribution. However, the concept does stress that the size and structure of a population are not only the result of the environment affecting such qualities as speed of maturation, fecundity and longevity, but that these are also dependent on an inborn factor on the part of the animal itself. According to Andrewartha and Birch, (1954) the intrinsic rate of natural increase under ideal conditions is as characteristic of the species as any distinctive morphological feature.

The parameter r_m can be calculated for a particular species under various conditions, bearing in mind those which must remain standard and optimal, or it can be calculated for various species under constant conditions. In all instances there is a common denominator: the parameter refers only to a population with a stable age distribution. Thus it can serve as a means of comparison not only of those physiological qualities associated with increase between different animals under similar environmental conditions, but also between groups of the same kind of animals living under different environmental conditions. It can be used as the measure of preference of a species for a particular environmental feature.

Another feature of the intrinsic rate of natural increase is that it gives an indication of the theoretical potential of the species to increase under certain conditions. If two species occupy the same habitat but have differing intrinsic rates of natural increase for the particular conditions which prevail when a catastrophe strikes, the one with the higher intrinsic rate of natural increase will repopulate the habitat more quickly.

When considering the bulinid snails which serve as intermediate hosts for bilharziasis, it is important to determine how the various species respond to catastrophic disarrangement of the habitat, both natural and artificial. In the first instance many waterbodies dry out periodically, a situation to which the species, particularly B. (Ph.) globosus, have adapted satisfactorily, and the second instance concerns the application of molluscicides to the habitat. If these applications are carried out efficiently at a period when environmental circumstances are unfavourable to the species, that is when r_m is low, the effect may be more drastic to the population than if it happened during a period of high r_m. Thus the parameter may indicate the frequency and the timing at which catastrophes must occur in order to keep the population numbers at a very low level.

When dealing with field populations it is important to distinguish between r_m, the abstraction which although it is of biological significance, is based on features which do not exist in nature, and 'r' the rate of actual increase which is observed to occur in natural populations of the species. The rate of actual increase of a population is affected by two main groups of variables, those which affect the birth rate and fecundity of the individuals and those which affect death rate and longevity.

In the first category, those factors which affect the birth rate cause either a change in the rate of egg production or a change in the fertility of the eggs produced. There is reason to believe (Andrewartha and Birch, 1954) that both these features can be influenced by the numbers of other members of the same species present, that is by the degree of intraspecific competition which takes place. The aquatic snails considered here are hermaphrodite and it is unlikely that under-population is detrimental to the actual rate of increase. It has been shown (Perlowagora-Szumlewicz, 1958, Wright, 1960, and the author, unpublished results) that single unmated snails can produce large numbers of viable offspring. On the other hand it would appear to be a general rule in biology (Bodenheimer, 1938, Park, 1938, Allee et al, 1949, and other quoted in Andrewartha and Birch, 1954, Chernin and Michelson, 1957a, b, and Wright, 1960) that overcrowding has a depressing effect on fecundity. Temperature and the presence or scarcity of food are also factors which will affect the fecundity of poikilotherms.

The second group of factors which regulate the rate of actual increase act on longevity. These involve the influence of parasitism and predation which, for the most part, are constantly present but are seldom overwhelming. A choice of temperature is usually available in the habitat and within normal ranges, temperature has little effect on longevity. Scarcity of food must influence survival: in a biotope such as that considered here where food is generally abundant, it cannot be of much significance. Probably the most influential regulatory factor in this category is that relating to catastrophic alteration of the habitat, either flooding or drying. Within a group which is capable of a high rate of reproduction without the restriction of compulsory cross fertilisation, the most effective method of decreasing longevity would be by some catastrophic event. In these circumstances it would appear that apart from drastic alteration of the habitat, the most likely natural means of regulating the rate of actual increase would be by those conditions which alter the birth rate. That this is the case will be demonstrated later when the effects of temperature on longevity and fecundity are discussed. It will be shown that egg production is more sensitive to temperature than is longevity during the most productive period of life.

The rate of actual increase which is the observed value in a natural population will vary continually. It will increase or decrease as a result of many independent or related factors, but when the population suffers as the result of either a natural or unnatural catastrophic event, the potential which is expressed in terms of the intrinsic rate of natural increase can indicate the rapidity with which the species may re-establish itself.

Application of intrinsic rate of natural increase to aquatic snails.

For the determination of the intrinsic rate of natural increase it is necessary to draw up comprehensive life tables based on recorded data obtained from actual experiments. As has been stated earlier, the parameter r_m is calculated so as to apply to animals living under certain prescribed and carefully controlled conditions. If the resulting information is to have any meaning in relation to natural conditions, then the choice of environmental variables must relate as close as possible to the situation in the field.

Working with Microtus agrestis, Leslie and Ranson (1940) drew attention to this fact when they mentioned that under experimental conditions the vole could reproduce throughout the year, whereas in the field normal reproduction took place for only approximately 26 weeks of the year. This meant that for a long period of time the community would be living under conditions resulting in a negative rate of increase, for, while being subjected to normal forces of mortality, the animals were getting older but they were adding no young to the population. It is therefore necessary to determine this parameter r_m for a series of conditions which will relate to circumstances in nature.

When considering the aquatic environment a wide variety of physical variables are involved. The amount of dissolved salts, the pH of the water, its oxygen content, the quantity and nature of dissolved or suspended organic matter and temperature are instances of the factors which may influence the resultant population.

The present knowledge of the ecology of freshwater molluscs would indicate that the most important factor to be investigated under laboratory conditions is the effect of temperature on the intrinsic rate of natural increase. This should be done keeping all other factors constant and using a water which is derived from some snail habitat. Among other factors to be considered, perhaps food and the chemical composition of the water are important, but for this particular work they were not investigated. Snails are gross feeders consuming not only algae but detritus, mud and decomposing vegetation. As they seldom increase to such proportions as to denude a habitat of these constituents, food would not appear to be a limiting factor. Waters in the highveld areas of Southern Rhodesia tend to be oligotrophic and research which has been directed to correlating chemical factors with snail habitat has, as yet, yielded no positive results. Alves (1958) and de Meillon et al (1958) have reported analyses of natural waters in Southern Rhodesia and in South Africa but have shown no satisfactory correlation between these and snail habitat. This is in agreement with work done by Abdel-Malek (1958) in the Sudan.

When any animal is reared in a restricted environment such as an aquarium tank, excessive crowding or overpopulating is a danger and may be detrimental. Therefore it is important to consider the degree of crowding which can be tolerated by snails before egg production becomes seriously affected. It has been shown by Wright (1960) that *Bulinus* (*Bulinus*) *forskalii* is greatly affected both in growth rate and egg production by a filterable product of its own metabolism when kept in overcrowded conditions. Similarly, Chernin and Michelson (1957a, b) claim to have shown that overcrowding retards both egg production and growth of *Australorbis glabratus*. In the present work, the reaction to crowding has been investigated for each species on which laboratory studies have been carried out. Data for the compiling of life tables were then collected from snails living under standard conditions of crowding which were a compromise between optimal conditions for the snails and practicable experimental procedure. A final point to be considered in the collection of these data under laboratory conditions is the presence of other animals within the aquaria. The method of snail culture which has been found satisfactory for the present experiments requires the use of conditioned water. It is impossible to exclude from this both bacteria and protozoa, but the presence of the cladoceran *Ceriodaphnia sp.* has been found to limit these contaminants. As it did not appear to be detrimental to the snails, *Ceriodaphnia* was deliberately introduced into all the aquaria.

2. Mean generation time.

The second population parameter which is considered in this work is the mean generation time. It is a calculated estimation of the time elapsing from birth of parents to the birth of offspring (Andrewartha and Birch, 1954).

All the young of a generation are not born at one instant in time but birth is usually spread out for a considerable part of the life span of the mother. Young are born from parents as they progress through several age groups and therefore it is difficult to arrive at a true mean generation time. In a life table the young are indicated in the l_x column as l_0 and add up to 1.0000. These are the sum of several components $\frac{l_x m_x}{R^x}$ each of which is born from parents of age x. The average age weighted by reproduction is a near estimate of the average time from egg to egg, the mean generation time.

Thus the mean generation time is calculated from life table data as follows:-

$$\text{M.G.T.} = \frac{\sum \frac{x l_x m_x}{R^x}}{\sum \frac{l_x m_x}{R^x}} = \sum \frac{x l_x m_x}{R^x}$$

(By definition, since R is obtained by making the denominator equal to 1.)

(Dr. N. Hairston, personal communication).

3. Rate of growth.

The rate of growth is not a population parameter but it is a useful tool in the study of population ecology. An average growth rate compiled from data recorded under various constant conditions enables estimates to be made of the age structure of field populations, and therefore average growth curves have been produced for *Bulinus* (*Physopsis*) *globosus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis*.

With the spired shells, the maximum height from the base of the aperture to the apex has been measured, and with the discoidal shell of *B. pfeifferi* the maximum diameter was measured.

V. SPECIAL APPARATUS.

1. Temperature Control.

The collection of life table data at various temperatures required the maintenance of several aquaria at those temperatures for long periods of time. For levels above room temperature, a hot room or water baths could be used, but for lower temperatures refrigeration was required and specially constructed cabinets were used. These constant temperature cabinets were based on a design of Dr. Cotterell and were constructed by Messrs. William Jacks Ltd. of Salisbury. The ava ilable space within the cabinet measured 61 cm. x 61 cm. x 61 cm. and the necessary shelving provided adequate room for ten aquaria. The constant temperature chamber had a false bottom beneath which was a small 300 ohm. heating pad, a condenser connected to a refrigeration unit which was in the base of the cabinet, and a continually operating fan designed to circulate hot or cool air through the chamber. The chamber was roofed with a double layer of glass with air space between the sheets in order to minimise heat exchange. Above the glass was installed a 61 cm. 40 watt fluorescent tube which illuminated the chamber, and the whole top was enclosed with a light-proof lid.

Temperature was controlled by means of a thermostat situated within the chamber. This, operating through a hot wire vacuum relay, activated either the 1/6 h.p. refrigeration unit or the heating pad. In this way the temperature within the chamber could be regulated within a range of ± 0.5°C. and within the aquaria themselves the temperature fluctuation was seldom in excess of 0.1°C.

2. A device for quantitative sampling of some snail habitats.

All samples which were taken either in the Foyle ponds or in the Marlborough pond were collected with a modified Eckman dredge (see Fig. V_1). Two different samplers were used, both of similar dimensions and involving similar principles.

The original sampler was hand operated, the jaws being closed and kept shut by the operator pulling on a wire cable. This was later modified by the incorporation of a small winch to tension the cable. The second sampler was spring-loaded and easier to manage. This latter apparatus was designed and manufactured by G. Demblon Esq. of Carnie and Maddocks Ltd., Salisbury. It was a square metal box constructed of 1.5 mm. steel plate with a cross-sectional area of 1/20th sq. metre.

The top was closed by means of two hinged metal flaps each provided with a gauze window to allow movement of water. Distally the box was provided with hinged jaws which, when opened, allowed unrestricted access to the base and when closed, provided an almost watertight joint enclosing plants and debris within the box. Gauze-covered windows in the jaws and on two sides of the box allowed the escape of excess water during sampling operations. The jaws were spring-loaded and were held in juxtaposition by coil springs set horizontally on each side of the apparatus. Each arm of an inverted U-shaped bracket was connected by means of a swivel linkage to each jaw. The cross-piece of the U was attached to a steel rod which could be used to pull open the jaws against the action of the spring, or to push the jaws shut as a supplement to the spring action. This steel rod was attached to a lever, the fulcrum of which was a pole made of 2.4 cm. conduit piping which served as the vertical handle of the dredge.

Toopen the jaws, the operating lever was pulled upwards. This drew back the jaws (see Fig. $V._2$) against the tension of the springs; if the jaws were opened sufficiently for the springs to pass above

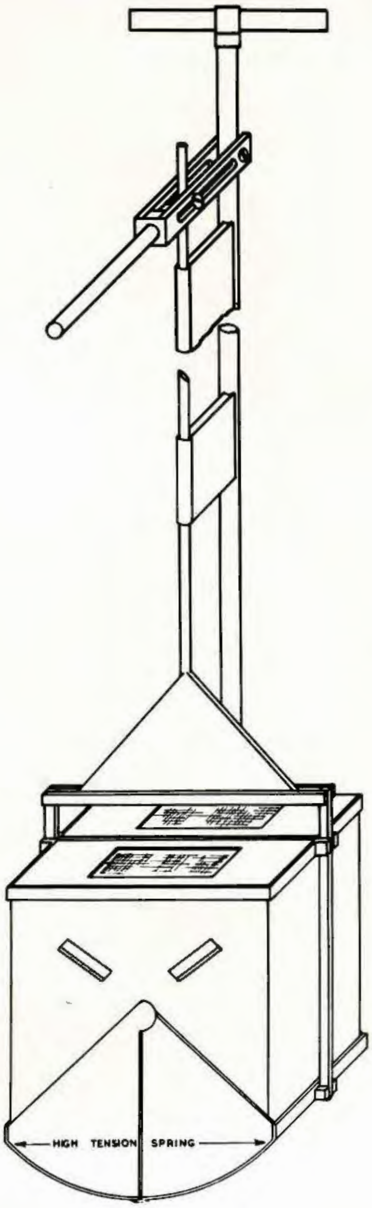


FIG. V.$_1$ Modified version of Eckman dredge in closed position.

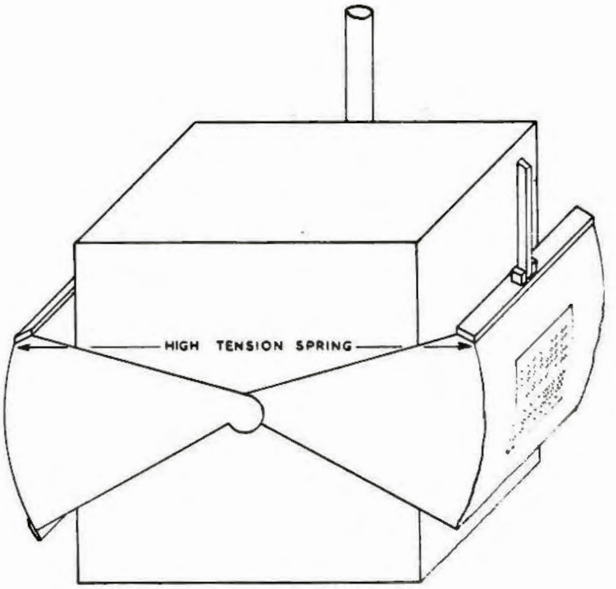


FIG. V.$_2$ Modified version of Eckman dredge set open. Note position of springs.

the pivot (see Fig. $V._2$), they would then start contraction and hold open the jaws. The box would then be lowered gently over the area to be sampled, the base being kept parallel with the water surface, and when it had settled on the bottom, the lever would be pulled downwards thus forcing the jaws past the horizontal position so allowing the tension of the springs and leverage on the handle to effect closure. When the jaws were being closed, the action of the springs could be augmented by the operator bearing down on the lever. In this way considerable pressure could be applied to the jaws which were able to sever heavy growths of Typha and Courtoisia and retrieve mud to a depth of several centimetres. The whole apparatus was then lifted up and the sample thus obtained washed into an enamel basin, transferred to a large polythene bag and returned to the laboratory for detailed examination. The samples were washed and minutely examined in large white photographic dishes (30 x 45 cm.). The complete examination of one sample took approximately three man hours.

VI. BIONOMICS OF BULINUS (PHYSOPSIS) GLOBOSUS IN RELATION TO TEMPERATURE.

1. General.

Bulinus (Physopsis) globosus is widely distributed throughout the territories of Central Africa, often occurring in waterbodies which are frequented by man. The species is the most important intermediate host of the southern African form of the blood fluke, Schistosoma haematobium. The snail inhabits a wide variety of waterbodies, and as yet, no successful effort has been made to describe them systematically. Gordon et al (1934) cite Blacklock in support of their observations that B. (Ph.) globosus appeared to be limited to slow running, weedy or shady streams and was found only in places where mud formed the bed of the waterbody. These somewhat sweeping statements do not apply in general to the species as it occurs in Southern Rhodesia, where it has been found in relatively new dams, in temporary waterholes and in streams, both sluggish and moderately fast flowing and where mud, sand or rock form the bed of the waterbody. Some attempts have been made (Alves, 1958, de Meillon et al, 1958) to define the chemical constituents of habitats suitable to the species but no attempts were made to investigate the finer details of microclimate, and no positive correlations were noted.

Of all the physical factors influencing life within a body of fresh water, temperature is generally recognised as exerting the most profound effects, both in the collective sense as limiting geographical distribution and in the individual sense as affecting metabolic processes. Not only does temperature alter the rate at which a poikilothermal animal can go about its normal trophic activities, but it affects the rate of organic decomposition, the oxygen saturation coefficient of the water along with other factors affecting the micro and macro habitats in the biotope.

Further, because in tropical regions it is seldom that sunlight is in short supply, temperature has a direct effect on the growth of phytoplankton. Thus when dealing with freshwater pulmonates which generally inhabit stagnant pools or slow moving streams, it would appear that temperature, by means of both direct and indirect influences, will cause profound and dramatic changes in the life patterns of the snails.

In general, the localities preferred by the bulinid and lymnaeid snails of Southern Rhodesia seem to be clear open water more or less covered with aquatic vegetation but without much overhead shade. In these conditions the habitat will be subjected to daily insolation and during the summer this will result in wide diurnal temperature fluctuations in the surface levels. At night, with normal temperature inversion taking place, the temperature of the waterbody will become stable at a minimal figure.

In Chapter III the records made at three habitats, Foyle, Derbyshire and Marlborough, were given. The following comments refer to all these waterbodies.

During the summer period of October to April surface maxima were high, even exceeding 30°C., with wide differences between diurnal maxima and minima. At a depth of 25 cm. maxima for the same period were also high, always in excess of 22°C., but here the temperature differential between minimum and maximum was far less, generally of the order of two or three degrees. There was little difference between minima recorded at the surface and minima at the lower depth. During the winter period of May to August surface maxima became progressively lower until August. After this there was a sharp rise as summer conditions approached. Throughout the winter, surface minima were fairly representative of the minima within the whole waterbody, there being little difference between these temperatures and those at a depth of 25 cm. Maxima at this depth were at their lowest during July and August.

It is probably safe to infer that the temperature records from Derbyshire, Marlborough and Foyle are a representative picture of water temperatures in the upper levels of small dams and ponds in the highveld areas of Southern Rhodesia.

If this be the case, then it is apparent that, although surface maxima rise very high, it is seldom that heat will affect the snails to any great extent. Even when the surface temperature exceeds 30°C. there is usually a steep temperature gradient between the surface layers and water at a depth of 25 cm. Thus to escape from the heat the snails have merely to migrate downwards until conditions become more favourable and they may then continue feeding at that depth. The situation is somewhat different during the winter. When the surface maxima are low, the snails are unable to seek out warmer conditions and thus their metabolic processes must be limited by the water temperature although, if low temperatures are sustained, acclimation may occur. Nevertheless, it is highly probable that at this period the snails encounter their most direct limiting temperatures.

From the ecological viewpoint it would seem that the most interesting range of temperature to be considered with regard to its effects on these snails would be from winter surface minima to summer maxima at the 25 cm. level, these conditions being representative of the range of conditions available to the snails within the waterbody. Applying this to the range of temperatures recorded in the Derbyshire weir, we find that the normal range to which these aquatic snails are exposed lies between 11.1°C. and 26.1°C. Considering these figures in relation to probable extremes which might occur in the aquatic environment, it is doubtful whether minimal temperatures ever drop much lower than 11° but it is quite probable that in small shallow waterbodies the maximal temperature to which the snails may be subjected would be several degrees in excess of 26°C. A range of 11 - 30°C. should cover the extreme temperatures to which the snails normally would be subjected. The effects of temperatures within these ranges on the snails form the main considerations of these laboratory experiments.

The choice of locality for the investigation of the population dynamics of B. (Ph.) globosus has been influenced, of necessity, by two features, the presence of large numbers of snails, and the suitability of adequate sampling procedure. In the first instance the Nyachivi stream was chosen because of the presence of reasonable numbers of snails and because it provided a typical contact point habitat where schistosome transmission occurred. Unfortunately, the snail population decreased steadily and after a particularly heavy flood, so few snails could be collected that sampling had to be discontinued in favour of the more satisfactory site on Foyle Farm.

2. Life tables and the rate of increase.

In Chapter IV the various parameters associated with the population dynamics have been considered. These will be calculated for B. (Ph.) globosus reared under standard conditions at different temperatures and should indicate the most suitable temperature for increase and the theoretical potential under those conditions.

The species lays eggs in clutches or egg masses of up to 40 eggs per egg mass, thus it was convenient to consider the progeny of a single egg mass along with progeny from other egg masses as the initial cohort of snails from which the life table data were obtained. The egg masses were chosen at random, the only requirements being reasonable size, from eight to 30 eggs, and that they had reached a stage of development where it was possible to distinguish infertile eggs. When the selected egg mass was removed from the parent aquarium it was placed in a small container and kept at the experimental temperature. The brood was nurtured through the early stages of life in the manner described in Chapter II and from time to time counts of survivors were made. When the snails were approximately four millimetres in length they were transferred to the large aquarium tanks. Depending on the numbers of survivors from each egg mass, one two or more large aquaria were used for maintenance. It was important to ensure that the snails were not overcrowded (snails were kept at a density of 1 - 1.5 snails per litre, with never more than six adults in a tank). Water in these aquaria was changed approximately every two months or whenever it appeared to be 'going off'. The aquaria were tended daily when food was changed, deaths recorded and eggs marked and counted. As the eggs developed, those infertile were recorded and the egg mass removed from the tank. The experiments were run under these prescribed conditions for as long as possible, with a minimum of 16 fortnights, by which time most of the relevant data for the calculation of the intrinsic rate of natural increase were available. In some cases cohorts were kept under the set conditions until all the snails were dead so as to be able to compile a comprehensive life table for the species. This yielded interesting information on the absolute maximum life expectancy under particular conditions and the actual pattern of egg production with respect to age.

To gain some insight into the response to temperature of a field population, cohorts of snails were reared at 18.0 ± 0.1°C., 22.5 ± 0.5°C., 25 ± 0.5°C., 27 ± 0.1°C. and room temperature. Data from these were used to calculate population parameters for each set of conditions.

(a). Life table : 25 ± 0.5°C.

The initial size of the cohort reared at this temperature was 114 individuals, all of which were used for the collection of mortality data; fecundity records were made from 34 of these snails. As each snail is capable of producing eggs, the data should be adequate and comprehensive. The results are presented in Table VI.$_1$ and in Fig. VI.$_1$

TABLE VI.1

Life table of *Bulinus (Physopsis) globosus* reared at a constant temperature of 25° ± 0.5°C. Nett reproductive rate (R_o) calculated for 26 fortnights. Pivotal age in fortnights.

x (Pivotal Age)	Total Snails	l_x (Survivorship)	Total Eggs	Egg laying snails	m_x (Eggs/Snail)	$l_x m_x$
0	114	1.0000				
.5	81	0.7105				
1.5	60	0.5263				
2.5	60	0.5263				
3.5	59	0.5175				
4.5	59	0.5175	115	34	3.382	1.750
5.5	54	0.4737	674	33	20.424	9.675
6.5	52	0.4561	1063	31	34.290	15.640
7.5	51	0.4474	2018	31	65.097	29.124
8.5	51	0.4474	2251	31	72.613	32.487
9.5	50	0.4386	2052	31	66.193	29.032
10.5	50	0.4386	2230	31	71.935	31.551
11.5	50	0.4386	2103	31	67.839	29.754
12.5	49	0.4298	2145	30	71.500	30.731
13.5	49	0.4298	1976	30	65.867	28.310
14.5	49	0.4298	2755	29	95.000	40.831
15.5	47	0.4123	2358	29	81.310	33.524
16.5	46	0.4035	1832	27	67.852	27.378
17.5	45	0.3947	1295	27	47.963	19.060
18.5	44	0.3860	1528	27	56.593	21.845
19.5	40	0.3509	1249	25	49.960	17.531
20.5	39	0.3421	1160	25	46.400	15.873
21.5	35	0.3070	1051	24	43.792	13.444
22.5	34	0.2982	1110	23	48.261	14.391
23.5	32	0.2807	265	22	12.045	3.381
24.5	30	0.2632	399	20	19.950	5.251
25.5	26	0.2281	346	17	20.353	4.643
26.5	23	0.2018	199	17	11.706	
						455.206

R_o = 455.206

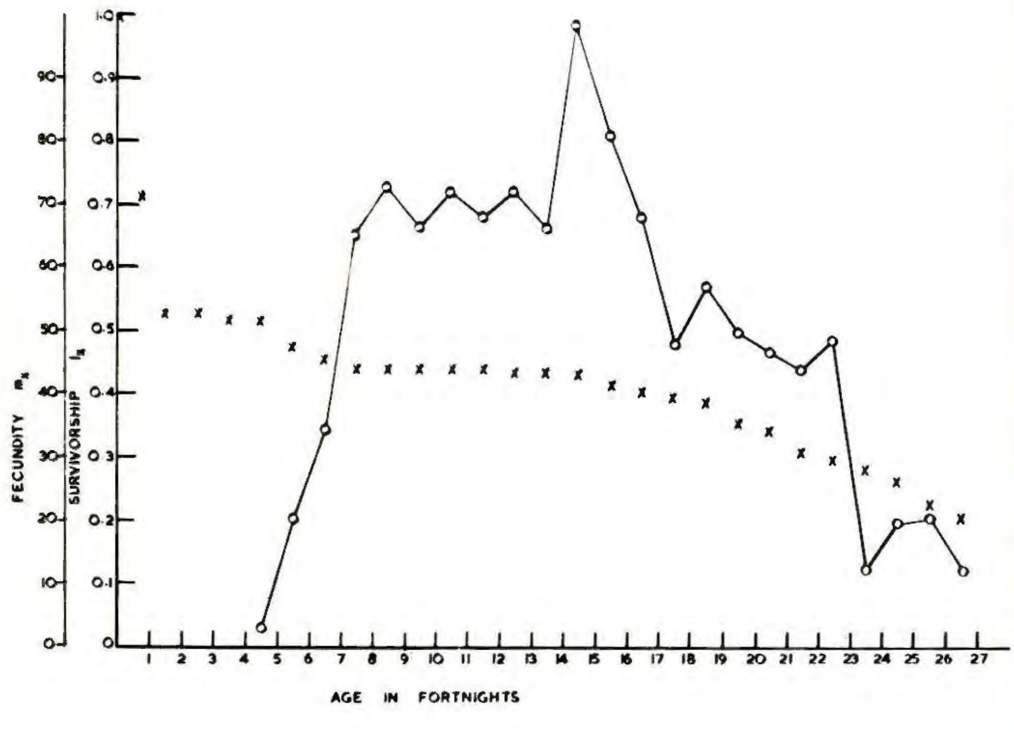


FIG. VI.1 Graphical representation of the life table of *Bulinus* (*Physopsis*) *globosus* reared at a temperature of 25 ± 0.5°C. The points marked 'x' signify survivorship (l_x), and those marked with a circle denote fecundity in eggs per snail (m_x).

At this temperature there was a high initial mortality among the newly hatched snails, but after approximately one month, the death rate decreased and remained fairly static; there was only a ten per cent. loss of the population between the third and fifteenth fortnights. After this the mortality rate again increased with some 22% of the original cohort surviving a complete year. The life table only extended for 28 fortnights with 20% of the population surviving. The longest recorded life span for B. (Ph.) globosus at 25°C. was 490 days. The egg laying pattern for this species can be explained most clearly with reference to the graph, Fig. VI.$_1$, where the l_x and m_x data are plotted against time. Egg production commenced during the fifth fortnight and continued throughout the period of observation, although during the last few intervals eggs were produced at a reduced rate. Initially egg production rose steeply from 3.38 eggs per snail in the fourth fortnight to approximately 70 eggs per snail in the seventh fortnight. This level was maintained until the 13th interval after which there was a dramatic rise in egg production. This was followed by a decline to a level which for six fortnights fluctuated around 48 eggs per snail. Finally, another drop in the 22nd fortnight brought egg production down to a level of between 10 and 20 eggs per snail.

In Table VI.$_1$ and subsequent life tables, the data have been recorded at the mid-points of each time interval. This was necessary for the calculation of the intrinsic rate of natural increase, as it enabled the approximation from integration to summation to be made. For the calculation of r_m and other parameters the data accumulated up to the 16th fortnight have been used.

(b). Life table : 27 ± 0.1°C.

An initial group of 37 eggs made up of three egg masses was reared in aquaria kept in a waterbath thermostatically regulated to 27°C. Shortage of space precluded the use of a larger number of snails, especially for mortality data. However, the information obtained shows an interesting pattern and can be compared with the data obtained from the other cohorts.

The data are given in Table VI.$_2$ and Fig. VI.$_2$ It will be seen that the pattern of mortality was for the most part very similar to that exhibited by the 25°C. cohort. After the 18th fortnight the death rates of these two cohorts separate, a higher mortality being recorded at the warmer temperature. Approximately 16% of the original cohort survived a full year and by the 31st fortnight one snail remained. This individual survived 481 days. The pattern of egg production at 27°C. was somewhat peculiar: there appeared to be cyclic rhythm of peak and trough repeated throughout the reproductive life of the cohort. Water in the aquaria was changed fairly regularly, but never were all the tanks drained and refilled at the same time; it is unlikely that the cyclic pattern was a response to refreshened conditions. At this temperature the snails matured rapidly but no faster than at 25°C. The initial pattern of egg production was very similar to that at 25°C. after which the warmer conditions restricted egg laying. At no time did the rate of egg production approach the high levels recorded at 25°C. Apart from four instances, egg production fluctuated between six and 25 eggs per snail until the 29th fortnight after which no more eggs were laid.

(c). Life table : 22.5 ± 0.5°C.

The progeny of four egg masses, totalling 48 individuals, were reared in aquaria kept in a thermostatically controlled constant temperature cabinet. Illumination was provided by means of a 40 watt fluorescent tube controlled by means of a time switch. The snails were reared for a total of 20 fortnights, the data being given in Table VI.$_3$ and Fig. VI.$_3$

It is unfortunate that the observations did not cover the duration of the life span under these conditions, but for the period covered, B. (Ph.) globosus shows a consistently high survival, of the

TABLE VI.$_2$

Life table of *Bulinus* (*Physopsis*) *globosus* reared at a constant temperature of 27 ± 0.1 °C. Nett reproductive rate (R_o) calculated for 26 fortnights. Pivotal age in fortnights.

x (Pivotal Age)	Total Snails	l_x (Survivorship)	Total Eggs	m_x (Eggs/Snail)	$l_x m_x$
0	37	1.0000			
.5	36	.9730			
1.5	25	.6757			
2.5	25	.6757			
3.5	19	.5135			
4.5	19	.5135	100	5.263	2.703
5.5	17	.4595	393	23.118	10.623
6.5	17	.4595	520	30.588	14.055
7.5	16	.4324	223	13.938	6.027
8.5	16	.4324	257	16.063	6.946
9.5	16	.4324	226	14.125	6.108
10.5	16	.4324	349	21.813	9.432
11.5	16	.4324	401	25.063	10.837
12.5	16	.4324	371	23.188	10.026
13.5	16	.4324	144	9.000	3.892
14.5	16	.4324	234	14.625	6.324
15.5	16	.4324	104	6.500	2.811
16.5	16	.4324	221	13.813	5.973
17.5	14	.3784	263	18.786	7.109
18.5	13	.3514	84	6.462	2.271
19.5	10	.2703	293	29.300	7.920
20.5	10	.2703	223	22.300	6.028
21.5	9	.2432	62	6.889	1.675
22.5	7	.1892	93	13.286	2.514
23.5	7	.1892	282	40.286	7.622
24.5	7	.1892	111	15.857	3.000
25.5	6	.1622	177	29.500	4.785
26.5	5	.1351	167	33.400	
27.5	4	.1081	0		138.681
28.5	4	.1081	21	5.250	
29.5	3	.0811	0		
30.5	2	.0541	0		

$R_o = 138.681$

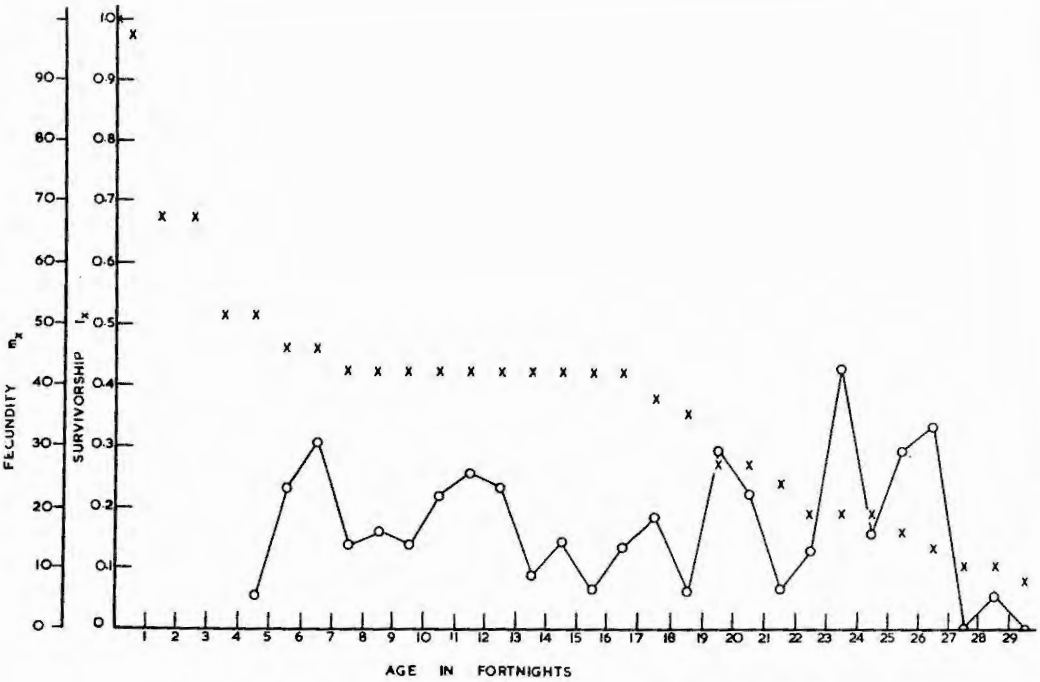


FIG. VI.$_2$ Graphical representation of the life table of *Bulinus* (*Physopsis*) *globosus* reared at a temperature of 27 ± 0.1°C. The points marked 'x' signify survivorship (l_x), and those marked with a circle denote fecundity in eggs per snail (m_x).

