Some aspects of the ecology of two freshwater pulmonate gastropods; Limnaea stagnalis (L.) and Planorbis planorbis (L.).

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Contents.

General Introduction

The study outlined in the following thesis was made over a period of nine months, between November 1965 and August 1966. The object of the study was to examine the life cycles, growth rates, and any possible interactions, of the two species of freshwater gastropods, *Limnaea stagnalis* (L) and *Planorbis planorbis* (L).

Both species belong to the pulmonate gastropod suborder Basommatophora, members of which are characterised by having only one pair of tentacles, with eyes at the base of the tentacles. In common with all other pulmonate gastropods, these animals are hermaphrodite. They breed seasonally, laying batches of eggs held together in masses of jelly. The young develop without an intervening larval stage.

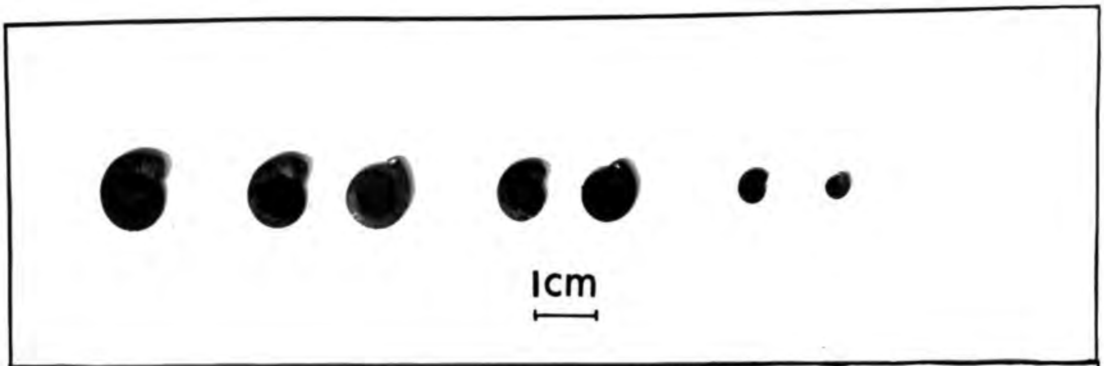
Limnaea stagnalis (L.), the Great Pond Snail, (Plate 1), which belongs to the family Limnaeidae, may attain a height of 6 cm. and a breadth of 3 cm. It is restricted to all hard water areas of the British Isles and prefers waters having a calcium content of at least 20 mg./1. (Boycott, 1936). Thus it is present throughout England, (except the south west), eastern Wales, the lowlands of Scotland, and in Ireland it is quite widespread, but absent from the peat districts of West Cork, Kerry, Wicklow and the north east of Donegal (Ellis, 1951). In 1965, Berrie, working on a *Limnaea stagnalis* population in Lanarkshire, demonstrated a biennial life cycle for this species. This was the first fully substantiated work to show that this species, unlike other British freshwater snails (Hunter, 1957; Duncan 1959;), had a life cycle which lasted for more than a year.

Planorbis planorbis (L.), (= *umbilicatus* Muller; = *marginatus* Draparnaud; = *complanatus* Jeffreys;) is now classified in the Planorbidae. It grows up to 18 mm. in breadth and 4 mm. in height. In the British Isles this species is very similar in range to *Limnaea stagnalis*, being restricted to hard water districts, in which the calcium concentration of the water is at least 20 mg./1. Like *Limnaea stagnalis*, it is found in rivers, canals, ponds, ditches and swamps. It is generally found in smaller bodies of water than its near relative *Planorbis carinatus*, (Ellis, 1951; Boycott, 1936). In these habitats it is found in the calmer waters, which are rich in aquatic weeds on which it seems to be more dependent than members of the Limnaeidae, (Janus, 1965). This study appears to be the first attempt to clarify the nature of the life cycle of this species.

PLATE 1.

(a). Examples of the species <u>Planorbis planorbis</u>.

(b). Examples of the species Limnaea stagnalis.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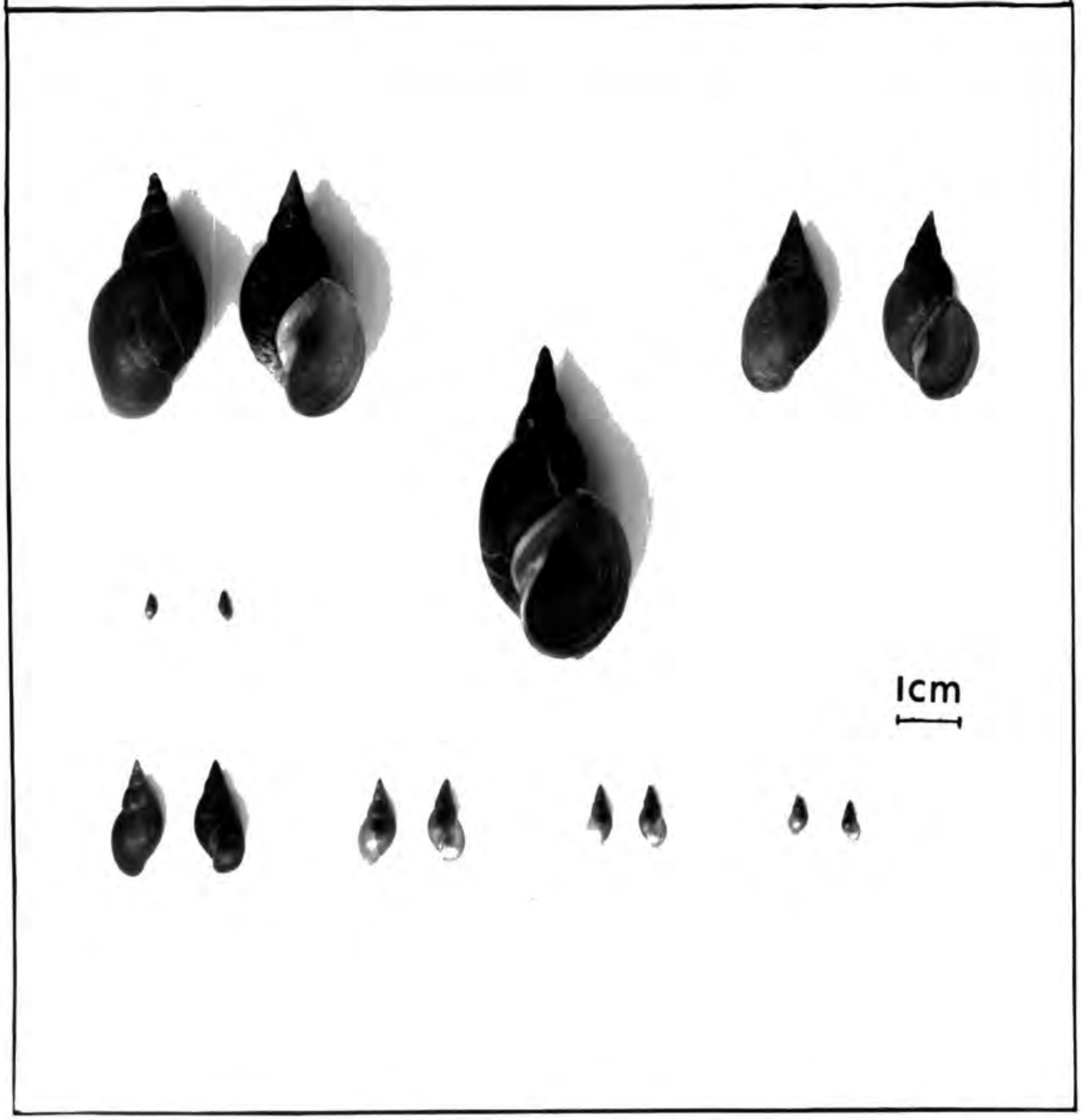
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LIFE CYCLE STUDIES

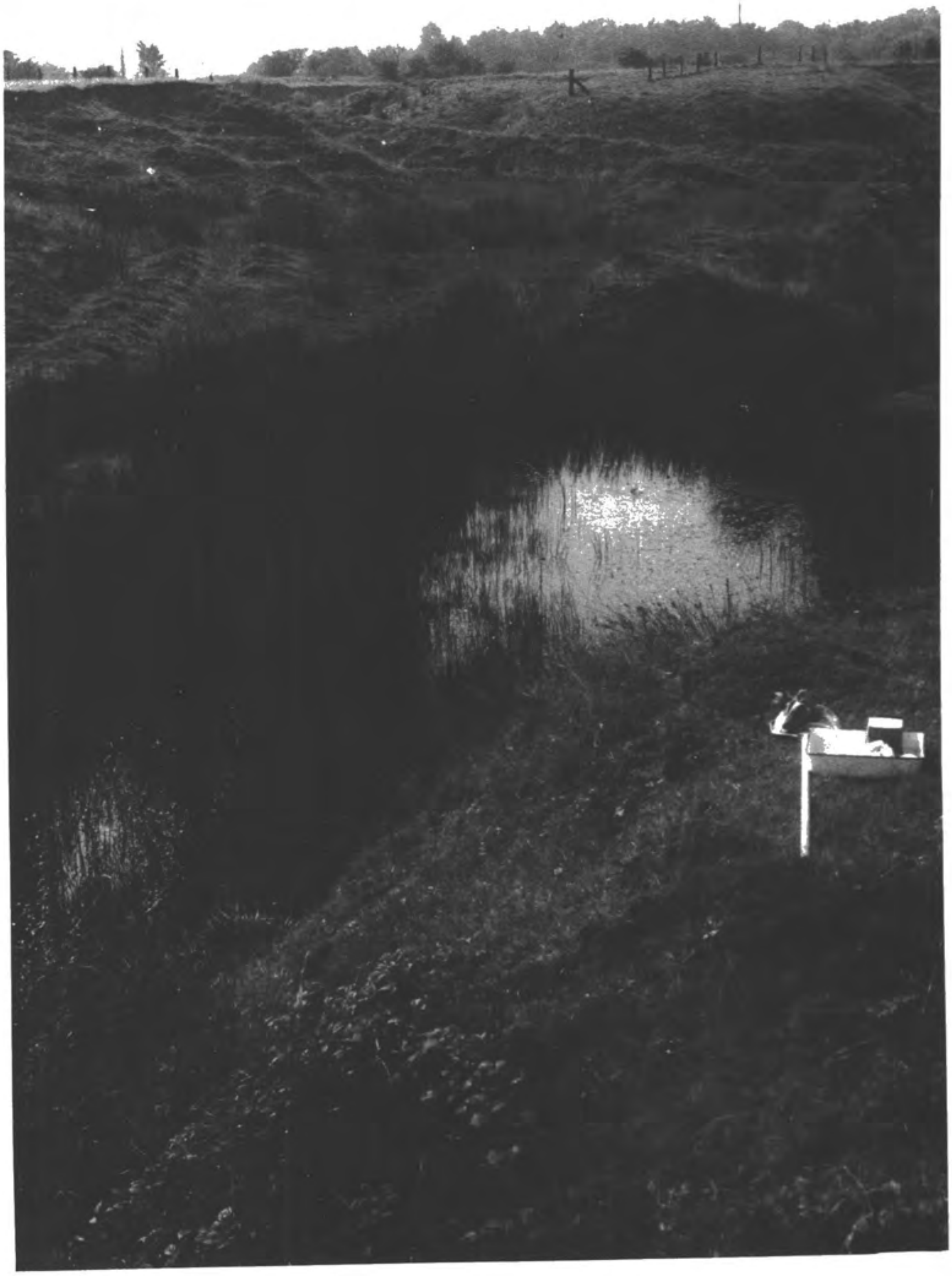
(a) Introduction and description of habitat.

The site selected for the study of life cycles was in an area near to the village of Brasside (Map Reference: NZ 45/290452) which is situated two miles (3.2 km.) to the North east of Durham City. The locality, which stands approximately 200 feet (60. 96 m.) above sea level, lies on the laminated clays of the old submerged valley of the River Wear (Maling, 1955). At this point the deposits are about 70 feet (21.3 m.) thick and consist of interlayed beds of sands and laminated clays, which overlie a thin bed of boulder clay, which in turn rests on the bed rock of the Durham coal measures. This area has been excavated for clay and is therefore characterised by a mosaic of brick diggings which, when excavation ceased about 20-30 years ago, became filled with rain water to form ponds which were then invaded by aquatic plants and animals. In the immediate locality there are about nine ponds (Figure 1) in an area of 2-3 acres (0.8 - 1.2 hectares). Ponds A-H lie in a depression which is about 8-10 feet (2.4-3 0m.) below the level of the surrounding ground and thus forms an artificial drainage system. Pond I is dammed with clay at its northern end but persistent leakage through the clay is sufficient to form a stream which stocks ponds H, G and A1, and possibly pond A during severe flooding. Pond I is on a similar level to the surrounding land and therefore stands 8-10 feet (2.4-3 0m.) above the other ponds in the system. The ground adjacent to the ponds is used as rough grazing for cattle, horses and pigs.

FIGURE 2. Detailed map of Pond A.

FIGURE 1. Map showing the system of ponds at Brasside.

PLATE 2. View of Pond A.



Pond A (figure 2) was selected for the detailed studies of life cycles, for unlike the other ponds in the system it contained both _Limnaea stagnalis_ and _Planorbis planorbis_. This pond, which was approximately 1000 sq. ft. (92.9 sq.m.) in area and 2-3 feet (0.6-0.9 m.) deep, had no definite inflow, but as stated above, it is possible that during severe flooding it may have received water from the stream which supplied ponds H, G and A1, and which originates in Pond I. Under normal weather conditions however, Pond A seemed to derive its water from direct precipitation and drainage, from the higher ground above its eastern bank. During the period of study, Pond A was observed to remain entirely separate, and there was no known direct contamination from any of the other ponds in the system, including pond A1. The outlet stream of Pond A joined the main outflow from the system. The limb of pond A, which ran southwards, became increasingly shallower with distance from the main pond and during long dry periods became discontinuous to form a string of pools a few inches deep. During drought this limb would probably have ceased to exist.