TABLE VI.$_3$

Life table of *Bulinus* (*Physopsis*) *globosus* reared at a constant temperature of 22.5 ± 0.5°C. Nett reproductive rate (R_o) calculated for 26 fortnights. Pivotal age in fortnights.

x (Pivotal Age)	Total Snails	l_x (Survivorship)	Total Eggs	Egg laying snails	m_x (Eggs/Snail)	$l_x m_x$
0	48	1.0000				
.5	44	0.9167				
1.5	30	0.6250				
2.5	30	0.6250				
3.5	30	0.6250				
4.5	30	0.6250				
5.5	29	0.6042				
6.5	27	0.5625	52	31	1.677	.943
7.5	26	0.5417	189	30	6.300	3.413
8.5	26	0.5417	626	30	20.867	11.304
9.5	26	0.5417	1156	30	38.533	20.873
10.5	26	0.5417	1230	30	41.000	22.210
11.5	26	0.5417	1327	30	44.233	23.961
12.5	26	0.5417	1273	30	42.433	22.986
13.5	26	0.5417	1062	30	35.400	19.176
14.5	26	0.5417	1163	30	38.767	21.000
15.5	26	0.5417	1073	30	35.767	19.375
16.5	25	0.5208	1175	29	40.517	21.101
17.5	24	0.5000	943	28	33.679	16.839
18.5	24	0.5000	1184	28	42.286	21.143
19.5	24	0.5000	1198	28	42.786	21.393
20.5	23	0.4792	1108	27	41.037	19.665
21.5	23	0.4792	900	27	33.333	15.973
22.5	23	0.4792	864	27	32.000	15.334
23.5	21	0.4375	838	25	33.520	14.665
24.5	20	0.4167	763	24	31.792	13.248
25.5	19	0.3958	629	22	28.591	11.316
						335.918

R_o = 335.918

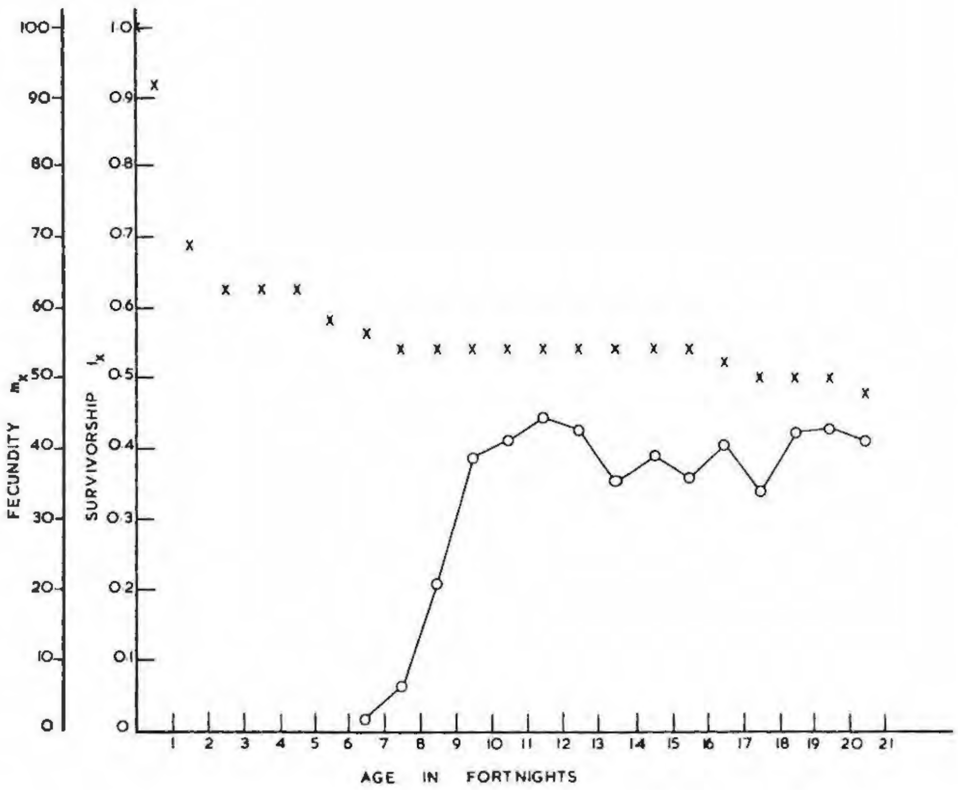


FIG. VI.$_3$ Graphical representation of the life table of *Bulinus* (*Physopsis*) *globosus* reared at a temperature of 22.5 ± 0.5°C. The points marked 'x' signify survivorship (l_x), and those marked with a circle denote fecundity in eggs per snail (m_x).

order of ten per cent. better than that of the snails kept at 25°C. The pattern of egg production was somewhat different from that observed at both 25 and 27°C. The onset of maturity was delayed for two fortnights by the lower temperature, the first eggs being laid during the seventh fortnight. By the tenth fortnight egg production had reached the level of approximately 40 eggs per snail and it fluctuated around this figure for the duration of the observations. Egg production per snail at this temperature was again in excess of that recorded for the species at 27°C.

(d). Life table : 18 ± 0.1°C.

An original group of 40 eggs derived from three egg masses was maintained in aquaria kept in a constant temperature cabinet set at 18°C. Conditions of illumination were identical to those in the 22.5°C. cabinet. The observations were maintained for only 17 fortnights and did not extend for the life span of the cohort; however, the pattern of survival and egg production was clear enough for comparison with the other groups, and adequate for the calculation of the population parameters.

As can be seen from the data given in Table $VI._4$ and Fig. $VI._4$ the initial mortality at this temperature was somewhat lower than that observed under warmer conditions; by the third fortnight some 75% of the initial population were still alive. During the next two fortnights the snails suffered a high mortality but after the sixth fortnight the survivors were better able to survive the cool conditions and no further deaths were recorded for the duration of observations.

At this temperature the onset of maturity was greatly delayed, no eggs being produced until the 12th fortnight. Egg production proceeded at a low level and at no time during the period of observation did it exceed 12 eggs per snail per fortnight. It is clear, however, that although the species could barely maintain its numbers at this temperature, gonad development was not inhibited by the cold.

TABLE VI.4

Life table of *Bulinus* (*Physopsis*) *globosus* reared at a constant temperature of 18 ± 0.1°C. Nett reproductive rate (R_o) calculated for 19 fortnights. Pivotal age in fortnights.

x (Pivotal Age)	Total Snails	l_x (Survivorship)	Total Eggs	m_x (Eggs/Snail)	l_xm_x
0	40	1.0000			
.5	39	.9750			
1.5	30	.7500			
2.5	30	.7500			
3.5	27	.6750			
4.5	21	.5250			
5.5	19	.4750			
6.5	17	.4250			
7.5	17	.4250			
8.5	17	.4250			
9.5	17	.4250			
10.5	17	.4250			
11.5	17	.4250	65	3.824	1.625
12.5	17	.4250	114	6.706	2.850
13.5	17	.4250	136	8.000	3.400
14.5	17	.4250	75	4.412	1.875
15.5	17	.4250	16	0.941	0.400
16.5	17	.4250	3	0.176	0.075
17.5	17	.4250	69	4.059	1.725
18.5	17	.4250	67	3.941	1.675
					13.625

R_o = 13.625

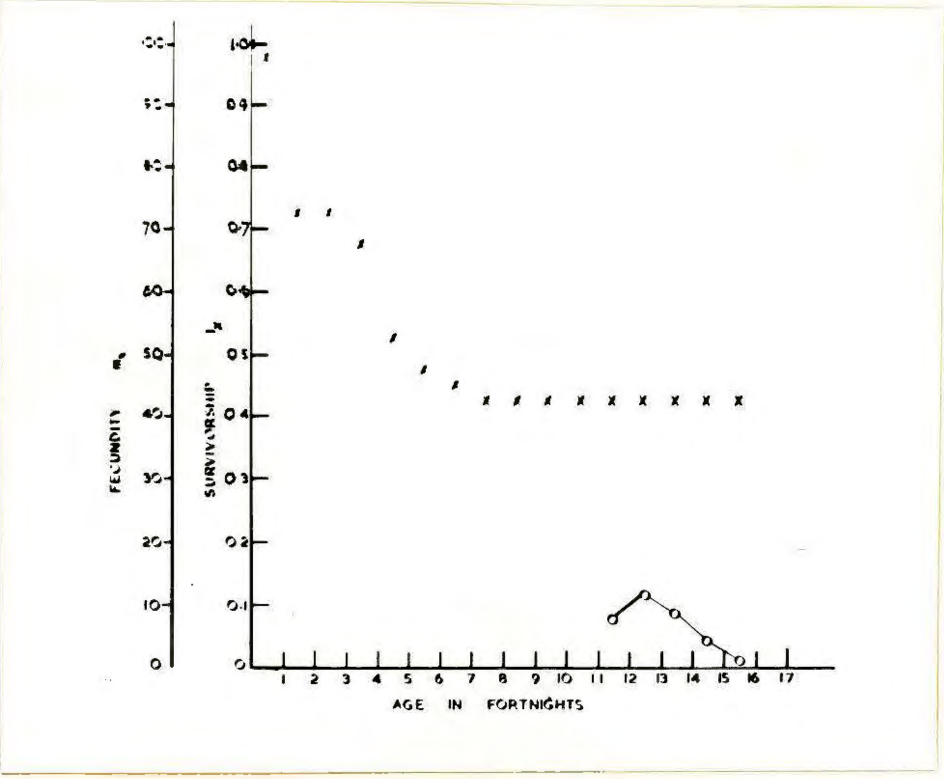


FIG. VI.$_4$ Graphical representation of the life table of *Bulinus* (*Physopsis*) *globosus* reared at a temperature of 18 ± 0.1°C. The points marked 'x' signify survivorship (l_x), and those marked with a circle denoted fecundity in eggs per snail (m_x).

(e). Life table : room temperature, March, 1961 to June, 1962.

Temperature conditions in a room cannot duplicate the pattern of extremes which may occur in natural waterbodies but they will follow the seasonal trends which occur out of doors. To provide a comparison with the four sets of preceding data all gathered under conditions of constant temperature, a life table for B. (Ph.) globosus was compiled from data recorded in a series of aquaria kept in an unheated room from March, 1961, onwards. An initial group of 85 eggs derived from four egg masses of similar age was used. The data are given in Table $VI._5$ and in Fig. $VI._5$. Daily maximum and minimum temperatures were recorded in an aquarium and the weekly averages of these values are included in Fig. $VI._5$

The mortality rate of the snails under these conditions was very similar to that recorded at 22.5°C. which must be close to the optimum for survival. Snails of this cohort have shown an extremely long life span, four of the original 85 survived two years, although they had long since ceased egg production. Almost 40% of the snails survived one year, which was the highest survival rate recorded in this work. Egg production showed an interesting pattern. The onset of maturity appeared to be delayed by winter conditions, temperatures dropped just before the snails could have been expected to lay, and egg production did not commence to any extent until temperatures began to rise in the early summer. The fecundity rate was never very high and fluctuated in relation to temperature when this altered considerably.

The significance of this life table is not to demonstrate the potential of the species to exist under changing temperature conditions but to show how prolonged conditions such as winter may affect the whole reproductive pattern of the species, although conditions for survival remain good. It draws attention to the fact that this species is very sensitive to temperature change and can tolerate only a restricted range. The high potential at temperatures lower than the optimal range represents an adjustment to winter conditions and

TABLE VI.5

Life table of *Bulinus* (*Physopsis*) *globosus* reared at room temperature from March, 1961 to June, 1962. Nett reproductive rate (R_o) calculated for 26 fortnights. Pivotal age in fortnights.

x (Pivotal Age)	Total Snails	l_x (Survivorship)	Total Eggs	m_x (Eggs/Snail)	$l_x m_x$
0	85	1.0000			
.5	85	1.0000			
1.5	51	.6000			
2.5	51	.6000			
3.5	51	.6000			
4.5	51	.6000			
5.5	51	.6000			
6.5	51	.6000			
7.5	51	.6000			
8.5	50	.5882	8	.160	.094
9.5	50	.5882	20	.400	.235
10.5	49	.5765	0		
11.5	49	.5765	73	1.489	.858
12.5	49	.5765	245	5.000	2.883
13.5	49	.5765	393	8.020	4.624
14.5	49	.5765	1243	25.367	14.624
15.5	47	.5529	1808	38.468	21.269
16.5	45	.5294	486	10.800	5.718
17.5	42	.4941	390	9.286	4.588
18.5	38	.4471	228	6.000	2.683
19.5	36	.4235	548	15.222	6.447
20.5	36	.4235	290	8.056	3.412
21.5	36	.4235	609	16.917	7.164
22.5	36	.4235	500	13.889	5.882
23.5	35	.4118	354	10.114	4.165
24.5	33	.3882	456	13.818	5.364
25.5	31	.3647	621	20.032	7.306
26.5	30	.3529	567	18.900	
27.5	30	.3529	422	14.067	97.316
28.5	28	.3294	188	6.714	
29.5	27	.3176	151	5.593	
30.5	24	.2824	164	6.833	

$R_o = 97.316$

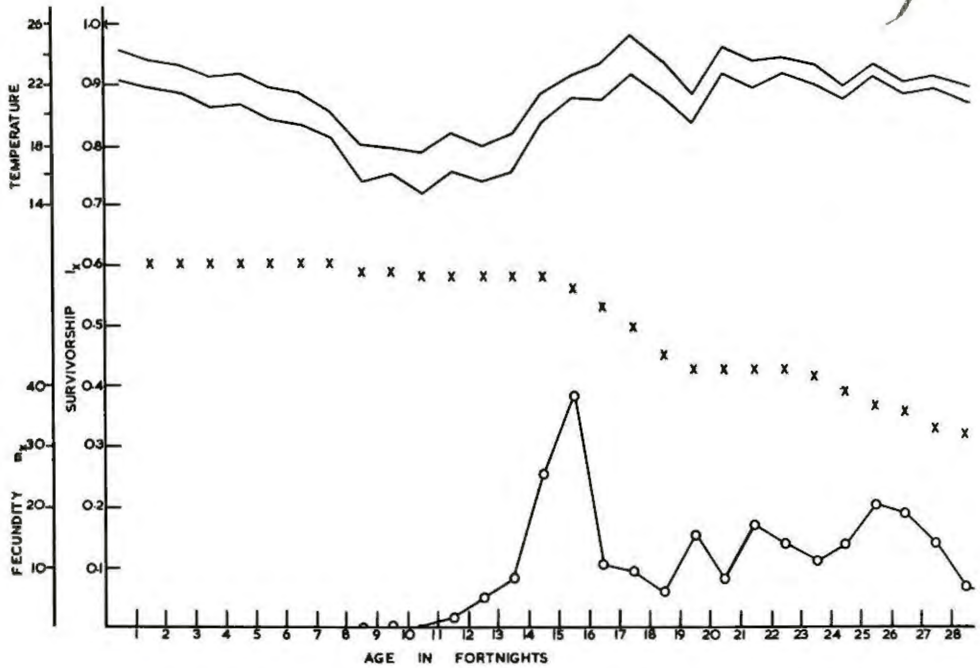


FIG. VI.5 Graphical representation of the life table of *Bulinus* (*Physopsis*) *globosus* reared at room temperature from March, 1961 to June, 1962. The points marked 'x' signify survivorship (l_x), and those marked with a circle denote fecundity in eggs per snail (m_x). Weekly averages of daily maximum and minimum temperatures are given.

leaves the population numerically well equipped to survive the hot pre-rain season. This information is liable to be overlooked when only constant temperatures are considered.

Significance of the life tables.

The life tables discussed above provide the necessary data for the calculation of the intrinsic rate of natural increase for each set of conditions. Bearing in mind the definition of r_m, it will thus be possible to determine the optimal temperature conditions for the species. This has ecological value because, with the help of this parameter, the potential increase of the species during the various seasons can be predicted. A knowledge of the rate of increase for a range of temperature conditions also provides information on the limiting effects of these conditions with regard to distribution of the species.

In Table $VI._6$ are summarised the calculated values of various population parameters for B. (Ph.) globosus under the various temperature conditions. In Fig. $VI._6$ is shown the relationship between the finite rate of increase (R) and temperature. At a temperature of 18°C. the species can only just maintain itself, R is slightly in excess of unity. This is purely an effect of temperature on fecundity because, as can be seen from the life table (Fig. $VI._4$), the species can survive quite well at 18°C. Egg production is not inhibited but the onset of maturity is considerably delayed, and the egg production which does occur is hardly sufficient to maintain the species even in the absence of adverse biotic influences. Thus it is unlikely that the species would exist under natural conditions where maximal temperatures do not exceed 18°C. throughout the year. However, it can tolerate conditions where temperatures fall to this level during part of the year.

When temperature conditions are maintained at 22.5°C. the finite rate of increase for B. (Ph.) globosus is 1.599 per fortnight. This temperature is suitable for the species although the rate of increase

TABLE VI.6

Population parameters of *Bulinus* (*Physopsis*) *globosus*, as calculated from life tables at 18, 22.5, 25 and 27°C. All values are based on a time interval of one fortnight.

R = finite rate of natural increase
r_m = infinitesimal or intrinsic rate of natural increase
M.G.T. = Mean Generation Time (fortnights)
B = birth rate
D = death rate.

	R	r_m	M.G.T.	B	D
18 ± 0.1°C.	1.247	0.2208	12.84	1.0079	0.1033
22.5 ± 0.5°C.	1.599	0.4695	9.86	1.5931	0.1474
25.0 ± 0.5°C.	1.935	0.6601	7.00	2.3015	0.2259
27.0 ± 0.1°C.	1.8217	0.6026	6.17	1.9504	0.1592

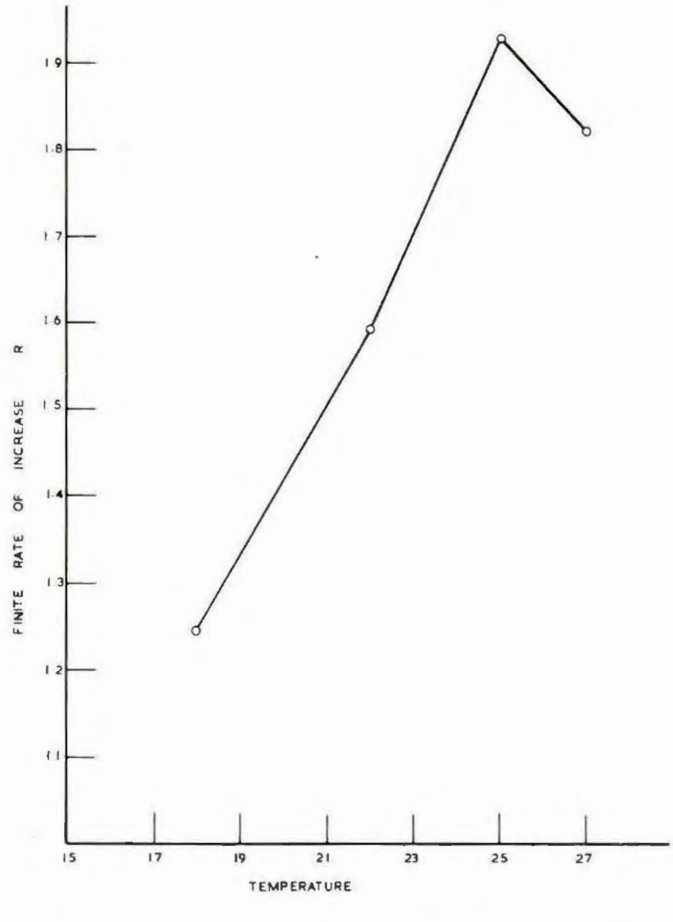


FIG. VI.$_6$ The realtionship between the finite rate of increase (R) of *Bulinus* (*Physopsis*) *globosus* and temperature.

is not very high. Under these laboratory conditions, in ten fortnights each individual would potentially give rise to 109 snails. Survival is favoured at 22.5°C. and there is evidence that the species would be long lived under these conditions. A result of this is the high nett reproductive rate, R_o, after a long period of time. Where maximal temperatures do not exceed 22.5°C. but remain close to that level, the species can survive well and increase at a slow rate; in a stable environment this response is likely to be of value to the species.

At a constant temperature of 25°C. the species exhibits a maximal rate of increase, R = 1.933. Temperature conditions are ideal for rapid development and egg production soon rises to a high level which is maintained for some time. Conditions for survival , especially during the effective reproductive period, are good although maximal life span is lower than under cooler conditions (see Fig. $VI._5$). At this temperature the potential of one individual would be to give rise to 729 snails in ten fortnights. As will be seen from the records of temperature within the various waterbodies (Chapter III), 25°C. is not at all unusual in nature especially in the upper levels and at those times of the year when the species may be recovering from catastrophic reductions in the population. In early summer waterbodies have usually been greatly reduced in size or even dried out completely, therefore a high rate of increase is necessary when the first rains fall. Towards the end of summer after the floods and flushing rains common in February, the warm weather during March and April once again provide ideal conditions for recovery.

At a constant temperature of 27°C. the rate of increase for the species is somewhat lower than at 25°C. The optimal temperature has been exceeded although the rate of increase is still high, R = 1.827. Under these stable conditions, in a period of ten fortnights one individual would give rise to 444 snails. As can be seen from the life table (Fig. $VI._2$), the rate of development is just as rapid as at 25°C., but the production of eggs is somewhat curtailed. The picture of mortality throughout the life span is very similar to that of the species reared at 25°C. as is the maximal recorded duration of life. What is significant is the great drop in egg production caused by a two degree rise in temperature.

3. The influence of temperature on egg production.

From the preceding data it is clear that there is a restricted range of temperature within which the species can both exist and increase in numbers. Under natural conditions however, aquatic snails will have to tolerate, for indefinite periods, temperature variations beyond this range. It is unnecessary to determine life tables for these wider conditions for, in all probability, the species will not survive long enough for adequate data to be amassed, or development may be inhibited. In any case the species could not live in a habitat in which extreme conditions prevailed for any length of time. What is important to know is the effect on the species of temperature changes of short duration. Therefore the following series of experiments were undertaken to study this.

(a). Seasonal conditions at room temperature.

Records of egg production made from a large number of *B. (Ph.) globosus* show an association between temperature and egg production. In Fig. VI.$_7$ the average weekly egg production per snail from five different aquaria, commencing 26th January, has been presented. Daily temperatures were recorded by means of a 'Sixes' thermometer kept permanently in an aquarium. Weekly averages of maxima and minima are included in the figure. It will be seen that there was a marked fall-off in egg production as temperatures dropped below the average figure of 20°C. Correspondingly, when temperatures rose above 20°C. after the winter period, egg production increased. An analysis of these figures has been carried out by the Biometry Unit of the Agricultural Research Council of Rhodesia and Nyasaland, who investigated the sample estimators of the cross serial correlation

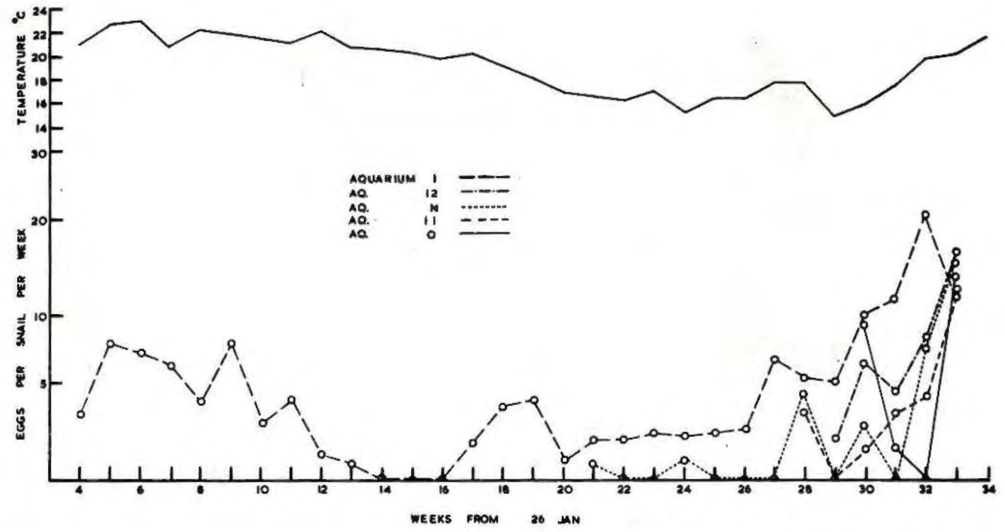


FIG. VI.$_{7}$ The average weekly egg production of *Bulinus* (*Physopsis*) *globosus* maintained at room temperature as from the 26th January, 1961. Individual records from five different aquaria and average weekly temperatures are given.

coefficients (see Fig. VI.$_8$). The data which are presented in Table VI.$_7$ and Fig. VI.$_7$ have been derived from individual records of several aquaria. For each separate aquarium the product moment correlation coefficient of the eggs laid per snail in a given week, is plotted for the range +1 to -1, and the temperature observed over a range of four weeks previous to and including the week of egg production. The snails of each aquarium were of the same age but as can be seen from Table VI.$_7$, the various aquaria were of different age groups. In all instances age zero was taken when the snails in the aquaria were of a size at which egg production would normally commence. Aquarium 1 was initiated in January whereas Aquarium 12 was at age zero in June, Aquaria 11 and 'N' both reached age zero in July and Aquarium 'O' in early August. This means that at any particular time, the prevailing temperature was influencing the various aquaria at different ages. It can be seen from Fig. VI.$_8$ that within each aquarium there is a lagged temperature effect: Aquaria 'N', 11 and 'O' show a positive correlation between egg production and temperature one, two and three weeks previously. With Aquarium 12 there is a distinct negative correlation with temperatures four weeks prior to egg production but the correlation becomes positive when temperatures only two weeks prior to the egg laying, are considered. This is not the case with the oldest group, Aquarium 1, where it would appear that the main effect of increased previous temperatures would be to depress egg production, and temperatures nearer the week of egg laying appear to have little effect on the eggs produced per snail. Clearly egg production is influenced not only by temperature per se, but also by a factor relating temperature to the age of the snails, and the younger the snails, the more positive is the correlation between increased egg production and temperature. This would infer that in the younger snails, temperature conditions both in the present and for several weeks before, influence the development and maturation of ova and the rate of oviposition, but in older snails with active

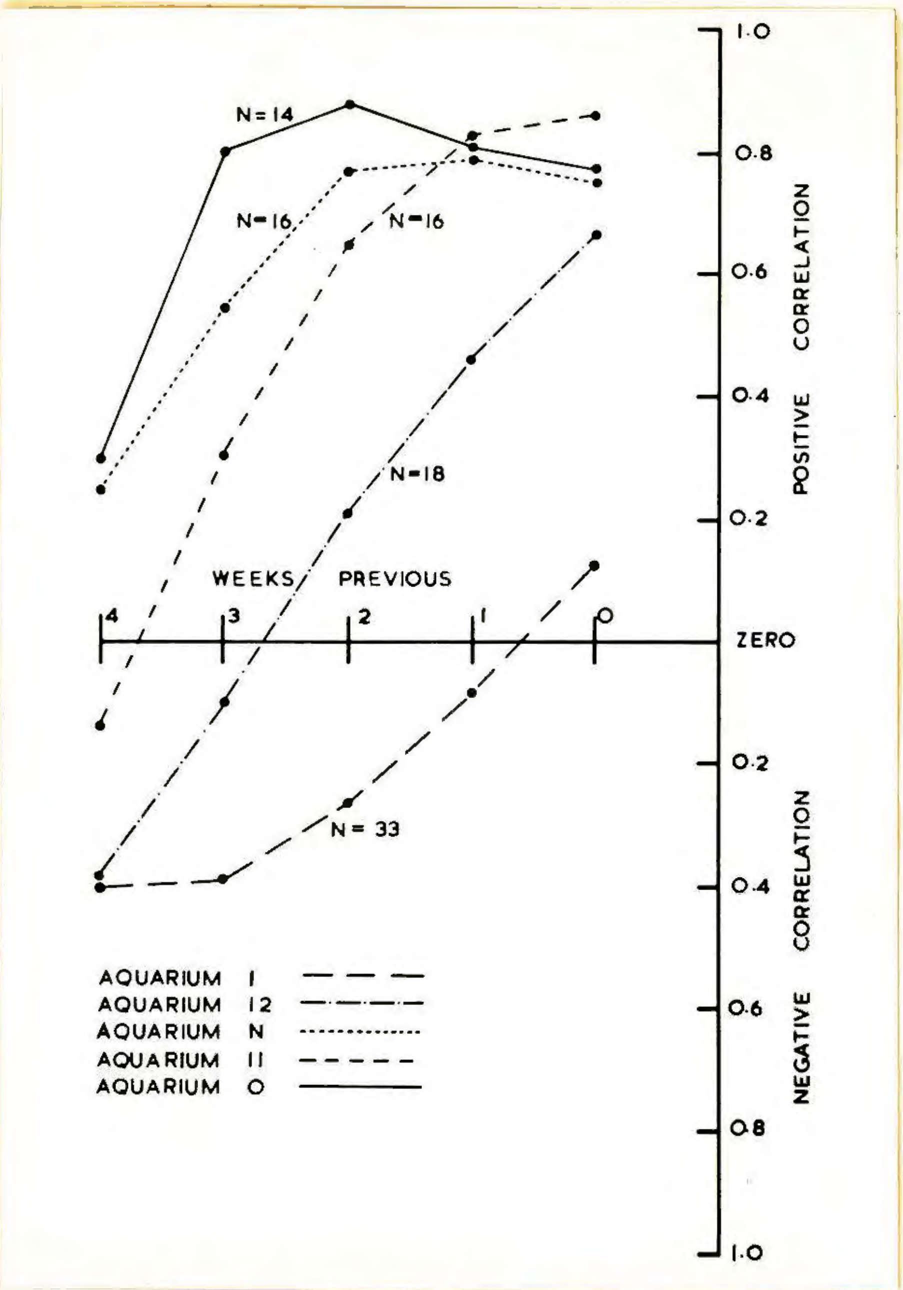


FIG. VI.8 Product moment correlation coefficients for *Bulinus* (*Physopsis*) *globosus* showing the influence of temperature during the current week and for four weeks previously on egg production at room temperature. Data for analysis were derived from Table VI.7 The actual age in weeks of each aquarium at the end of the series is given as 'N'.

TABLE VI.7

Egg production of *Bulinus* (*Physopsis*) *globosus* at room temperature, 26th January to 4th October, 1961. Age zero was taken when the snails were of an average size of 8 mm. and therefore capable of egg production.

	Aquarium 1			Aquarium 12			Aquarium 11			Aquarium N			Aquarium O				
Weeks from 26th Jan.	Eggs	Snails	Eggs/ Snail	Eggs	Snails	Eggs/ Snail	Eggs	Snails	Eggs/ Snail	Eggs	Snails	Eggs/ Snail	Eggs	Snails	Eggs/ Snail	Av.Max. Temp.	Av.Daily Temp.
1	0	21														22.8	21.9
2	0	21														23.1	22.3
3	0	21														22.6	21.8
	Age	Zero															
4	66	21	3.1													22.1	21.0
5	162	21	7.7													24.2	22.7
6	147	21	7.0													23.9	23.0
7	130	21	6.2													22.8	21.9
8	80	21	3.8													23.2	22.3
9	161	21	7.7													22.9	22.0
10	55	21	2.6													22.7	21.6
11	83	21	4.0													22.2	21.3
12	23	21	1.1													23.2	22.3
13	14	21	0.7													21.7	20.9
14	0	21	0													21.9	20.7
15	0	21	0													21.3	20.5
16	0	21	0													21.1	20.0
17	35	21	1.7													21.3	20.3
18	77	21	3.7													20.7	19.3
				Age	Zero												
19	85	21	4.0	0	15											19.3	18.4
20	17	21	0.8	0	15											18.3	16.9
							Age	Zero		Age	Zero						
21	38	21	1.8	0	15		0	12		8	12	0.6				17.3	16.4
22	38	21	1.8	0	15		0	12		0	12	0				17.3	16.1
													Age	Zero			
23	46	21	2.2	0	15		0	12		0	12	0	0	11		17.8	17.0
24	43	21	2.0	0	15		0	11		10	12	0.8	0	11		16.6	15.5
25	45	21	2.2	0	15		0	11		0	12	0	0	11		17.9	16.5
26	50	21	2.4	0	15		0	11		0	12	0	0	11		17.7	16.5
27	138	21	6.6	0	15		0	11		0	12	0	0	11		19.3	18.0
28	114	21	5.4	0	15		35	11	3.2	53	12	4.4	0	11		18.9	17.9
29	108	21	5.1	28	15	1.9	0	11	0	0	12	0	0	11		16.5	15.3
30	216	21	10.3	96	15	6.4	14	11	1.3	30	12	2.5	100	11	9.1	17.8	16.8
31	241	21	11.5	68	15	4.5	36	11	3.2	0	12	0	15	11	1.4	19.1	17.7
32	437	21	20.8	123	15	8.2	46	11	4.2	88	12	7.3	0	11	0	20.9	19.8
33	245	21	11.7	243	15	16.2	122	11	12.2	180	12	15.0	150	11	13.6	21.5	20.2
34	234	21	11.1	159	15	10.6	189	11	17.2	145	12	12.0	243	11	22.1	22.2	21.6
35	229	21	10.9	104	15	6.9	97	11	8.8	166	12	13.8	357	11	32.5	22.3	21.6
36	13	21	0.6	35	15	2.3	85	11	7.7	481	11	43.7	229	11	20.8	22.4	21.7

and fully developed gonads, the influence of rising temperature even exerts a retarding effect on egg production.

For further investigations into the influence of temperature on egg production, two groups of five B. (Ph.) globosus were kept for several weeks at a constant temperature of 25°C. The temperature was then reduced abruptly to 18°C. and maintained at this level for five weeks after which the temperature was increased again to 25°C. The results are given in Table VI.$_8$ In both aquaria egg production during the initial period at 25°C. fluctuated considerably, but egg production was depressed to a consistently low figure when the temperature fell. It is interesting to note that when conditions returned to 25°C. egg production rose considerably. It would appear that the change in temperature from 18 to 25°C. produced an initial spurt of egg production for one to two weeks, a week after the change took place.

(b). Limiting effects of temperature on egg production.

Using a thermostatically controlled constant temperature cabinet, observations were made on the limiting effect of temperature on egg production. Two series were carried out, the first covering lower temperatures and the second, higher temperatures. The first experiment considered a range of temperatures between 14 and 29°C. The initial temperature was 23°C. which was maintained for a fortnight after which the temperature was reduced to 21°C. This process of reduction was gradual, approximately two degrees per step. Allowing 14 days at each temperature, the process was continued to the minimum of approximately 14°C. After this, temperatures were increased stepwise at a similar rate to 29°C., with a final return to 25°C. The experiment lasted 11 fortnights.

Twenty-six mature snails approximately six months old were used in the experiment. It was found that some snails ceased producing eggs at a particular temperature especially when this was high. Those which did not recommence egg laying after four weeks at the

TABLE VI.8

Showing the effects of drastic temperature changes on the egg laying of *Bulinus* (*Physopsis*) *globosus*. Five snails in each aquarium.

Date	Aquarium 1		Aquarium 2		
	Total Eggs	Eggs/ Snail	Total Eggs	Eggs/ Snail	Temperature °C.
24/8 - 30/8	84	16.8	11	2.2	25
31/8 - 6/9	98	19.6	7	1.6	25
7/9 - 13/9	95	19.0	22	4.4	25
14/9 - 20/9	25	5.0	38	7.6	25
21/9 - 27/9	78	15.6	65	13.0	25
28/9 - 4/10	160	32.0	73	14.4	25
5/10 - 11/10	27	5.4	10	2.0	18
12/10 - 18/10	29	5.8	12	2.4	18
19/10 - 25/10	27	5.4	4	0.8	18
26/10 - 1/11	28	5.6	0		18
2/11 - 8/11	0		9	1.8	18
9/11 - 15/11	31	6.2	69	13.8	25
16/11 - 22/11	265	53.0	118	23.6	25
23/11 - 29/11	143	28.6	88	17.6	25
30/11 - 6/12	72	14.4	101	20.2	25
7/12 - 13/12	93	19.2	114	22.8	25
14/12 - 20/12	118	23.6	203	40.6	25

final temperature were considered to be physiologically deranged and were not included in the experiment from the time of their last egg deposition. This is the reason for the sharp drop off in the number of snails towards the end of the series. The results are given in Table VI.$_{9}$ and are analysed graphically in Figs. VI.$_{9}$ and VI.$_{10}$

The second series investigated egg production ranging from 17.5 to 34.4°C. The initial temperature was 25°C. which was maintained for two weeks after which the temperature was dropped abruptly to 17.5°C. and kept at that level for a further fortnight. The temperature was then increased in steps to 34.4°C. This temperature was maintained only for one week because of the obvious distress of the snails. The temperature was finally reduced to 25°C. for a four week recovery period.

Thirty-one snails three to four months old initiated the experiment. The snails laid fewer eggs than those used in the first series; however, the data as seen in Table VI.$_{10}$ and Figs. VI.$_{11}$ and VI.$_{12}$ show similar trends. A drop in temperature from 25 to 17.5°C. more than halved the rate of egg production which was re-established as the temperature rose to 20.4, 21.9 and 24.1°C. A temperature of 31.4°C. caused a drop in egg production, and with a rise to 34.4°C., egg production was completely inhibited.

A consideration of these preceding data indicates that *B.* (*Ph.*) *globosus* is capable of producing eggs within a wide range of temperature from some figure below 14.2°C. to a temperature in excess of 31.4°C. but less than 34.4°C.

The fact that in the preceding data it has been shown that the species is capable of producing eggs over a wide temperature range does not conflict with the life table data. This latter information is of much greater value for it relates to the ability of the snail to increase its numbers. The correlation of temperature and egg production as demonstrated in Figs. VI.$_{6}$, VI.$_{10}$ and VI.$_{12}$ indicates

TABLE VI.9

Egg production of *Bulinus* (*Physopsis*) *globosus* at various temperatures. Snails were exposed to each temperature category for a period of 14 days (one fortnight). Temperatures were maintained at ± 0.5°C. excluding 14.2°C. which was ± 1.0°C.

Week	Temp. °C.	Total Eggs	Total Snails	Average eggs per snail per week
1	23.1	1151	26	
2	23.1	1085	26	43.00
3	21.1	839	26	
4	21.1	924	26	33.91
5	19.1	608	26	
6	19.1	494	24	21.98
7	17.0	184	24	
8	17.0	221	24	8.44
9	14.2	59	23	
10	14.2	65	22	2.76
11	16.9	104	22	
12	16.9	188	21	6.84
13	20.2	277	20	
14	20.2	477	20	18.85
15	23.1	289	20	
16	23.1	377	20	16.65
17	25.9	265	19	
18	25.9	464	13	24.82
19	29.7	98	10	
20	29.7	89	10	9.35
21	25.0	259	10	
22	25.0	251	8	28.63

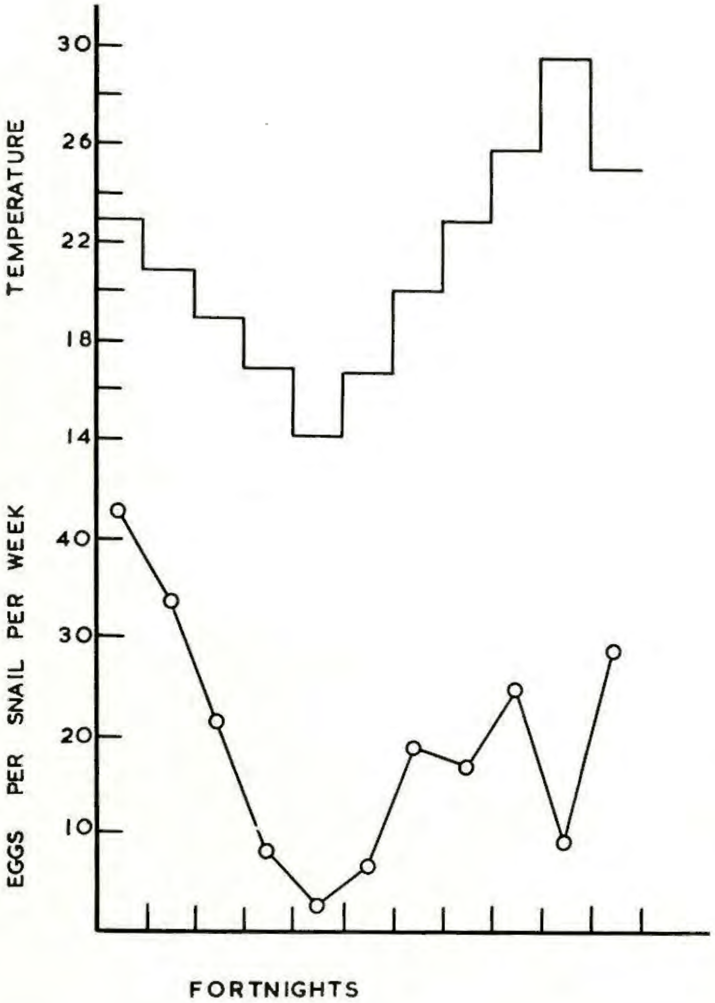


FIG. VI.9 Graph showing the rate of egg production of Bulinus (Physopsis) globosus expressed in eggs per snail per fortnight (circles) of a cohort of snails kept at temperatures ranging from 14.2 to 29.7°C. Each temperature was maintained for a period of two weeks (cf. Table VI.9)

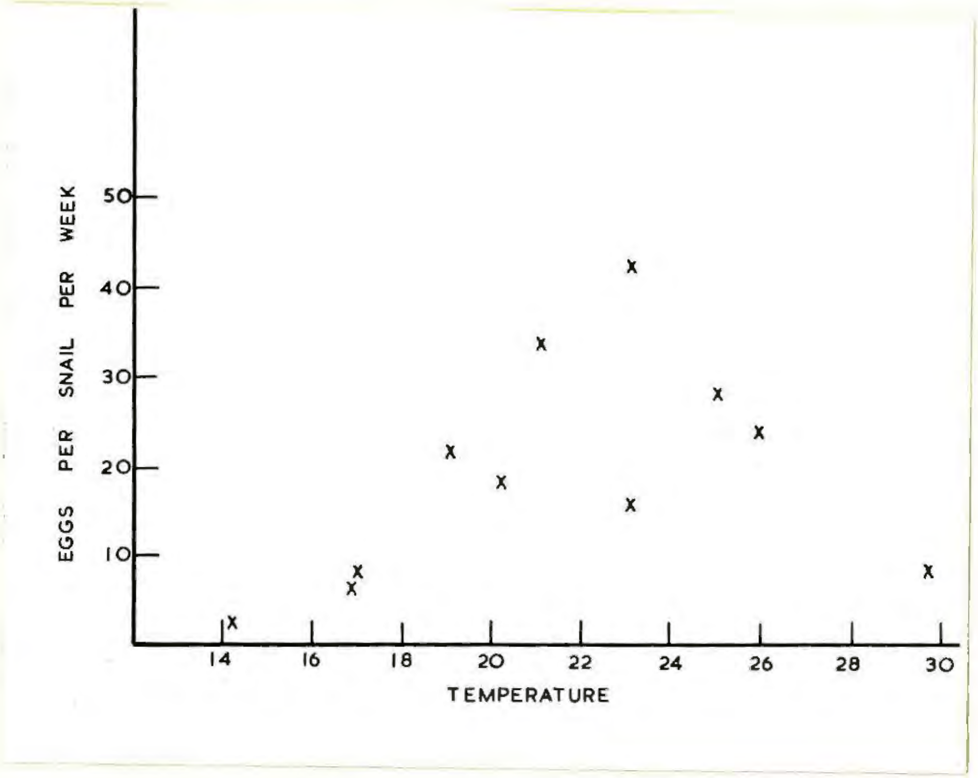


FIG. VI.$_{10}$ Graph showing the correlation of egg production in Bulinus (Physopsis) globosus with temperatures ranging from 14.2 to 29.7°C. (cf. Table VI.$_9$)

TABLE VI.10

Egg production of *Bulinus* (*Physopsis*) *globosus* at various temperatures. Snails were exposed to each temperature category for a period of 14 days (one fortnight). Temperatures were maintained at ± 0.5°C.

Week	Temp. °C.	Total Eggs	Total Snails	Average eggs per snail per week
1	25.0	334	31	
2	25.0	494	30	13.62
3	17.5	206	30	
4	17.5	96	30	5.03
5	20.4	175	30	
6	20.4	370	30	9.08
7	21.9	367	30	
8	21.9	234	29	10.15
9	24.1	298	29	
10	24.1	678	29	16.83
11	25.1	307	28	
12	25.1	417	28	12.93
13	31.4	159	19	
14	31.4	116	17	7.59
15	34.4	0	10	Nil
16	25.0	63	10	
17	25.0	253	10	15.80

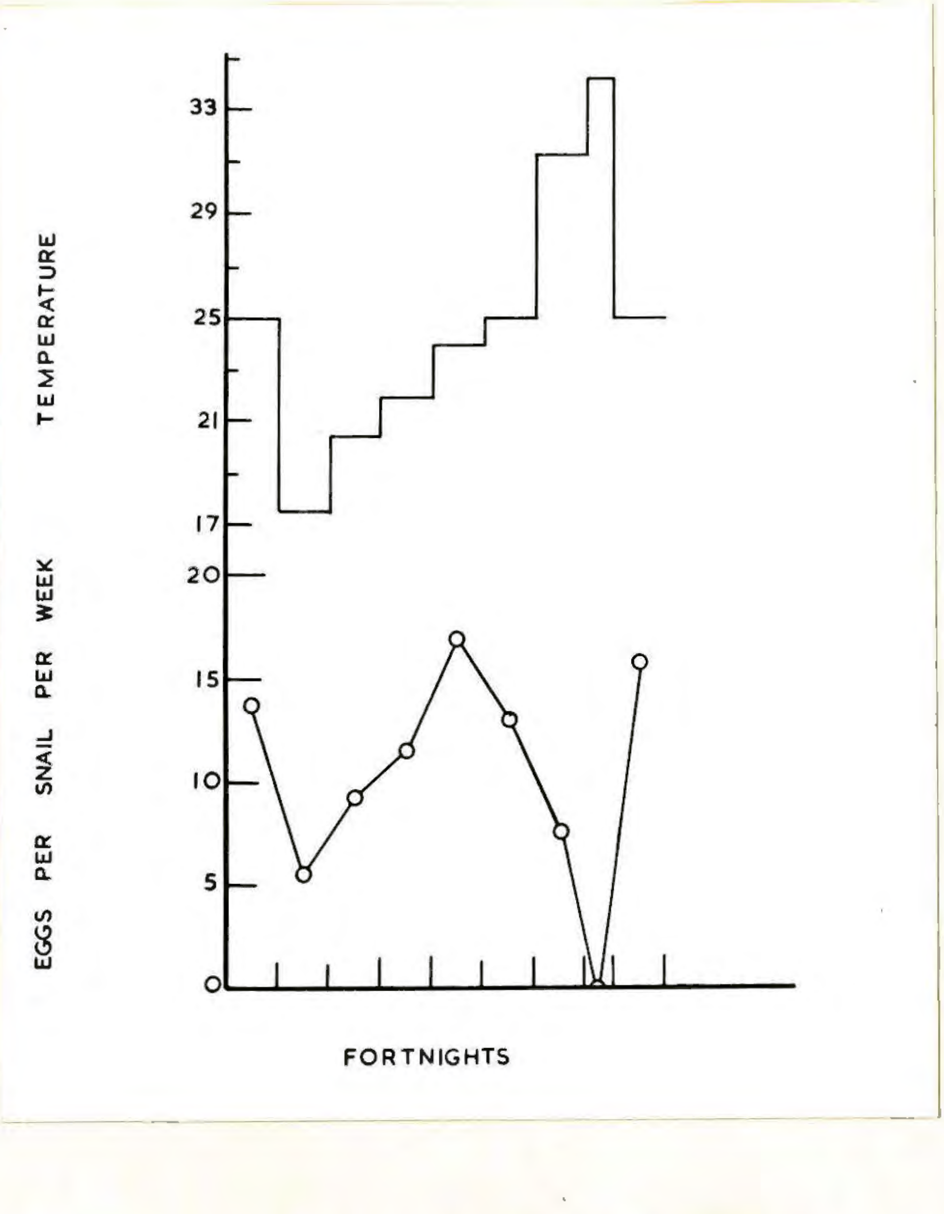


FIG. VI.$_{11}$ Graph showing the rate of egg production of Bulinus (Physopsis) globosus expressed in eggs per snail per week (circles) of a cohort of snails kept at temperatures ranging from 17.5 to 34.4°C. Each temperature was maintained for a period of two weeks (cf. Table VI.$_{10}$).

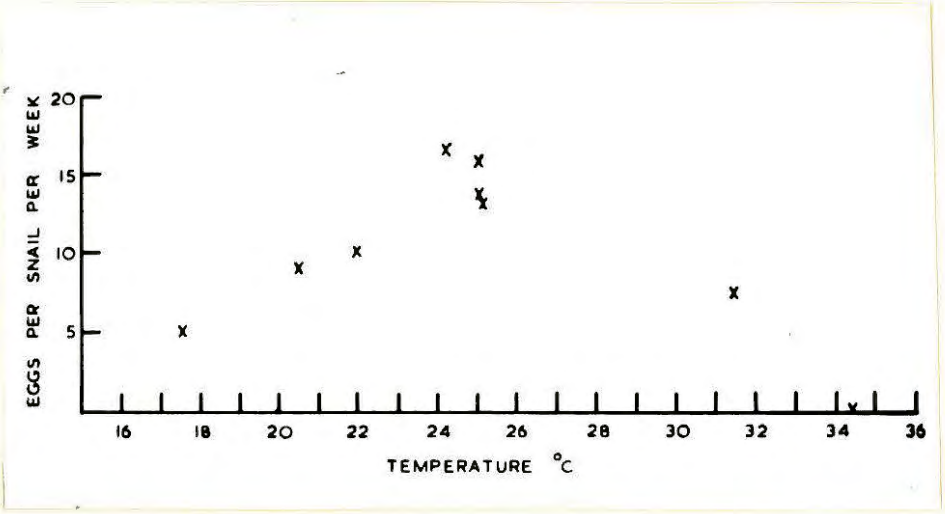


FIG. VI.$_{12}$ Graph showing the correlation between egg production in *Bulinus* *(Physopsis)* *globosus* with temperatures ranging from 17.5 to 34.4°C. (cf. Table VI.$_{10}$)

the temperature range in which *B.* (*Ph.*) *globosus* can produce eggs. If this information alone is considered, an inaccurate appraisal of the species' tolerance can be obtained. In fact, the more intimate population parameters have described the limitations of temperature more precisely.

Hubendick (1958) has inferred that freshwater snails are euryok, this is tolerant of wide ranges of conditions. This is not the case with *B.* (*Ph.*) *globosus* in respect to temperature. Certainly, in nature, temperatures do vary considerably but a glance at the records of temperature fluctuations at various levels within a waterbody shows that there is usually a wide range of conditions available for choice.

There are times when the choice becomes limited. When waterbodies become very shallow there is little escape from warm conditions during the day, but this would probably be of short duration prior to aestivation in the mud. During winter, the whole waterbody cools down and there is no escape from the cold except on sunny days when the uppermost layers of water will be slightly warm. At this time the species, although unable to increase effectively, is well equipped to survive the cold with a low mortality.

4. *The growth of Bulinus (Physopsis) globosus under laboratory conditions.*

(a). *The effect of temperature on the rate of growth under laboratory conditions.*

In order to interpret population data from field studies it is necessary to estimate the growth of some measurable index. In general, the height of the shell is used and with this it is possible to estimate the age of a natural population, given the size distribution of this character. McMullen (1947) measured the rate of growth of *Oncomelania quadrasi* (Moll) by comparing the modes of successive size frequency curves. Pesigan *et al* (1958) and Webbe

(1962) have applied this technique, supplemented by laboratory observation, to determine the growth rates of *Q. gundrasi* and *Bulinus* (*Physopsis*) *nasutus productus* (Mandahl-Barth). Neither of these authors appears to have attempted to correlate the rate of growth with temperature or season. This may not be important when dealing with a small snail which grows slowly (*Q. quadrasi*), or a snail which grows rapidly (*Lymnaea natalensis*, see Chapter VIII). But with the medium size snails it would appear to be important and is being considered here.

The growth rate of *B.* (*Ph.*) *globosus* has been studied in the laboratory under various temperature conditions. From these data four average growth curves have been compiled. These are given in Fig. VI.$_{13}$ where comparisons can be drawn. In addition to the average curves the progress of the fastest growing snails under each set of conditions is given. This is to emphasise the highest potential for growth under those conditions. In a restricted environment such as an aquarium there is a considerable degree of individual variation and a few stunted individuals would influence the estimate of the mean growth rate. In nature it is unlikely that these individuals would survive long and so influence the natural growth picture. In order to record the degree of variation relevant data are given in Table VI.$_{11}$ The curves representing average growth rates have been based on mean measurements taken from numbers of snails reared throughout their life under standard conditions. As the snails were not all measured on the same date or at exactly the same age it has been difficult to obtain sufficient measurements at particular ages in order to calculate standard deviations. However, standard deviations have been calculated for some points on each growth curve. It should be noted that in some instances the mean value of the point in the table (VI.$_{11}$) does not correspond with the appropriate value on the curve. This is because the curve is a graphical representation of the size of a larger number of snails than those used for the calculation of the standard deviation.

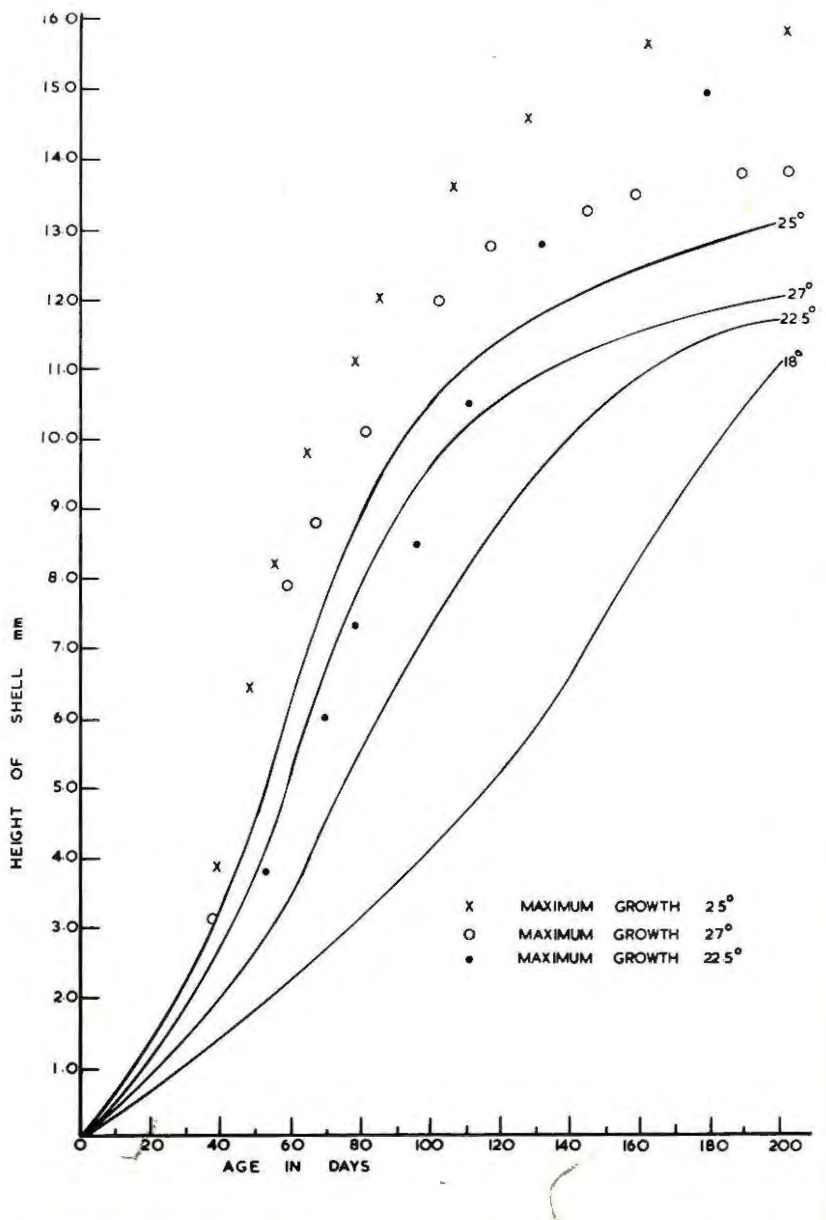


FIG. VI.$_{13}$ Average growth curves of <u>Bulinus</u> (<u>Physopsis</u>) <u>globosus</u> taken from snails reared under standard conditions at 18°, 22.5°, 25° and 27°C. The individual spots mark the maximum rate of growth recorded for any particular snail under these conditions.

TABLE VI.$_{11}$

Showing variation in the rate of growth of *Bulinus* (*Physopsis*) *globosus* at different temperatures under laboratory conditions.

Temperature °C.	Age in Days	Mean Size mm.	Standard Deviation	Number of Replicates
22.5 ± 0.5	41	2.45	0.374	17
	60	3.21	1.321	30
	95	6.26	1.428	18
	135	9.69	1.556	26
25 ± 0.5	35	2.08	0.503	18
	54	5.62	1.283	19
	62	7.08	1.239	27
	106	11.24	1.447	22
	123	11.76	1.194	15
	163	12.35	1.454	18
	200	12.80	1.399	15
27 ± 0.1	28	1.76	0.331	19
	55	4.64	1.691	17
	77	7.50	2.248	17
	115	10.03	1.738	16
	145	11.08	1.518	16
	201	11.98	1.536	16

The curves have been extrapolated to zero time which corresponds with the laying of the eggs, and the average incubation period at each temperature is given by the intercept at 0.8 mm., the average length of B. (Ph.) globosus at hatching.

The growth pattern (Fig. VI.$_{13}$) of the species at 18°C. was abnormal, indicative of rather unsuitable conditions, and is discounted. On the average, snails grew more slowly at 22.5°C. than at 27°C., but at 25°C. the best average rate of growth was recorded. This situation closely resembles the various values for intrinsic rate of natural increase mentioned above. It would appear to be significant, however, that at all three temperatures, the progress of the fastest growing snails was well in excess of the average and that there was a similarity between the maximal patterns of growth both at 25 and 27°C. At a temperature of 22.5°C. growth up to approximately the 100th day was slow, but after this time, although there was little change in the average figure, the fast growing snails approached the size of those at the other temperatures.

It is important to correlate these growth curves with the patterns of growth of the species under natural conditions and to determine whether a single average growth pattern will suffice to age snails in the field throughout the whole year or whether several growth curves must be compiled for various seasonal periods.

(b). The effect of density on the rate of growth under constant temperature conditions.

It would appear from preceding work that the growth rate of Bulinus (Physopsis) globosus is dependent on the prevailing temperature and as with the intrinsic rate of natural increase, growth is optimal at 25°C. Here it is intended to use the rate of growth of snails as a measure of response to various degrees of crowding, temperature being kept at the optimum. This will not have direct application to field conditions because snails seldom occur naturally at the densities which are considered here.

Its importance lies in determining the degree of crowding which the species can tolerate in the confines of a small aquarium. Chernin and Michelson (1957a, b) and Wright (1960) have discussed the relationship between crowding and growth, indicating that stunting occurs where conditions become overcrowded. In this work the growth of *B.* (*Ph.*) *globosus* living in one litre capacity aquaria at densities between one to ten snails per litre is considered. The optimal rate of growth should indicate the best conditions for the species.

All observations were carried out at a constant temperature of 25 ± 0.5°C. All aquaria were the same size (one litre cylindrical glass dishes 145 mm. in diameter) therefore surface area and area of bottom were constant for each set of conditions. Apart from the observations made at a density of one snail in 500 ml., all aquaria were kept full. Young snails of approximately the same size were taken from stock tanks and reared under the defined conditions. All aquaria were drained and refilled with conditioned water every three weeks.

The results over a period of 97 days with standard deviations are given in Table VI.12 As can be seen from the results there was a clear trend towards reduced growth rate and increased individual variation in size as the snails were more crowded, indicating that, of the conditions tested, one snail per litre was optimal. However, at a density of one snail in 500 ml., snails grew much faster than at a density of two snails in one litre. This would suggest that apart from actual density in relation to the volume of water, the number of snails present in the aquarium is of importance. This may not be true in large tanks, but the implications cannot be denied when small aquaria are considered. Densities of less than one snail per litre were not investigated because it is generally not feasible to use such conditions in a laboratory where space and apparatus are limited. In fact it was found necessary to keep

TABLE VI.12

Showing the effect of density on growth of *Bulinus* (*Physopsis*) *globosus* reared at 25 ± 0.5°C. One litre capacity aquaria were used for all experiments. Water was changed every three weeks. Values in parentheses are standard deviations, and values marked with an asterisk (*) indicate the number of replications. Measurements are given as the mean value for height of shell in mm.

Day	Density				
	1 per litre	1 per 500 ml.	2 per litre	5 per litre	10 per litre
0	3.37 (0.635) 3*	4.00 (0.245) 6*	4.46 (1.114) 6*	3.40 (0.840) 5*	3.57 (0.602) 10*
20	6.47 (0.666) 3*	7.12 (0.171) 6*	6.96 (1.034) 6*	5.54 (1.119) 5*	5.13 (1.187) 10*
41	8.40 (0.200) 3*	8.46 (0.377) 6*	6.83 (0.700) 6*	7.30 (1.483) 5*	6.03 (0.711) 10*
62	11.00 (0.519) 3*	10.50 (0.825) 6*	8.78 (0.658) 6*	8.63 (1.800) 5*	7.28 (0.839) 10*
84	12.03 (0.709) 3*	11.60 (0.828) 6*	9.88 (0.543) 6*	9.33 (0.783) 5*	8.07 (0.844) 10*
97	13.10 (0.656 3*	12.16 (0.622) 6*	10.20 (0.182) 6*	9.73 (0.971) 5*	8.30 (1.033) 10*

B. (*Ph.*) *globosus* at a density of the order of 1 to 1.5 snails per litre with never more than six snails in a tank. To have exceeded this would have introduced a factor of overcrowding into the previously described experiments.

5. A naturally occurring population of *Bulinus* (*Physopsis*) *globosus*.

A natural population of *B.* (*Ph.*) *globosus* occurring in the habitat on Foyle farm (see Chapter III) has been studied for the period March, 1962 to March, 1963. Apart from September and October when the ponds were completely dry, quantitative sampling of the waterbody was undertaken each month. Using the modified version of the Eckman dredge, described in Chapter V, a series of samples were taken, each some five to six metres apart. Coverage of all vegetation types and open water was attempted so that the composite results of a sampling would give a general picture of the distribution of snails within the habitat. The dredge proved ideally suited to the ponds and as the substratum was muddy with only occasional pebbles or broken bricks littered around, each sample consisted not only of emergent, floating or bottom vegetation, but of a quantity of mud as well. Apart from the months when the waterbody was decreasing in size, 30 samples were taken on each occasion, 20 from the larger upper pool and 10 from the lower pool. As the two ponds were interconnected by runnels of water for most of the year, they were considered as a single ecosystem and all estimates of the population refer to the habitat as one unit. In no place was the waterbody very deep, 80 cm. being the maximum depth recorded. The sides were fairly steep and the bottom somewhat undulating. The distribution of vegetation was irregular but because of the small size of the ponds, access to all vegetation types was almost unrestricted.

It may be possible to estimate the snail population with respect to volume of the waterbody, but the difficulty of associating the volume of various vegetation types sampled with the volume of that ecotype available would lead to extensive approximations. The snails do not distribute themselves evenly throughout the waterbody but tend to cluster in certain well defined regions: to sample these alone or to lay traps which may attract snails for egg deposition or merely as a resting place, would be biased and likely to exaggerate grossly some particular feature of the population.

Perhaps the best and least complex estimate of the population is simply to relate the area actually sampled with the dredge to the total surface area of the waterbody, irrespective of various vegetation types, volume or depth. Errors are inherent in this but would be consistent as long as the ratio between the vegetation types and open water remained fairly constant and was sampled accordingly. In fact, this is the method used in subsequent estimations of population numbers.

All the samples taken were sorted in the laboratory and snails found were measured to the nearest 0.1 mm. from base to apex, using hand calipers for large snails or a microscope fitted with an eyepiece micrometer for small snails. All snails in excess of 5.0 mm. were examined for trematode infection by exposure to strong light in glass specimen tubes. After this all snails were returned to the waterbody. Eggs taken were examined microscopically so as to differentiate between fertile and infertile eggs.

The habitat was sparsely populated with _Bulinus_ (_Bulinus_) _forskalii_ throughout the season. It is difficult to differentiate between the egg masses of this species and those of _B_. (_Ph_.) _globosus_, but if kept in the laboratory until the young snails are due to hatch, the _B_. _forskalii_ characteristics become clear and identification is simple.

Parasites and predators.

Information on the extent of parasitism within the habitat is inadequate. It was felt that it was more important to return the snails promptly to the habitat than to attempt to shed cercariae from them over a long period of time or to kill and examine a proportion of the snails collected. A total of 16 infected snails were found of which 15 were shedding cercariae of mammalian type identified by exposure to hamsters (*Mesocricetus auratus*) as *Schistosoma mattheei* Veglia and Leroux, the other solitary case was a strygeid infection.

As in all aquatic habitats, predatory fauna abound, but during the period of observation no instance of actual predation of the snails was observed.

Distribution within the habitat.

As can be seen from the map of the waterbody (Fig. III.$_1$) *Courtoisia cyperoides* occurred in clusters in both ponds. This plant was favoured by *B.* (*Ph.*) *globosus* as an egg laying site. Occasionally eggs were found on *Heteranthera callifolia* or on the very common *Scirpus sp.* and sometimes on sticks or fragments of dead grass. Those grasses which became inundated for a short while when the ponds were full were never used for egg deposition. Because of this distribution of eggs, younger snails were usually found on or near clusters of *C. cyperoides* although larger snails wandered further afield and were often found on any floating vegetation. In the warm weather when algal growth was rich, snails were not to be found among the filamentous pads. On hot sunny days snails were seen crawling on the bottom and several samples taken over open water without vegetation, collected snails which therefore must have been on the bottom. From April to July snails were sometimes seen, at any time of the day, adhering to the stems of emergent vegetation several centimetres above the waterlevel. When water temperatures were low, on sunny days, large numbers of snails could be found clustering at the surface, apparently basking in the sunshine.