The other two ponds relevant to this study are H and B, which were used as chemical and biological controls. The former receives its water supply from Pond I and its outflow feeds several other ponds in the system. Pond B, like pond A, is completely separated from all the other ponds in the system, being situated on slightly higher ground and is an entity in its own right, having no definite inflow or outflow.

(b) Methods.

The field work performed on the three ponds falls into three sections, firstly, a qualitative survey of the vegetation and fauna of the three ponds, secondly, a quantitative study of certain physical and chemical factors; and finally the actual sampling of the two species under examination.

(i) General Ecology.

The dominant plant species were noted and their distributions and densities estimated by eye. An ordinary fine mesh pond net was used to determine the components of the fauna of the three ponds, and estimates were made of their comparative abundance.

(ii) Chemical and physical factors.

Amount of sunshine, temperature and rainfall data were supplied by the Durham University Observatory, which is situated about 2½ miles (4.0 km.) from the study area. Water samples were taken at monthly intervals, in 250 c.c. reagent bottles. Each sample was filtered through a Whatman No. 1 filter paper and then stored in a cold incubator at 3 deg.C, thus reducing biological and chemical activity to a minimum.

The pH of each sample was measured using an E.I.L. Model 23A Direct Reading pH meter, and the electrical conductivity using a Taylor Model 110c C & R Bridge in conjunction with a Mullard conductivity cell, with a cell constant of 0.23. All conductivity measurements were performed at 22 deg. C.

Alkalinity, total hardness, magnesium and calcium concentrations were measured for each sample using the methods suggest by Mackereth (1963), with the modifications put forward by Cheng et al (1953) for calcium and magnesium titrations.

(iii) Population Studies.

Initially it was intended to study the vertical distributions of the two species by employing three methods of sampling. It was considered that if a sampler could be devised to sample the whole water column, a pond net used to sample the open water and a bottom sampler to assess the benthic component, then by difference, one might gain an approximation of any differences in vertical distribution of the two populations. To this end a column sampler was constructed; a modification of the type used by Garnett and Hunter (1965). However, after several trials, this method proved unsatisfactory for such a small system, for in order to acquire an adequate sample, many samplings were required, and these caused considerable destruction of the benthic and floating flora of the pond. Therefore, the column sampling was discontinued. For the major studies a fine mesh pond net was used. An attempt was made to standardise the sampling procedure, so that each sample consisted of a 15 second sweep, through approximately 8 cubic feet (226 litres) of water. At each sampling date, two samples were taken, one from station 4, the other from station 4A. The contents of the net were placed in a large white enamel tray and all the specimens of both species were collected and taken back to the laboratory. Using a pair of callipers, the breadth and height of each specimen were measured and recorded and then all specimens were returned to the pond. Height in the case of Limnaea stagnalis and breadth in Planorbis planorbis are the most conspicuous indicators of growth, as it is in these planes that it is most rapid.

Therefore using these dimensions, the results were plotted as histograms. Further experiments, whereby sample time and hence sample size was varied, showed that the 15 second sweep was sufficient to give a reliable picture of the population structures.

Bottom samplers were constructed using a 5x8 inch (12.7 x 20.3 cm.) framework of angled stainless steel, to form a rectangular tray, into the bottom of which was soldered phospher bronze gauze (18 mesh to the inch.). Trays were placed at ten stations down the length of the pond (figure 2), at the period when eggs were beginning to hatch, in order to examine the possibility of localised breeding. The intervals between each station are as follows:-

Stations.	Distance between stations. feet	metres. (approx)
1 - 2	10	3
2 - 3	10	3
3 - 4	10	3
4 - 5	20	6
5 - 6	20	6
6 - 7	20	6
7 - 8	45	13.7
8 - 9	20	6
9 - 10	20	6

During August, quantities of the dominant plant species were collected from ponds A and H, taken back to the laboratories and examined for egg masses. The number of egg masses and number of eggs per mass was counted for each type of plant, and recorded. As the breeding season of Planorbis planorbis is limited to the period between April and July, this study was confined to Limnaea stagnalis.

(c) Results.

(i) General Ecology.

At the outlet stream of pond A, that is station 1, the water was about 6 inches (15.2 cm.) deep, and Juncus articulatus, Myosotis species, Epilobium parviflorum, together with the benthic plants, Lemna trisulca and Drepanocladus exannulatus were the dominant plants. Stations 2 - 6 constituted the main pond and here the depth varied from 1 - 2½ feet (30.5 - 76.2 cm). The dotted line in figure 2 shows the 2 foot (61 cm.) contour. The main pond was skirted around its margins by Juncus effusus, Juncus conglomeratus, Epilobium parviflorum and Myosotis species. In the deeper water of stations 2 - 4 inclusive, Potamogeton natans predominated, and was most dense at station 3, the deepest station. In this region there was a sparse benthic flora, consisting of Drepanocladus and Chara species. In the shallower marginal water of the main pond, Eleocharis palustris was common. Between stations 4 and 5, Potamogeton decreased in its abundance when compared with stations 2 - 4, and was replaced by a thick luxuriant mat of benthic plants, of which Chara was the dominant. Towards station 6, the pond narrowed and the water was more shallow so that at station 6 it was only 6 - 9 inches (15-23 cm.) deep. Here there was a profusion of Juncus species and Eleocharis. In the water between each clump of rushes there was a thick growth of Chara, Lemna trisulca and Drepanocladus. At station 7, the flora was similar qualitatively to that of station 6. However, a decrease in Lemna trisulca was apparent, and Juncus articulatus was more, and Myosotis less common than at station 6. At station 8, Eleocharis was dominant, as was also the case at stations 9 and 10, but at the latter two stations it was associated with Epilobium, patches of Juncus, and a thin cover of Equisetum. Stations 8 - 10 were characterised by a predominance of emergent plants and a large area of bare mud surface due to the absence of submerged macrophytes.

At the outlet stream of pond A, station 1, both Hydrobia jenkinsi and Pisidium species were found to be common. At stations 9 and 10, there was one occurence of Limnaea truncatula and one of Limnaea pereger. Limnaea stagnalis and Planorbis planorbis occured at all stations down the pond, the shells of the older specimens supporting exotic growths of the epiphtic alga Chaetophora incrassata. Other components of the fauna included Notonecta glauca, Corixa species, Haliplidae, Nepa cinerea, the larvae of Ephemeroptera, case bearing Trichoptera, Pyrrhosoma, Coenagrion, Culicidae, and Chaoborus, also included were Asellus aquaticus, Hydracarines, Cladocerans and Copepods.

Pond A represents an intermediate stage in the hydrological seral process, whereas the other two ponds, H and B, represent early and late stages respectively. The eastern end of pond B is characterised by an intertwined mass of Potamogeton natans, which predominated over the deeper water, which was up to 3 feet (91 cm.) deep in places. At the western end of the pond, the terrestrialisation process was well advanced. Juncus effusus and Juncus conglomeratus were present, and Typha latifolia was encroaching upon the deeper, open waters of the pond. In the deeper waters the dominant species was the floating Riccia, which replaced the Potamogeton seen at the eastern end. Gastropods were absent from pond B, except for a single specimen of Limnaea pereger, taken during March, 1966. Other animals present included Notonecta glauca, Corixa species, Haliplidae, Asellus aquaticus, Cladocerans, Copepods, and the larvae of Pyrrhosoma, Coenagrion, Enallagma, Ishnura, Aeshna, Ephemeroptera, case bearing Trichoptera, Chaoborus, Chironomids and Ceratopogonidae.

Pond H has an area of approximately 300 sq. feet (27.9 sq.m.) and is about 3 feet (91.4 cm.) deep at its centre. Potamogeton was the only floating macrophyte represented, of which there was only a small stand. With no benthic macrophytic flora represented, the mud surface was naked. The water of this pond had a murky appearance due to the presence of a heavy suspension of clay particles, probably derived from seepage through the clay dam at the northern end of pond I. The pond margins were dominated by dense stands of Juncus effusus, Juncus conglomeratus, and Epilobium parviflorum, whilst Eleocharis palustris thrived in the shallow waters of the pond. The main components of a sparse fauna included Limnaea stagnalis, of which there was a small population of very large individuals, Planorbis alba, Asellus aquaticus, aquatic Coleoptera, and Ephemeroptera larvae.

(ii) Physical and Chemical Factors.

Figure 3 shows meteorological data which were considered to be relevant to the study. The temperature curves, monthly mean maximum, monthly mean minimum and monthly mean, show the same trends. A rapid drop in temperature between October and November was followed by a more gradual decrease in January, and from then onwards up to June there was a steady increase, although

FIGURE 3. Weather conditions in the Durham area during the study period, November 1965 to August 1966.

Monthly mean temperature (deg. C.) ---------

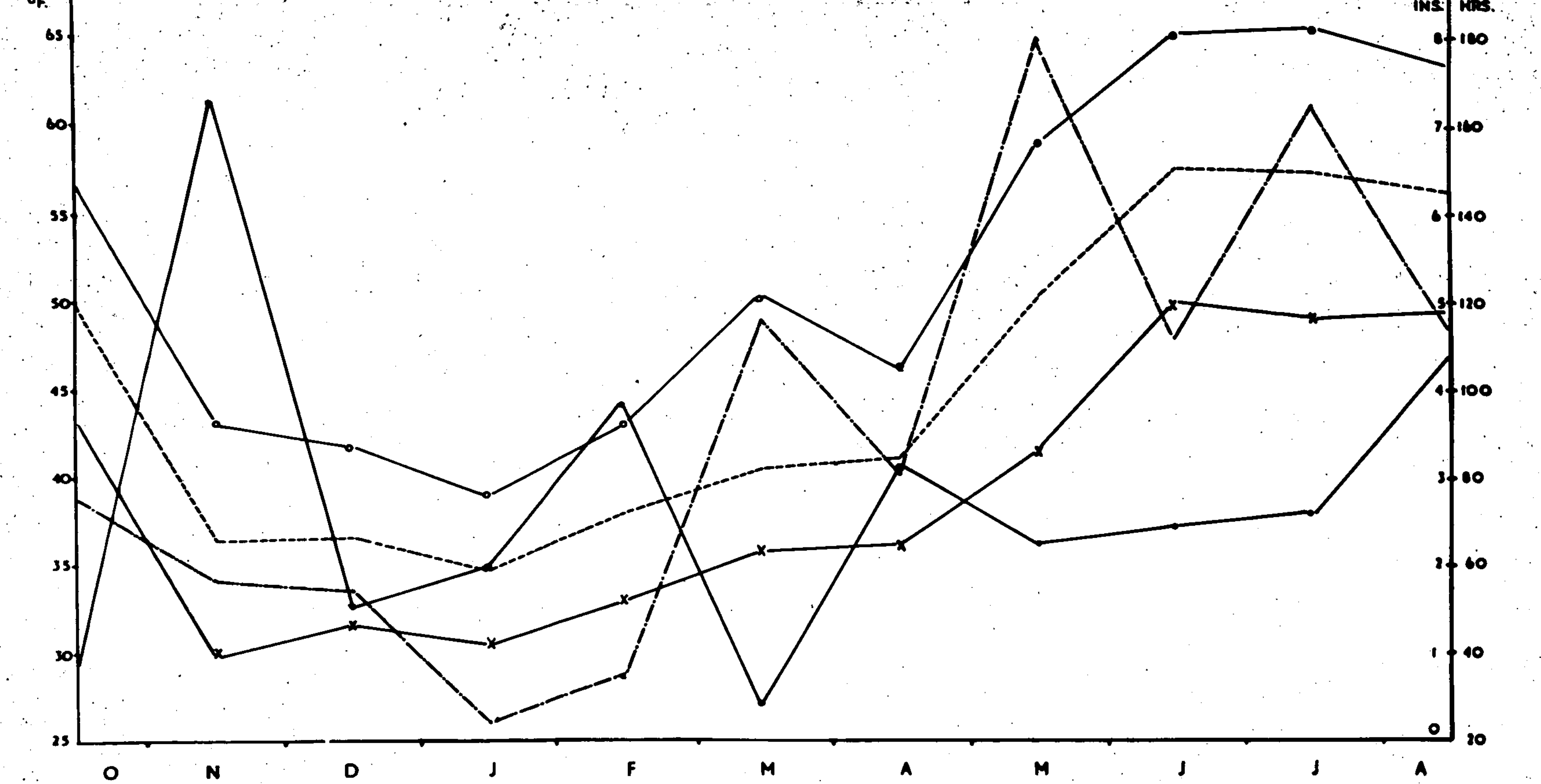
Monthly mean maximum temperature (deg.C.)

Monthly mean minimum temperature (deg.C.)

Hours of sunshine per month.

Rainfall (inches per month).

WEATHER CONDITIONS



there was a slight drop during March and April. Thereafter, the general trend of increase recovered and during June and July a summer maximum was reached. Figure 3 also shows the hours of sunshine per month which followed the temperature curve quite closely, but in June there was a deep depression in the curve, which was not reflected in the temperature curves. Finally, Figure 3 shows rainfall with a large peak in November, smaller peaks in February and April, and troughs in October, December and March, whereas during May, June and July it remained fairly constant.