Seasonal population fluctuations.

During the period March, 1962 to March, 1963 the population of *B.* (*Ph.*) *globosus* underwent a progression of fluctuations which help throw light on the bionomics of the species. There was a strong correlation between these fluctuations and the major seasonal influences. In the cold weather breeding was depressed to virtual inhibition and during times of flooding, large numbers of snails were lost. The species was able to utilise the relatively short favourable periods of calm weather to increase in numbers to such an extent as to survive the adversities. The seasonal fluctuation of the population is shown in Fig. $VI._{14}$ and can be understood best with reference to seasonal temperature, rainfall and the size distribution of the population (Figs. $VI._{15}$ and $VI._{16}$). In both March, 1962 and March, 1963 the snail density was low, with a large number of eggs being produced and the various size groups were relatively evenly distributed throughout the population. The slight difference which existed can probably be ascribed to the fact that in 1962 flooding rains ended early, whereas in 1963 heavy rain fell during the first ten days of March.

In April, water movement became slight with temperatures high. These conditions were favourable for increase and the snails responded with an outburst of egg production. Conditions for survival had improved and correspondingly there was an increase in numbers. By May, water movement throughout the habitat had ceased but water temperatures had fallen. The latter factor was probably responsible for the sharp decline in egg production although, with conditions for survival satisfactory, the snail population was still increasing in numbers. The cold conditions during May and June were reflected in the absence of eggs from the habitat and the high rate of survival as indicated by the progeny of the May cohort of eggs (see Table $VI._{20}$). An interesting comparison can be made between these data and the life table data collected in the laboratory where it has been shown that the survivorship at 22.5°C. (Fig. $VI._{3}$) or at room temperature (Fig. $VI._{5}$) was better than that at 25 or 27°C. (Figs. $VI._{1}$ and $VI._{2}$), similarly egg production in the laboratory declined with temperatures below 25°C.

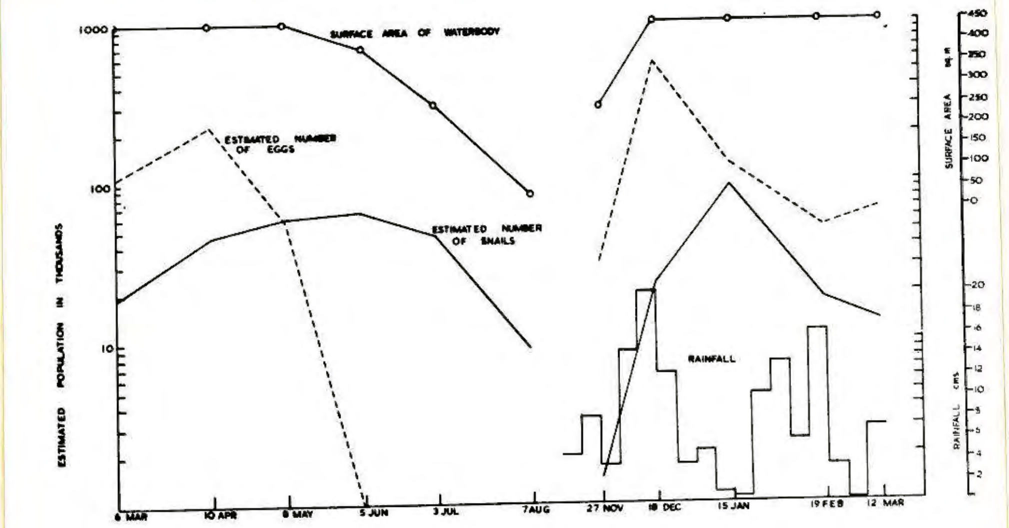


FIG. VI.14 Seasonal fluctuations of the estimated population of *Bulinus* (*Physopsis*) *globosus* in the Foyle habitat during the period March, 1962 to March, 1963. The estimated number of snails (continuous line) and eggs (broken line) is given on a logarithmic scale whereas the surface area of the waterbody (circles) and the rainfall histograms are on normal scales.

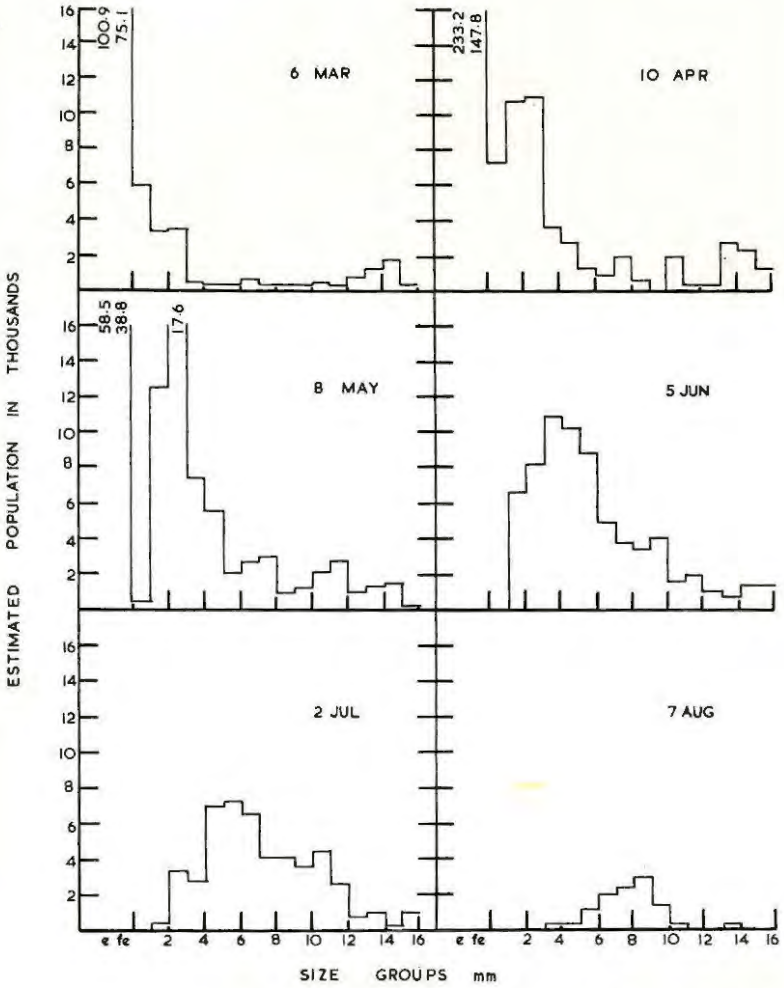


FIG. VI.15 Histograms showing the size distribution of the *Bulinus* (*Physopsis*) *globosus* population in the Foyle habitat, March, 1962 to August, 1962.

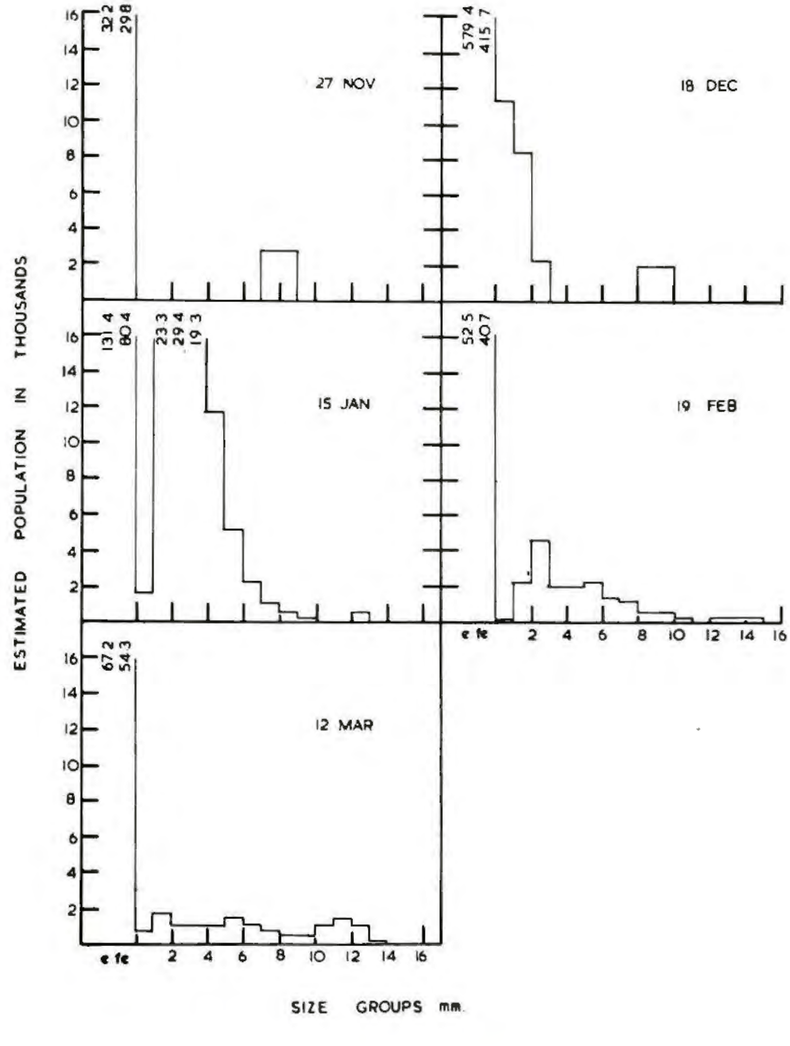


FIG. VI.16 Histograms showing the size distribution of the *Bulinus* (*Physopsis*) *globosus* population in the Foyle habitat, November, 1962 to March, 1963.

At the time of the June sampling the population was at the densest yet recorded but from then onwards another factor was influencing the snail population. Apart from winter conditions, the waterbody was drying up. This resulted in a reduction of the population during July and in early August, when the habitat finally became dry, those snails which were stranded on the surface succumbed. Large numbers of ants (Formicidae : unidentified) roamed the damp mud at this time, actively seeking and feeding on the helpless snails. Only those snails which had penetrated the mud and become sealed off were in a position to escape predation. Thus the only live snails found in the habitat during the dry season were embedded some 10 to 12 cm. deep in the bottom deposits.

Rain fell in the area towards the middle of November but it was not until the 22nd November that the habitat started to fill. Samples were taken on the 27th of that month when it was found that an estimated 1,459 snails had survived aestivation. These snails had already produced appreciable numbers of eggs. By the 18th December the waterbody was completely full, the water was warm and no excessive flooding had occurred. Conditions were ideal for breeding and this was proceeding at a remarkably high rate. By now there were an estimated 2,020 snails, all survivors from the previous season which had produced 579,354 eggs at the time of the sampling. The maximum period within which these eggs could have been laid was 12 days, the average duration of incubation at 22.5°C. These figures imply that eggs were being produced at the rate of 23.6 eggs per snail per day. This is in excess of any of the average figures from which life table data have been compiled, but in isolated cases, egg production of this order has been recorded in the laboratory at 25°C.

By mid-January, although rainfall had been heavy, water run-off was still low due to absorbtion into the soil. The snail population had risen to a peak figure in excess of 95,000, made up mainly of young snails, the progeny of the immense outburst of egg production which occurred in December. Egg production in January had declined and at this stage was not entirely due to the old generation of snails which was dying off, but to a new generation which by this time had reached maturity. During January and February excessive flooding occurred. Heavy rainstorms and saturated soil conditions resulted in massive volumes of water pouring through the habitat. To this must be ascribed the immense destruction of the snail population as indicated by the February and March samples. Egg production continued at a fairly constant level, held in check no doubt by the excessive movement of water. The snail population could survive the flooding only by virtue of large numbers present prior to the adversity. As flooding subsided, no doubt large numbers of eggs would once more be produced.

Rate of growth of *Bulinus* (*Physopsis*) *globosus* under natural conditions.

It has been shown in Chapter IV that the growth rate of *B.* (*Ph.*) *globosus* is dependent on temperature: therefore, with the wide range of temperatures which normally exist in the freshwater biotope throughout a year, it would be unreasonable to expect a single average growth curve for the species to apply to all seasonal conditions. The size distribution data in Figs. VI.$_{15}$ and VI.$_{16}$ show the progression of several groups which were discernible in the monthly samples. These data enable the growth of groups of snails within the samples to be measured.

The pond was first sampled on the 6th March, 1962, when it contained a large number of eggs and conditions had become favourable for survival. By the 10th April, the group originating from these eggs was between 1 and 3 mm. long. At the time of the next sampling, the 8th May, the snails had grown to 6 to 8 mm. long and by the 5th June were in the range 10 to 12 mm. The cohort was still discernible on the 3rd July by which time the snails were 12 to 14 mm. long.

On the 10th April evidence was found of a massive outburst of egg production, the progeny of which could be followed thus: 8th May, 1 to 3 mm.; 5th June, 3 to 6 mm.; 3rd July, 4 to 7 mm.; 7th August, 8 to 10 mm. The growth curves derived from these data are given in Fig. VI.$_{17}$ It will be seen that the initial rate of growth was similar for the two groups but the growth curves soon diverged. This was most probably the result of falling temperatures in May which affected the growth of the younger April cohort of snails more drastically than the larger survivors of the March cohort. The April cohort became stunted by the conditions in July and August, as did the March cohort although to a lesser extent. In November ideal conditions for rapid growth existed. The pond filled on the 22nd November when the first of a new generation appeared as eggs. The growth of this group during December, January and February was remarkably rapid, far in excess of the growth of the March cohort and even in excess of the absolute maximum growth achieved by a snail under ideal laboratory conditions (see Fig. VI.$_{17}$).

It is as well to draw attention to a point which should be remembered when comparing laboratory and field data. Laboratory data are derived mainly from average results based on the reaction of a group of individuals living in a highly protected environment. The slow maturing and poorly developed members of the cohort will reduce the average figure somewhat. In nature these retarded individuals may not survive long and thus when field conditions are satisfactory, comparison should be made with the best individual records of laboratory animals. In the case of B. (Ph.) globosus they match field data in egg production and growth rate far more accurately than the average data.

A stunting effect due possibly to overcrowding.

The water temperatures in the habitats during November and December were very similar to those recorded in March and April yet the growth of the November cohort during this time was far in

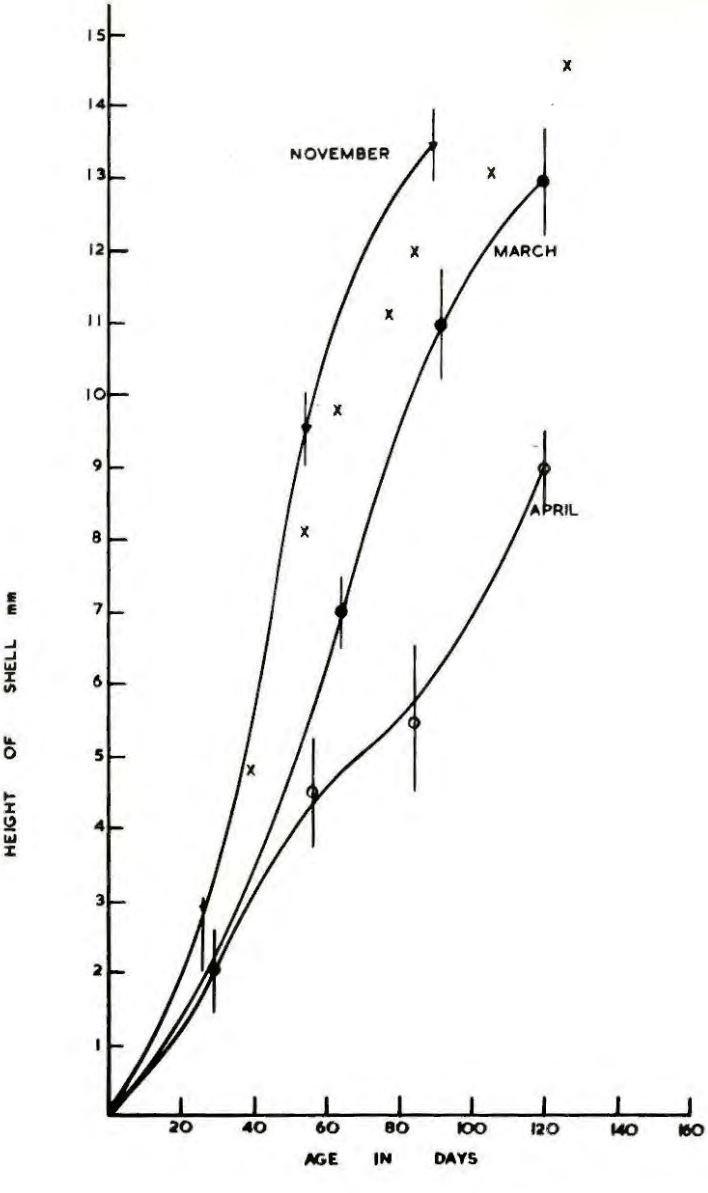


FIG. VI.17 Comparative growth curves of Bulinus (Physopsis) globosus at Foyle for cohorts originating in March, April and November, 1962. Mid-points and range of each group are given. Points marked 'x' indicate maximum growth recorded from a particular snail reared at 25°C.

excess of the growth of the March cohort over a similar period. Again, with regard to egg production, while both periods appeared favourable yet the few snails which existed in the pond in November and December laid a far greater number of eggs than the larger number of mature snails in the pond in March and April. Both periods marked a limited favourable existence for the snails, yet the one appeared to be far more successful than the other.

A striking difference in the habitat for these two periods was the actual snail population. In November very few snails were present in a large volume of water whereas in March considerably more snails were living in the same volume of water. Laboratory data in Chapter IV have shown that growth is sensitive to crowding and it may be that this effect is also operative in this natural population. Water in November was fresh, whereas in March pollution may have occurred to some extent.

6. The seasonal rate of increase of a natural population of Bulinus (Physopsis) globosus between March, 1962 and March, 1963.

(a). The calculation of seasonal mortality.

The age specific mortality rate, or its converse, the age specific survival rate of a population is one of the two basic measurements required for the establishment of the rate of natural increase of that population (see Chapter IV). In order to calculate this mortality rate from field data, two important assumptions must be made. These are based on observations carried out in the laboratory.

(i) The incubation period for eggs under natural conditions is similar to that observed in the laboratory at 22.5°C., namely 12 days.

(ii) The range of age within the cohort at any particular time will be the same as the incubation period of the eggs, also 12 days.

Water temperatures recorded within the surface levels of the habitat where most eggs are laid show a daily average in the region of 22.5°C. during the egg laying season.

The cohort which originated in March, 1962 was estimated to consist of 100,990 eggs 0 to 12 days old (see Table $VI._{14}$) and of these 75,860 were fertile. In April, 35 days later, the age of the cohort was between 29 and 40 days. From the growth curve of the March cohort (Fig. $VI._{17}$) these age limits correspond with a size range of 2.0 to 3.3 mm., which when applied to the estimated numbers of snails present at this time, indicate that there were 13,902 survivors. This is 13.77% of the original number of eggs or a survival of 0.1377. Similarly the cohort can be followed through May, June and July as can the other cohorts originating in April, May, November and December.

There was one discrepancy which must be noted. The February samples were taken at the time of heavy flooding and appear to be inaccurate. It may be that because of the swift movement of water some snails might have migrated into the shallow grassy verges which were inadequately represented in the samples. Thus in some cohorts, less snails were available in February than in March, which was incorrect. In such instances, graphical extrapolation was made between the January and March data.

It can be seen from the various life tables that as the temperatures dropped with the approach of autumn conditions, chances of survival improved. Both the March and May cohorts (Table $VI._{14}$) show very similar and high survival rates when compared with the November and December cohorts (Table $VI._{15}$). To some extent this is substantiated by laboratory data where it has been shown (Tables $VI._{1}$ to $VI._{5}$) that survival is favoured as maintenance temperature falls.

TABLE VI.13

Size distribution (in millimetres) of total estimated population of *Bulinus* (*Physopsis*) *globosus* in Foyle ponds, March, 1962 to March, 1963. (* = with evidence of aestivation).

Date	6/3/62	10/4	8/5	5/6	3/7	7/8	27/11	18/12	15/1/63	19/2	12/3
Eggs	100,990	233,229	58,508	Nil	Nil	Nil	32,240	579,354	131,346	52,523	67,243
Fertile eggs	75,080	147,840	38,797	Nil	Nil	Nil	29,760	416,680	80,538	40,702	54,257
Under 1 mm.	5,946	7,168	538	Nil	Nil	Nil		11,258	1,732	260	866
1.1 - 2.0	3,313	10,752	12,544	6,647	446	Nil		8,372	23,382	2,295	1,732
2.1 - 3.0	3,434	11,021	17,562	8,133	3,335	Nil		2,310	29,444	4,633	1,154
3.1 - 4.0	408	3,584	7,437	10,792	2,668	167			19,338	2,035	1,154
4.1 - 5.0	269	2,688	5,645	10,244	6,928	167			11,838	2,035	1,154
5.1 - 6.0	269	1,164	2,061	8,758	7,184	1,004			5,196	2,295	1,443
6.1 - 7.0	538	896	2,688	4,848	6,466	1,674	297*		2,312	1,429	1,154
7.1 - 8.0	269	1,796	2,957	3,597	4,002	2,176			1,152	1,169	866
8.1 - 9.0	279	582	896	3,284	4,002	2,679			580	563	577
9.1 - 10.0	269	Nil	1,165	3,910	3,541	1,172	297*	2,020*	286	563	577
10.1 - 11.0	408	896	2,061	1,486	4,413	167				260	1,154
11.1 - 12.0	269	269	2,688	1,799	2,463	Nil			580*	Nil	1,443
12.1 - 13.0	677	269	896	860	667	Nil	297*			260	1,154
13.1 - 14.0	1,087	2,688	1,165	626	872	167				260	287
14.1 - 15.0	1,753	2,329	1,434	1,173	205	Nil	496*			260*	
15+	269	1,164	269	1,173	872	Nil					
Size of pond (sq. metres)	448	448	448	391	256	44.9	248	448	448	448	448

TABLE VI.14

Estimated progression of the March, April and May cohorts in the Foyle ponds showing survivorship (l_x) and fecundity (m_x) where applicable.

MARCH						APRIL					MAY				
Date	Size	Age	No./Sn.	l_x	m_x	Date	Size	Age	No./Sn.	l_x	Date	Size	Age	No./Sn.	l_x
6/3	Eggs	0-12	100,990	1.0000		10/4	Eggs	0-12	233,229	1.0000	8/5	Eggs	0-12	58,508	1.0000
	Fertile Eggs		75,860	0.7512			Fertile Eggs		147,840	0.6339		Fertile Eggs		38,797	0.6631
10/4	2.0- 3.3	29-40	13,902	0.1377		8/5	1.3-2.6	22-33	19,318	0.0828	5/6	1.3-2.6	22-33	10,197	0.1743
8/5	5.8- 8.0	58-69	11,828	0.1171	0.299	5/6	4.0-5.0	50-61	11,323	0.0485	3/7	4.0-5.0	50-61	7,195	0.1230
5/6	10.3-11.6	85-96	2,268	0.0225	Nil	3/7	5.3-6.0	78-89	5,747	0.0246	7/8	5.3-6.0	85-96	1,339	0.0229
3/7	12.6-13.2	113-124	507	0.0050	Nil	7/8	8.1-9.3	113-124	3,031	0.0130					

TABLE VI.15

Estimated progression of November and December cohorts in Foyle pond showing survivorship (l_x) and fecundity (m_x). Items marked * are extrapolations from January and March data.

Date	Size	Age	Number	l_x	m_x (Table VI.17)	Date	Size	Age	Number	l_x	m_x
27/11	Eggs	0-12	32,240	1.0000		18/12	Eggs	0-12	579,354	1.0000	
	Fertile Eggs		29,760	0.9231			Fertile Eggs		415,680	0.7175	
18/12	1.1- 2.6	15-27	9,758	0.3027		15/1	1.9- 4.5	22-34	59,377	0.1025	
15/1	6.7- 9.6	43-55	2,827	0.0877		19/2	10.0-11.7	57-69	3,474*	0.0060	1.863
19/2	12.7-13.6	78-90	1,128*	0.0350	40.346	12/3	12.7-13.6	78-90	632	0.0011	69.623
12/3	13.9-14.3	99-110	56	0.0017	33.910						

TABLE VI. 16

Egg production apportionments according to a_x at 25°C.

Age in Fortnights	3 age groups present	5 age groups present	6 age groups present
4.5	0.058	0.003	0.002
5.5	0.352	0.107	0.080
6.5	0.590	0.178	0.133
7.5		0.335	0.250
8.5		0.374	0.279
9.5			0.255

TABLE VI.17

Corrected egg apportionments.

Sampling date	8/5	19/2	12/3
Fertile eggs available	38,797	40,702	54,257
Ages in fortnights			
4.5	No. snails 11,828 Proportion 969.896 Apportion .091	No. snails 3,474 Prop: 201.492 App: .159	No. snails: 2,452 Prop: 7.356 App: .014
5.5		No. snails 1,128 Prop: 1062.576 App: .841	No. snails: 1,526 Prop: 434.910 App: .811
6.5	No. snails 10,574 Proportion 9696.358 Apportion .909		
7.5			No. snails: 56 Prop: 18.760 App: .035
8.5			No. snails: 201 Prop: 75.375 App: .140
9.5			

TABLE VI.18

Life table for *Bulinus* (*Physopsis*) *globosus* from March to July, 1962, in Foyle pond. Calculated graphically from the data in Table VI.14

Age x	Survivorship l_x	Fecundity m_x	$l_x m_x$
0	1.0000		
0.5	0.7512		
1.5	0.4127		
2.5	0.1377		
3.5	0.1275		
4.5	0.1171	0.299	.035
5.5	0.0680	-	
6.5	0.0220	-	
7.5	0.0130	-	
8.5	0.005	-	
9.5	Nil		

TABLE VI.$_{19}$

Life table for *Bulinus* (*Physopsis*) *globosus* from April to August, 1962, in Foyle pond. Calculated graphically from the data in Table VI.$_{14}$
No eggs were laid by this cohort.

Age x	Survivorship l_x
0	1.0000
0.5	0.6339
1.5	0.2450
2.5	0.0740
3.5	0.0560
4.5	0.0410
5.5	0.0295
6.5	0.0205
7.5	0.0175
8.5	0.0130
9.5	

TABLE VI.$_{20}$

Life table for *Bulinus* (*Physopsis*) *globosus* from May to August, 1962, in Foyle pond. Calculated graphically from the data in Table VI.$_{14}$
No eggs were laid by this cohort.

Pivotal age in fortnights x	Survivorship l_x
0	1.0000
0.5	0.6631
1.5	0.4951
2.5	0.3350
3.5	0.1743
4.5	0.1499
5.5	0.1230
6.5	0.0845
7.5	0.0438

TABLE VI.21

Life table for *Bulinus* (*Physopsis*) *globosus* from November, 1962 to March, 1963, in Foyle pond. Calculated graphically from the data in Table VI.15

Age x	Survivorship l_x	Fecundity m_x	$l_x m_x$
0	1.0000		
0.5	0.9231		
1.5	0.3027		
2.5	0.1950		
3.5	0.0877		
4.5	0.0660		
5.5	0.0451	24.001	1.082
6.5	0.0249	38.500	0.959
7.5	0.0017	33.910	0.058
8.5	-		

finite rate of increase, R = 1.132

rate of actual increase, r = 0.1240

TABLE VI.22

Life table for *Bulinus* (*Physopsis*) *globosus* from December, 1962 to March, 1963 in Foyle pond. Calculated graphically from the data in Table VI.15

Age x	Survivorship l_x	Fecundity m_x	$l_x m_x$
0	1.0000		
0.5	0.7175		
1.5	0.2960		
2.5	0.0840		
3.5	0.0450		
4.5	0.0060	1.863	0.011
5.5	0.0049	47.250	0.232
6.5	-		
7.5	-		

finite rate of increase, $R = 0.7718$

rate of actual increase, $r = (\bar{1}.7409)$

$= -0.2591$

(b). The calculation of seasonal age specific fecundity.

The calculation of the age specific fecundity of B. (Ph.) globosus is somewhat more complicated than the calculation of the mortality data. Certain characteristics must be derived from laboratory observation but in view of the critical effect of temperature, it is problematical as to which set of laboratory conditions can be chosen as typical. My earlier results have indicated that a temperature of 25°C. is optimal for the species and as this temperature prevails at some point within the habitat for the greater part of the egg laying season (November to May) it is the temperature condition of choice. Mention should be made of the apparent discrepancy between 25°C. as the temperature chosen for the derivation of egg laying data and 22.5°C. for the data on incubation. Eggs are immovable and cannot select the region where temperature is optimal, therefore they may have to experience both favourable and unfavourable temperatures, certainly no better than average. This is not the case with snails which are mobile and can seek out the most favourable conditions available in the habitat.

Two assumptions are necessary to derive the age specific fecundity:

(i) As at 25°C. egg laying commences during the fourth fortnight.

(ii) Egg production at various age groups follows the same pattern as observed at 25°C. (see m_x column, Table VI.$_1$).

The eggs available at each sampling must be apportioned among the mature snails according to the pattern of egg production mentioned in the second assumption. Thus an apportionment is calculated (Table VI.$_{16}$) assuming that all age groups are equally represented at each sampling. As the age groups are not equally represented, each proportion must be multiplied by the number of snails in the appropriate age group. This will give the egg laying power of each group as represented in the sample and when this is cast into proportions, it will give the correct apportionment of available eggs among the age groups (Table VI.$_{17}$) (Dr. N. Hairston, personal communication).

The method of calculation was as follows: The data in Table VI.$_{17}$ represent the egg laying power of various age groups present at a particular time. Since information on specific cohorts only was required, representatives of other than those cohorts have been bulked and eggs apportioned accordingly. On the 8th May, the March cohort was between the fourth and sixth fortnight in age. There was an estimated total of 11,828 snails of this age which could have laid a proportion of 0.091 of the total fertile eggs available, this is 3,530.5 eggs. Thus 11,828 snails were responsible for producing 3,530.5 eggs, which means that 0.2985 eggs were produced per snail in that period, this is the m_x value (see Table VI.$_{14}$). Similarly the m_x data for the November and December cohorts can be calculated (see Table VI.$_{15}$).

(c). <u>Rate of actual increase</u>.

With life tables showing age specific schedules for mortality and fecundity available for various cohorts of B. (Ph.) globosus, it was possible to arrive at a figure representing the rate of actual increase (r) for each cohort through its existence. The relevant data are given in Tables VI.$_{18}$ to VI.$_{22}$ and it will be seen that in only two instances for the November cohort (Table VI.$_{21}$) and the December cohort (Table VI.$_{22}$) were sufficient data available for the calculation of this figure. From March until August the progressive inhibition of egg production due to the cold caused all these cohorts to register a negative rate of increase. This culminated in August with the loss of most of the population when the ponds dried out. A small number of snails succeeded in surviving the dry period in the mud, and were responsible for an outburst of egg production once the rains had set in and started filling up waterbodies.

The cohort which derived from these eggs showed a positive rate of increase but heavy flooding in January removed a large proportion of the population and influenced the survival rate of older snails. Egg production decreased and the population diminished. The December cohort carried this picture a stage further and showed a negative rate of increase.

In this case the calculation of the parameter r from life table data is misleading. It would express the dynamics of a more stable population in a satisfactory manner, but where frequent seasonal catastrohpes inflict a high mortality, an inadequate picture is obtained. The estimated population data for the species in Foyle, (Fig. $VI._{14}$) undergo fluctuations which cannot be reconciled with the almost static conditions indicated by the calculations of r based on the life tables (Tables $VI._{18}$ to $VI._{22}$). Therefore, with populations which suffer high mortalities and are capable of explosive bursts of reproduction by a small number of survivors, another method of calculating r is necessary. This is based on the formula:

$$N_t = N_o e^{rt}$$

where N_o = population at time zero

N_t = population at time t.

(see Chapter IV).

Knowing N_t, N_o and t, it is possible to calculate r. The method is crude and inaccurate because it is based on an assumption that the population, at both instants in time, has a stable age distribution. Nevertheless, for the situation in the Foyle habitat, this method will be more descriptive of the conditions and the state of dynamic increase or decrease within the population. It will neither be influenced by the long term picture which misses the explosive reproduction and increase based on the successful aestivating snails, nor will it tend to obscure the fluctuations which are an important part of the life pattern of the species. In Table $VI._{23}$ values for r,

TABLE VI.23

Calculated values of the rate of actual increase of Bulinus (Physopsis) globosus in the Foyle habitat for various periods from March, 1962 to March, 1963. Calculations are based on the formula $N_t = N_o e^{rt}$.

	PERIOD								
	6/3 - 10/4	10/4 - 8/5	8/5 - 5/6	5/6 - 3/7	22/11 - 27/11	27/11 - 18/12	18/12 - 15/1	15/1 - 19/2	19/2 - 12/3
Time (days)	35	28	28	28	6	21	28	35	21
N_o	94,537	195,106	100,839	67,330	1,387	31,147	440,640	176,378	59,019
N_t	195,106	100,839	67,330	48,064	31,147	440,640	176,378	59,019	68,972
r/fortnight	0.291	-0.329	-0.202	-0.168	7.260	1.750	-0.458	-0.438	0.044

calculated according to the numerical change in population, are given for various periods from March, 1962 to March, 1963. In order to compare with preceding data the value of r per fortnight is quoted.