Figures 4, 5 and 6 show the results of the quantitative analysis of certain chemical components for the ponds A, B and H respectively. For Pond A (figure 4), the curve for total hardness shows a trough in December, then rises steeply to a peak in January, followed by a stepped decrease and then a plateau from March to May 1. This is followed by another slight drop to a June/July plateau. The curve for magnesium concentration is a shallow version of the total hardness curve until March, when unlike the total hardness curve it shows a slight increase up to a peak in June and then falls away. The curve for calcium concentration is similar to the total hardness curve, except that from June to July there was an increase in calcium.

The pH curve for pond A, of which there was no data for October 1965, begins at a low level in December and January, and then increases at first steeply and then more gradually to a maximum in March, when it falls away to a trough in May, followed by a sharp peak in June, and thereafter decreases rapidly to a low level in July.

FIGURE 4. Pond A chemical data.

pH --------

Conductivity (mhos). ....

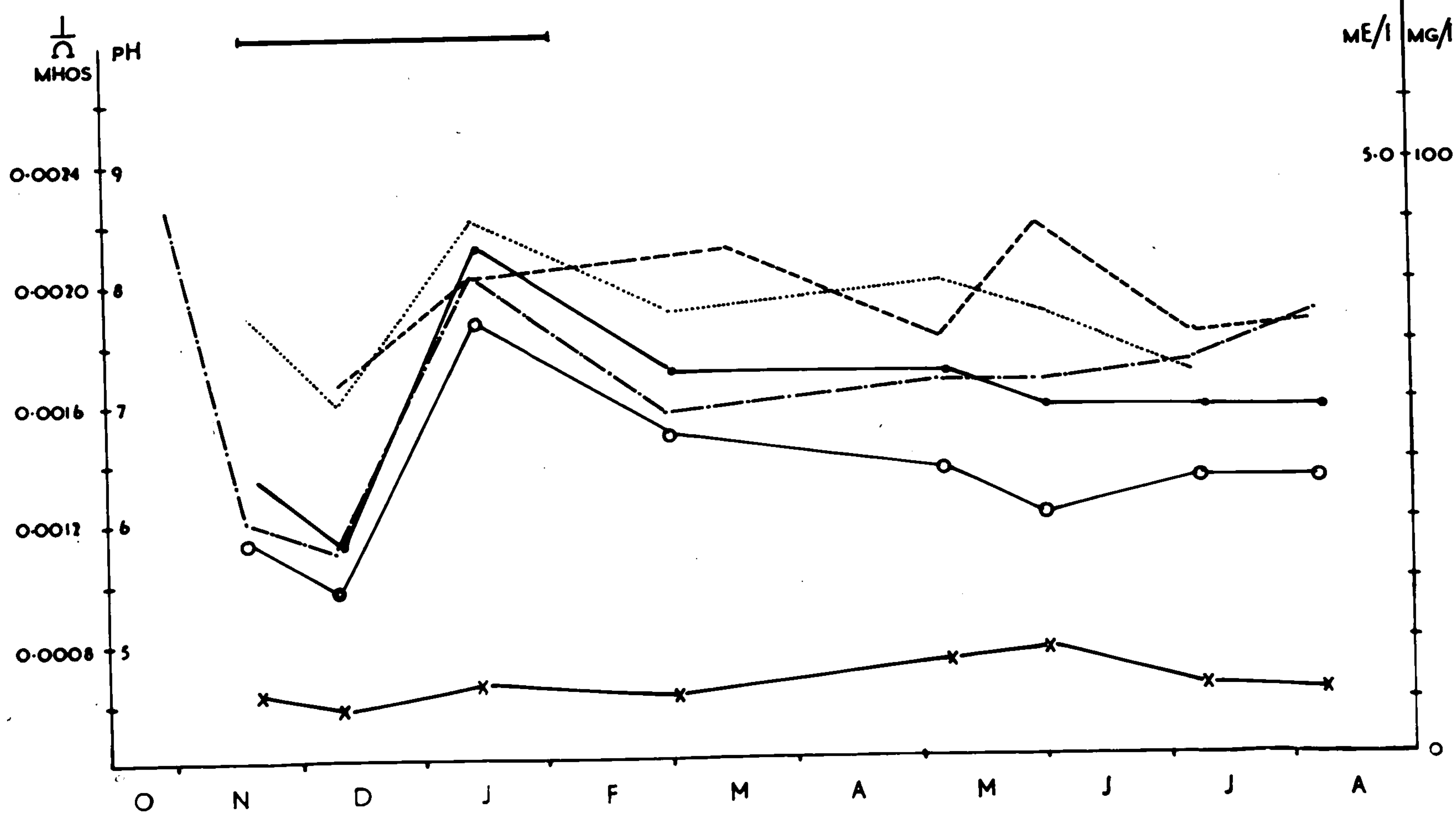
Alkalinity (mE/l.). —·—·—·—

Total Hardness (mg./l.). •———•———•

Calcium concentration (mg./l.). o———o———o

Magnesium concentration (mg./l.). x———x———x

POND A



1/Ω MHOS
pH
0·0024
9
0·0020
8
0·0016
7
0·0012
6
0·0008
5
ME/l
MG/l
5·0
100
0
O
N
D
J
F
M
A
M
J
J
A

Figure 5. Pond B chemical data.

pH - - - - -

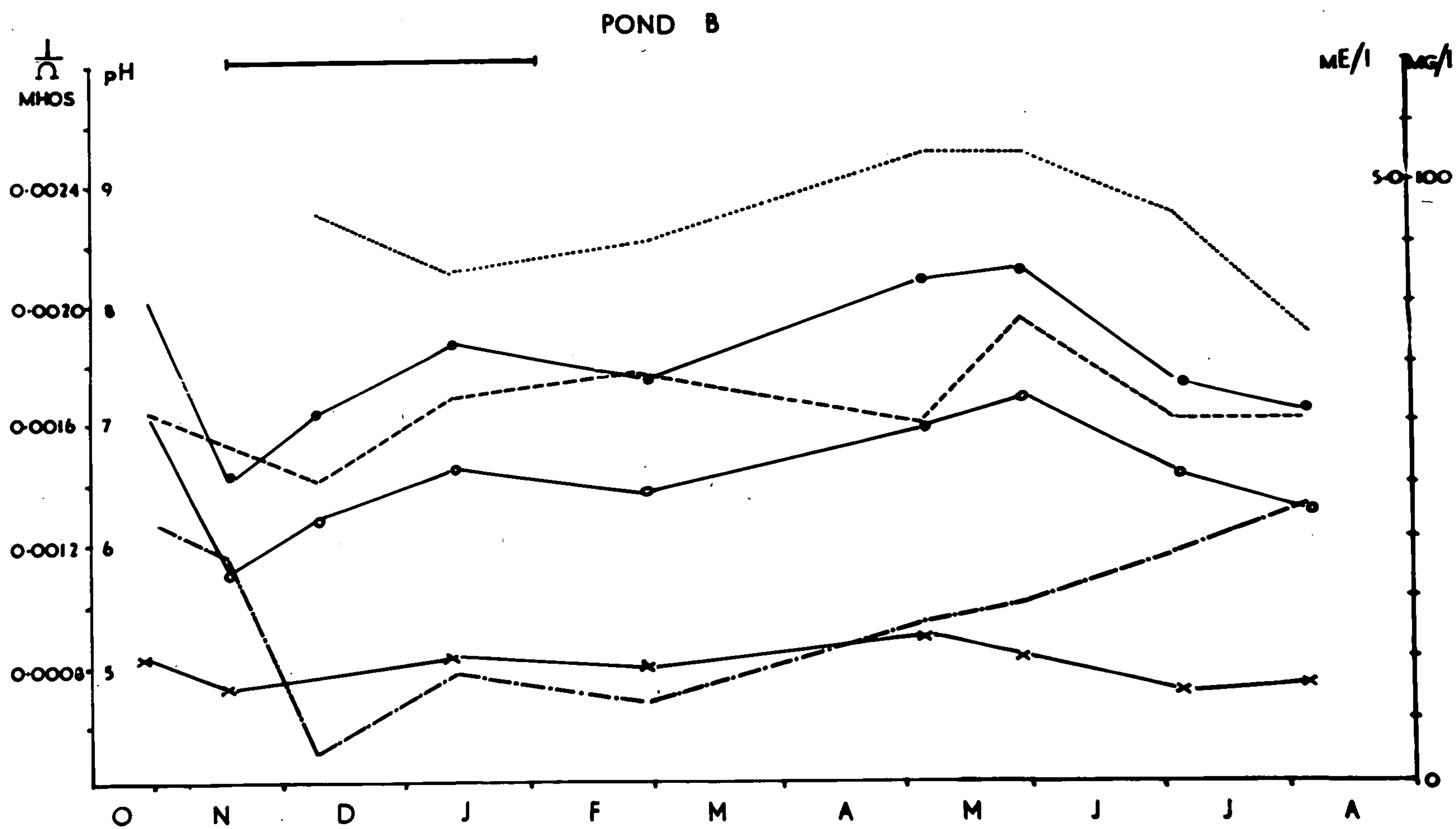
Conductivity (mhos). ··············

Alkalinity (mE./l.). —·—·—·—

Total hardness (mg./l.). •———•———•

Calcium contentration (mg./l.). o———o———o

Magnesium concentration (mg./l.). x———x———x



POND B
1/Ω MHOS
pH
ME/l
MG/l
0·0024 9
0·0020 8
0·0016 7
0·0012 6
0·0008 5
5·0 100
0
O N D J F M A M J J A

FIGURE 6. Pond H chemical data.

pH - - - - - - - -

Conductivity (mhos.). ....

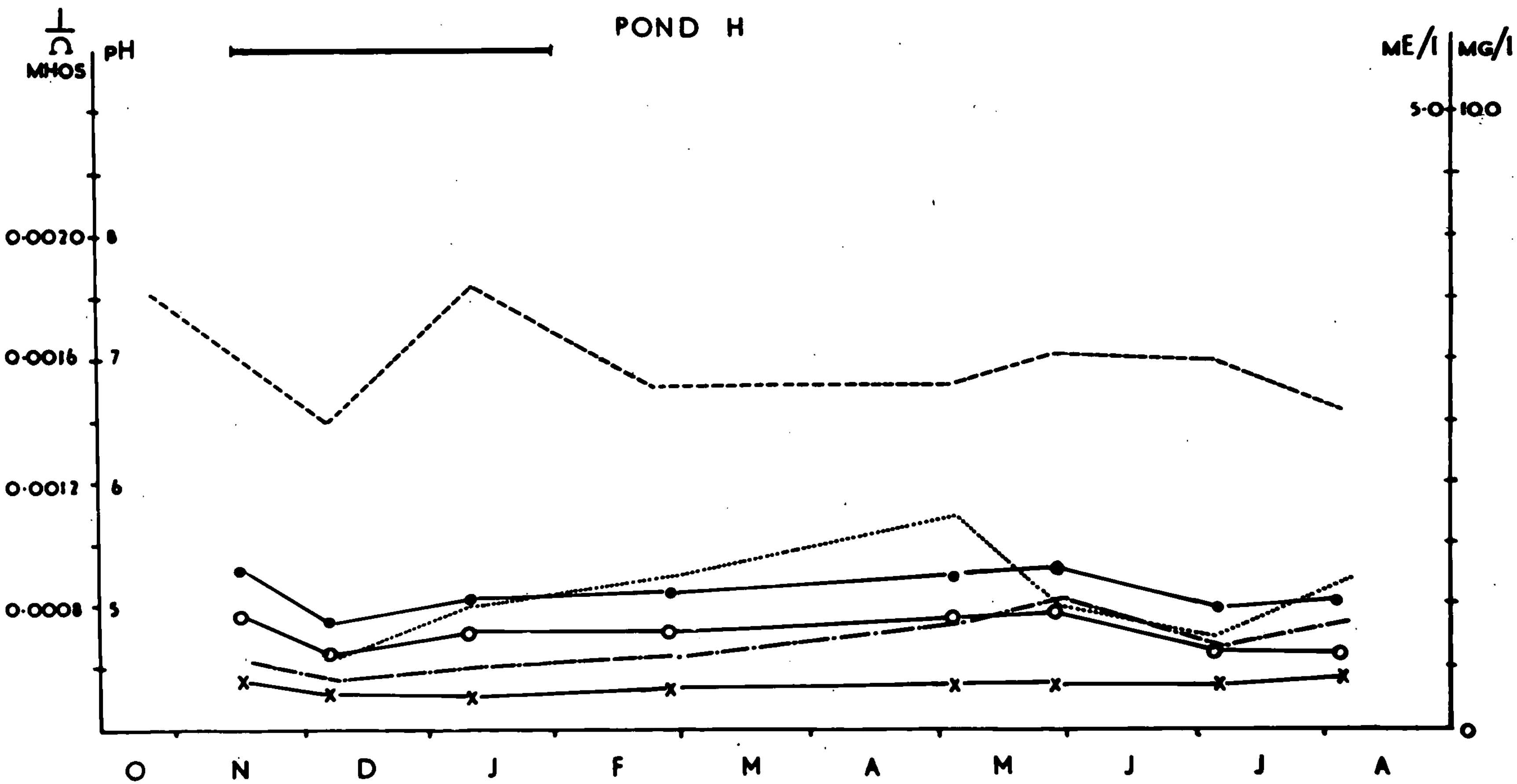
Alkalinity (mE./l.). —·—·—·—

Total hardness (mg./l.). •———•———•

Calcium concentration (mg./l.). o———o———o

Magnesium concentration (mg./l.). x———x———x

POND H



1/Ω MHOS
pH
ME/l
MG/l
5·0
100
0·0020
8
0·0016
7
0·0012
6
0·0008
5
0
O
N
D
J
F
M
A
M
J
J
A

The alkalinity curve shows a sharp decrease in November, but becomes more gradual from November, to a December minimum. This is followed by a rapid increase to a January peak, a decrease in February, and then onwards through the summer months there is a gradual increase.

Up to 1 March (figure 4), the conductivity curve is similar to the total hardness curve, but at this point there is a gradual increase up to the May level, followed by a decrease during June and July.

For Pond B (figure 5), the calcium, magnesium, and total hardness curves show the similar features of a trough in November and maximums in January and June. The alkalinity curve is also characterised by a November low, a slight peak in January running to a slight trough in March, and then onwards a gradual increase during the summer months. The pH curve is similar to that for pond A. The conductivity curve shows a slight trough in January and then gradually rises to a plateau in May and June, and then falls away.

The total hardness, calcium, magnesium and alkalinity curves for pond H (figure 6), show troughs in December, and then gradual increases up to maxima in June, after which there is a decrease. The pH curve drops from its November level to a minimum in December, followed by a rise to a January level, and then a more gradual rise to a higher March level. This is followed by a trough in May, a sharpish peak in June, and then another trough in July. There is no data for the November conductivity, but it increases from a low level in December to a peak in May, then decreases sharply and then more gradually during June and July.

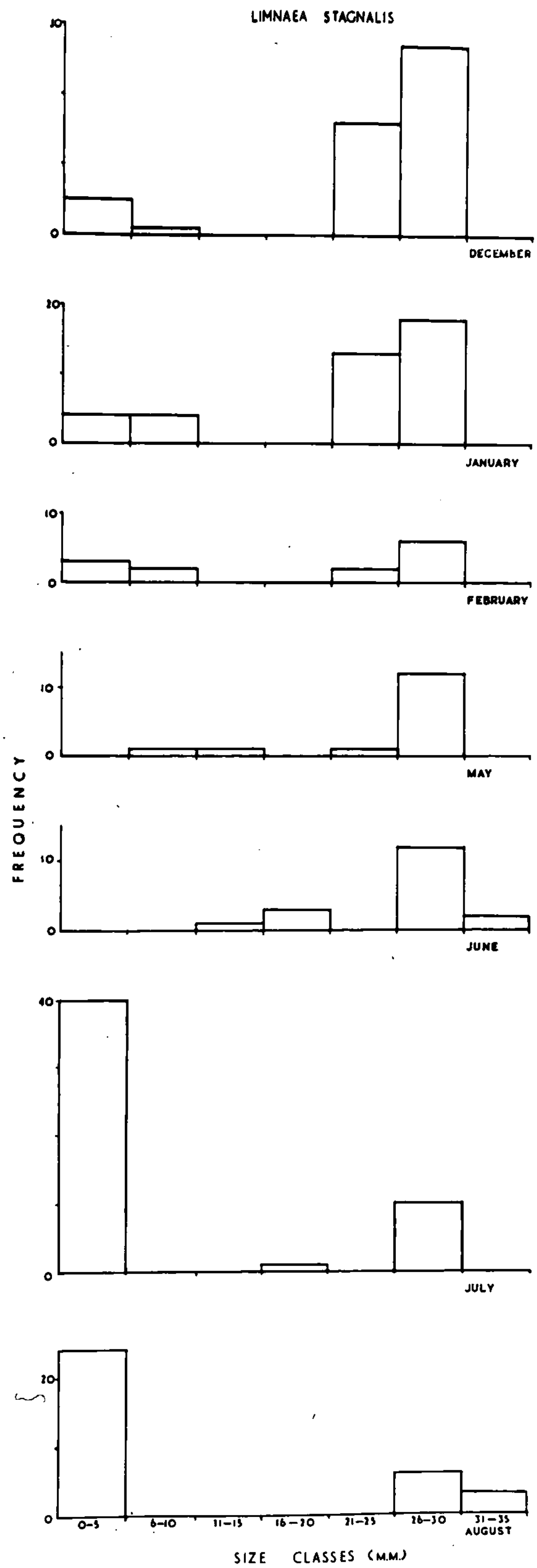
(iii) Population Studies.

(a) Monthly sampling at two stations.

No major differences were apparent between the net sweep samples taken at the two stations, 4 and 4A, when the population data was plotted as histograms. Therefore, the data for each of the two stations was pooled for the two species Limnaea stagnalis and Planorbis planorbis, and the resulting histograms are shown in figures 7 and 8.

Limnaea stagnalis. Figure 7 shows a distinct bimodal distribution for the December to June samples. It is clear that individuals of this species which hatched during the summer of 1965 passed the winter in the 0 - 10 mm. range, whereas those assumed to have hatched during the summer of 1964 overwintered at 20-30 mm, but see the discussion for further consideration. No significant growth occured until May when samples indicated that growth had recommenced, in that both generations had a greater mean height than in earlier samples. By June, the "1965" generations reached 10-20 mm. and the "1964" generation 25-35 mm. During July the 1966 generation was hatched and appeared in the 0-5 mm. size class, represented by a very large peak. During this time of the year the distribution was clearly trimodal, the oldest "1964" generation composed of the largest animals, the "1965" generation occupying the 15-20 mm. range, and the 1966 generation being represented by the smallest animals. During August the "1964" and 1966 generations continued to occupy the largest and smallest size categories, but the generation of the intermediate year was missed.

__FIGURE 7.__ Size distribution of *Limnaea stagnalis* specimens in successive collections from Brasside Pond A.


LIMNAEA STAGNALIS
FREQUENCY
DECEMBER
JANUARY
FEBRUARY
MAY
JUNE
JULY
AUGUST
0-5
6-10
11-15
16-20
21-25
26-30
31-35
SIZE CLASSES (M.M.)

From December until August, the "1964" and "1965" generations could be distinguished on a size basis, and the progress of the generations could be followed throughout the year. As the different generations remained distinct, the analysis technique of Berrie (1965) was adopted. However it must be emphasised that the numbers were not really adequate for this type of analysis and the ravages of a hard winter presumably caused such great mortality as to reduce the population to a very low level (see figure 9). Thus the sample became smaller with time. Therefore the results of the analysis, especially those given in table 1, must be treated with reservation and the only conclusions drawn are those which might document previous work.

Table 1 shows data obtained for the "1965" generation. This generation overwintered at a mean size of 4.5 mm., but after a temporary cessation of growth during the winter period, in which individuals remained in the 0-10 mm. size class (figure 7), growth rates apparently increased from May onwards. Note the decreased mean size in February; for the explanation of this anomaly, see the discussion.

Table 1. Summary of size and growth data for "1965" generation.

Date	Number	Range of lengths (mm.)	Mean Length (mm.)	Standard Deviation (mm.)	Size increases since previous sample. (%).	Growth Rate (mm./week).
14 Dec 65	6	2.0- 9.0	3.3	2.60	-	-
13 Jan 66	8	3.0- 9.0	5.6	2.18	69.6	0.46
28 Feb	5	2.3- 7.0	4.8	1.60	-19.1	-0.13
3 May	2	10.0-10.7	10.4	0.35	117.9	0.62
2 June	4	11.9-19.0	15.8	2.54	52.66	1.36
7 July	1	18.2	18.2	0	15.19	0.48

Table 2. Summary of size and growth data for "1964" generation.

Date	Number	Range of lengths (mm.)	Mean Length (mm.)	Standard Deviation (mm.)	Size increase since previous sample. (%).	Growth Rate. (mm./week)
14 Dec 65	43	23.0-30.0	26.05	1.64	-	-
13 Jan 66	31	23.0-29.0	25.77	1.76	-1.07	-0.06
28 Feb	8	23.3-28.0	26.13	1.38	1.40	0.06
3 May	13	25.0-29.5	27.50	1.38	5.24	0.15
2 June	14	26.1-31.5	28.65	1.73	4.18	0.28
7 July	10	28.0-30.3	28.85	0.63	0.70	0.04
8 Aug	9	26.0-32.5	28.84	2.32	0.03	0.002

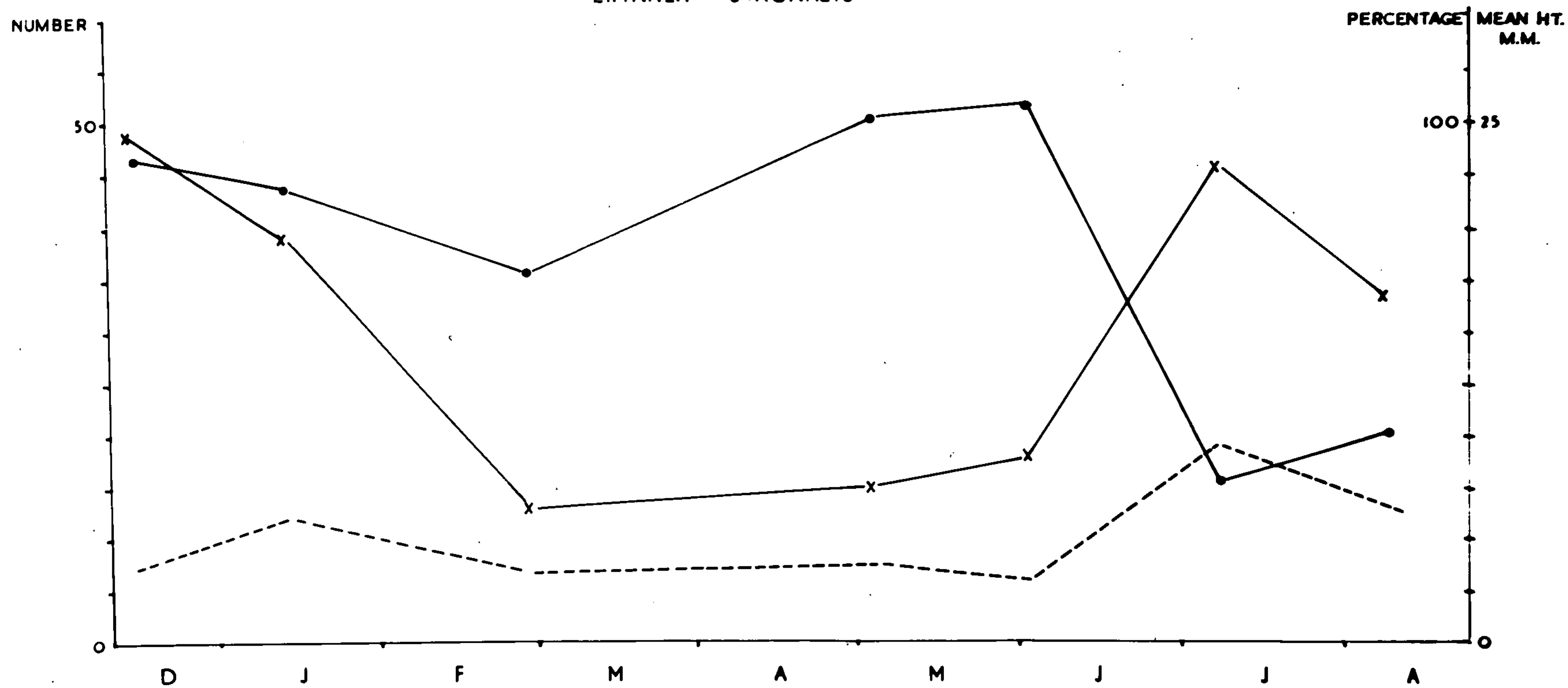
FIGURE 9. Population data for *Limnaea stagnalis* population of Brasside Pond A, for successive samples.

Population mean size (mm.). •———•———•

Numbers in each successive sample. x———x———x

Proportion of *Limnaea stagnalis* , as a percentage of the total snail population. – – – – – – – –

LIMNAEA STAGNALIS



In table 2, a similar cessation of growth during the winter period is apparent for the "1964" generation, which overwintered at an average size of 25 mm. Growth recommenced in May, but was clearly not as great as in the younger "1965" generation, at that period (see Table 1). Again, note the negative value for the January sample, which is commented upon in the discussion.

Figure 9 shows: the numbers of Limnaea stagnalis taken in two samples, at stations 4 and 4A, at each successive sampling date; the mean size of the animals in these two samples for each sampling date; and also the proportion of Limnaea stagnalis individuals present in the two samples, as a percentage of the total number of Limnaea stagnalis and Planorbis planorbis. The curve for numbers shows a decline during the winter months and reaches its nadir during February, remaining at this low level until recruitment from breeding commences after hatching, during June and July. The curve for mean size also shows a decline during the winter months with a trough towards the end of February, possibly associated with mortality of older and larger forms of the 1964 generation. With the onset of spring, growth rates increased and this was reflected in the increase in mean size of animals, until recruitment commenced in June and July (see figure 7). The curve showing the proportionate representation of Limnaea stagnalis at each successive sampling date is fairly constant for most of the year, but when hatching begins the proportion of Limnaea stagnalis in the samples increases.

Figure 11 shows the relationship between height and breadth for Limnaea stagnalis and shows that for this species growth is most rapid along the height axis.

FIGURE 8. Size distribution of *Planorbis planorbis* specimens in successive collections from Brasside Pond A.