The increase in the population from March to April was reflected in a positive value for r, 0.2912. From April to July was a period of continual decline in population and resulted in a series of negative values for r. Yet, during this period the improving conditions for survival of snails resulted in a decreasing negative value for r from May to June to July. The burst of egg laying by the few survivors from the previous season during the first few days after the pond filled in November, is reflected in the very high value for r recorded between the 22nd and 27th November. At this time r was 7.266 per fortnight. The increase continued but at a lower rate during December, r = 1.750, but a decrease in egg production in January resulted in a negative value for the parameter during that month, even though the number of snails (as opposed to eggs) increased. The floods during late January and February resulted in further negative values for r, but by March, a slight positive r reflected the revival of the population.

It must be remembered that these values are not accurate, but even so they do express the situation in the snail population with an essence of reality lost in the life table calculated values of the parameter.

Discussion: the temporary habitat.

Bulinus (Physopsis) globosus is not confined to temporary waterbodies but is ideally adapted to life in such habitats. It has been shown that the species is not tolerant of wide ranges of temperatures, in fact it functions best within very narrow limits. Yet within those limits it is capable of extremely rapid population growth. The range of temperature which is most suited to this species has been found to occur in the upper levels of waterbodies throughout the summer season, but as the weather becomes cool towards the end of the summer, egg production dwindles and finally stops altogether. Cool conditions however, are not a complete disadvantage to the species. Ample evidence has shown that under these conditions the snails survive well. Thus a large middle-aged population develops during the winter and is prepared for aestivation in the spring. Quite obviously the dry period is most hazardous because so few survive, yet up to a point the larger and more mature the population at the onset of the adverse conditions, the better the chances of individuals surviving. No evidence has been found of snails less than 6 mm. in length aestivating successfully.

It is apparent that the species requires warm stable conditions for optimal increase. These conditions did occur for a few weeks after the rains broke and before flooding occurred. During this time the snails which had survived from the previous season produced enormous numbers of eggs. If flooding had not occurred it is reasonable to assume that increase would have continued at an exceptionally high rate until such time as some density dependent factor reduced egg production. The species has been shown to be sensitive to overcrowding in the laboratory and a suspicion of this has been noted in the field where the snails have responded to factors other than temperature.

Towards the end of the rains when floods diminish, a second seasonal period of calm occurs. The result of this is a second burst of egg production in March and April caused by those snails which originated in and survived the flood conditions of January and February.

Conditions are arduous in small freshwater ponds but with the ability to reproduce rapidly during short periods of ideal conditions, the bulinid snail, B. (Ph.) globosus has evolved a means of overcoming the difficulties.

VII. THE INFLUENCE OF TEMPERATURE ON THE BIONOMICS OF BIOMPHALARIA PFEIFFERI.

1. General.

Biomphalaria pfeifferi is widespread throughout Southern Rhodesia, occurring in a variety of waterbodies and extending from the warm low-veld areas to the cooler regions of the eastern highlands. Apparently the species is somewhat eurythermal when compared with *Bulinus* (*Physopsis*) *globosus*. It has not been possible, as yet, to identify any preference for particular waterbodies: the species appears to thrive in reservoirs, streams, irrigation canals, night storage dams, ponds, etc.; dense populations are, however, usually associated with the more permanent man-made waterways, and do not occur in temporary ponds. All substrates apart from pure sand are suitable for the species, the snails often being found in large numbers even in cement-lined furrows.

B. pfeifferi has been found in the Marlborough pond and the Derbyshire reservoir. In these instances which cover most types of semi permanent waterbody in the highveld plateau, the range of temperature available to the snails follows the pattern outlined in Chapter VI. Hot weather is less likely to influence the snails adversely than cold weather, because at a depth of 25 cm. maximum temperatures are several degrees lower than maxima in the surface levels. However, unlike *B.* (*Ph.*) *globosus*, eggs of this species have often been collected in nature during the cold winter months. Apparently *B. pfeifferi* can thrive in cooler conditions than *B.* (*Ph.*) *globosus*.

2. Life tables and the rate of increase.

In Chapter IV the various parameters relating to population dynamics have been discussed. These were calculated for the species reared under standard conditions at different temperatures, 18, 25, 27°C.

and room temperature over a period of one year.

As with the other species, eggs are laid in clutches of up to 20 eggs, usually on floating vegetation or occasionally on the sides of the aquaria. The life table data were obtained from cohorts of snails derived from the progeny of several egg masses taken at random from a stock aquarium. Once mature, the snails were kept in three or four litre aquaria at a density not exceeding two snails per litre. The accuracy and significance of the work was marred by inexplicable behaviour of the snails which, on some occasions, persisted in emerging from the water for variable periods of time. The snails usually exhibited this behaviour pattern just prior to maturation when they were 4 to 6 mm. in diameter. They would crawl out of the water and adhere to the sides or the lids of the aquaria and if replaced in the water, which was a daily routine, would persistently climb out. This tendency to leave the water has been observed under all experimental conditions, but to a lesser extent at room temperature, yet no evidence that it occurs in natural populations has been found. While exhibiting this behaviour the snails neither fed nor grew: it resulted in a period of suspended development and had to be taken into consideration when the life tables were compiled. The room temperature and 25°C. cohorts showed this tendency to migrate from the water only occasionally: this had little influence on the final result, but at 27°C. the behaviour persisted for about two weeks and at 18°C. for nearly a month. For these cohorts two life tables will be presented, one showing the actual records and the other making allowances for these periods of suspended development.

Life table 18 ± 0.1°C.

An initial group of 30 eggs, derived from three egg masses, was reared in aquaria kept at a temperature of 18 ± 0.1°C. As with all other experiments the snails were fed daily with lettuce prepared according to Claugher (1960), and weekly with thin slices of raw carrot. The aquaria were cleaned out daily, uneaten food and faecal matter being removed by means of a pipette. In addition the aquarium water was conditioned once a week by the addition of a few drops of a five per cent. calcium carbonate suspension. When approximately 5 mm. in diameter the snails started leaving the water in the manner described, and after approximately one month this behaviour pattern ceased and normal feeding, behaviour and development was resumed. In Table VII.$_1$ two life tables are given, the second (b) excludes two fortnights of inactivity and because this behaviour is probably abnormal, part (b) will be considered as being more representative of natural conditions.

Maturation was delayed by the cold, the first eggs being produced during the 11th fortnight, thereafter egg output per snail rose slowly until the 19th fortnight when observations ceased. Mortality throughout the period was low, 76.67% of the cohort survived to maturity and by the 19th fortnight 73.3% were still alive.

Life table 25 ± 0.5°C.

An initial group of 60 eggs derived from four egg masses was reared in a constant temperature room for 18 fortnights. Maintenance and the degree of crowding were kept standard, as described above. Several attempts were made to culture batches of snails and of all these, this particular group showed the least tendency for the pre-maturation migration out of the water. The behaviour was restricted to a small number of snails and did not persist for long. Thus the actual records can be accepted as the normal life table at 25°C. (Fig. VII.$_1$ and Table VII.$_2$).

Egg production commenced during the sixth fortnight and rose rapidly to peak level during the ninth fortnight. Although fecundity at this temperature was low, the rapid rate of maturation was reflected in a high intrinsic rate of natural increase as this parameter is partially dependent on speed of development. Mortality during the period was low and evenly distributed throughout the age groups. A total of 83.3% survived to maturity and 68.3% of the original cohort were alive at the end of the period of observation.

TABLE VII.1

Life table for *Biomphalaria pfeifferi* reared under standard conditions of feeding and crowding at 18 ± 0.1°C. for a period of 18 fortnights (a) full-time life table, (b) minus two fortnights during which the snails persisted in leaving the water. Original cohort 30 eggs.

(a)			(b)			
Pivotal Age in Fortnights x	Survivorship l_x	Fecundity Eggs/Snail m_x	Pivotal Age in Fortnights x	Survivorship l_x	Fecundity Eggs/Snail m_x	$l_x m_x$
0	1.0000		0	1.0000		
0.5	0.9333		0.5	0.9333		
1.5	0.8000		1.5	0.8000		
2.5	0.8000		2.5	0.8000		
3.5	0.8000		3.5	0.7667		
4.5	0.7667		4.5	0.7667		
5.5	0.7667		5.5	0.7667		
6.5	0.7667		6.5	0.7667		
7.5	0.7667		7.5	0.7667		
8.5	0.7667		8.5	0.7667		
9.5	0.7667		9.5	0.7667		
10.5	0.7667		10.5	0.7667	.391	.300
11.5	0.7667		11.5	0.7667	1.435	1.100
12.5	0.7667	.391	12.5	0.7667	3.348	2.567
13.5	0.7667	1.435	13.5	0.7667	5.087	3.900
14.5	0.7667	3.348	14.5	0.7667	5.870	4.500
15.5	0.7667	5.087	15.5	0.7667	11.783	9.034
16.5	0.7667	5.870	16.5	0.7667	9.391	7.200
17.5	0.7667	11.783	17.5	0.7333	11.318	8.300
18.5	0.7667	9.391	18.5	0.7333	23.600	

Nett reproductive rate for 18 fortnights

$R_o = 36.901$

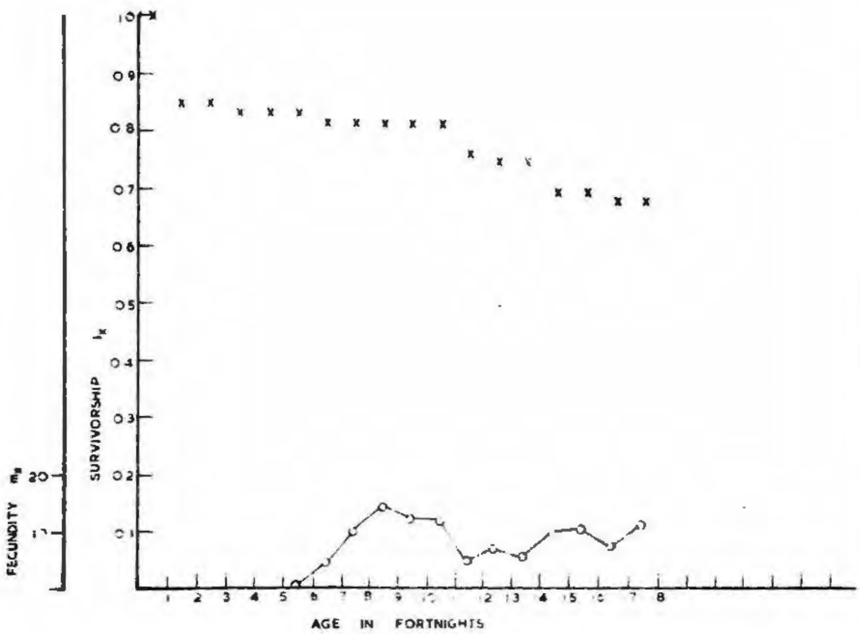


FIG. VII.1 Life table for *Biomphalaria pfeifferi* reared under standard conditions of feeding and crowding at 25 ± 0.5°C. for a period of 18 fortnights.

TABLE VII.$_2$

Life table for *Biomphalaria pfeifferi* reared under standard conditions of feeding and crowding at 25 ± 0.5°C. for a period of 18 fortnights.

Pivotal Age in Fortnights x	Total Snails	Total Eggs	Survivorship l_x	Fecundity Eggs/Snail m_x	$l_x m_x$
0	60		1.0000		
0.5	60		1.0000		
1.5	51		0.8500		
2.5	51		0.8500		
3.5	50		0.8333		
4.5	50		0.8333		
5.5	50	4	0.8333	.080	.007
6.5	49	287	0.8167	5.857	4.784
7.5	49	610	0.8167	12.449	10.167
8.5	49	856	0.8167	17.469	14.267
9.5	49	749	0.8167	15.286	12.484
10.5	49	723	0.8167	14.755	12.051
11.5	46	308	0.7667	6.696	5.134
12.5	45	429	0.7500	9.533	7.150
13.5	45	335	0.7500	7.444	5.583
14.5	42	615	0.7000	14.643	10.250
15.5	42	627	0.7000	14.929	10.450
16.5	41	470	0.6833	11.463	7.833
17.5	41	676	0.6833	16.488	11.266

Nett reproductive rate for 18 fortnights

$$R_o = 111.425$$

Life table 27 ± 0.1°C.

An initial group of 19 eggs derived from two egg masses was reared at a temperature of 27 ± 0.1°C. A waterbath was used to regulate the temperature of the aquaria and thus shortage of space precluded the use of a larger cohort. A prematuration period of migration from the water was exhibited by all the snails. This lasted for approximately two weeks after which a slow return to normal growth and activity took place. Because of this, Table VII.$_3$ shows two life tables and the second (b) which excludes one fortnight when the snails persisted in leaving the water, will be accepted as representing normal development (Fig. VII.$_2$).

Maturation was rapid at this temperature, the first eggs being produced during the sixth fortnight, but during the next four fortnights egg production was somewhat depressed. A considerable increase in fecundity occurred during the 10th and 11th fortnights reaching a level of egg production which fluctuated between 15 and 46 eggs per snail per fortnight until the 24th fortnight, after which egg production diminished. Mortality at this temperature was higher than under the cooler conditions: 68.42% of the original cohort survived to maturity, and by the 19th fortnight there were only 57.89% alive. After this the mortality rate increased and at the end of the period of observation 36.84% were left.

Room temperature, January, 1961 to January, 1962.

Water temperature in aquaria kept in an unheated laboratory will simulate in a subdued manner the seasonal trends which occur in nature. To observe the influence of daily fluctuation and seasonal change in temperature on mortality and fecundity in B. pfeifferi a batch of 79 eggs were reared in aquaria kept at room temperature for a full year. The results are given in Table VII.$_4$ and Fig. VII.$_3$

Temperatures were high during the early stages of development

TABLE VII.3

Life table for *Biomphalaria pfeifferi* reared under standard conditions of feeding and crowding at 27 ± 0.1°C. for a period of 18 fortnights (a) full time life table, (b) minus one fortnight during which the snails persisted in leaving the water. Original cohort 19 eggs.

(a)			(b)			
Pivotal Age in Fortnights x	Survivorship l_x	Fecundity Eggs/Snail m_x	Pivotal Age in Fortnights x	Survivorship l_x	Fecundity Eggs/Snail m_x	l_xm_x
0	1.0000		0	1.0000		
0.5	1.0000		0.5	1.0000		
1.5	0.8947		1.5	0.8947		
2.5	0.7895		2.5	0.7895		
3.5	0.7895		3.5	0.7895		
4.5	0.7368		4.5	0.7368		
5.5	0.6842		5.5	0.6842	.154	.105
6.5	0.6842	.154	6.5	0.6842	2.154	1.474
7.5	0.6842	2.154	7.5	0.6842	6.000	4.105
8.5	0.6842	6.000	8.5	0.6842	8.385	5.737
9.5	0.6842	8.385	9.5	0.6842	8.154	5.579
10.5	0.6842	8.154	10.5	0.6842	15.000	10.263
11.5	0.6842	15.000	11.5	0.6316	46.250	29.212
12.5	0.6316	46.250	12.5	0.6316	44.917	28.370
13.5	0.6316	44.917	13.5	0.5789	25.545	14.788
14.5	0.5789	25.545	14.5	0.5789	23.545	13.630
15.5	0.5789	23.545	15.5	0.5789	46.818	27.103
16.5	0.5789	46.818	16.5	0.5789	30.455	17.630
17.5	0.5789	30.455	17.5	0.5789	15.091	8.736
18.5	0.5789	15.091	18.5	0.5789	49.091	
19.5	0.5789	49.091	19.5	0.5789	35.182	
20.5	0.5789	35.182	20.5	0.5789	34.273	
21.5	0.5789	34.273	21.5	0.4737	19.333	
22.5	0.4737	19.333	22.5	0.4737	30.222	
23.5	0.4737	30.222	23.5	0.4737	20.444	
24.5	0.4737	20.444	24.5	0.3684	9.286	
25.5	0.3684	9.286				

Nett reproductive rate for 18 fortnights

$R_o = 166.732$

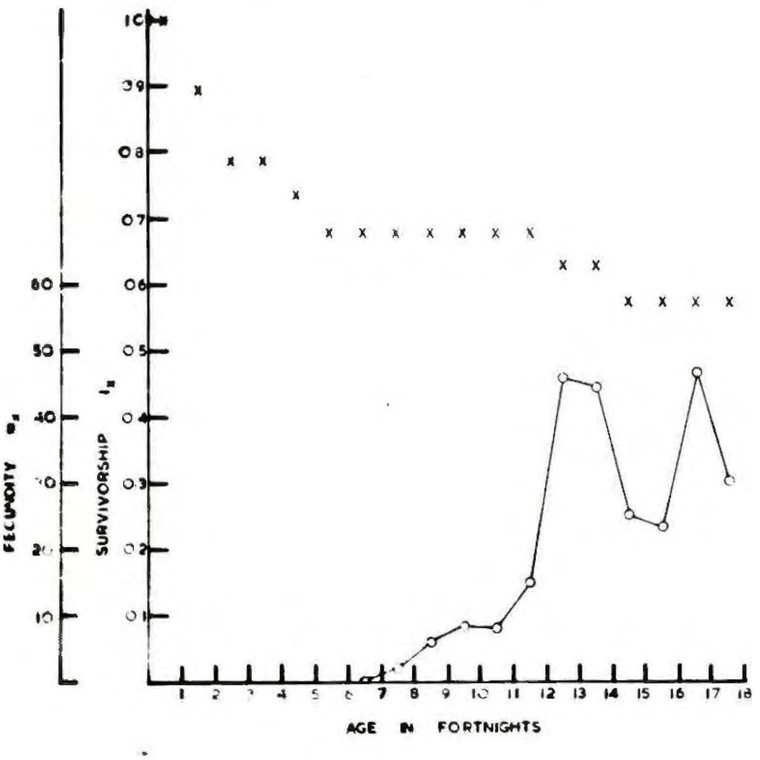


FIG. VII.$_2$ Life table for _Biomphalaria pfeifferi_ reared under standard conditions of feeding and crowding at 27 ± 0.1 °C. One fortnight during the prematuration period has been excluded from the data (see text).

TABLE VII.4

Life table for *Biomphalaria pfeifferi* reared under standard conditions of feeding and crowding at ambient room temperature for the period January, 1961 to January, 1962. Based on information derived from an original cohort of 79 snails.

Pivotal Age in Fortnights x	Survivorship l_x	Fecundity Eggs/Snail m_x	$l_x m_x$
0	1.0000		
0.5	0.9259		
1.5	0.8148		
2.5	0.8148		
3.5	0.8148		
4.5	0.8148		
5.5	0.8148	.047	.038
6.5	0.8148	1.186	.966
7.5	0.8148	.837	.682
8.5	0.8148	4.500	3.667
9.5	0.7778	5.050	3.928
10.5	0.7407	55.125	40.831
11.5	0.7407	46.000	34.072
12.5	0.7407	33.100	24.517
13.5	0.7407	67.000	49.627
14.5	0.7407	109.325	80.977
15.5	0.7037	64.333	45.271
16.5	0.7037	99.487	70.009
17.5	0.7037	97.462	68.584
18.5	0.7037	102.684	
19.5	0.7037	60.342	
20.5	0.7037	61.417	
21.5	0.7037	27.478	
22.5	0.7037	61.316	
23.5	0.6666	52.222	
24.5	0.6296	69.294	
25.5	0.5926	42.813	
26.5	0.5556	48.000	

Nett reproductive rate for 18 fortnights

$$R_0 = 423.169$$

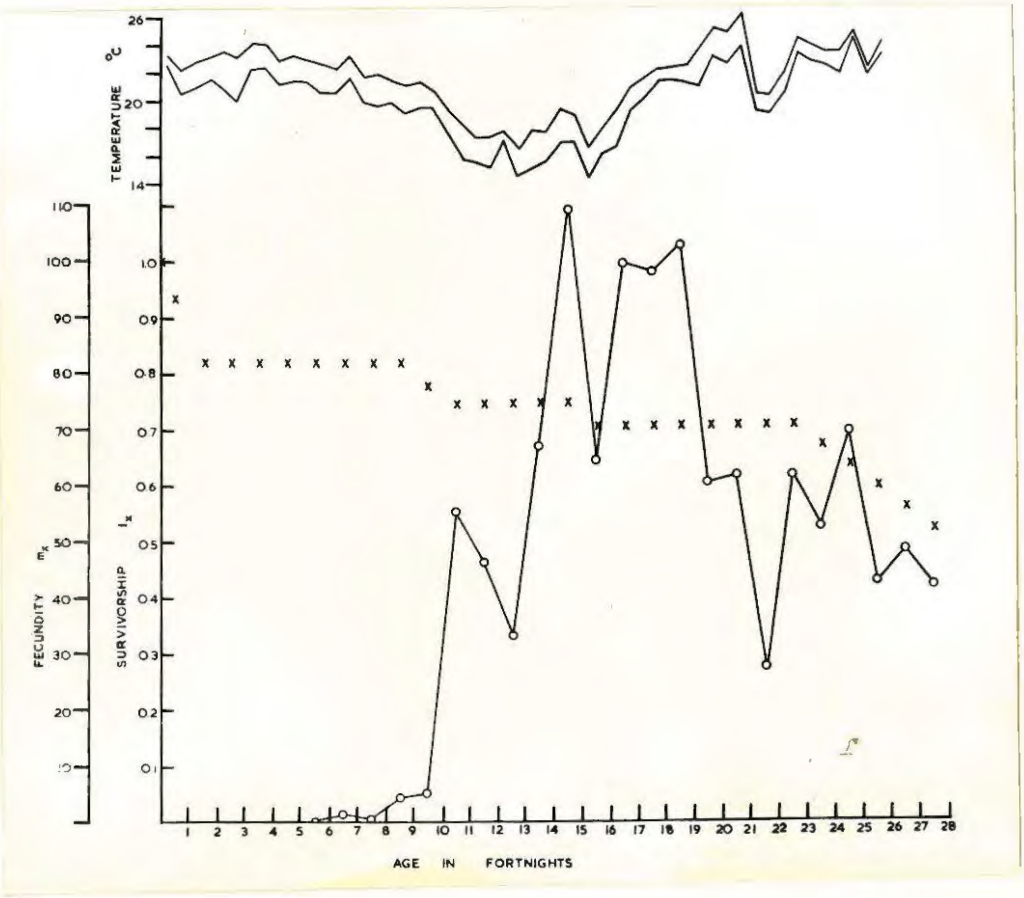


FIG. VII.3 Life table for Biomphalaria pfeifferi reared under standard conditions of feeding and crowding at room temperature for the period January, 1961 to January, 1962. Temperatures given are average weekly minima and maxima.

which took place rapidly, the first eggs being laid during the sixth fortnight. Declining temperatures during the seventh, eighth and ninth fortnights appeared to suppress egg production but during the tenth fortnight, even though temperatures were still dropping, egg production rose to a level far in excess of any value yet recorded in laboratory conditions. From this time on it would appear that room temperatures exerted little influence on egg production.

Mortality over the whole period was low, 81.48% of the original cohort survived to maturity and over 50% survived one year. It would appear that these conditions are admirably suited to *B. pfeifferi*.

The intrinsic rate of natural increase.

Various population parameters calculated from the life table data are given in Table VII.$_5$. From these it would seem that of all the temperature conditions investigated, 25°C. appeared to be most favourable even though fewer eggs were produced at this temperature than at 27°C. or at room temperature. This is because at 25°C. maturation took place earlier and egg production rose rapidly during the early period. It is this period which has the most significant effect on the intrinsic rate of natural increase. The large output of eggs at room temperature was offset by the early retardation of egg laying caused by the fluctuating temperature, yet in actual fact these latter conditions are probably best suited to the species.

A feature of all the life tables is the high survival rate of the species under laboratory conditions. Even at 27°C. which is close to the upper limit for egg production, survival is good. In spite of this, the intrinsic rate of natural increase under all conditions investigated is low when compared with *Lymnaea natalensis* and *B. (Ph.) globosus*. This is because development is relatively slow and egg production does not reach maximum until the ninth or tenth fortnights.

TABLE VII.5

Values of the intrinsic rate of natural increase (r_m) and the finite rate of increase (R) for *Biomphalaria pfeifferi* maintained at various temperatures.

Temp. °C.	r_m	R
18 ± 0.1°	0.2374	1.268
25 ± 0.5°	0.4798	1.616
27 ± 0.1°	0.4376	1.549
Seasonal Room Temp.	0.4643	1.591

3. The influence of temperature on egg production.

Using a thermostatically controlled constant temperature cabinet observations were made on the limiting effect of temperature on egg production. Two series were carried out, the first investigating effects of lower temperatures and the second covering higher temperatures. The first series considered egg production per fortnight in the range 14.2° to 29°C. The initial temperature was 21.1°C. which was maintained for a fortnight after which the temperature was reduced to 19.1°C. The process of reduction was gradual to 17°C. and then 14.2°C. allowing 14 days at each temperature. After this temperatures were increased stepwise to 29.7°C. with a final return to 25°C.

The experiment was started with 19 mature snails which were maintained in three 4-litre aquaria. Sixteen snails survived the experiment which extended over ten fortnights. The results are given in Table VII.$_6$ and Fig. VII.$_4$.

The second series investigated egg production in the range 17.5°C. to 34.4°C. The initial temperature was 25°C. which was maintained for 14 days after which the temperature was dropped abruptly to 17.5°C. and kept at that level for a further fortnight. The temperature was then increased in six steps to 34.4°C. and then reduced to 25°C. for 14 days and finally to 20°C. for a further two weeks recovery.

Six mature snails were used in the experiment although, while under observation, two died and only four snails survived. The results are given in Table VII.$_7$ and Fig. VII.$_5$.

It would appear from these data that temperatures falling from 25° to below 20°C. cause a reduction in egg laying but there is a suggestion that if temperatures are high (29.4°C.) a fall to 25°C. results in an increase in egg production. This is not the case if temperatures have risen to 34.4°C., at which not only is egg production arrested, but four weeks recovery at more equitable temperatures failed to revive egg laying. Below 22°C., rising temperatures cause

TABLE VII.6

Egg production of *Biomphalaria pfeifferi* at various temperatures. Snails were exposed to each temperature category for a period of one fortnight. Temperatures were maintained ± 0.5°C. except for 14.2°C. which was ± 1.0°C.

Week	Temp. °C.	Total Eggs	Total Snails	Average eggs/snail/ week
1	21.1	660	19	
2	21.1	496	19	30.42
3	19.1	399	19	
4	19.1	254	19	17.18
5	17.0	94	18	
6	17.0	23	18	3.25
7	14.2	60	18	
8	14.2	137	18	5.47
9	16.9	173	18	
10	16.9	90	18	7.31
11	20.2	484	18	
12	20.2	194	16	19.51
13	23.1	282	17	
14	23.1	147	17	12.62
15	25.9	168	17	
16	25.9	45	17	6.26
17	29.7	53	16	
18	29.7	1	16	1.69
19	25.0	137	16	
20	25.0	63	16	6.25

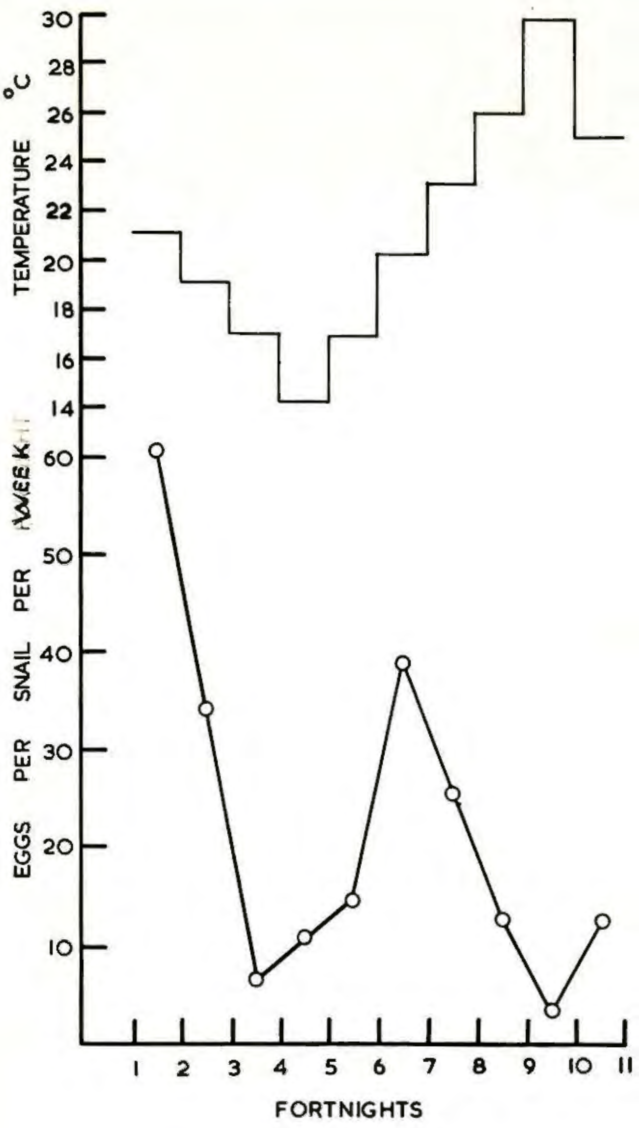


FIG. VII.4 Graph showing the influence of temperature on egg production in *Biomphalaria pfeifferi* maintained at various temperatures ranging from 14.2° to 29.1°C. Snails were kept at each temperature for one fortnight.

TABLE VII.7

Egg production of *Biomphalaria pfeifferi* at various temperatures. Series 2.
Snails were exposed to each temperature category for a period of one fortnight except for 34.4°C. when exposure lasted only seven days. Temperatures were maintained at ± 0.5°C.

Week	Temp. °C.	Total Eggs	Total Snails	Average eggs/snail/ week
1	25.0	18	6	
2	25.0	290	6	25.67
3	17.5	107	6	
4	17.5	26	6	11.08
5	20.4	112	6	
6	20.4	174	6	23.83
7	21.9	208	5	
8	21.9	202	5	41.00
9	24.1	200	5	
10	24.1	178	5	37.80
11	25.1	66	5	
12	25.1	192	5	25.80
13	31.4	34	5	
14	31.4	0	5	3.40
15	34.4	0	5	
16	25.0	0	5	0.00
17	25.0	0	4	
18	20.0	0	4	0.00
19	20.0	0	4	

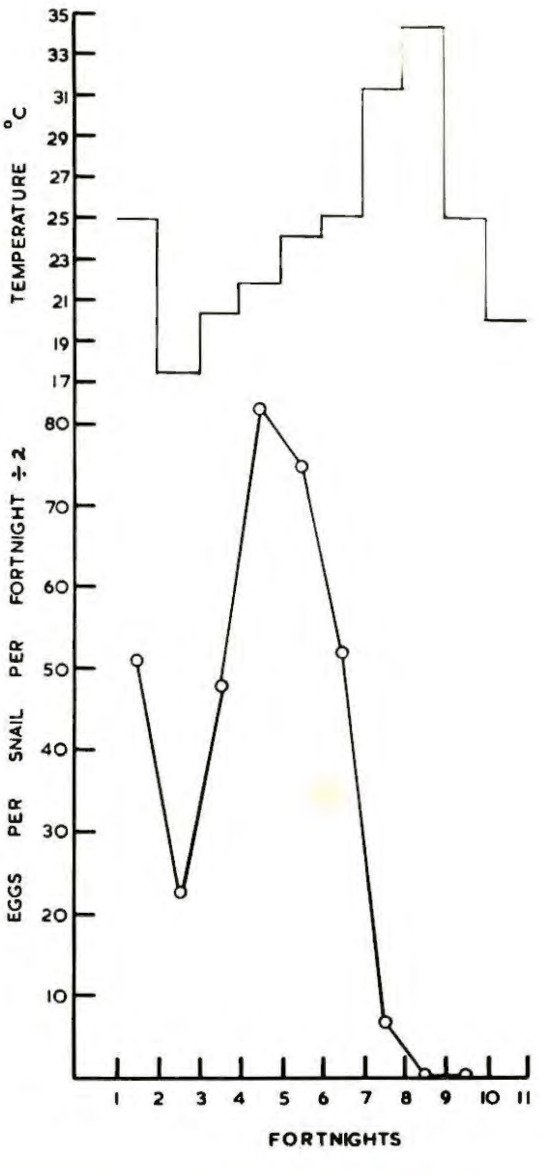


FIG. VII.5 Showing the influence of temperature on egg production in *Biomphalaria pfeifferi* maintained at various temperatures ranging from 17.5° to 34.4°C. Snails were kept at each temperature for one fortnight except for 34.4°C. which was maintained for one week only.

an increase in egg production but as temperatures exceed this figure a progressive drop in egg laying occurs.

It is interesting to note that the upper temperature threshold for egg production in *B. pfeifferi* is 31.4°C. which is lower than that for *B.* (*Ph.*) *globosus*. The preceding data also indicate that *B. pfeifferi* can produce more eggs than *B.* (*Ph.*) *globosus* at lower temperatures. The results fit well into the general pattern which suggests that *B. pfeifferi* can exist in somewhat cooler conditions than can *B.* (*Ph.*) *globosus*, a situation borne out by field observation.

It was not possible to determine the optimal temperature for the species from the preceding data but it would appear to lie between 20° and 23°C. although a far wider range, from 18° to 27°C., can be tolerated. Data in Chapter III show that in winter, temperatures in waterbodies fall well below 18°C. and it has been shown that even at 14°C. *B. pfeifferi* is capable of laying eggs. It is clear that the species can survive temporary cold conditions although it would not be able to increase in number during that time.

4. A naturally occurring population of *Biomphalaria pfeifferi*.

Biomphalaria pfeifferi was present in the Marlborough pond (see Chapter III) during the period June, 1961 to June, 1962. During this time the pond was sampled once every month except for January, 1962, when the sampling apparatus broke down. The modified Eckman dredge described in Chapter V was used and the method has been outlined in Chapter VIII, section 3.