PLANORBIS PLANORBIS

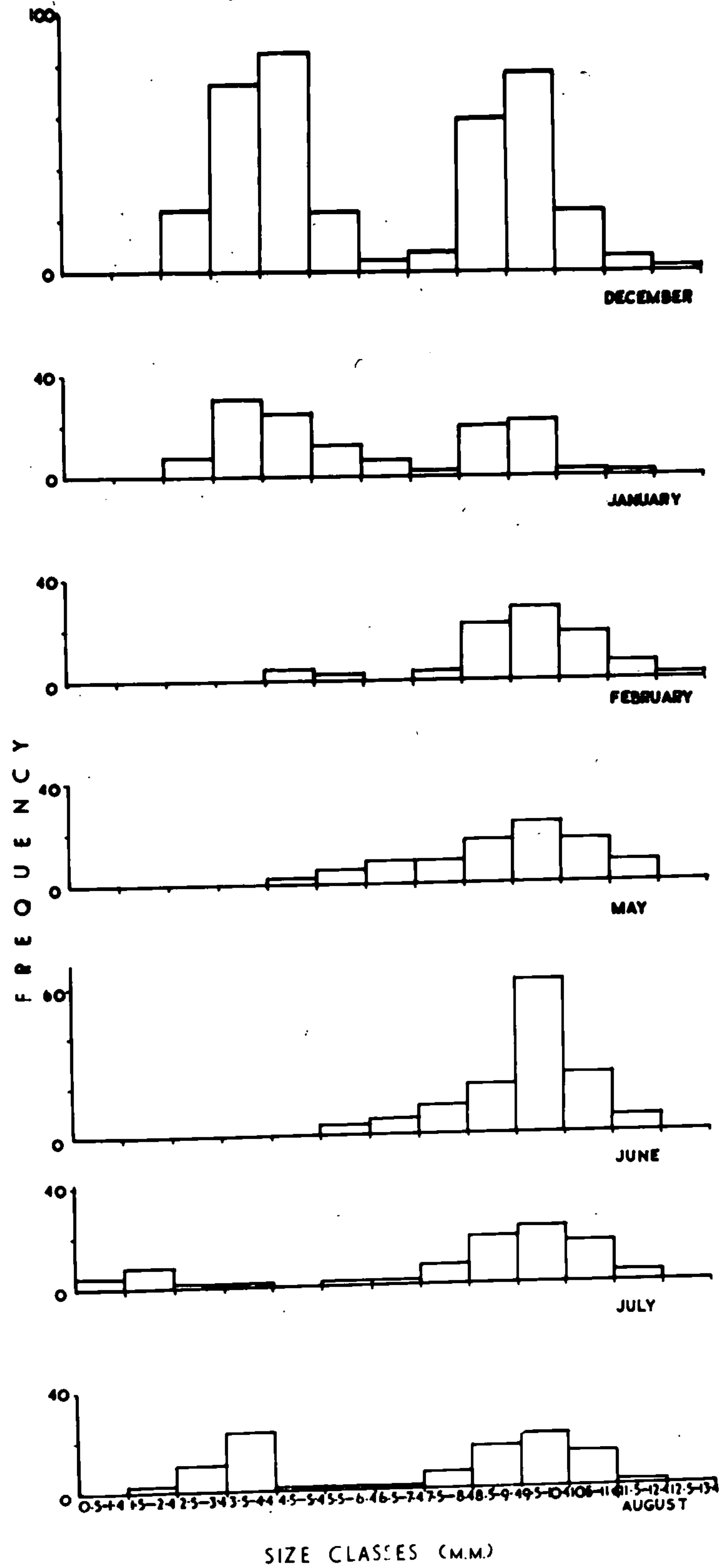


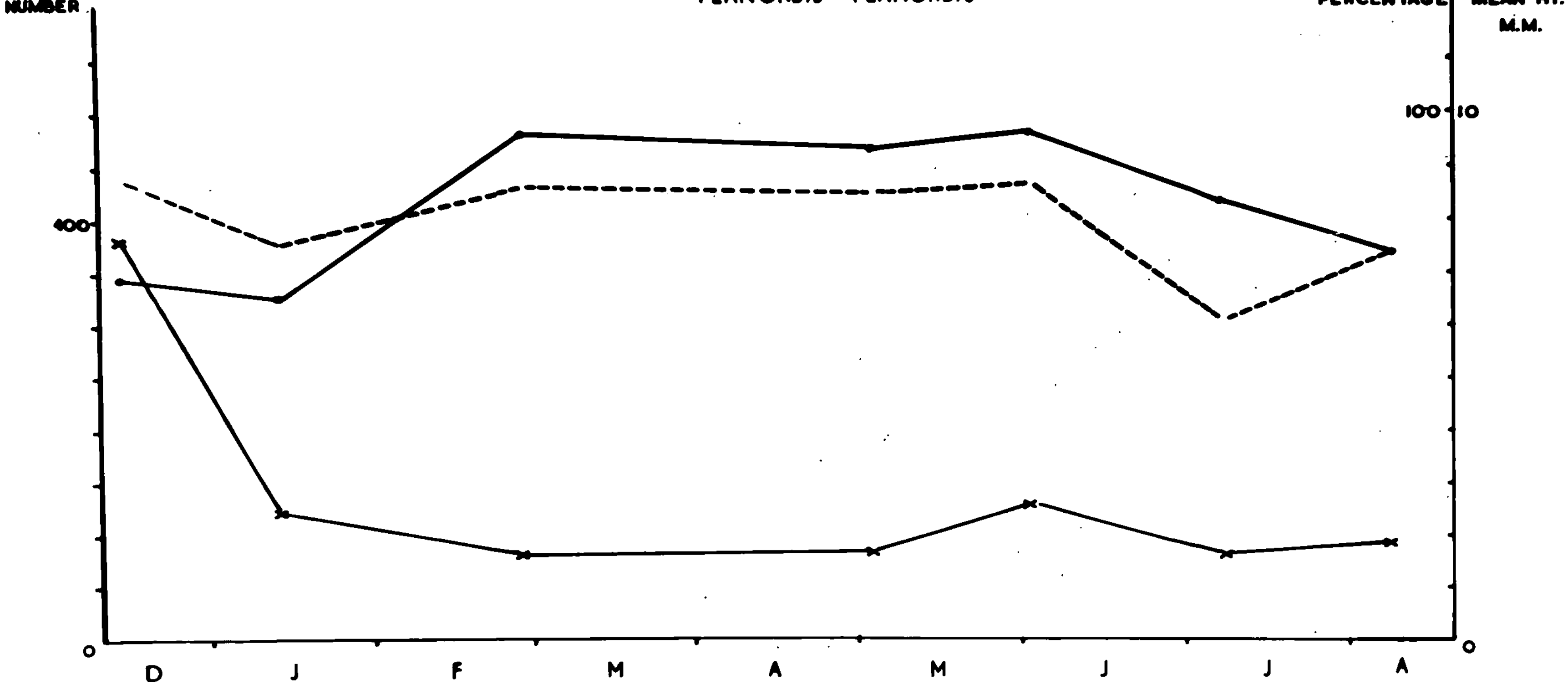
FIGURE 10. Population data for *Planorbis planorbis* population of Brasside Pond A, for successive samples.

Population mean size (mm.). •————•————•

Numbers in each successive sample. x————x————x

Proportion of *Planorbis planorbis*, as a percentage of the total snail population. --------

PLANORBIS PLANORBIS



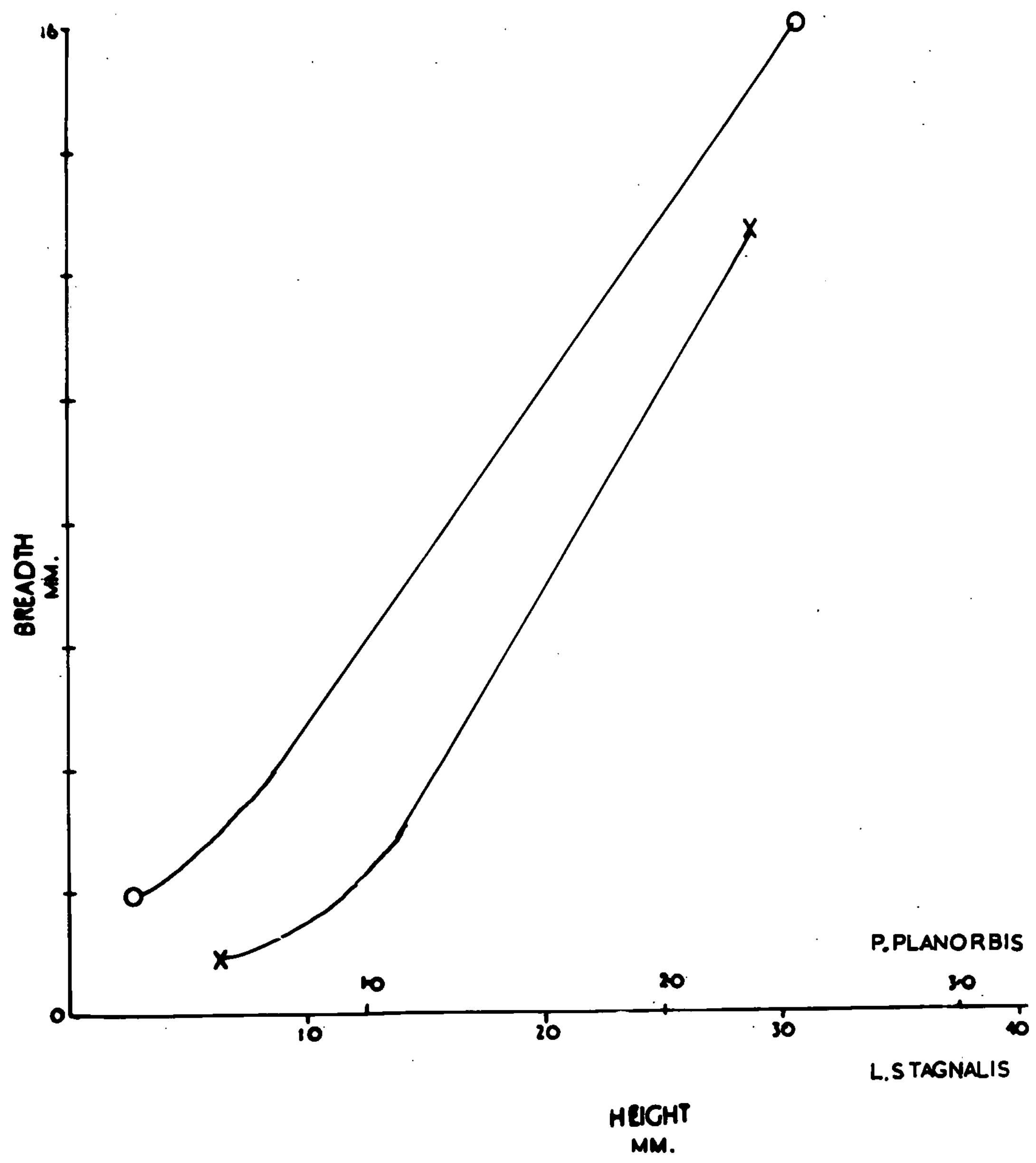
Planorbis planorbis. As with ~~the~~ Limnaea stagnalis, sweep net data, from the two sampling stations, (4 and 4A,) of Pond A, were pooled. Figure 8 shows the population to have a distinct bimodal distribution during December 1965 and January 1966, with the 1965 generation grouped around the 5 mm. peak, and the generation which hatched in 1964, grouped around the 10 mm. peak. From December 1965 to June 1966 the size range of each year class became smaller as the larger and older individuals died off. The smaller individuals of the 1965 generation grew rapidly, eventually to form the adult group which lies in the range of 8-14 mm. in breadth. During July, the 1966 generation appeared and the histogram again shows a bimodal distribution. However, the generations can only be clearly distinguished for little more than a month, for in August the size classes of the two generations begin to overlap. This precluded the possibility of examining the growth rates of the two component generations of the population separately, as was done for Limnaea stagnalis (after Berrie, 1965).

Figure 10 shows: the numbers of Planorbis planorbis taken in successive samples at station 4 and 4A, the mean size of the animals in the population at these two sampling stations at each sampling date: and also, the proportion of Planorbis planorbis individuals as a percentage of the total number of Planorbis planorbis and Limnaea stagnalis present at the two stations at each successive sampling date. The curve for numbers shows a steep decline from December to January and then a more gradual drop to a minimum in late February. From this point onwards, the numbers remained

FIGURE 11. Relationship between height and breadth for the two species, *Planorbis planorbis* and *Limnaea stagnalis*.

Planorbis planorbis: x————————x

Limnaea stagnalis: o————————o



16
0
BREADTH
MM.
P. PLANORBIS
10
20
30
10
20
30
40
L. STAGNALIS
HEIGHT
MM.

constantly low until July, when recruitment to the population began. However, there is a slight peak in June, but as no hatching had occured and recruitment from any other source seems unlikely, this reflects a slight inconsistency in the sampling for that month. The curve for population mean size shows a decrease to a January minimum, followed by a rise to a peak at the end of February, and then a plateau from February to May.

The relationship between breadth and height for Planorbis planorbis is shown in figure 11, and it is apparent that growth is most pronounced in the breadth dimension.

(b) Bottom tray sampling.

Results are shown in Figure 12, and represent data accumulated from four consecutive weeks of sampling from stations 1-10 (see Figure 2) between 14 July and 8 August.

Limnaea stagnalis. The largest numbers of newly hatched 1966 generation were found at station 1, and here the size group composed of the largest animals ranks second in importance. At the other stations the size classes containing the largest and intermediate sized animals predominated, except at stations 7 and 10 where no Limnaea stagnalis were taken. Young also appeared in the samples taken at stations 2, 4 and 6. The significance of this distribution is dealt with in the discussion.

Planorbis planorbis. The histogram shows that at station 1 there is a large proportion of the size class containing the largest animals and a considerable representation of the intermediate size group. This station ranks fourth in order of abundance of animals hatched in 1966. Station 2 had a much smaller number of individuals

FIGURE 12.

(a). Size distribution of Planorbis planorbis snails taken at 10 stations along Pond A, at four sampling dates, by bottom tray sampling.

0 - 3.9 mm. size class

4 - 7.9 mm. size class

8 - 11.9 mm. size class

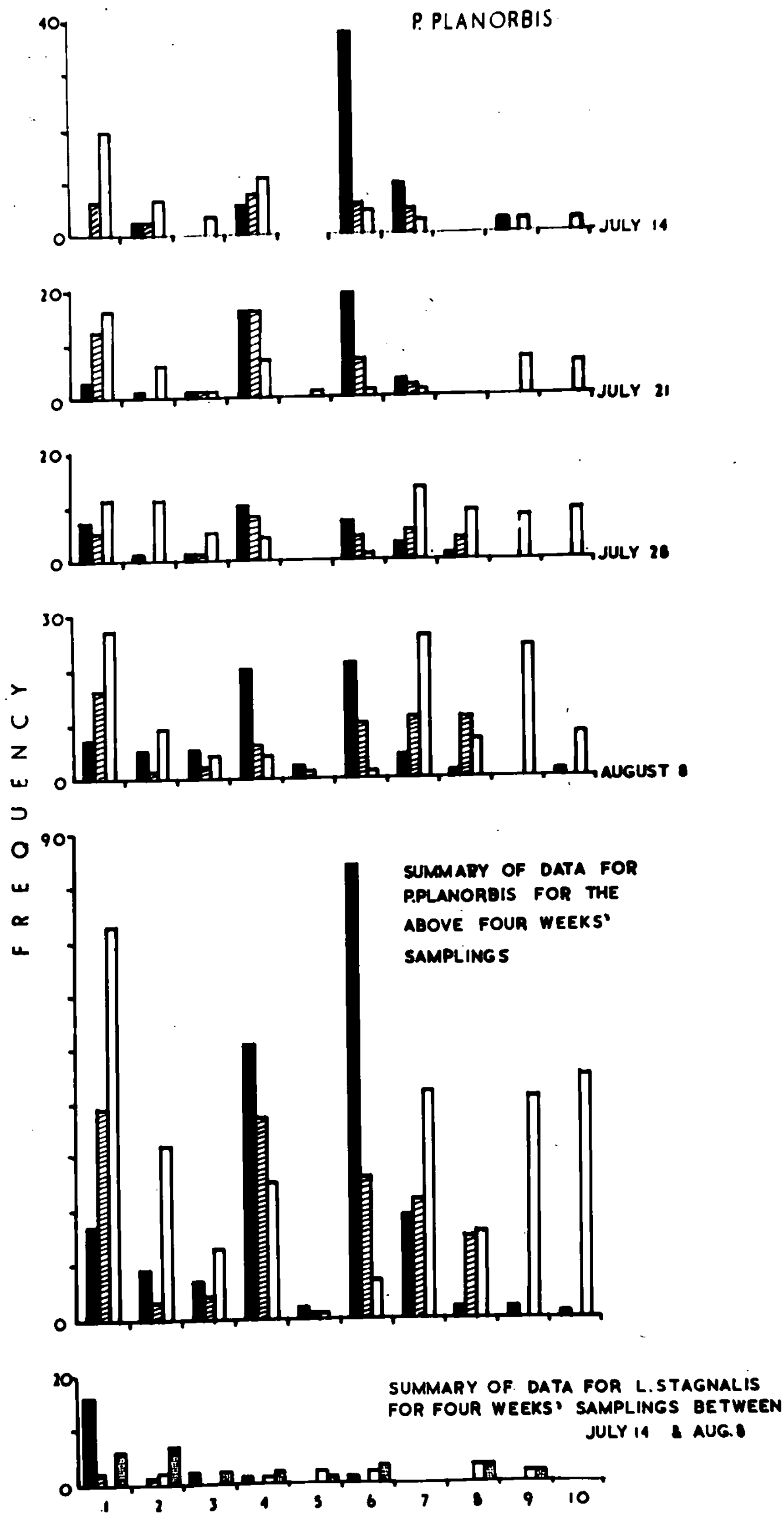
(b). Size distribution of Limnaea stagnalis snails taken at 10 stations along Pond A by bottom tray sampling. The data from four consecutive sampling dates has been pooled.

0 - 4.9 mm. size class

5 - 14.9 mm. size class

15 - 24.9 mm. size class

25 - 34.9 mm. size class


P. PLANORBIS
40
0
JULY 14
20
0
JULY 21
20
0
JULY 28
30
0
AUGUST 8
FREQUENCY
90
0
SUMMARY OF DATA FOR
P.PLANORBIS FOR THE
ABOVE FOUR WEEKS'
SAMPLINGS
20
0
SUMMARY OF DATA FOR L.STAGNALIS
FOR FOUR WEEKS' SAMPLINGS BETWEEN
JULY 14 & AUG.8
1
2
3
4
5
6
7
8
9
10

and is characterised by a small number of animals in the intermediate size category, whereas the class containing the smallest sized individuals ranks second in importance to the dominant large animal size category. A similar situation exists at station 3. At stations 4 and 6 the situation is completely reversed, for the 1966 generation predominates and the intermediate size class ranks second in importance. At station 5 there were very few individuals. At station 7 a similar situation to that found at station 1 occurs, whereas at station 8, although the same order of importance to that at station 7 was observed, the 1966 generation was only poorly represented as was also the case at stations 9 and 10. At the latter two stations the intermediate size class was absent and here the largest sized animals predominated. It was here that the largest specimens of the whole study were taken, some reaching 14.5 mm. in breadth, and often the shells of these giants were festooned with the epiphytic algae, Chaetophora incrassata. See the discussion for the consideration of the distribution of the different size classes.

(c) Study of egg capsules.

The results of this study are seen in Table 3. It is apparent that Limnaea stagnalis prefers the sites offered by Potamogeton, regardless of station or pond, and qualitative observations suggest that it is the undersides of the floating leaves of this species which are most favoured. In pond A where there were dense stands of Potamogeton, eggs were not found on other types of vegetation. In pond H, however, where there was very little Potamogeton, many egg capsules were laid on the limited supply of leaves, and in fact the egg capsules collected from this pond were taken from 3 leaves and one stem, whereas in the Pond A sample,50 leaves and stems were examined. It appears that when the supply of preferred sites is limited, as in Pond H, the animals resort to other plant species for oviposition sites. Thus in pond H,egg capsules were also found on Juncus articulatus and Eleocharis palustris.

The other significant result of this study was that egg capsules, laid by the larger individuals of the pond H population, contained about twice as many eggs per capsule as those laid by the smaller individuals of the Pond A population.

Table 3. Summary of egg count data for *Limnaea stagnalis*, made from collections of vegetation from ponds A and H on 8 August.

Pond	Station.	Plant.	Mean size of mature animals (mm.)	Standard Deviation (mm.)	Range of sizes (mm)	Number of egg masses	Mean number of eggs per mass	Standard Deviation	Range of number of eggs/mass
A	1	Chara	28.8	2.32	26.0-32.5	0	0	0	0
A	4	Potamogeton	28.8	2.32	26.0-32.5	14	16.3	18.8	7-30
A	5	Chara	28.8	2.32	26.0-32.5	0	0	0	0
A	4-5	Potamogeton	28.8	2.32	26.0-32.5	14	18.1	25.4	2-34
A	6	Lemna & Chara	28.8	2.32	26.0-32.5	0	0	0	0
A	4	Dreparocladus	28.8	2.32	26.0-32.5	2	18.0	2.8	16-20
B	-	Potamogeton	41.4	5.1	38.7-44.8	12	41.2	158.3	6-80
B	-	Eleocharis	41.4	5.1	38.7-44.8	2	30.0	33.9	6-54
B	-	Juncus	41.4	5.1	38.7-44.8	2	51.0	1.4	50-54

(d) Discussion

The use of the pond net as the major means of sampling must first be appraised as subsequent discussion assumes the integrity of this form of sampling procedure. Animals such as *Limnaea stagnalis* and *Planorbis planorbis*, even though they are slow moving, obviate a very rigorous form of sampling procedure, for they have very extensive habits; frequenting open water, crawling through vegetation, floating to the surface, and burying themselves in the mud (Germain, 1931). Various methods have been pursued in an attempt to surmount this problem, and theoretically that devised by Garnett and Hunt (1965) would seem to be the best, in that it samples the whole water column and the mud as well. However, as mentioned in the methods section, this system proved unsatisfactory and furthermore, it could not be used successfully to sample animals crawling through floating vegetation, such as *Potamogeton*, as it merely brushed aside this type of plant.

Berrie (1965), in his study of *Limnaea stagnalis* gathered 40 specimens by hand from the part of the pond where the bottom was covered with large stones. Berrie allows that this method might favour the larger specimens but states that "there is no reason to believe that the results have been unduly biased in this way". However the present author finds himself unable to agree with this statement and suggests that this method gives an exaggerated picture, of the importance numerically, of the large sized individuals in the population, whilst on the other hand it gives an inaccurate picture of the importance of recruitment in this species. Duncan's (1959) work emphasises the importance of very close scrutiny. In the present study a small white enamel tray was used, a much more confined area in which to work, with less possibility of error, and yet smaller individuals were frequently nearly overlooked. When data from the present study were compared with the data given by Berrie, it was found that, after the first batch of Limnaea stagnalis had hatched, the proportion of young newly hatched in the Bellshill population was 30% in July 1957 and 43% in July 1958, compared with 78.4% for July 1966 in the present study. However, it may be argued that inthis study, sampling was performed in the middle of a centre of high breeding, but even if this were the case,it gives a more accurate picture of the whole population structure, and gives the right emphasis to the importance of recruitment in this species. However, it may be that the size of recruitment varies from one population to another, according to the prevailing conditions. Berrie's sampling technique may also be biased in that individuals were removed from one station and were not returned to the system. This removal of what Berrie terms "a very significant proportion of the total population" must certainly throw doubt upon the importance to be attached to his growth rate data, as an interference of this magnitude into the interaction between animal numbers, size and food supply, cannot but cause some fundamental change in the pattern of population structure and growth rates. Finally the anomaly in Berrie's results for January 1958 in which small sized individuals apparently appear out of the blue,suggests that these small sized individuals were overlooked in the previous samples.

Another technique, which was used by Berrie (1965), though unsuccessfully, is collecting for a unit period of time. This again would be open to the criticism that it favours the larger sized individuals.

Bottom trays were used in this study, but if vertical differences in the distribution of species existed (see later), this method would give an inaccurate picture, if used without some supplementary form of sampling procedure to sample the upper layers of water.

Duncan (1959) used the pond sweep method in his study of Physa fontinalis, but sampled at random stations at monthly intervals. However, sampling at fixed stations was favoured in this study, as it was considered important that successive samples should be comparable, in an effort to determine differences between the two stations, but as has been stated no differences of this kind were found to exist. Thus, in this study, it is probable that a degree of integrity has been sacrificed for want of a comparison. Nevertheless, certain behavioural activities of the animals suggest that successive samples would not be strictly comparable. Shelford (in Ellis, 1926), noted that members of the family Limnaeidae had the habit of moving into the light open water on dull days, and retreating amongst the vegetation when the sunshine was too bright. Thus samples at predetermined stations might not be comparable if light intensities at subsequent sampling dates differed significantly. Certain authors (Rimmer, 1907; Jeffreys 1862;) have stated that Limnaea stagnalis is gregarious which also poses problems in sampling. Members of the freshwater pulmonate group, Basommatophora, of which Limnaea stagnalis and Planorbis planorbis are members, lack gills and an operculum and have to respire by means of a capillary network, which forms a lung in the roof of the respiratory chamber. Although this cutaneous arrangement is geared to aquatic breathing, individuals have the habit of floating to the surface in order to expel effete air from their respiratory chamber, and replenish their supply of oxygen. This is especially the case in foul waters and during warm summer weather, when the oxygen tension of the water is low (Ellis, 1926). In accordance with the surface area/volume relationship, it is usually the larger individuals which behave in this fashion, as they have to meet greater oxygen requirements. Further, the present author, has observed, that once an animal is at the surface, it is at the mercy of the surface currents and a slight breeze is sufficient to carry individuals to the margins of the pond. These behavioural characteristics pose further problems and lay the pond sweep method open to some criticism. Localisation or concentration of the population in some centre would also affect the results and the integrity of the sampling. All members of the Basommatophora have a radula, and therefore they can be selective in their feeding. Boycott (1936) suggested that there was no obligatory relationship between snail species and food plant species, and that what may superficially seem to suggest that such a relationship might exist, may merely have been that both species have a particular preference for a certain type of locus. This would give rise to an indirect association. However, Boycott was dealing with macrophytes, and it must be emphasised that such a relationship is still undecided in the case of microphytes, especially in those algae which form a felt like cover over vegetation.

stones and mud surfaces. If certain species of these algae are preferred in the diet, this might give rise to concentration of the population over centres of abundance of the food organism. Concerning breeding sites, it seems possible from the present work that snail species prefer a particular type of site for oviposition, and this, as was the case in Berrie's study (1965), may mean, that unless one is aware of this preference, one might either hit or miss the importance of recruitment. In the case of Berrie's study, the sampling station was removed from the centre of breeding, and as he states, it was some time before the newly hatched generation colonised the area which he was sampling.

Despite all these problems which make sampling procedure very difficult, though the pond net method fell short in many respects, a glance at the results suggests that this method, despite its inadequacies, gave a fairly good picture of the population structure for the two species studied. However, a bias may exist, which, it is suggested, favoured _Limnaea stagnalis_ during the breeding season, and possibly underestimated the importance of recruitment in _Planorbis planorbis_, (see later).