At no time was the population of *B. pfeifferi* very dense but during the period when the pond was under observation it remained fairly constant, varying between an estimated 220,000 and 70,000 snails. The population was at its lowest in September, October and November, which corresponded with high temperature and low water. Three peaks in numbers of snails present occurred during the year, in August, December and April. Apart from the period June to July both in 1961 and in 1962, eggs were laid in low numbers throughout

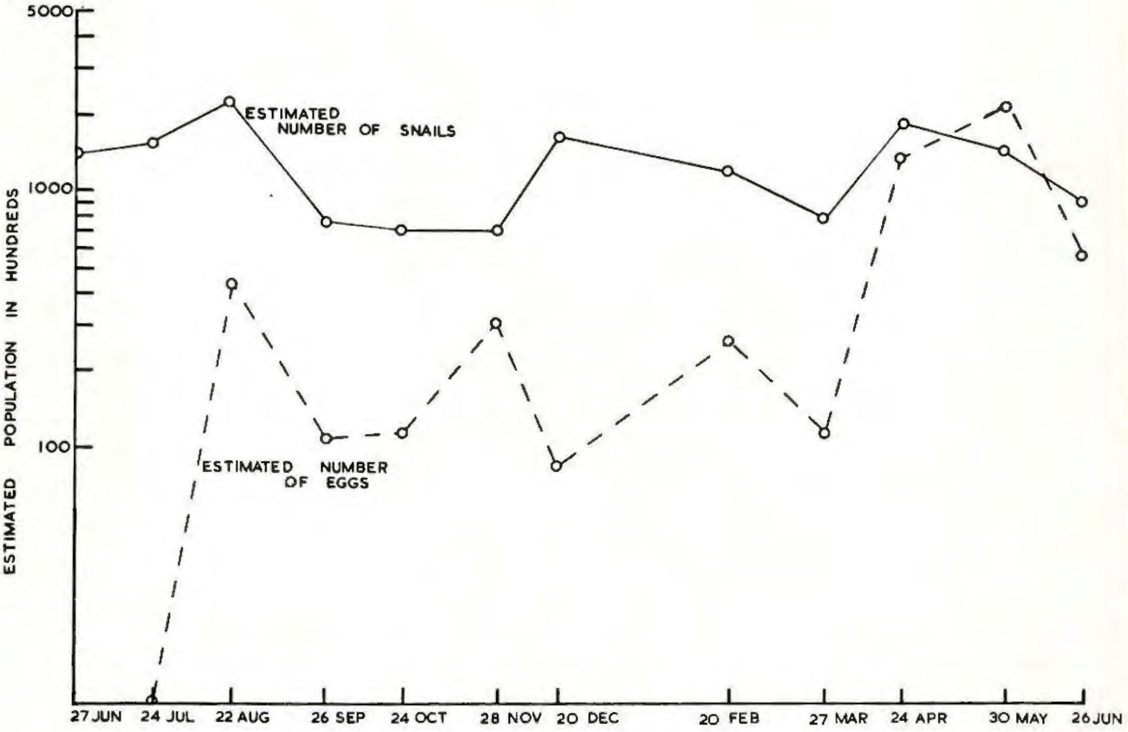


FIG. VII.$_6$ Estimated population fluctuations of *Biomphalaria pfeifferi* in the Marlborough pond during the period June, 1961 to June, 1962.

the year with highest production in April and May. This period corresponded with falling temperatures at the end of the summer, and with the pond still nearly full after the rains, conditions were probably ideal for reproduction. This is what would be expected from laboratory data.

Population fluctuations.

It is almost impossible to deduce any trends in population fluctuation from the data available. The changes in the numbers of snails collected do not follow a logical pattern and when analyses are made of the population with reference to size distribution, it can be seen that the method of sampling was somewhat inadequate. In a stable or increasing population the younger and therefore smaller individuals should be more numerous. The size distribution of the estimated population is shown in Table VII.$_8$. Only on two occasions were the smaller size groups more abundant than the larger ones and these corresponded with the peak populations of the 20th December and the 24th April.

It would appear that the population of B. pfeifferi in Marlborough pond was small but fairly stable. In such a large volume of water the snails were sparsely distributed according to some unknown habitat preferences, and the number of samples used was inadequate to estimate the actual population with any degree of accuracy. This would not appear to be the case with Lymnaea natalensis which was present in large numbers (Chapter VIII) or Bulinus tropicus which was also abundant and showed normal age distribution in the sampled population.

If the number of snails taken in the samples has been influenced by distribution of a sparse population in the habitat, the situation is not necessarily the same with regard to eggs. These are laid on plants and if all vegetation types in the waterbody are sampled, the relative abundance of eggs during various seasons should be indicated in the samples.

There were four clear peaks of egg production: the first was in August and was probably a response to rising temperatures after winter

TABLE VII.8

Estimated population of *Biomphalaria pfeifferi* in Marlborough pond during the period June, 1961 to June, 1962. Diameter of snails given in millimetres.

Size of pond m^2	27/6/61	24/7/61	22/8/61	26/9/61	24/10/61	28/11/61	20/12/61	20/2/62	27/3/62	24/4/62	30/5/62	26/6/62
	1,415	1,415	1,296	988	807	1,020	1,365	1,640	1,640	1,640	1,534	1,400
Eggs	Nil	Nil	43,740	10,980	11,540	30,600	8,530	26,240	11,480	139,400	219,362	67,200
Under 1	Nil	Nil	Nil	Nil	Nil	Nil	1,706	14,760	1,640	6,560	Nil	Nil
1.1 - 2.0	3,538	Nil	1,620	Nil	Nil	5,100	29,002	8,200	14,760	37,720	6,136	8,400
2.1 - 3.0	26,535	19,459	11,340	Nil	2,308	5,100	35,826	16,400	8,200	37,720	15,340	15,400
3.1 - 4.0	28,304	22,997	24,300	Nil	2,308	7,650	20,472	11,480	1,640	27,880	12,272	8,400
4.1 - 5.0	40,687	51,301	48,600	7,686	Nil	6,375	10,236	34,440	3,280	16,400	13,806	8,400
5.1 - 6.0	30,073	47,763	89,100	24,156	15,002	6,375	18,766	21,320	18,040	26,240	18,408	15,400
6.1 - 7.0	7,076	5,307	25,920	35,136	40,390	19,125	35,826	14,760	16,400	11,480	39,884	16,800
7.1 - 8.0	1,769	Nil	14,580	7,686	9,232	19,125	11,942	Nil	11,480	13,120	23,010	12,600
8.1 - 9.0	Nil	5,307	3,240	1,098	1,154	1,275	Nil	Nil	1,640	11,480	9,204	5,600
9.1 - 10.0	Nil	Nil	1,620	Nil	Nil	Nil	Nil	Nil	1,640	Nil	6,136	1,400
10 +	1,769	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil
Total snails	139,751	152,134	220,320	75,762	70,394	70,125	163,776	121,360	78,720	188,600	144,196	92,400

minima. At this time evaporation from the waterbody was excessive and a reduction in size of the habitat may have caused the subsequent fall-off in egg production. By November rain had fallen and a second burst of egg production followed the dilution of the waterbody. However, with continued rain in December a large amount of the vegetation became swamped and egg production declined, probably because there was insufficient vegetation near the surface to provide adequate egg laying sites. The situation improved slowly during February and March although surface temperatures were high and may have influenced egg production adversely. The major outburst of egg production occurred during the late summer period of stability from March until June.

Parasites and predators.

Numbers of *B. pfeifferi* were infested with trematode parasites although, strangely, none of these were of the genus *Schistosoma*. During the period June, 1961 to July, 1962, of the 1,042 snails of this species which were examined for parasitic infection, 99 were infected. Of these 84 were hosts of "cystophorous" cercariae, probably *Cercaria bulla* Fain, 12 were immature trematode and three were amphistomes. Trematode infections were most common during the period March to July.

It is not feasible to attempt to draw any conclusions about the population of *B. pfeifferi* in the Marlborough pond except those referred to above concerning the egg laying, and that the population was small and fairly stable. There did not appear to be any gross fluctuation in numbers during the period of observation.

It is possible that the snails have some obscure behaviour patterns which rendered the sampling methods inconclusive with regard to this species: it is clear that further sampling in smaller or more densely populated habitats must be carried out before the dynamics of fluctuation of *B. pfeifferi* in waterbodies on the highveld plateau of Southern Rhodesia can be understood.

VIII. THE INFLUENCE OF TEMPERATURE ON THE BIONOMICS OF *LYMNAEA NATALENSIS*.

1. General.

Lymnaea natalensis is the commonest and most widely distributed pulmonate snail in Rhodesia, and with its high degree of adaptability has established itself in a great variety of waterbodies ranging from large lakes to small ornamental ponds. Van Someren (1946), working in East Africa, has reviewed the habitats and tolerance ranges of *L. caillaudi*, which is a northern form conspecific with *L. natalensis* (Connolly, 1939). Certainly the species in Rhodesia occupies habitats similar to those described for *L. caillaudi*. It would seem that both species are best suited to clear, slow moving water whether in *vleis* or streams. Large open pools in riverbeds, dams or in excavations also offer satisfactory conditions, but then as pointed out by Boycott (1936) these waterbodies can be compared with slow moving streams in that "the effective occupied (by snails) volume of water is in contact with a larger volume of 'free water' promoting cleanliness and diluting the products of activity and decay ....." Neither species appears to tolerate rapidly flowing water and flood conditions, and *L. caillaudi* is reported by van Someren as not occurring in shallow stagnant water in which there are heavy red flocculent precipitates of iron compounds. This is generally the case with *L. natalensis* but occasionally this species has been collected from such water bodies.

L. natalensis has been collected from the three localities described earlier but has not been taken in large numbers at Foyle, whereas in both the Derbyshire weir pool and the Marlborough pond the species has been well represented, especially in the latter habitat. When full, these two waterbodies are similar in that there is an abundance of clean water and therefore are comparable to gently moving streams. However, Marlborough pond is subjected to annual fluctuations, rising during the rains and falling during the dry season. At the low level which generally occurs toward the end of October, the waterbody becomes much smaller and cluttered up with dense growths of aquatic plants (*Typha*, *Potamogeton* and *Nitella*).

As the species is so widespread it is impossible to find a single typical *L. natalensis* habitat, and thus it was decided to utilise the Marlborough pond merely because of convenience, an assurance from the local authority that it would not be tampered with, and because for the period under consideration it contained a large number of snails.

2. Life tables.

As with the other species discussed above, a desirable prerequisite to the investigation of field population dynamics is the compilation of life tables under laboratory conditions. This permits the calculation of basic population parameters, namely the intrinsic rate of natural increase, the mean generation time and birth and death rates under specified conditions. These values can be compared with calculated parameters based on field data collected at various stages of population fluctuation and, it is hoped, will provide some idea of the conditions which are favourable or unfavourable for increase, the theoretical capabilities of the species to increase and the extent to which this does occur under natural circumstances. For the same reason as with the other species discussed, the laboratory work has been confined to the investigation of the effects of temperature, keeping other conditions such as feeding, crowding, water and other animals, constant throughout the experiment. Shortage of space has restricted this work to two sets of conditions, one at room temperature from March, 1962 to January, 1963, and the other for a period of ten months at a constant temperature of 25°C.

Life table : room temperature, March, 1962 to January, 1963.

An initial batch of 53 eggs laid by a group of snails collected from the Marlborough pond were reared under standard conditions of feeding and crowding at room temperature from March, 1962 to January, 1963 (see Table VIII.$_1$). Daily records of maximum and minimum temperatures were made from a 'Sixes' thermometer kept immersed in an aquarium. Weekly averages are incorporated in Fig. VIII.$_1$ which also shows the life table of the cohort of snails over a period of 22 fortnights.

There was a high loss of newly hatched snails but after the sixth fortnight no further mortality occurred for the remainder of the period of observation. Egg production commenced during the sixth fortnight and slowly increased to a maximum output during the 15th fortnight, after which eggs were laid at a fairly constant rate for the duration of the experiment.

As was pointed out in Chapter IV, sufficient data for the calculation of the intrinsic rate of natural increase are usually available by the 16th fortnight. As this is the case with this cohort, the nett reproductive rate has been given for 16 fortnights only. The values for the intrinsic rate of natural increase (r_m), the finite rate of increase (R), as well as the mean generation time, the birth rate and death rate for the conditions specified above are given in Table VIII.$_3$, along with similar parameters calculated for the species maintained at 25°C.

Life table : 25 ± 0.5°C.

Shortage of space in the constant temperature room precluded the use of large numbers of snails, however, the information obtained from the culture of the progeny of an initial batch of 17 eggs provides an interesting comparison with that obtained from snails living at room temperature. Data were collected over a period of 22 fortnights and are given in Table VIII.$_2$ and Fig. VIII.$_2$. As before, the nett reproductive rate has been calculated only up to the 16th fortnight.

At this temperature, mortality among the younger snails was not as high as sustained at room temperature, but by the 8th fortnight, survival was of the same order as that recorded under the cooler

TABLE VIII.$_1$

Life table for *Lymnaea natalensis* reared at room temperature for the period March, 1962 to February, 1963.

Pivotal Age in Fortnights x	Total Eggs	Total Snails	Survivorship l_x	Fecundity Eggs/Snail m_x	$l_x m_x$
0		53	1.0000		
0.5		50	.9434		
1.5		30	.5660		
2.5		30	.5660		
3.5		30	.5660		
4.5		30	.5660		
5.5	44	28	.5283	1.571	0.830
6.5	379	28	.5283	13.536	7.151
7.5	477	28	.5283	17.036	9.000
8.5	693	28	.5283	24.750	13.075
9.5	556	28	.5283	19.857	10.490
10.5	824	28	.5283	29.429	15.547
11.5	863	28	.5283	30.821	16.283
12.5	1,178	28	.5283	42.071	22.226
13.5	1.423	28	.5283	50.821	26.849
14.5	2,026	28	.5283	72.357	38.226
15.5	1,819	28	.5283	64.964	34.320
16.5	1,869	28	.5283	66.750	
17.5	2,177	28	.5283	77.750	
18.5	2,001	28	.5283	71.464	
19.5	1,918	28	.5283	68.500	
20.5	2,163	28	.5283	77.250	
21.5	1,386	28	.5283	49.500	

Nett reproductive rate for 16 fortnights

$$R_o = 193.997$$

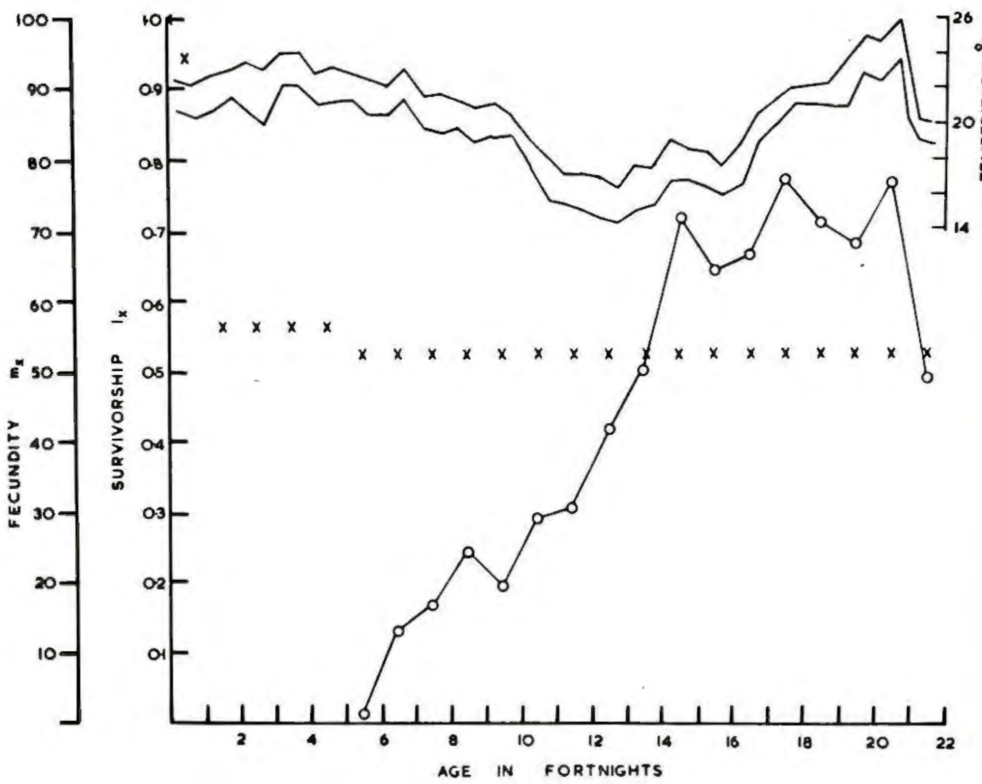


FIG. VIII.₁ Life table for Lymnaea natalensis reared under standard conditions of feeding and crowding at room temperature during the period March, 1962 to February, 1963. The temperatures given are weekly averages of maxima and minima as measured in a sample aquarium.

TABLE VIII.$_2$

Life table for *Lymnaea natalensis* reared under standard conditions of feeding and crowding at a constant temperature of 25 ± 0.5°C.

Pivotal Age in Fortnights x	Total Eggs	Total Snails	Survivorship l_x	Fecundity Eggs/Snail m_x	$l_x m_x$
0		17	1.0000		
0.5		17	1.0000		
1.5		16	0.9412		
2.5		16	0.9412		
3.5		12	0.7059		
4.5	275	12	0.7059	22.917	16.177
5.5	338	12	0.7059	28.167	19.883
6.5	314	12	0.7059	26.167	18.471
7.5	445	10	0.5882	44.500	26.175
8.5	219	10	0.5882	21.900	12.882
9.5	263	10	0.5882	26.300	15.470
10.5	84	10	0.5882	8.400	4.941
11.5	382	10	0.5882	38.200	22.469
12.5	284	10	0.5882	28.400	16.705
13.5	339	10	0.5882	33.900	19.934
14.5	508	10	0.5882	50.800	29.881
15.5	309	10	0.5882	30.900	18.175
16.5	397	10	0.5882	39.700	
17.5	310	10	0.5882	31.000	
18.5	247	10	0.5882	24.700	
19.5	269	10	0.5882	26.900	
20.5	137	8	0.4706	17.125	
21.5	36	6	0.3529	6.000	

Nett reproductive rate for 16 fortnights

$$R_o = 221.163$$

TABLE VIII.3

Population parameters of *Lymnaea natalensis* calculated from life table data.
R is finite rate of natural increase per fortnight.
r_m is infinitesimal rate of natural increase per fortnight.

Value for	Ambient Room Temp. March - Nov.	Const. Temp. 25 ± 0.5°C.
R	1.662	2.173
r_m	0.5080	0.7761
Mean generation time	8.5 fortnights	5.4 fortnights
Birth rate	2.2035	2.2762
Death rate	0.1811	0.0348

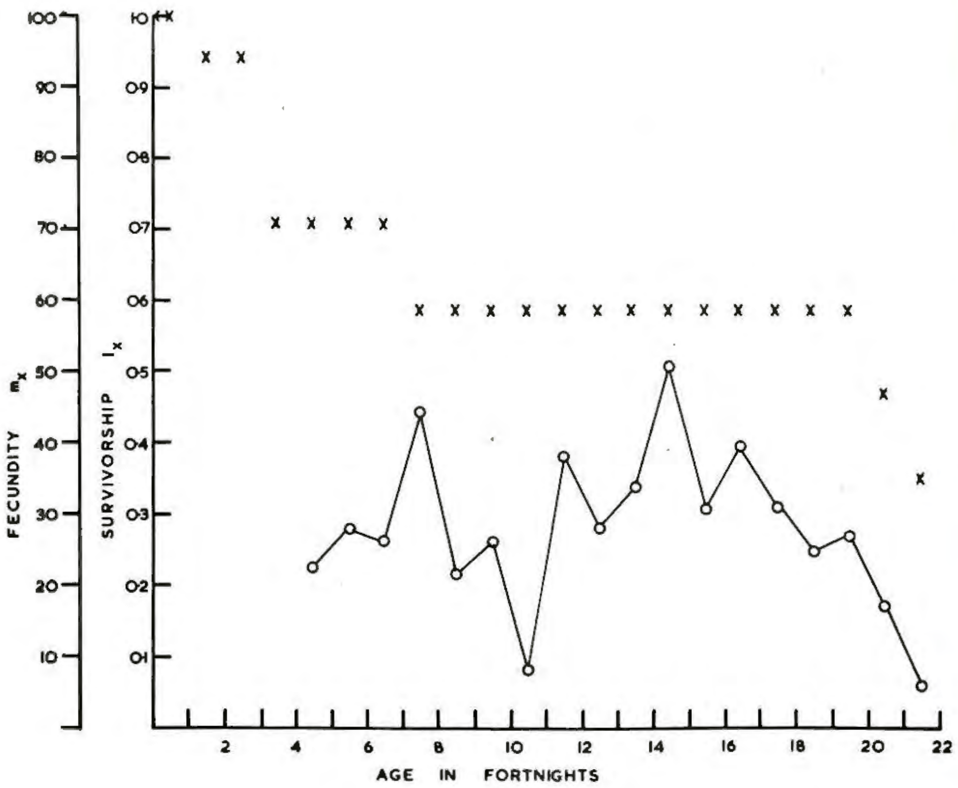


FIG. VIII.$_2$ Life table for *Lymnaea natalensis* reared under standard conditions of feeding and crowding at a constant temperature of 25 ± 0.5°C.

conditions. A long period elapsed during which no mortality occurred but by the 20th fortnight the cohort began to die off. There was a great deal of similarity between the two survivorship patterns; it would seem that the higher temperature had little effect on the survival of individuals during the first 20 fortnights. The picture was somewhat different with regard to egg production. The first eggs were produced during the fifth fortnight, after which the snails laid eggs at a fairly constant rate until the 20th fortnight, after which fecundity of the snails decreased. Egg production never approached the high level recorded at room temperature, yet due to the rapid rate of maturation, the nett reproductive rate for 16 fortnights was higher at 25°C. than at room temperature. From these data and the population parameters in Table VIII.$_5$, it can be seen that although there was no striking increase in egg production with the small rise in temperature, the finite rate of increase rose from 1.66 at room temperature to 2.17 at 25°C. The mean generation time was reduced from 8.5 fortnights to 5.4 fortnights.

Under these experimental conditions, L. natalensis is capable of very high rates of increase. At 25°C. this is far in excess of the other species examined. Under these ideal conditions one snail would in the course of ten fortnights, give rise to 2.17^{10} or 2,274 individuals at the observed rate of increase. The high intrinsic rate of natural increase is probably an important reason why the species is so widespread.

3. A naturally occurring population of Lymnaea natalensis.

The Marlborough pond has been described in Chapter III, and for the period June, 1961 to June, 1962, was found to contain a large fluctuating population of L. natalensis. During this time, using a modification of the Ekman dredge outlined in Chapter V, the pond was sampled once every month except for January, 1962 when the apparatus broke down. Samples were taken along two transects, one east to west and the other north to south, which were marked by a rope held taught by assistants on each bank. The sampler was operated from a small dinghy and samples were taken at approximately five metre intervals. No attempt was made to mark the position of each sample, these were merely taken from approximately the same regions month after month, except, of course, when the locality became exposed as the water receded. There was no replacement of those snails taken in the samples, it was considered to be unnecessary because the amount of material removed at each sampling was very small in relation to the size of the habitat.

Depending on the surface area of the pond, from 14 to 20 samples were taken each month. Except for the *Phragmites*, an average cover of all vegetation types, including the dense beds of *Typha*, was achieved. The sampler was able to sever the *Typha* stems and roots but not the much harder *Phragmites*. However, it should be pointed out that a possible error exists in the *Typha* samples because the stiff upright plants were inclined to raise the hinged flaps covering the top of the sampler and some snails on the stems may have been lost.

The purpose of this method of sampling was to obtain some form of quantitative estimate which, although it would not necessarily reflect the actual number of snails present in the whole pond, would provide comparative figures for the month by month samplings. It would be most difficult to estimate the actual number of snails in a pond such as Marlborough which has an uneven bottom and is colonised by various vegetational types, the actual extent of which change significantly from time to time. The whole pond would have to be divided into various major ecotypes and the size of each determined in relation to the whole, the population in each category could then be expressed as the number of snails per unit volume of the ecotype.

From these data it might be possible to compute a figure representing the actual population of snails within the whole pond, but this type of population assessment would be beyond the compass of these studies. What must, therefore, be accepted is an estimation based on the population density per unit area which takes into consideration the changing surface area of the pond. It is evident that, unless there is an accompanying high mortality as the pond decreases in size, snails will become more crowded and more dense per unit area. This may obscure the actual state of the population, so that any estimation of the population must take into consideration the density of snails per unit area, and the total surface area of the pond. This may not be acceptable in larger waterbodies, but in the small, well defined Marlborough pond, in fact all the ecotypes are available to the snails all the time. There is no effective barrier between them.

It may be argued that the number of samples taken was too small, but the mere physical difficulty of sorting large amounts of vegetation and mud together with measuring, crushing and microscopic examination of every snail taken precluded the collection of more samples. Each snail was measured with an eyepiece micrometer or hand callipers to the nearest 0.1 mm. and then examined for trematode infection. No attempt was made to identify the trematodes further than general types.

For the period June, 1961 to March, 1962 the numbers of L. natalensis in the pond were far in excess of both other species. For the period March to June, 1962, the population declined dramatically. No reason for this was sought, it was merely recorded as a period of positive increase, stability and then decline. This cycle was not followed by the populations of other snails present in the pond so that the decline recorded from March to June was purely a feature of the L. natalensis population.

During the period of increase and stability L. natalensis was distributed all over the pond although it appeared to prefer the broad leafed Polygonum on which were laid most Lymnaea egg masses. During the period of decline the species occurred spasmodically at all sampling stations with the highest concentrations again in association with Polygonum.

Commensals and Parasites.

L. natalensis in the Marlborough pond was particularly free of parasitic infestation: 14 of the 4,337 snails examined were found to have trematode infections, of which four were immature trematode infections, six amphistome infections, three with xiphidiocercariae and one was apparently infected with *Fasciola gigantica* Cobbold.

The commensal oligochaete worm *Chaetogaster* sp. c.f. *lymnaei* occurred in almost all of the snails examined and in general there were several of these worms present in each snail.

Food.

No attempt was made to identify the particular food preferences of *L. natalensis* but from the crushings carried out on the snails the following points are worth noting. In all snails the gut appeared to be crammed full with mud, grains of quartz and very frequently spore capsules of *Nitella*. From this it seems that although the snails browse on plant material they consume a good deal of bottom detritus which is, of course, rich in nourishment and always plentiful.

Population fluctuations.

Conditions in the Marlborough pond during June, July and August, 1961 seemed to be ideal for *L. natalensis*. For most of that period water temperatures were generally low and loss of water by evaporation was minimal. The area of the pond did not decrease significantly until mid-August at which time temperatures had begun to rise. From June until August the *L. natalensis* population, including both eggs and snails, increased, (see Fig. VIII.-3) rising in August to a peak of nearly four million, of which 2.8 million were eggs. This peak declined abruptly until October, and thereafter until May fluctuated around the one million mark.

This gross population figure is somewhat over simplified, a point which becomes clear when the population figures are broken down into eggs and snails separately. The snail population as distinct from the eggs rose twofold from 495,040 in June to 1,033,560

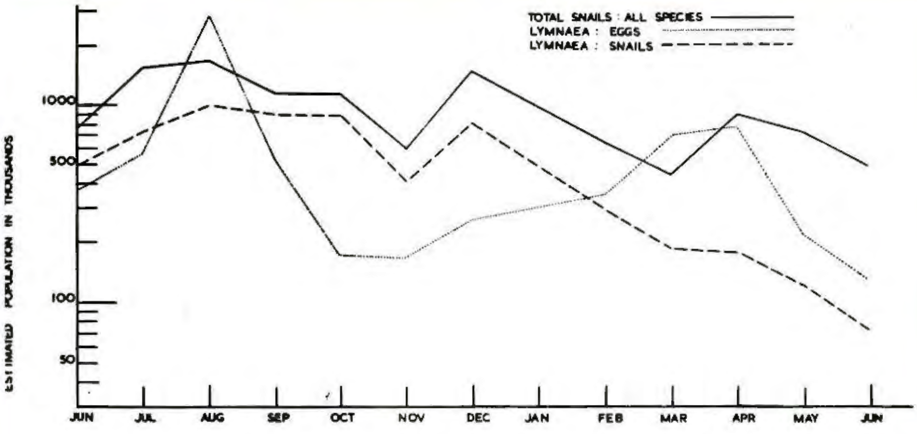


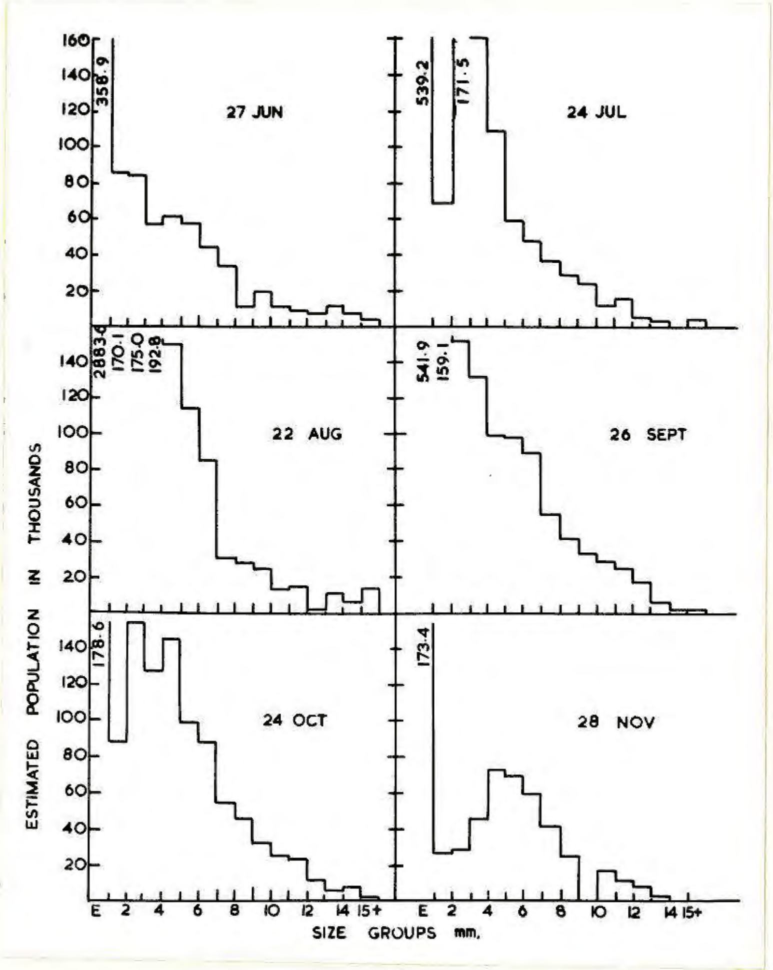
FIG. VIII.3 Showing seasonal fluctuations in estimated populations in thousands during the period June, 1961 to June, 1962, in the Marlborough pond, of *Lymnaea natalensis*, and other species.

in August and maintained approximately that level during September and October. This state of affairs broke down in November with the flooding of the habitat at the beginning of the rainy season, and although the snail population rallied somewhat in December, subsequently a general decline in numbers took place which by April began affecting the number of eggs in the habitat. This decline was followed until the end of the period of observation in June, 1962. As can be seen in Fig. VIII.$_3$, which shows the Lymnaea population in relation to the total number of snails present, the drop in L. natalensis from March to June, 1962 was not matched by a general drop in numbers of the total snail population, thus it can be concluded that decline in the L. natalensis population was a feature of that species only.

Size distribution within the population, month by month.

For close analysis of the population trends during the period under investigation, snails were measured to the nearest 0.1 mm. so that the size structure of the population, month by month, could be investigated. These data are presented in a series of histograms (Figs. VIII.$_4$ and VIII.$_5$) and show the size frequency at 1.0 mm. intervals. As will be seen later, this is adequate for determining the age of the population. The actual figures presented are the estimated populations of the pond based on surface area and, for the sake of convenience are expressed in thousands. The most important information that can be derived from this series of histograms is the estimation of the rate of growth of L. natalensis under field conditions. If this is found to resemble measurements of snails carried out in the laboratory, then it will be possible to compile a growth curve for the species and to convert size frequency into age structure, month by month. This can then be used to make estimates of such data as age specific mortality, fecundity, and the rate of actual increase in the field.

An examination of the histograms in Figs. VIII.$_4$ and VIII.$_5$ shows a definite progression of a peak from 24/10, where there was a maximum



FIGS. VIII.$_4$ Histograms showing the size group frequency (1.0 mm. intervals) of *Lymnaea natalensis* in Marlborough pond as estimated on the quoted sampling dates. (E = eggs).