The assumption that size may serve as an index of age, must also be appraised. As seen from the results (tables 1 and 2), the relationship is not a simple one, but depends upon pregailing conditions and is probably governed ultimately by food supply, although other factors, such as temperature and the concentration of certain minerals, must not b$ underrated. Semper (in Step, 1945) found maximum size obtained to be directly related to the volume of water in which an individual developed. Boycott (1936) however, suggested that this was more likely to be a food relationship, the larger the system the more the food. The present work does not support the findings of Semper, for in pond A there was a large population of individuals which never exceeded 35 mm. in height, whereas in the smaller and more oligotrophic pond H, the adults in the population were much larger, though the actual population was much smaller. In a sample taken in pond H during August, all the adult members of the population were over 38 mm. in height.

The functioning of a hierarchical system (Wynne-Edwards, 1962; Macan, 1965;) and the possibility of secretion of growth inhibitors, is still speculative and, as yet, has not been documented for freshwater snails. Thus discounting this possibility, and also regarding genetical differences in the size of individuals, in an isolated population, as negligible, it seems reasonable to assume that all animals have fairly equal chances of obtaining a given quantity of food from an enclosed system, and of converting this into their own body substance. Thus, size should, in these circumstances give a fairly good indication of the age structure of an isolated snail population.

In general, British freshwater pulmonate snails have been found to have annual life cycles (Duncan, 1959; Hunter, 1953; 1957; 1961a; 1961b;) or more than one cycle per year, however Berrie in 1965, showed Limnaea stagnalis to have a biennial life cycle which was contrary to the view held by Boycott (1936). After extensive studies in the south of England, Boycott concluded that all freshwater snails were annuals, with the possible exception of Planorbarius corneus. Whereas Hunter, (1957), considered Limnaea stagnalis, Limnaea auricularia, and Planorbarius corneus, to be the only species likely to have life cycles of more than a year's duration. Up to the present, therefore, Limnaea stagnalis appears to be the only fully documented case of a British freshwater pulmonate snail having a life cycle of more than a year.

Limnaea stagnalis. Although the present study was confined to a period of nine months, the results obtained support the conclusion made by Berrie (1965) concerning the biennial life cycle of this species. Berrie showed that most animals could breed in the year in which they were hatched and again in the spring and summer of the following year, when individuals were a year old. However, data presented in this paper appear to conflict, in part, with this conclusion, for it would seem that snails breed in the early spring and summer of the two years following the summer in which they were hatched. This would suggest that snails might have a life span of two years or more, whereas Berrie's data suggests that snails live 18-20 months. In the light of Berrie's work, it seems likely that the group termed, for convenience, in the result section, the "1964" generation, (see table 2 and Figure 7), is probably composed of the older 1964 individuals together with animals hatched early in 1965, whereas the group contained in the 0-10 mm. size category and termed the 1965 generation, represents individuals hatched in the late summer of 1965.

After December, the 21-25 mm. animals (see Figure 7) presumably grow to form the 26-30 mm. class, replacing the older and larger members of the 1964 generation, many of which probably died during the winter period. This view is substantiated in figure 9, where from December 1965 to January 1966, decreases in both numbers and population mean size are apparent, presumably the result of the cold, hard winter of 1965/66. A preferential mortality of larger individuals would explain the spectacular decrease in mean size of the population during the winter period. This view is also substantiated in Tables 1 and 2.

Data in tables 1 and 2 suggest that during the winter period growth was slight, a finding in accordance with Berrie's results. Although growth probably did occur, it is only clearly evident in the younger sector of the population, data for which is presented in table 1. The reduced growth rates for the summer period (apparent in table 2), in the large animal component of the population, can be explained on the grounds already suggested, that the group, the "1964" generation, is in fact a mixture of early hatched 1965 animals and late hatched 1964 individuals. The explanation would be that death of the last surviving members of the 1964 generation, which would most probably be the largest, would have the effect of reducing the mean size of this portion of the population.

An anomaly noted in these results was the occurence of two negative results in the February data in table 1, and for the January data in table 2. These discrepancies point to an inadequany in the sampling technique. But, at a time when growth rates are minimal, if one or two of the largest specimens died or failed to be included in a small sample, this would have the effect of reducing the mean size to a value less than that of the preceding sample.

After the quiescent winter period, temperatures and sunshine began the annual climb to their respective summer maxima. During April, May and June improvement in weather conditions was particularly rapid and presumably had the effect of increasing the supply of plant food, which in turn increased the oxygen content of the water, and as plant cover increased, was partly responsible for the translation of sunlight energy into heat in the pond system. This rapid amelioration in conditions, probably accounts for the burst of growth which occured during the spring months, which can be observed in figures 7 and 9 and table 1. Although this trend is not so apparent in table 2, these low values are probably inaccurate, as stated above, and reflect the death of the last surviving individuals of the 1964 generation, The general trend of increased growth rates is especially manifest in the population mean size curve in figure 9. The increase observed, suggests that growth rates were sufficient to offset any setback which might have been incurred through loss of the largest and oldest of the 1964 generation. Growth rates in both groups are seen to reach a maximum during June, (tables 1 and 2, and figure 9), which might be attributed to the high mean temperature of this month, (Figure 3).

Assuming that hatching takes 21 days (Berrie, 1965; Germain 1931;), the individuals taken in the July samples were probably laid during the first or second week in June, at which time temperatures were increasing rapidly. The appearance of the first batch of newly hatched young, apparent in Figures 7 and 9, causes the spectacular drop in population mean size, due to recruitment into the population of young small sized animals. This decrease is, probabby enhanced by the disappearance, due to death, of the large sized animals, 31-35 mm. in height, of the 1964 generation, which were present in the June sample, and further by the small representation of the intermediate size class of animals 16-20 mm. in height. This small representation of the intermediate size group and absence from the August sample, suggests that the data for these two months are inadequate.

The present results can be used to support the conclusions made by Berrie (1965), that Limnaea stagnalis has a biennial life cycle. However, the possibility remains that a life cycle longer than two years, duration might be the case. Berrie comments on some work performed by Campion (in Berrie, 1965) at Malham Tarn, about 50 miles to the south west of Durham City, in which it was stated that Limnaea stagnalis had a simple annual life cycle. Further, Berrie has made unpublished observation in southern England which also suggest an annual life cycle. Nevertheless, it must be emphasised that, with a calcium concentration of more than 40 mg./1. and taking into account the altitude and lattitude of the present study area, the Durham habitat cannot be considered as marginal for this species. This suggests that conditions are especially favourable at Malham, which is a calcareous region. However, the altitude at Malham would appear to be unfavourable, as this is the highest station at which *Limnaea stagnalis* has been recorded in Britain. (Boycott, 1936). Clearly more work must be done before any definite statement can be made, as to the length of the life cycle of this species.

Planorbis planorbis. Though the nature of the size distributions in this species precluded the possibility of an analysis of the type adopted for *Limnaea stagnalis* (after Berrie, 1965), deductions can be made and several conclusions drawn from the examination of the data presented in figures 8 and 10. It seems feasible to assume that the peak in the range of the small sized animals in the December 1965 sample (Figure 8) represents animals hatched during the spring of that year, whilst the peak in the large animal size categories is probably formed from the 1964 generation, but the earliest hatched animals of the 1965 generation probably contribute towards the latter group. Mortality between December 1965 and January 1966 is sufficient to register as a decrease in population mean size in Figure 10, but this is not very large, and the later recovery of the mean size curve suggests that many of the surviving members of the 1964 generation probably the largest animals, died during the December to January period, when conditions were extreme. After January, when conditions appeared to be improving, especially mean temperature, a fairly rapid growth of the younger and smaller members of the population occured, and this is manifest in the mean size curve in Figure 10. This increase in mean size could also have been caused by high mortality amongst the smaller animals in the population. However, scrutiny of the histograms for the succeeding months (Figure 8), suggests that a general shift has occured and that as growth rates continued to be fairly high throughout the winter, the smaller individuals grew to replace the remnant of the 1964 generation, in the ranks of the large sized animal categories. That the last of the 1964 generation had died out by February, seems, quite a plausible deduction, as after this period, until recruitment in July, the population remains fairly constant with regard to numbers, mean size, and population structure.

When compared with Limnaea stagnalis, in which there is a quiescence in growth during the winter period, it appears that Planorbis planorbis is geared to continue its growth during the adverse winter period, for growth rates seem to be much greater for this species, than for Limnaea staghalis, during the winter period. Observations (see later) suggest that this species has one burst of reproductive activity when conditions improve, and that after this short period of breeding, though conditions may remain optimal, no further breeding in fact takes place. Thus, it seems likely that this species relies on maintaining fairly high growth rates during the winter period, so that when opportunities first occasion the possibility of breeding in the spring, animals are mature with regard both to size and reproductive condition.

In contrast to Limnaea stagnalis, it is seen that the mean size in Planorbis planorbis (Figure 10), reaches a maximum during February, and thereafter decreases slightly during March and April. This decrease could either be due to mortality in the large sized animal categories, whilst growth rates remain high, or alternatively to small mortality of the large animals, whilst growth rates remain comparatively small. The fact that there are no obvious differences in the structure and distributions of the histograms during this period, suggests that growth rates are reduced, and that the slight decrease registered in the mean size curve (Figure 10) is due to death of a small number of the larger animals in the population.

During July recruitment commenced, but unlike Limnaea stagnalis, this species seemed to confine its reproductive activity to a few weeks during the late spring and early summer. On the other hand, Limnaea stagnalis, continued to breed right up to August when the study ended. Searches made for the egg capsules of Planorbis planorbis after the last week in July, were in vain; before this period, egg capsules were found in abundance, especially amongst the benthic vegetation, amidst such plants as Drepanocladus and Lemna trisulca. According to Germain (1931), the eggs are laid between April and July, and hatching takes 14 - 16 days after oviposition. This suggests that the eggs of the 1966 generation were laid some time during the second or third week in June. Again, the only factor, of those measured, which shows coincident change, is increase in temperature. None of the other factors measured appear to be relevant. The stimulation of oviposition and copulation in other species has been shown to be quite complex, and as yet unsolved, (Timmermans, 1959; Duncan 1959;) thus it would be precipitate to suggest that temperature is the sole stimulating factor. Nevertheless, in the absence of more data, the tentative suggestion is made that temperature was the limiting factor in this case, and that all other relevant conditions for breeding had been satisfied. This is further suggested, since in 1966, spring was late. The appearance of the 1966 generation caused a dramatic drop in the population mean size curve, but this is not reflected so conspicuously in the curve for numbers (Figure 10).

The development of thermal stratification, in small and shallow ponds, is extremely unlikely, since precipitation or slight wind would be sufficient to cause overturn. Therefore, it is assumed that the concentration of all the chemical components of the water remained uniform throughout the system, and that exchanges between the mud surface and water, spread through the system quite rapidly, and were not localised in the bottom layer. In the main, variations in the concentration were probably due to dilution, caused by precipitation and also to the absorption of minerals by the organisms.

High rainfall during November, which caused water levels to rise very high, probably accounts for the marked drop in ponds A and B, of total hardness, calcium concentration, conductivity, alkalinity and to a lesser extent magnesium concentration, (Figures 4 and 5). The peak of these factors during January (the samples of which were taken under ice) may reflect the drier weather conditions during this month. The increase in calcium, and hence in alkalinity and total hardness, may reflect the return of calcium, in the form of vacated shells, to the system, since many dead shells were observed on the pond floor during this period, especially in the case of pond A, where the peak is more pronounced. However this effect may have been only slight. It seems possible that the increased concentrations were magnified by the ponds being frozen over during this period. Mortimer (1941) states that ice, when melted, gives quite a pure grade of distilled water. This fact, in itself, would have a concentrating effect. Furthermore, although there are no data for oxygen concentration, if anaerobix conditions did appertain during this period of ice cover, it is possible to speculate that the redox potentials might have been reduced and more minerals released from the mud surface, (Mortimer 1941).

After January the chemical data, in general, reflects the amount of precipitation and evaporation. pH is a poor indicator, for it is known to vary considerably during the day. The trough in the pH curve during May in ponds A and B (Figures 4 and 5), probably reflects high respiration rates, due to increase in sunshine. It is interesting to note that in pond A (Figure 4) during the remainder of the study period, after January, there was a decrease in calcium concentration, reflected in the total hardness curve, which is not evident over the same period for pond B (Figure 5). This might be due to calcium uptake by a large, rapidly growing, snail population present in pond A. This decrease is not observed in the results for pond B, where snails were absent. The fall in June, in calcium and magnesium concentrations and total hardness, in pond A, and the concomitant continued increase in alkalinity is inexplicable, and suggest an error in measurement. Except for the period of ice cover, therefore, it is suggested that variations in the chemical components of the pond water reflect the realtionship between precipitation and evaporation. In such systems as those studied, a weekb rain or a weeks sunshine would have sufficient effect to cause considerable variation in concentrations, through precipitation and evaporation, and it is believed that if more precise data of this kind were available, the explanation for the variations would become more apparent.

Conditions in pond H present a special case, since here there is continual flow of water. This might explain the apparent constancy of the chemical components. Furthermore, it is quite different from the other two ponds being oligotrophic, when compared with the eutrophic enclosed status of the ponds A and B.

Therefore, although there appears to be no apparent corelation between the beginning of breeding and the chemical factobs measured, the importance of these factors must not be underestimated.

Working with Planorbis planorbis, Timmermans (1959) found that a gradual rise in temperature to 25 - 28 deg. C. stimulated oviposition within one or two hours, provided that the temperature on the preceding day did not fall below 21 deg. C. Moreover, this species showed better oviposition after a yeast diet. Timmermans suggested that plant material and oxygen concentration might also be of importance. Limnaea stagnalis is stimulated to oviposit in aquaria, by the introduction of lettuce leaves, or certain other plants which float on the surface. A sudden rise in oxygen concentration or gradual rise in temperature are both known to stimulate oviposition in this species (Timmermans, 1959).

Working with *Physa fontinalis*, Duncan (1959) also found temperature to be an important factor. He suggested that it might have the indirect effect of controlling the rate of development, which might regulate the time of reproduction, and that there might be a critical temperature, below which oviposition does not occur. Duncan concluded that when the action specific energy had built up to a maximum, then any environmental variation such as a rise in temperature, or change in water, might be sufficient to initiate oviposition. Thus, due to the intricacy of the problem, all that can be concluded in the present study, is that breeding in both *Limnaea stagnalis* and *Planorbis planorbis* coincided with the relatively rapid increase in temperature, which occured during the spring and summer months. It seems relevant to observe that sunlight, proposed by Hunter (1961a) to be the stimulating factor of oviposition in *Ancylus fluviatilis*, a herbivorous animal, would be of no value as a proximate factor, stimulating oviposition in the breeding processes of *Limnaea stagnalis* and *Planorbis planorbis*, as neither species are obligatory herbivores. Furthermore sunshine data (Figure 3), substantiates this view, as no corelation is apparent. However, the data is not refined enough, and day to day observations on behaviour and prevailing conditions would be required, before any really valuable deductions could be made.

The results of bottom sampling at 10 stations along pond A (Figure 12), during the months of July and August, suggests that there were centres of breeding. Higher frequencies of young *Planorbis planorbis* were recorded at stations 4 and 6 and a fairly high number of the 1966 generation were also observed in the samples taken at stations 1,2,3 and 7. These centres of breeding, seem to coincide with the occurence of a thick layer of benthic plants, of the species Drepanocladus exannulatus, Lemna trisulca and Chara. However, at station 5, where there was a pure stand of Chara, the frequencies of both young and old were very low, suggesting that conditions here were too exposed, there being no emergent or floating vegetation. Thus it is suggested that eggs were laid, and therefore young concentrated, in centres were there was a thick mat of benthic plants, and where the sites were unexposed, either by being situated under dense stands of Potamogeton in deep water, or in the shallower water between rushes. As no quantitative data relating to actual oviposition is available, the evidence must remain circumstantial. It is interesting to note that egg capsules of Planorbis planorbis were found to be abundant in the rich benthic vegetation during July.

The data for Limnaea stagnalis are interesting in that the highest frequencies of small young animals, hatched during July 1966 and thereafter, were recorded in the bottom samples taken at station 1 (Figure 12). The egg data (Table 3) suggested that Potamogeton was the preferred oviposition site for this species, in this pond. As will have been observed, there was no Potamogeton present at station 1. Therefore, it must be assumed either that this reflects the presence of a small breeding centre at the outlet stream, station 1, where in the absence of Potamogeton, egg capsules are oviposited in the benthic vegetation, or alternatively that this represents dispersion, colonisation or carriage of young individuals from stations 2, 3 and 4, where it is considered that most of the breeding occured. Since eggs were recorded from the type of situation existing at station 1 (Table 3), it seems probable that the former interpretation is quite plausible. The very small representation of young Limnaea stagnalis in bottom samples, taken at stations 2, 3 and 4, where Potamogeton was abundant, is also explicable. If the percentage of young in the bottom samples, taken in four weeks of sampling at station 4, is calculated, it is found to be 25% and that for the pooled data of the three Potamogeton dense stations 2, 3 and 4, is found to be 16.7% and the percentage of young in all ten samples, taken over four weeks of sampling, is found to be 37.7%. When this is compared with the percentage of young 1966 hatched animals, in the August net sweep sample, which was 72.7%, a remarkable disparity is apparent. It was noted, during the egg count study, that large numbers of young newly hatched animals of this species were found adhering to the stems and leaves of the Potamogeton, possibly feeding on the algal epiphytes. It is therefore suggested that newly hatched members of the population remain high up in the water column, amongst the higher branches of the floating vegetation, and that the newly hatched animals taken in the bottom samples, are those which have either dropped or descended from the above vegetation. This zonation of the bulk of the young members of the Limnaea stagnalis population in the higher water layers, may either be due to feeding activity, or merely be a consequence of the situation of the breeding sites.

When similar calculations were made for Planorbis planorbis, for July and August, it was found that the net samples for these months contained 17.3% and 38.2% respectively, of the 1966 generation, whereas the bottom samples taken at station 4, for the same two months, contained 21.8 and 66.7% of the animals hatched in 1966. Thus, it is apparent that, at the deep water stations, the young newly hatched Planorbis planorbis predominate at the bottom of the water column, but it seems that they ascend the emergent and floating stems, to appear in the net samples taken further up the water column.

It appears that young Limnaea stagnalis was situated high up in the water column, whereas young Planorbis planorbis predominated at the bottom. These relationships were probably a consequence of their respective breeding positions in the system. One would expect that the results from the net sampling might reflect an increase in the proportion of Limnaea stagnalis in the sample, since this technique samples the higher water zones. This is, in fact, the case in Figures 9 and 10, where an increase in the proportion of Limnaea stagnalis in the sample is observed, and a decrease in the case of Planorbis planorbis.

Recruitment in Limnaea stagnalis is manifest by an increase in numbers (Figure 9), but in Planorbis planorbis the increase in numbers between July and August, after breeding has taken place, is so slight, that it suggests that little breeding takes place in the surface layers of water, at that station. The fact that the mean size curve for Planorbis planorbis (Figure 10) continues to decrease during August, suggests that colonisation of the higher water zones by newly hatched, small sized animals is still proceeding. This is, furthermore, reflected by a small increase in numbers (Figure 10) and by the return of the curve showing the proportion of Planorbis planorbis in the samples to its former level.

Thus, it is suggested that during the breeding season, the distribution of the two species differs, due to the difference in their breeding sites. This difference in distribution possibly disappears when the newly hatched individuals disperse from the breeding centres and invade the rest of the system. Qualitative observations support a more uniform distribution of adult forms. Nevertheless, it may be that oviposition is fairly general throughout the habitat and that the results in Figure 12 merely reflect the degree of success in hatching and development, at the different stations, due to variations in conditions.

According to Germain (1931), the egg capsules of Limnaea stagnalis contain 40 - 100 eggs, but sometimes as many as 140. However, Bondesen (in Berrie, 1965) states that there are on average 100 eggs per capsule, with a maximum of up to 150, whereas Schodduyn (in Berrie, 1965) gives an average of 35 eggs per capsule. Berrie (1965) found 35 eggs per capsule, whereas in the present study 2 - 80 eggs per capsule were noted, (Table 3). It was found that the number of eggs per capsule could be corelated with the mean size of the breeding individuals. Thus the breeding animals of the pond A population, which never exceeded 35 mm. in height, laid egg capsules containing not more than 34 eggs per capsule, whereas those of the larger pond H animals, which were more than 38 mm. in height, laid egg capsules containing up to 80 eggs per capsule, and on the average had twice as many eggs per capsule as those laid by the pond A animals. It seems, therefore, that clutch size can be related to the size of the breeding adults in the population; the larger the animal the larger the clutch size. In his study of Physa fontinalis, Duncan (1959) found that brood size decreased at each successive laying. On the other hand, Berrie (1965) states that certain authors have noted that the first capsules, layed by individual snails, were smaller than those produced later. Thus these results, from ponds A and H, may not be strictly comparable.

Berrie found the average number of eggs per capsule to be 35.0 with a maximum of 55. He concluded that the reason for the clutch size being smaller in the Bellshill population, than that observed by other workers elsewhere, was because of the marginal nature of the habitat which caused the population to be composed of small sized individuals. However, evidence from the present study suggests that there can be large differences in clutch size, even between two adjacent water bodies. Pond H has a calcium concentration of about 13 mg./1. which would be considered marginal, according to Boycott (1936), whereas pond A has a calcium concentration of 45-55 mg./1. Thus one would expect the conditions, prevailing in pond A, to be more conducive to the growth and reproduction of Limnaea stagnalis, than those existing in pond H. Therefore, it is suggested that in pond H, a considerable loss of individuals maintained the population density at a low level, but sufficiency of food, in this pond, allowed the residual population to reach larger dimensions and, in consequence, lay a greater number of eggs per capsule. Thus with high losses, the residual population is able to make amends, but if the clutch size was not plastic in this way, extinction of the population might be imminent. In pond A, it is suggested that losses are not as great, therefore more individuals are present, but due to the limitations set by a factor such as food supply, the animals do not attain such large dimensions, and this is reflected in the smaller clutch size.

Other data, presented in Table 3, suggest that Limnaea stagnalis prefers Potamogeton to other species of plants, for its oviposition sites, but where this plant is in short supply, as in pond H, the species first utilises existing sites to the full, but resorts to other plants when the favourite sites are all taken up.

Comparing the two species, it appears that in Limnaea stagnalis, with its probable biennial life cycle and high egg laying capacity which can extend throughout the late spring and summer, recruitment is on a large scale, whereas in Planorbis planorbis, there is a limited breeding period; a smaller egg laying potential, with only 8-20 eggs per capsule (Germain, 1931) and only an annual life cycle. As the proportion of Limnaea stagnalis in the total snail population of pond A is small, when compared with the Planorbis planorbis population, it can be concluded that Limnaea stagnalis in the present study, experiences much greater losses than that experienced by Planorbis planorbis.

Summary

1. A comparative study of two species of freshwater pulmonate snails. *Limnaea stagnalis* and *Planorbis planorbis* was made at a system of ponds near Durham City, during a period of nine months, between November 1965 and August 1966. Bottom tray sampling, in conjunction with net sampling, was suggested as the best means of assessing the population structure.
2. Population data and physico-chemical factors were examined.
3. The snail population of the three ponds studied differed markedly, but no obvious factors responsible for these differences in distribution were discovered.
4. It was suggested that *Limnaea stagnalis* had a biennial life cycle in contrast to *Planorbis planorbis* which had an annual life cycle. Differences in the growth rates between the two species were observed during the winter period, and it was suggested that the growth rates of *Limnaea stagnalis* were influecned by weather conditions, whereas those of *Planorbis planorbis* were thought to be related to the length of the life cycle.
5. The choice of different oviposition sites, *Limnaea stagnalis* preferring the leaves of *Potamogeton*, and *Planorbis planorbis* preferring benthic plants, conferred a difference in the vertical distribution of the young animals; *Limnaea stagnalis* predominating in the surface waters and *Planorbis planorbis* in the benthos.

Summary (continued)

6. Amount of egg production was found to vary considerably from pond to pond, and this was corelated with the size of the breeding adults in the populations. It was suggested that such plasticity allows a species to inhabit a wider range of aquatic habitats.

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References.

Berrie, A.D., 1965. On the life cycle of Limnaea stagnalis (L.) in the West of Scotland. Proc. Malac. Soc. Lond. 36. 283-295.

Boycott, A.E., 1936. The habitats of freshwater Mollusca in Britain. J. Anim. Ecol. 5. 116-186.

Cheng, K.L., Melsted, S.N. and Bray, R.H., 1953. Removing interfering metals in the versenate determination of calcium and magnesium. Soil Sci. 75. 37-40.

Duncan, C.J., 1959. The life cycle and ecology of the freshwater snail Physa fontinalis (L.). J. Anim. Ecol. 28. 97-117.

Ellis, A.E., 1926. British Snails, Oxford.

Ellis, A.E., 1951. Census of the distribution of British non-marine Mollusca. J. Conch. 23, 171-244.

Forbes, E. and Hanley, S. 1853. A history of the British Mollusca and their shells. London.

Garnett, P.A. and Hunt, R.H., 1965. Two techniques for sampling freshwater habitats, Hydrobiol. 26, 114-120.

Germain, L. 1931. Mollusques terrestres et fluviatiles. Faune de France 21. Paris.

Hunter, W. Russell, 1953. On the growth of the freshwater limpet, Ancylus fluviatilis Muller. Proc. zool. Soc. Lond. 123, 623-636.

Hunter, W. Russell, 1957. Studies on freshwater snails at Loch Lomond. Glas. Univ. Publ., Stud. Loch Lomond 1, 56-95.

Hunter, W. Russell, 1961a. Annual variations in growth and density in natural populations of freshwater snails in the West of Scotland. Proc. zool. Soc. Lond. 136, 219-253.

Hunter, W. Russell, 1961b. Life cycles of four freshwater snails in limited populations in Loch Lomond, with a discussion of infraspecific variation. Proc. zool. Soc. Lond. 137, 135-171.

Janus, H., 1965. The young specialist looks at land and freshwater molluscs. London.

Jeffreys, J.G., 1862. British Conchology. London.

Lack, D., 1955. The natural regulation of animal numbers. Oxford.

Macan, T.T., 1965. Self-controls on populationssize. New Scientist. 801-803.

Maling, D.H., 1955. The Geomorphology of the Wear Valley. Ph.D. Thesis. Durham.

Mortimer, C.H., 1941. The exchange of dissolved substances between mud and waters in lakes. J. Ecol. 29, 280-329.

Rimmer, R., 1907. Land and freshwater shells of the British Isles. Edinburgh.

Step, E., 1945. Shell Life. London.

Timmermans, L.P.M., 1959. Stimulation of oviposition in some land and freshwater snails. Proc. ned.Akad.Wet.Amst. 62C, 363-372.

Wynne-Edwards, V.C., 1962. Animal dispersal in relation to social behaviour. Oliver and Boyd.