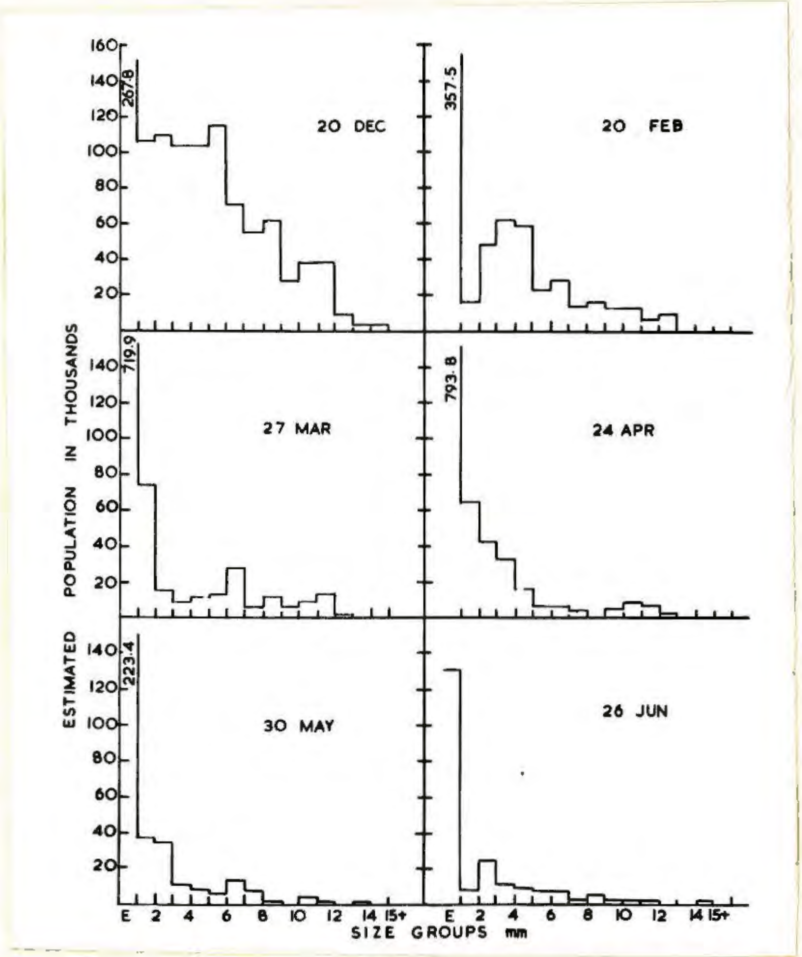


FIG. VIII.5 Histograms showing the size group frequency (1.0 mm. intervals) of *Lymnaea natalensis* in Marlborough pond as estimated on the quoted sampling dates. (E = eggs).

between 2.1 and 5.0 mm., to 28/11 when this had moved to the 5.1 to 8.0 mm. range. It was still apparent on 20/12 as a peak in the range 10.1 to 12.0 mm. and probably the remnants were responsible for the small peak in the range 12.1 to 13.0 mm. on 20/2. A second series can be followed in a less definite manner from 27/7 where the peak occurred in the range of 2.1 to 4.0 mm. The corresponding group on 22/8 appeared to be in the range 4.1 to 7.0 mm. The sampling on 26/9 was influenced by the enormous numbers of young snails present during the previous month and it is not possible to point at any particular grouping with certainty, however, if growth had proceeded in a manner comparable to the first series outlined then the previous group would probably be represented by the range 8.1 to 11.0 mm. on 26/9 and 11.1 to 12.0 mm. on 24/10.

It is possible to estimate the rate of growth of *L. natalensis* in the field from these data and then to make a comparison between this and results obtained from keeping the species under laboratory conditions.

Three groups of *L. natalensis* were reared under laboratory conditions and were measured periodically. The details of measurements and standard deviations are given in Table VIII.$_4$. The curves showing average growth rate for the different conditions can be compared in Fig. VIII.$_6$. It will be seen that the two curves representing growth rate at room temperature during different seasons are far more similar than that for *L. natalensis* at a constant temperature of 25°C.

Fig. VIII.$_7$ shows the average growth rate for the snails reared at room temperature compared with the series from Marlborough for the period 24/10 to 22/2 and for the period 27/6 to 28/11: the range of each peak is given. Submitting these figures to the chi square test for goodness of fit, it is clear that the points are associated with the average growth rate at room temperature, for in both series P is greater than 0.3. The association is not so strong when the field data are compared with the average growth rate at 25°C., in these instances P is only slightly greater than 0.05. Thus it would appear

TABLE VIII.4

Details of measurements of three groups of *Lymnaea natalensis* reared under standard conditions of feeding and crowding at 25 ± 0.5°C. and at room temperature, Number 1 initiated in April and Number 2 in March. Measurements in mm. Standard deviation in parentheses.

	25°C.		Room temperature			
			No.1		No.2	
Age in days	Mean height of shell	Replicates	Mean height of shell	Replicates	Mean height of shell	Replicates
32	3.79 (1.23)	16	3.48 (0.57)	11	2.28 (0.54)	19
43	6.66 (2.28)	12	5.20 (0.98)	11	4.95 (1.88)	18
52	7.48 (2.59)	12	6.24 (1.33)	11	6.77 (2.61)	18
65	10.65 (2.83)	12	9.40 (1.55)	11	8.05 (2.62)	18
87			11.11 (1.21)	11	10.92 (1.44)	17
105			12.02 (1.33)	11	12.31 (1.03)	17
150	16.70 (1.17)	10	13.35 (1.27)	11	13.54 (0.85)	17

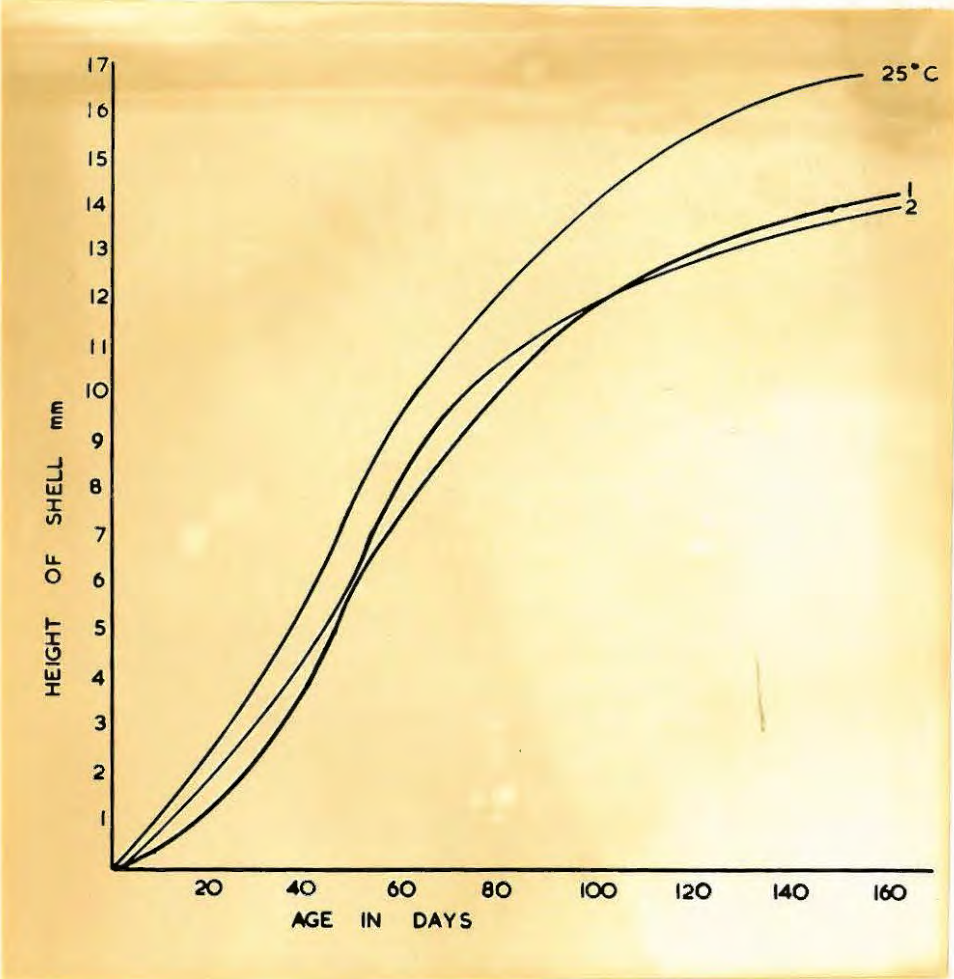


FIG. VIII.6 Average growth curves of Lymnaea natalensis as determined in the laboratory under various temperature conditions: 25°C.; 1 = room temperature March to July; 2 = room temperature April to August.

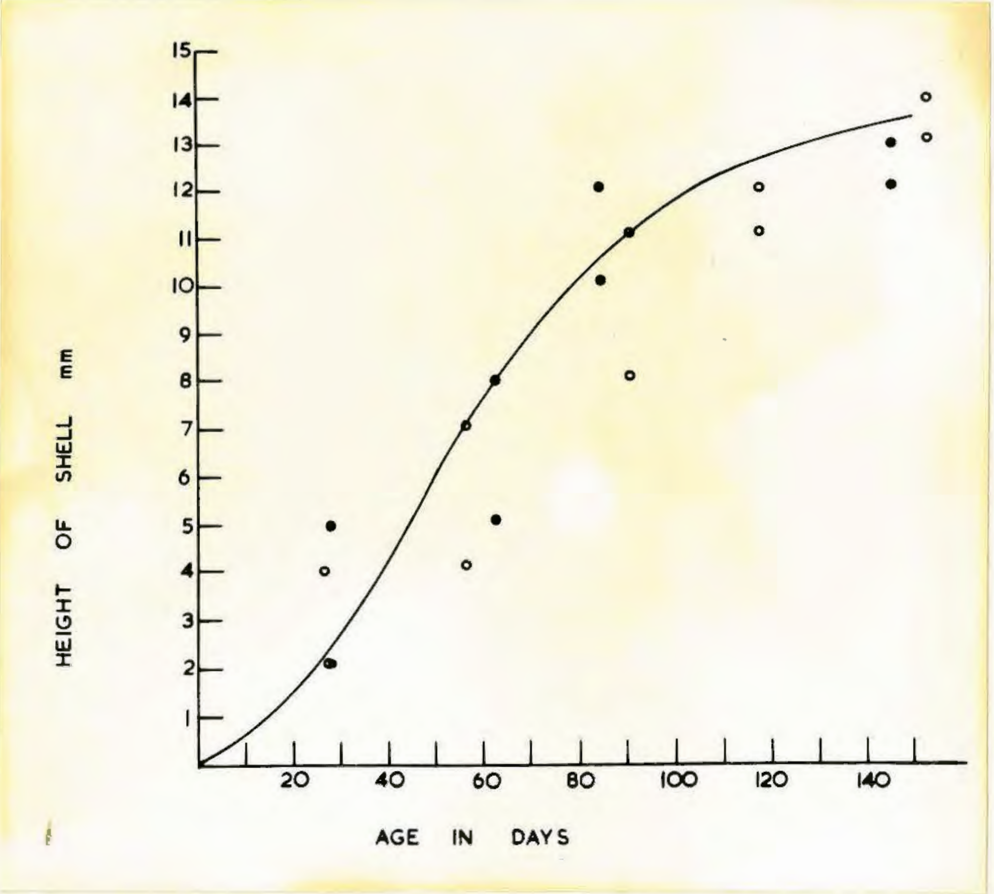


FIG. VIII.7 Average growth rate of *Lymnaea natalensis* reared at ambient room temperature March to September compared with the estimated growth rate in Marlborough pond. Hollow circles represent the range of peaks for the population existing from 27/6 to 28/11, solid circles represent the range of peaks for the population existing from 24/10 to 20/2.

that the growth rate estimated by the measurements of snails bred at room temperature in the laboratory represents a fair indication of the growth of the species under field conditions, both for the late winter and the summer period.

Age structure of the L. natalensis population in Marlborough pond month by month.

With the establishment of an average growth rate for L. natalensis under field conditions as they existed at Marlborough, it is possible to consider the age structure of the population in that pond as it changed month after month, and from this to calculate the percentage survival of various age groups as they grew older.

Because the rate of growth of L. natalensis is very rapid, it was decided to estimate the population in ten day periods. As no attempt was made to age the eggs collected, eggs and young snails up to 1.5 mm. long were considered to be in the group 0 to 20 days old. The next group of snails between 1.6 and 2.5 mm. long fell into the age group 21 to 30 days old and so on as indicated in Table VIII.$_5$. These data are presented in a series of histograms in Figs. VIII.$_8$ and VIII.$_9$ and give graphical demonstration of the changing age structure of the population of Marlborough pond month by month. It can be seen that the population becomes younger for the period June to August and that apart from the drop in eggs and very young snails (age 0 to 20 days) the population structure for August, September and October was fairly similar. In November flooding took place and this resulted in the loss of younger (21 to 40 days) and older (111 +) snails. However in some instances the December groups contained more snails than their November predecessors which means that the decrease recorded in November was probably the result of sampling error and not completely due to mortality of snails. It is probable that because of some reaction to the diluting effect of the flooding which took place in November, a proportion of the population was missed and therefore the November figures will be used to a minimum extent for mortality and

TABLE VIII.5

Estimated population of *Lymnaea natalensis* in Marlborough pond for the period 27.6.61 to 26.6.62 showing calculated age distribution based on laboratory growth rate (Fig. VIII.7).

Age in days	Size in mm.	27/6	24/7	22/8	26/9	24/10	28/11	20/12	20/2/62	27/3	24/4	30/5	26/6
0 - 20	Eggs - 1.5	429,624	565,760	2,953,260	607,738	201,600	197,625	310,492	364,080	754,400	823,280	234,090	133,000
21 - 30	1.6 - 2.5	76,024	123,760	196,020	160,162	120,960	16,575	107,478	34,440	27,880	59,040	39,780	11,200
31 - 40	2.6 - 4.0	77,792	251,056	272,160	223,788	193,536	31,875	167,188	85,280	16,400	45,920	32,130	26,600
41 - 50	4.1 - 6.0	114,920	167,960	264,060	198,557	244,224	116,025	216,662	80,360	24,600	21,320	15,300	15,400
51 - 60	6.1 - 7.5	53,040	63,648	105,300	104,215	103,680	105,825	87,006	31,160	26,240	6,560	19,890	7,000
61 - 70	7.6 - 9.0	31,824	47,736	37,260	65,820	78,336	54,825	98,948	27,880	21,320	-	1,530	7,000
71 - 80	9.1 - 10.0	19,448	22,984	24,300	34,007	32,256	22,950	27,296	13,120	11,480	3,280	-	1,400
81 - 90	10.1 - 11.0	10,608	12,376	12,960	27,425	24,192	17,850	39,238	13,120	6,560	8,200	4,590	1,400
91 - 100	11.1 - 12.0	8,840	14,144	14,580	26,328	23,040	12,750	39,238	4,920	8,200	4,920	1,530	1,400
101 - 110	12.1 - 12.3	1,768	3,536	-	6,582	4,608	7,650	5,116	3,280	4,920	-	-	-
111 - 120	12.4 - 12.7	3,536	1,768	-	4,388	5,760	-	3,412	3,280	4,920	1,640	-	-
121 - 130	12.8 - 12.9	-	-	1,620	5,485	1,152	-	3,412	3,280	-	-	-	-
131 - 140	13.0 - 13.2	5,304	-	3,240	2,194	-	-	-	-	4,920	-	-	-
141 - 150	13.3 - 13.5	1,768	1,768	-	1,097	2,304	-	-	-	-	-	-	-
151 +	13.6 +	17,680	5,304	30,780	4,388	10,368	1,275	-	-	-	1,640	1,530	1,400

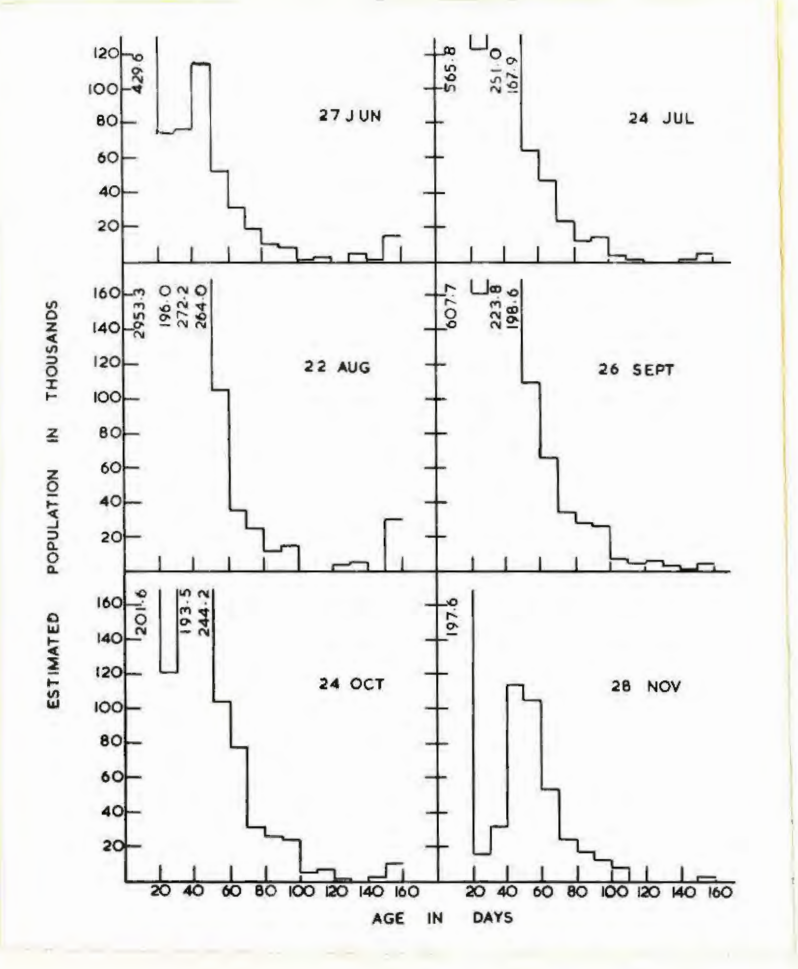


FIG. VIII.8 Histograms showing the age group frequency (10 day intervals) of Lymnaea natalensis in Marlborough pond as estimated on the quoted sampling dates.

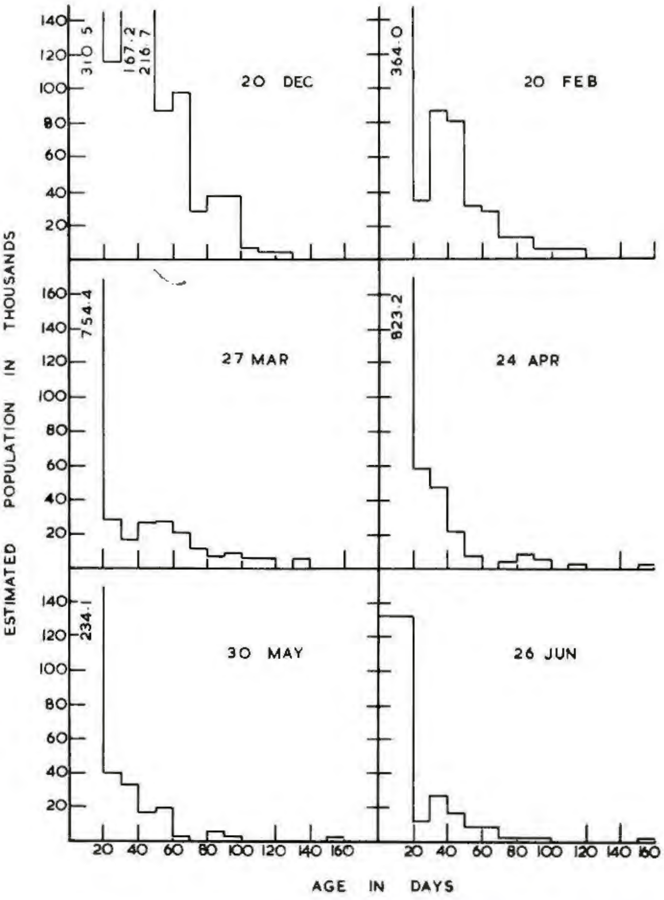


FIG. VIII.$_9$ Histograms showing the age group frequency (10 day intervals) of *Lymnaea natalensis* in Marlborough pond as estimated on the quoted sampling dates.

fecundity calculations. No samples were taken in January and by February, apart from very young snails (0 to 20 days) the population was beginning to decline with a mortality reflected generally throughout all ages. A similar picture is seen through March and April with the population becoming younger but smaller until May and June when the general decline of adult snails began to cause a drop in the population of eggs and younger snails.

The calculation of age specific mortality for Lymnaea natalensis in the field at various periods between June, 1961 and June, 1962.

It is possible to use the age structure of the population month by month to obtain several population parameters such as age specific mortality, and estimates of the rate of actual increase. The age specific mortality of a field population is not a constant figure which can be applied generally to any population. It must refer specifically to the situation studied and should be calculated at different seasons of the year if it is to have any application to groups other than those from which it was measured.

The L. natalensis population in the Marlborough pond has been studied for a full year and during this time the species went through a period of increase, stability and decline. The age specific mortality rate has been calculated for several periods during the year. To do this it has been necessary to take 20 day age groups as this was the duration of the youngest category in the age structure data. Thus the total number of individuals falling into this period at time zero are taken as originators of the group and refer to 100% survival. At the second sampling, which normally would be about one month later, the exact time lapse is known, the actual age which the original group would have attained is calculated. From the appropriate data in Table VIII.$_5$, the number of survivors in the nearest corresponding periods are computed, and thus a percentage survival for the period is obtained. The data are given in Tables VIII.$_8$ to VIII.$_{12}$: Table VIII.$_8$ will be taken as an example. At the sampling on 27/6 there were 429,624

TABLE VIII.$_6$

Apportionments of egg production of *Lymnaea natalensis* assuming all age groups to be equally represented. Based on fecundity data from laboratory observations (see m_x data Table VIII.$_1$). (After Dr. N. Hairston).

Age (x)	5 age groups present	6 age groups present
5.5	0.020	0.015
6.5	0.176	0.128
7.5	0.222	0.160
8.5	0.323	0.233
9.5	0.259	0.187
10.5		0.277

TABLE VIII.7

Apportionments of egg production of *Lymnaea natalensis* in age groups, based on the number of snails available at each sampling.

Sampling date		24/7	22/8	26/9	24/10	28/11	20/12	20/2	27/3	24/4	30/5	26/6
	Eggs	539,240	2,883,600	541,918	178,560	173,400	267,814	357,530	719,960	793,760	223,380	130,200
Age in days	x											
71-84	5.5	0.068	0.034	0.058	0.055	0.089	0.056	0.069	0.044	0.052	0.027	0.044
85-98	6.5	0.388	0.194	0.414	0.372	0.532	0.626	0.388	0.291	0.515	0.504	0.376
99-112	7.5	0.174	0.036	0.180	0.146	0.308	0.196	0.204	0.264	0.088	0.048	-
113-126	8.5	0.053	0.018	0.140	0.109	-	0.099	0.277	0.200	0.139	-	-
127-140	9.5	-	0.055	0.073	0.007	-	0.023	0.063	0.201	-	-	-
140+	10.5	0.317	0.663	0.135	0.310	0.070	-	-	-	0.206	0.420	0.580

TABLES VIII.$_{8-12}$: A series showing progression of various estimated populations of *Lymnaea natalensis* in Marlborough pond. For explanation of apportionments see text.

TABLE VIII.$_8$

Sampling Date	Actual Age (Days)	Period Used (Days)	Individuals Present	Survivorship l_x	Pivotal Age in Fortnights	Proportion of Eggs Laid	Eggs Available at Sampling	Est. Eggs Laid	Mature Snails	m_x
27/6	0-20	0-20	429,624							
24/7	28-47	31-50	419,016	0.9753						
22/8	57-76	51-70	142,560	0.3318	5.0	0.034	2,883,600	98,042	29,448	3.329
26/9	82-101	81-100	53,755	0.1251	7.0	0.180	541,918	97,545	12,725	7.666
24/10	109-129	111-130	6,912	0.0161	9.0	0.007	178,560	1,249	460	2.715
28/11	144-164	145+	1,275	0.0030						

TABLE VIII.$_9$

Sampling Date	Actual Age (Days)	Period Used (Days)	Individuals Present	Survivorship l_x	Pivotal Age in Fortnights	Proportion of Eggs Laid	Eggs Available at Sampling	Est. Eggs Laid	Mature Snails	m_x
24/7	0-20	0-20	565,760							
22/8	30-49	31-50	536,220	0.9478						
26/9	65-84	61-80	99,827	0.1764	5.0	0.058	541,918	31,431	43,997	0.714
24/10	93-112	91-110	27,648	0.0489	7.0	0.146	178,560	26,069	10,368	2.514
28/11	128-147	131-150	-	0.0000						

TABLE VIII.$_{10}$

Sampling Date	Actual Age (Days)	Period Used (Days)	Individuals Present	Survivorship l_x	Pivotal Age in Fortnights	Proportion of Eggs Laid	Eggs Available at Sampling	Est. Eggs Laid	Mature Snails	m_x
22/8	0-20	0-20	2,953,260							
26/9	35-55	31-50	422,345	0.1430						
24/10	63-83	61-80	110,592	0.0374	5.0	0.055	178,560	9,820	41,932	0.234
28/11	98-118	101-120	7,650	0.0026	7.5	0.308	173,400	53,407	9,690	5.512
20/12	120-140	121-140	3,412	0.0012	9.5	0.023	267,842	6,160	1,366	4.510

TABLE VIII.$_{11}$

Sampling Date	Actual Age (Days)	Period Used (Days)	Individuals Present	Survivorship l_x	Pivotal Age in Fortnights	Proportion of Eggs Laid	Eggs Available at Sampling	Est. Eggs Laid	Mature Snails	m_x
24/10	0-20	0-20	201,600							
28/11	35-55	31-50	147,900 ?	0.7336 ?	November results doubtful					
20/12	57-77	61-80	126,244	0.6262	5.0	0.056	267,842	14,999	42,992	0.349
20/2	119-139	121-140	3,280	0.0163	9.0	0.063	357,530	22,524	1,312	17.168
27/3	154-174	150+	-	-						

TABLE VIII.$_{12}$

Sampling Date	Actual Age (Days)	Period Used (Days)	Individuals Present	Survivorship l_x	Pivotal Age in Fortnights	Proportion of Eggs Laid	Eggs Available at Sampling	Est. Eggs Laid	Mature Snails	m_x
20/12	0-20	0-20	310,492							
20/2	62-82	61-80	41,000	0.1320	5.0	0.069	357,530	24,669	18,368	1.343
27/3	97-117	101-120	9,840	0.0032	8.0	0.264	719,960	190,069	7,544	25.195
24/4	125-145	121-140	-	-						

TABLE VIII.$_{13}$

Age and average size at onset of egg production in *Lymnaea natalensis* in the laboratory.

Temp. Conditions	No. Snails	Age in days at which 1st Eggs Appear	Av. Size
Ambient March-Aug.	53	89	9.70
Ambient Aug.-Dec.	17	82	9.82
Const. Temp. 25 ± 0.5°C.	17	60 day	9.40 mm.

individuals of age 0 to 20 days old in the pond, according to the recognised method of sampling. The pond was sampled 27 days later on 24/7 by which time the actual age of the selected cohort of snails would be between 27 and 47 days. As the data given in Table VIII.$_{5}$ fall into 10 day intervals the nearest groups must be used, i.e. age 30 to 50 days, and on 24/7 there were 419,016 of this group left, 97.53% of the original number, or a survival of 0.9753 for that period of time and that particular age group. Thus knowing the number present at time zero and by following the group through to its extinction, it is possible to calculate age specific survival (l_x), information which is essential for calculation of more intimate population statistics.

The calculation of age specific fecundity for *Lymnaea natalensis* in the field at various periods between June, 1961 and June, 1962.

In order to compile life tables from these field data and to calculate the rate of actual increase it is necessary to calculate a further component of the population, the age specific fecundity rate (m_x). As with the species discussed above, *L. natalensis* is hermaphroditic and no sex ratio can be determined, thus maturity is calculated from the time egg production commences and each snail is considered as a potential female. Two characteristics of the species have to be determined under experimental conditions, the age or size at which egg production commences and the general pattern of egg production in relation to age. These will permit the egg population as recorded in the field to be apportioned according to age and thus the age specific fecundity figures (m_x) can be calculated. The age and size at which egg production commenced was recorded from several batches of snails reared in the laboratory (see Table VIII.$_{13}$). It would appear from these data that size rather than age is correlated with the onset of egg laying and that when the average size of a group of snails is 9.4 mm., egg production can commence. This is an approximate figure based on averages. It is not acceptable to select a particular size or age and categorically state that this marks the onset of maturity. It is more satisfactory to accept that egg production commences during the sixth fortnight (see Table VIII.$_1$), between 70 and 84 days of age.

Earlier in this section it was shown that the average rate of growth of snails reared at room temperature in the laboratory was in agreement with calculated rates of growth derived from field data at various times of the year. Because of this it was decided to use the pattern of egg production of this group of snails to represent that which could be expected from a field population under various seasonal temperature conditions. It was then necessary to apportion the eggs available at each sampling among the mature snails according to the pattern of egg production observed in the laboratory (see Table VIII.$_1$, m_x). Thus an apportionment was calculated similar to that for *B.* (*Ph.*) *globosus* in Chapter VI, assuming that all age groups were equally represented, (Table VIII.$_6$). As the age groups were not equally represented, each proportion was multiplied by the number of snails in the appropriate age group. This would give the egg laying power of each group as represented and this must be cast into proportions which would then give the correct apportionment of available eggs among the age groups (see Table VIII.$_7$).

The age specific fecundity rate (m_x) given in Tables VIII.$_{14}$ to VIII.$_{18}$ has been calculated from field data and was based on two assumptions:-

(i) Egg production commenced during the sixth fortnight.

(ii) The relation between age and egg production in the field is similar to that recorded under laboratory conditions and is represented by the m_x Column in Table VIII.$_1$

The method of calculation was as follows: in Table VIII.$_8$, the survivorship (l_x) has been calculated merely by the progression of

TABLE VIII.$_{14}$

Theoretical seasonal life table for *Lymnaea natalensis* in Marlborough pond compiled from data collected between 27/6 and 28/11 with the number of eggs available in May estimated theoretically, and other data calculated graphically from Table VIII.$_{8}$

Age in days	Estimated population	Survivorship l_x	Date
0 - 20	429,624	1.0000	May
28 - 48	184,932	0.4304	27/6
56 - 76	80,984	0.1885	22/8
91 - 111	33,349	0.0776	26/9
119 - 139	1,728	0.0040	24/10
153+	1,275	0.0030	28/11

Pivotal Age in Fortnights x	Survivorship l_x	Eggs/Snail m_x	l_xm_x
0	1.0000		
0.5	1.0000		
1.5	0.775		
2.5	0.485		
3.5	0.335		
4.5	0.215		
5.5	0.1504	1.313	0.197
6.5	0.1099	19.250	2.116
7.5	0.066	35.600	2.350
8.5	0.030	22.250	0.668
9.5	0.004	9.015	0.036

finite rate of increase, $R = 1.262$

rate of actual increase, $r = 0.2327$.

TABLE VIII.15

Seasonal life table for *Lymnaea natalensis* in Marlborough pond compiled from data collected between 27/6 and 28/11 and calculated graphically from Table VIII.8

Pivotal Age in Fortnights x	Survivorship l_x	Fecundity Eggs/Snail m_x	$l_x m_x$
0	1.000		
0.5	0.995		
1.5	0.980		
2.5	0.970		
3.5	0.620		
4.5	0.360		
5.5	0.215	3.329	0.716
6.5	0.125	5.500	0.688
7.5	0.044	7.666	0.337
8.5	0.016	5.210	0.083
9.5	0.008	2.715	0.022

finite rate of increase, R = 1.100

rate of actual increase, r = 0.095

TABLE VIII.$_{16}$

Seasonal life table for *Lymnaea natalensis* in Marlborough pond compiled from data collected between 22/8 and 20/12 and calculated graphically from Table VIII.$_{10}$

Pivotal Age in Fortnights x	Survivorship l_x	Eggs/Snail m_x	$l_x m_x$
0	1.000		
0.5	0.740		
1.5	0.400		
2.5	0.220		
3.5	0.119		
4.5	0.061		
5.5	0.027	0.234	0.006
6.5	0.010	2.898	0.029
7.5	0.003	5.512	0.017
8.5	0.002	5.025	0.010
9.5	0.001	4.510	0.005

finite rate of increase, $R = 0.6918$

rate of actual increase, $r = -0.3684$.

TABLE VIII.$_{17}$

Seasonal life table for *Lymnaea natalensis* in Marlborough pond compiled from data collected between 24/10 and 20/2 and calculated graphically from Table VIII.$_{11}$

Pivotal Age in Fortnights x	Survivorship l_x	Eggs/Snail m_x	l_xm_x
0	1.000		
0.5	0.945		
1.5	0.860		
2.5	0.781		
3.5	0.715		
4.5	0.645		
5.5	0.345	0.349	0.120
6.5	0.153	4.545	0.695
7.5	0.067	8.800	0.590
8.5	0.029	13.025	0.378
9.5	0.013	17.168	0.223

finite rate of increase, $R = 1.098$

rate of actual increase, $r = 0.094$.

TABLE VIII.18

Seasonal life table for Lymnaea natalensis in Marlborough pond compiled from data collected between 20/12 and 27/3 and calculated graphically from Table VIII.12

Pivotal Age in Fortnights x	Survivorship l_x	Eggs/Snail m_x	$l_x m_x$
0	1.000		
0.5	0.815		
1.5	0.555		
2.5	0.373		
3.5	0.255		
4.5	0.172		
5.5	0.080	1.343	0.107
6.5	0.019	13.180	0.250
7.5	0.005	25.195	0.126

finite rate of increase, $R = 0.894$

rate of actual increase, $r = -0.112$.

the numbers of snails as they grew older, month by month. For the calculation of the m_x data, the process is more complex. The data in Table VIII.$_7$ represents the egg laying power of each age group present at a particular time. To find out the number of eggs the group of age 71 to 84 days could have produced on 22/8, the total number of eggs available, 2,883,600, is multiplied by .034 and the result is 98,042. The snails available have been recalculated from Table VIII.$_5$ to fortnight intervals. Of the cohort which originated in June, there were 29,448 snails in the sixth fortnight by the 22/8. Dividing this into 98,042 gives an estimate of m_x or age specific fecundity rate. Further calculations follow this pattern.

<u>Calculation of the rate of actual increase from field data for various seasonal periods</u>.

With the estimation of the pattern of age specific fecundity and mortality, it is possible to arrive at a figure expressing the rate of actual increase for various cohorts of snails within the Marlborough pond. The factors influencing this rate of actual increase have been discussed in Chapter IV and need not be mentioned here, however, it will probably be as well to point out that the rate of actual increase (r) is an expression of increase calculated for a naturally occurring population. It does not necessarily fall into line with the definition of intrinsic rate of natural increase although it may approach this figure under ideal conditions.

Seasonal life tables for <u>L. natalensis</u> have been compiled (Tables VIII.$_{14}$ to VIII.$_{18}$) and with reference to these it is possible to discuss the state of various elements of the population within the general picture obtained from the gross numerical fluctuations of <u>L. natalensis</u> (see Fig. VIII.$_3$). The cohort originating in June shows a small positive rate of increase (0.0953) whereas the gross population during the period June, July and August was increasing rapidly. To account for this it is necessary to appreciate that the snails which contributed to this increase by virtue of egg production originated prior to the first sampling which was taken in June, 1962. If it is assumed that a similar number of eggs were produced in May as occurred in June, then it is possible to work out a hypothetical life table for a cohort of L. natalensis originating in May, 1962. If the assumption is accepted, then using the data in Tables VIII.$_5$ and VIII.$_7$, a life table has been compiled, Table VIII.$_{14}$. It can be seen that the actual rate of increase for this May cohort, r = 0.2327, was far in excess of that of either the June or July cohorts. The cohort which originated in August had a negative value for r, this was a reflection of the high mortality afflicting the vast number of eggs which were laid in the pond during August. The October cohort returned to the normal trend showing a slight positive rate of increase, r = 0.0936, but in the following cohorts originating in December and March the decline in the population (see Fig. VIII.$_3$) was reflected as high negative rates of increase (December, -0.1118). This situation was due to the very high mortality rates exhibited by these cohorts which could not be offset by high fecundity rates.

It is of interest to compare the various patterns of mortality in successive cohorts. The conditions in the pond were best suited to the survival of L. natalensis from June to August and October to February, but the latter period was followed by several months of consecutive decline which resulted in a considerable fall in the numbers of this species within the habitat. In all instances the snails were strikingly short lived. Even though the general picture was one of high survival among the younger snails, as they approached an age of 50 to 60 days the survival rate dropped; by 80 to 100 days after their origination only low numbers of snails remained.

4. The effects of crowding on egg production in Lymnaea natalensis.

The possibility of density dependent factors operating on the population of L. natalensis in the Marlborough pond suggested a series of investigations which were carried out in the laboratory. The intention was to assess the effect on egg production of snails at various densities and then to compare this with egg production of snails at a certain density, but varying the number of individuals in proportion with the volume of water within the aquaria.

Three series of experiments were carried out, the first, at a constant temperature of 22.5°C., with single snails in one litre aquaria to determine the variability of egg production (Table VIII.$_{19}$). The other two series were conducted at room temperature. These two did not run concurrently and therefore are not strictly comparable with each other. The experiments were carried out during the months September to November. Each experiment lasted seven weeks, one week for acclimatisation and six weeks for recording. All snails were of similar age and no mortalities occurred during the investigations. An abundance of fresh food was given daily when aquaria were cleaned out by means of a pipette. Once during each series all the aquaria were drained and refilled with fresh biologically conditioned water. This appeared to have little direct effect on egg production.

Table VIII.$_{19}$ shows the variation recorded in weekly egg production of 40 replicates of single individuals kept at a density of one snail per litre for six weeks. The mean number of eggs per snail per week was 57.9 ± 14.14. In Table VIII.$_{20}$ the results indicate that within the above range of variability an increase in density in snails per litre resulted in a decrease of egg production. There was a remarkable similarity in the egg production of the four replicates of two snails in one litre. In the second series (Table VIII.$_{21}$) a different pattern was exhibited. In this experiment two levels of density were used, either two snails per litre or one snail per litre. This was merely a proportion because the number of snails and the volume of water were adjusted to give increasing populations at constant density. Considering these results on their own, there appeared to be a depressing effect on egg production when the number of snails in an aquarium was increased, irrespective of the actual density of those snails. This was best demonstrated when four or eight snails

TABLE VIII.19

To show the degree of variability of egg production in *Lymnaea natalensis* kept individually in one litre aquaria maintained at 22.5 ± 0.1°C. over a period of six weeks.

No. Replicates	Mean Egg Production per week	Standard Deviation
40	57.9	14.14

TABLE VIII.20

Effect of density on egg production (Series 1). *Lymnaea natalensis*. 3/9 to 8/10. Snails reared at room temperature.

Density Sn./litre	No. Snails	Vol. litre	Total eggs in 6 weeks	Egg/Snail/Week
1	3	3	1,067	59.28
2	2	1	369	30.75
2	2	1	380	31.67
2	2	1	443	36.92
2	2	1	429	35.75
3	6	2	735	20.42
3.66	11	3	745	11.29

TABLE VIII.$_{21}$

Effect of density and volume of water available on egg production (Series 2). *Lymnaea natalensis*. 15/10 to 19/11. Snails reared at room temperature.

Density Sn./litre	No. Snails	Vol. litre	Total eggs in 6 weeks	Egg/Snail/Week
2	1	.500	458	76.33
2	1	.500	400	66.67
2	1	.500	566	94.33
2	2	1.000	475	39.58
2	4	2.000	391	16,29
2	8	4.000	750	15.63
1	1	1.000	455	75.85
1	2	2.000	334	27.83
1	2	2.000	327	27.25
1	3	3.000	444	24.67
1	3	3.000	568	31.55

were maintained in a single aquarium. This phenomenon has been discussed previously and has been reported by other workers using Bulinus (Bulinus) forskalii (Wright, 1960) and Australorbis glabratus (Chernin and Michelson, 1957). Thus it would seem that with L. natalensis the number of snails present as well as the density of snails has an effect on egg production.

When the L. natalensis population in the Marlborough pond is considered, the apparent sensitivity of egg production to numbers of individuals within the habitat, rather than to the actual density per unit volume of water available, seems to tie in with observations.

If the estimated number of mature snails available is divided into the estimated number of eggs present in the pond at that time, a figure expressing the average egg production per mature snail can be obtained for that particular time. These figures can then be plotted graphically against the total estimated population of L. natalensis snails present at that time, as has been done in Fig. VIII.10. In that figure the solid circles refer to this relationship and apart from an instance marked 'a' all the points fit remarkably well on a regular curve correlating numbers of snails to egg production per mature snail. The point 'a' was the relationship calculated for August and corresponded with a general rise in temperatures after the winter period.

It is of interest to record this apparent relationship between numbers and egg production. There is no doubt that if it were possible to compare density per unit volume with egg production per mature snail, some correlation would be found but due to the large volume of water available for most of the year, it is unlikely that the numerical density per litre would be very great. Certainly the density only once attained the figure of one snail per litre.
A rough calculation based on the area of the pond at minimum level in October shows that there were approximately 800 cubic metres of water available for 900 thousand snails, at no other time during the period was this high density achieved.

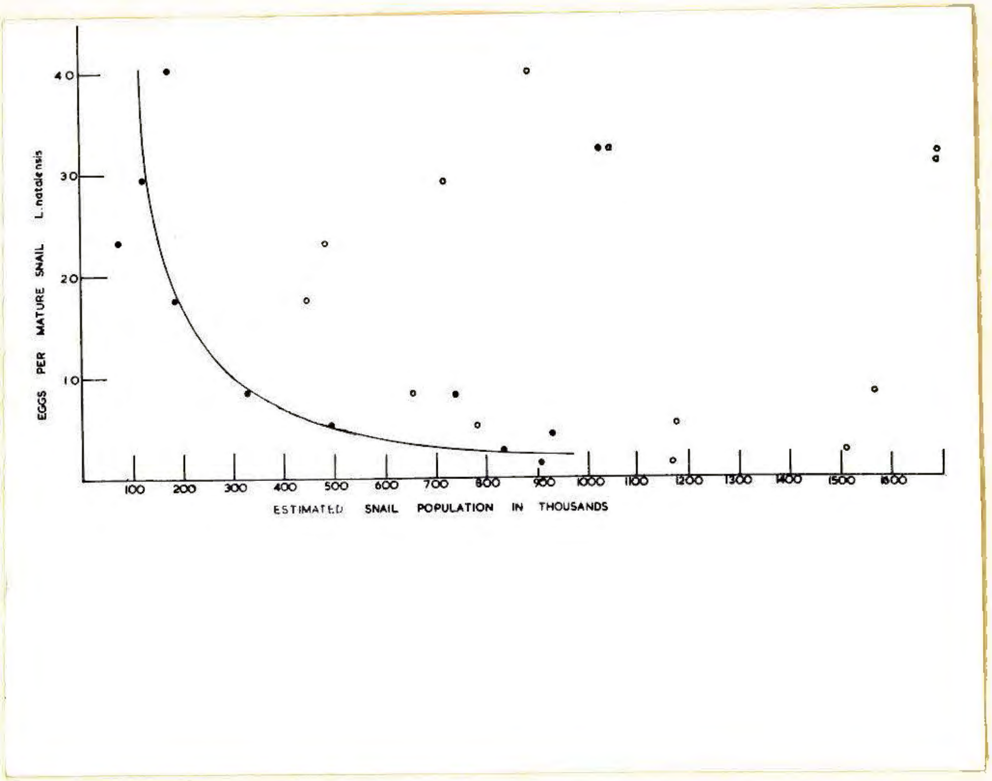


FIG. VIII.10 Showing the relationship between total estimated number of eggs produced per mature *Lymnaea natalensis* in Marlborough pond. Solid circles represent the relationship based on *Lymnaea* population only; hollow circles represent relationship based on total snail population; 'a' refers to sampling in August, 1961.

In order to determine whether other snails present entered into this apparent effect on the *L. natalensis* egg production, Fig. VIII.10 contains points, hollow circles, showing the relationship between eggs produced per mature *L. natalensis*, and the gross snail population including total estimated mature *L. natalensis*, *Bulinus tropicus* and *Biomphalaria pfeifferi*.

In this case there appears to be a wide degree of scatter suggesting that under the conditions that prevailed in the Marlborough pond for the period under consideration, other species of snails had little effect on the egg production of *L. natalensis* even when those other species were present in fairly large numbers.

5. Discussion.

L. natalensis is a most adaptable snail which can tolerate a wide variety of conditions. It has been shown to have a high intrinsic rate of natural increase and that in the field when conditions are suitable, the species is capable of a high rate of reproduction. Nevertheless, these outbursts of egg laying are generally followed by a high mortality of the young, which results in a very low nett rate of actual increase.

L. natalensis grows very rapidly and under warm conditions reaches maturity in a very short time. Even in winter, the snails can mature in less than 80 days. Egg production does not necessarily build up rapidly to a maximum, the process is gradual, with peak production being reached after about seven months. Few snails, however, appear to survive as long as that in the field and those that do represent a very small proportion of the original cohort.

Its high intrinsic rate of natural increase whether at 25°C. or at room temperature represents an ideal adaptation to most waterbodies in Rhodesia and in fact, in central Africa.

IX. DISCUSSION.

It is well to consider the results obtained from the work reported here in the light of a pertinent statement made by Park (1955) to a Symposium on population numbers: "Research in laboratory population ecology should take its orientation from some phenomenon known, or suspected to occur in nature and known or suspected to have significant ecological consequences. Its object is not to erect an indoor ecology but, rather, to illuminate conceptually the general problem to which it is addressed. The research is thus the handmaiden of field investigation; not the substitute."

Sentiments such as these have motivated the present investigation because the influence of temperature on the ecology of freshwater snails has not been critically studied. Previous workers have tended to limit their attention to the responses of snails at extremes of temperature, possibly in the hope of determining whether or not these acted as limiting ecological factors. Thus Gordon et al (1934) found that in Sierra Leone Planorbis (=Biomphalaria) pfeifferi would survive for a fortnight or longer in aquaria maintained at 35°C. and for months at 15°C. Lowest death rates were obtained over the range 25 to 33°C. They further observed that Physopsis globosa could live for many months at 15°C. and could survive exposures of two hours to temperatures as high as 40°C. Since these temperature extremes were not encountered in the natural habitats, these authors concluded that temperature was not a limiting factor in the distribution of the snails. Again, McCullough (1957), working in Ghana, came to a similar conclusion since the temperature of the snail habitats did not go much outside the range of 23 to 27°C. The same opinion, but for precisely the opposite reason, is voiced by Watson (1958) in connection with Bulinus truncatus in Iraq. Here he found the water temperatures of snail infested canals to vary from 18°C. to "near blood heat" and this led him to the view that temperature was of negligible importance to the snails.

These varying results suggest that temperature per se is not a limiting factor in the ecology of the snails in any direct way. That is, there will not be a simple correlation between thermal tolerances as determined in the laboratory and the temperatures which occur within the habitats of the snails. Nevertheless this does not imply that temperature, by means of its influence on the rate of growth of populations, may not be a significant ecological factor. The present investigations strongly suggest that temperature does exert a greater influence on both the distribution and the abundance of various species of freshwater snails than had previously been thought.

The influence of temperature on population numbers.

The intrinsic rate of natural increase, r_m, and the nett reproductive rate, R_o, have been discussed earlier in Chapter IV. Here it is necessary to mention only the ecological significance of these parameters. It has been shown by Slobodkin (1962) that r_m and R_o are associated in terms of the mean generation time. This means that if r_m decreases with R_o remaining constant, the mean generation time must have increased. In the discussion which follows, the temperature at which r_m is maximal will be referred to as the "optimal" temperature. If a population with a high r_m at optimal temperature lives in an environment in which the prevailing temperature approaches this optimum for the species, the population would expand rapidly until such time as other factors start restricting this increase. If, on the other hand, temperature conditions were suboptimal for r_m with R_o the same in both cases, and if the population were to expand to the same stable state as in the former situation, the mean generation time would have to be longer. This would mean that the species would be more vulnerable to a change in the environment because of the longer time taken for the population to build up in numbers. If r_m is lower, the nett reproductive rate, R_o, may be equally high but the population would take longer to achieve this. Selection favours those members of any population that leave the greatest number of eventual descendants. Thus a high r_m is advantageous to species that live in temporary environments where favourable and unfavourable conditions alternate.

This hypothetical case seems to apply to B. (Ph.) globosus which, in Rhodesia, exists in two distinct types of habitat: temporary ponds as exemplified by the Foyle habitat and permanent or semi-permanent waterbodies such as lakes, reservoirs or large pools in streams.

It is extremely difficult to appreciate the full ecological implications of temperature with only recordings of the absolute weekly maximum and minimum temperatures. An average of these values will not give a true picture of the prevailing temperature conditions. It is important to know the duration of warm conditions during the day, whether brief or long lasting. B. (Ph.) globosus has a high r_m at 25°C. If the reason for its success in temporary environments is because of this feature, this temperature must occur at some depth in the waterbody for some minimal period to allow the snails to realise the potential high rate of increase. Records of temperature in Foyle were made by a thermograph set 5 cm. below the surface of the water. From these data it has been possible to calculate the average number of hours per day during which the temperature at that depth was in excess of 25°C. The data are given in Table $IX._1$. It will be seen that this temperature occurred in the waterbody daily during the months March to April and December to January. The excessive flooding of the habitat in February depressed temperatures somewhat.

There are no comparative data for more permanent habitats but it is possible that in these situations, high temperatures may be of shorter duration because of the greater buffering effect of the larger water volume. If this is the case, longevity with moderate but not maximal egg production would constitute a satisfactory adaptation to

TABLE IX.1

Temperature records 5 cm. deep in the Foyle habitat, March, 1962 to March, 1963. Average number of hours per day during which the prevailing temperature exceeded 25°C.

Date	Average Daily Hours
March, 1962	7.28
April	4.41
May	0.35
June	Nil
July	Nil
August	0.12
September	Dry, no records
October	Dry, no records
November	Dry, no records
November 27 to December	4.17
January, 1963	9.40
February	2.12
March	5.57

the habitat. This is because the nett reproductive rate, R_o, of an individual surviving a long time under conditions which are suboptimal for r_m may be almost as great as the reproductive capacity for individuals living at a higher rate. Indeed at 22.5°C., B. (Ph.) globosus shows a high nett reproductive rate over the period of one year (see Fig. $IX._1$) which is the result of a high survival rate coupled with a moderate rate of egg production over a long period of time. Thus the species is capable of surviving and reproducing slowly in a waterbody in which maximum temperatures may be low - of the order of 20 to 23°C. In response to a rise in prevailing temperature to 25°C. for a minimal period each day, the snail population will tend to increase considerably. Insofar as temperatures of this order generally precede such adverse situations as flooding, drying out or the winter season, conditions will be satisfactory for the species.

Extending this to Biomphalaria pfeifferi which, under both cool or warm conditions, has rather a low intrinsic rate of natural increase. Survival, however, is good and this coupled with a high rate of egg production in older snails results in a high nett reproductive rate, particularly at room temperature. As with B. (Ph.) globosus at 22.5°C., this pattern of life is suggestive of an adaptation for existence in a stable type of habitat. B. pfeifferi is not capable of a large increase in r_m in response to a rise in temperature to 25°C. and is therefore unlikely to be able to utilise the short, warm, calm periods which precede catastrophes - the situation in temporary ponds. This species would therefore appear to be adjusted to the permanent or semi-permanent, but not to the temporary type of habitat. As well as this, the species both at 18°C. and at room temperature seems to be able to increase more rapidly under cool conditions than does B. (Ph.) globosus and therefore may extend further into the cooler regions of the country before the nett reproductive rate declines to zero.

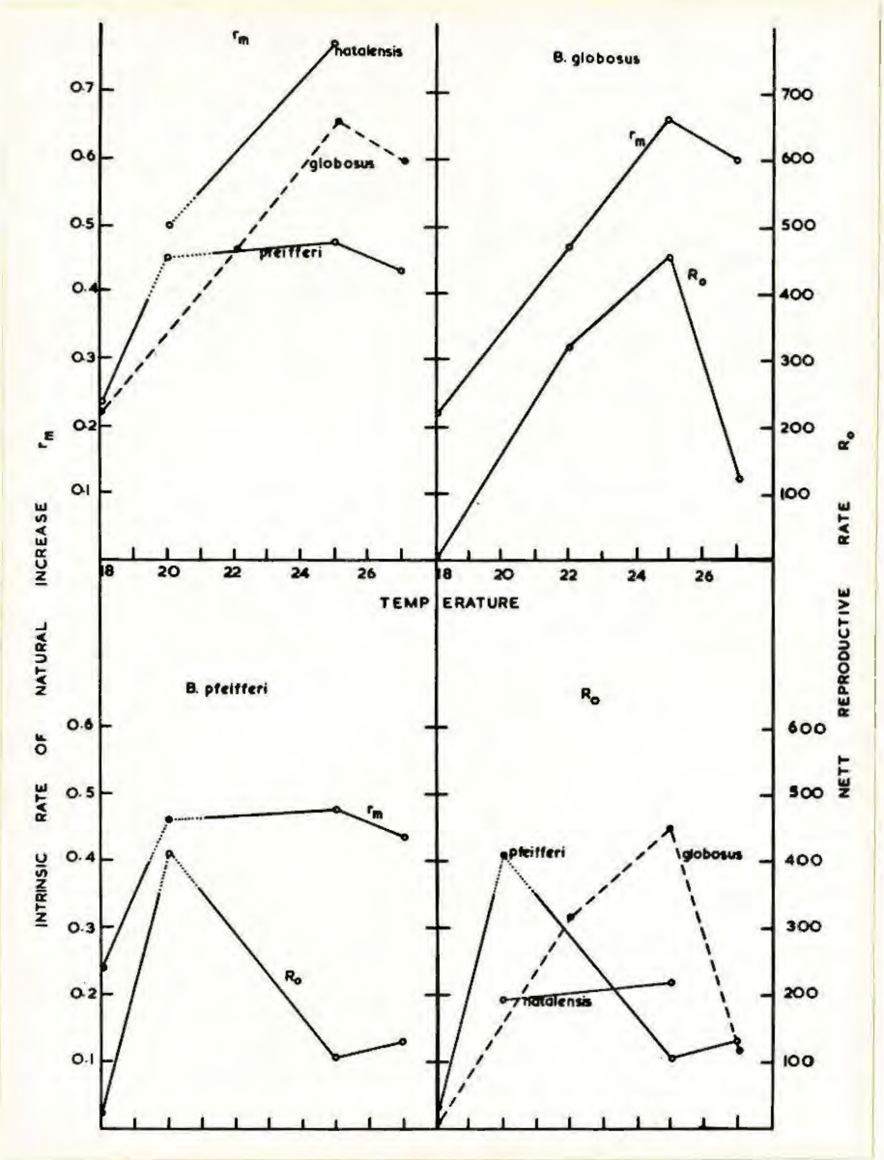


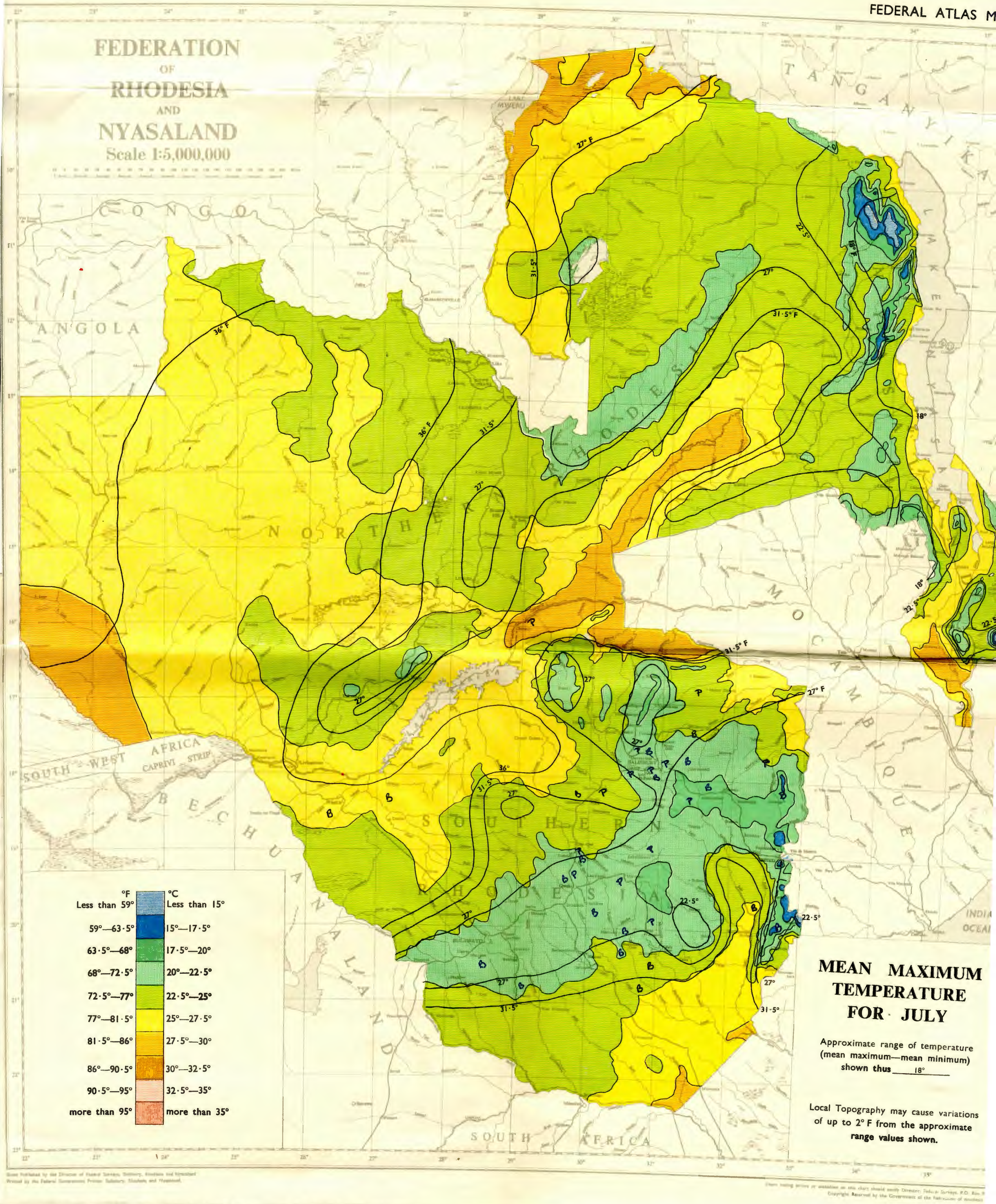
FIG. IX.$_1$ Comparative graphs showing the calculated values for the various parameters of Bulinus (Physopsis) globosus, Biomphalaria pfeifferi and Lymnaea natalensis in relation to temperature. R_o, the nett reproductive rate, for B. pfeifferi is calculated over 18 fortnights, for B. (Ph.) globosus 26 fortnights and for L. natalensis for 16 fortnights.

The various parameters for *B. (Ph.) globosus* and *B. pfeifferi* are summarised in Fig. IX.$_1$. In Fig. IX.$_2$ the distribution of winter isotherms in Southern Rhodesia indicate the cooler and warmer regions of the country.

The actual distribution of these two species of snails fits well into the predictions of habitat which can be made from a study of the influence of temperature. *B. (Ph.) globosus* is found only in the warmer areas in both temporary and permanent waterbodies, whereas *B. pfeifferi* is found in warm or cold waterbodies, but only where they are fairly permanent. This association could be ascribed to the relative ability of the two species to survive the dry conditions which occur annually in temporary ponds. Yet Shiff (1960) has shown that under comparative conditions, relative humidity 92% and temperatures between 15 and 27.5°C., 70% of a sample of *B. pfeifferi* survived out of water for 50 days whereas in *B. (Ph.) globosus* 59% survived only 30 days. It is therefore unlikely that *B. pfeifferi* is absent from temporary pools because it cannot aestivate effectively.

Lymnaea natalensis has a high intrinsic rate of natural increase both at room temperature, which exemplifies cool conditions, and at 25°C. The nett reproductive rate for a period of 16 fortnights is similar under both these conditions of temperature, see Fig. IX.$_1$, but there is an indication that if average temperatures exceed 25°C., the capacity for increase would drop. This species by virtue of its high nett reproductive rate at room temperature and its high intrinsic rate of natural increase at 25°C., would appear to be adjusted to existence in permanent, semi-permanent or temporary waterbodies. This is confirmed by field observation.

The inter-relationships of the various population parameters for the three species given in Fig. IX.$_1$ thus allow certain predictions to be made about the distribution of the various species with respect to temperature and type of habitat. Nevertheless, it is clear that temperature, although important, is not the only factor regulating the



MEAN MAXIMUM TEMPERATURE FOR JULY

Approximate range of temperature (mean maximum—mean minimum) shown thus 18°

Local Topography may cause variations of up to 2° F from the approximate range values shown.

FIG. IX.$_2$ Map of Rhodesia and Nyasaland showing average maximum temperatures for July. The distribution of *Bulinus* (*Physopsis*) *globosus* is marked 'P' and of *Biomphalaria* *pfeifferi* is marked 'B'. The points shown are definite records and are not the only localities of these species.

distribution and abundance of these species, thus Williams (unpublished work) suggests that chemical factors such as bicarbonate ions may affect certain freshwater snails.

Temperature and egg production.

It is now necessary to consider another aspect of the influence of temperature on freshwater snails. Within the range examined it is clear that temperature has a greater effect on fecundity than on longevity. At temperatures of the order of 18°C. B. (Ph.) globosus lays fewer eggs than it does at 25°C. This is a common phenomenon among poikilothermal animals and appears to be due to an effect of temperature on oogenesis. Precht (1955) states that in Planorbis corneus L. and Lymnaea truncatula (Muller) there is a seasonal periodicity in egg production and that with the onset of cold weather egg production is initially inhibited by endogenic factors which are later superceded by the effect of mere cold. In Cepea nemoralis L. only oocytes are formed in the hermaphrodite gland when the temperature is less than 23°C. Above this level, spermatogenesis occurs with progressive inhibition of oogenesis (Bouillon, 1956). The analysis of egg production of B. (Ph.) globosus at room temperature in Chapter VI shows that the positive temperature effect on egg production of younger snails (16 to 18 weeks) is lagged by about two weeks. This means that in these snails an increase of temperature will lead to an increase in egg production in two weeks time; so that within the range considered, temperatures were possibly influencing the extent of oogenesis within the hermaphrodite gland and not the act of egg laying. By contrast, with older snails (33 weeks) an increase in temperature caused a reduction in egg production 3 to 4 weeks later. This is extraordinary, but again indicates an association between oogenesis and temperature, dependent on the maturity of the snail. It may be that in older snails an increase of temperature induces spermatogenesis in favour of oogenesis in a manner similar to that in C. nemoralis, reported above.

Auto-inhibition of egg production.

The phenomenon of auto-inhibition of growth and reproduction has been demonstrated in a variety of animals. Chernin and Michelson (1957a, b) reported that overcrowding depressed egg production and growth in *Australorbis glabratus* while Wright (1960), demonstrating a similar phenomenon in *Bulinus* (*Bulinus*) *forskalii*, showed that the inhibiting factor was in the water of crowded aquaria and that it could be removed with activated charcoal. Both these authors noted that the inhibiting effect increased not only with increased crowding in snails per litre, but also with absolute increased population even if the ratio of snails per litre was kept constant, thus five snails in 2.5 litres laid more per unit time than did ten snails in five litres. Recently Maguire (1962) has demonstrated auto-inhibition of reproduction with increased crowding in a turbellarian *Cura formanii* and Berrie and Visser (1963) have extracted a chemical from a natural pond overcrowded with *Biomphalaria sudanica*. This chemical proved toxic to laboratory cultures of the same species. In the present work auto-inhibition of egg production has been clearly demonstrated with *Lymnaea natalensis* in the laboratory both with respect to increased crowding and increased population in single aquaria. What is interesting is the correlation between egg production per mature snail and the total estimated *L. natalensis* population in a natural pond (Chapter VIII, Fig. VIII.$_{10}$). The correlate between the estimated *L. natalensis* population and egg production per mature snail is real. Including the aberrant point 'a' (using the Spearman rank correlation test), P is only just greater than 0.05.

While it might be that this correlation was due purely to fortuitous factors, it may also indicate the presence of some factor which is specific to *L. natalensis* and dependent on the size of the *L. natalensis* population at any particular time. The third explanation indicates the possibility of complementary interaction between a *Lymnaea* specific factor auto-inhibiting egg production, and such non-specific factors as weather, chemistry, etc., which together have produced this relationship between egg production per individual and the snail population.

The freshwater biotope and sub-specific forms.

Finally, it is well to mention that these three species of snails as well as other Basommatophora propagate, to a large extent, by self fertilisation. Copulation is indiscriminate, occurring almost at random between snails of various species of the same genus and even between species of different families (Hubendick, 1954). It is likely that in temporary pools the various individuals will be genotypically similar and because freshwater biotopes are, in general, fairly well isolated, various microgeographic races are likely to develop. Yet from time to time the transference of individuals from habitat to habitat by floods or other natural means must result in genetic interchange, therefore this isolation is not normally sufficient to produce real geographic races. In this way the life time of isolated populations is too short for the development of different sub-species. However, if some form of geographic barrier does exist, even though it may not be very effective for more mobile creatures, there is every likelihood that the populations of freshwater snails on each side of the barrier will develop different characteristics. The number of different so-called sub-species which have been described within the genera Biomphalaria and Bulinus (Physopsis) is indicative of this situation.

The significance of these considerations in the light of the present work is that the results reported here are based on data derived from snails taken from a single locality and refer in particular to that population. Yet the broader implications of the parameters which have been discussed apply in general to the species.

In conclusion.

This work represents an attempt to assess the influence of temperature on populations of the three species of snails considered. This was done by keeping experimental aquaria under conditions which were as constant and as near optimal as possible for each species and varying only temperature. It is realised that absolute control of other variables in the environmental factors is impossible and they must have influenced the results obtained. Nevertheless, these laboratory experiments have yielded information which can be applied, with a remarkably high degree of predictive success, to conditions as they exist in the field. It is realised that the influence of temperature on the complex inter-relationships of the environment of freshwater snails is but a small part of the ecology of these animals. The complete picture will be apparent only when all the interdependent factors are resolved, assessed independently and finally combined to form an integral whole.

X. SUMMARY.

1. This study attempts to assess the influence of temperature on the ecology of individuals and populations of *Bulinus* (*Physopsis*) *globosus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis*, freshwater snails of importance in Southern Rhodesia.
2. The techniques developed and used in the maintenance of these snails in the laboratory are discussed.
3. Data were obtained both from laboratory and field studies: sampling of snail populations in the field presented initial problems but these were overcome by the development of a sampling implement which is described.
4. Temperature records are given from three localities.
5. Populations were studied from several localities but detailed results are presented from two of these, a semi-permanent pond and a temporary habitat. These data include the age structure and size of the snail populations in relation to seasonal influences.
6. In the laboratory the snails were maintained at various temperatures, all other physical conditions being kept as near standard as possible.
7. For each cohort of snails daily records were kept of mortality, egg production and the fertility of eggs laid. From this it is possible to determine the age specific fecundity and survival of each cohort at different temperatures. From these data were calculated the mean generation time, the finite rate of increase (R), and the intrinsic rate of natural increase (r_m) for each set of conditions. The rate of growth was also estimated at each temperature.

8. The effect of crowding on growth of B. (Ph.) globosus and on egg production of L. natalensis was studied.
9. From the data obtained in the laboratory it was possible to predict the distribution and population potential of each species of snail for various environmental conditions. These predictions were, in fact, confirmed by field observation.

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