A study on the bioenergetics of a fresh water gastropod, planorbis planorbis l., in a small pond

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A study on the bioenergetics of a fresh water gastropod, Planorbis planorbis L. , in a small pond.

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CONTENTS

INTRODUCTION

The application of thermodynamic principles in ecology is of fairly recent origin. Lindemann (1942) provided a framework for the concepts of trophic levels and their interactions, that stimulated much further work. If an ecological unit is considered as a closed system, then the laws of thermodynamics can be applied to it, and the total amount of energy leaving the system must be equivalent to the total amount entering it. Then all matter and changes in matter, within the system, can be considered in terms of potential energy content and kinetic energy flow and so one has a generalised way of describing processes within the unit, which may also be compared with other units.

Within an ecosystem, the paths of energy flow depend on the species composition. The role that any one species population plays in any one path, depends on its' numbers, rate of growth, life span and respiratory and faecal output. The following equation expresses the energy flow through a species population:

$$C = A + F$$

where C = food consumed, A = food assimilated and F = faecal production; all expressed in terms of energy content.

The food assimilated represents the energy that is metabolized by the species population and its' fate is shown by the following equation:

$$A = R + P$$

where R = the energy content of respiratory loss due to total metabolism and P = the increase in potential energy in the form of growth and reproduction.

In order to assess the role of a species population, the study ideally should be made over a whole year and take into account the whole life span of the species (Phillipson, 1966). Apart from a direct role in promoting energy flow, a population may play an important part in an ecosystem indirectly: as a by-product of its' activity, matter may be transformed into a state where its' energy is made more readily available to other species populations e.g. faecal material.

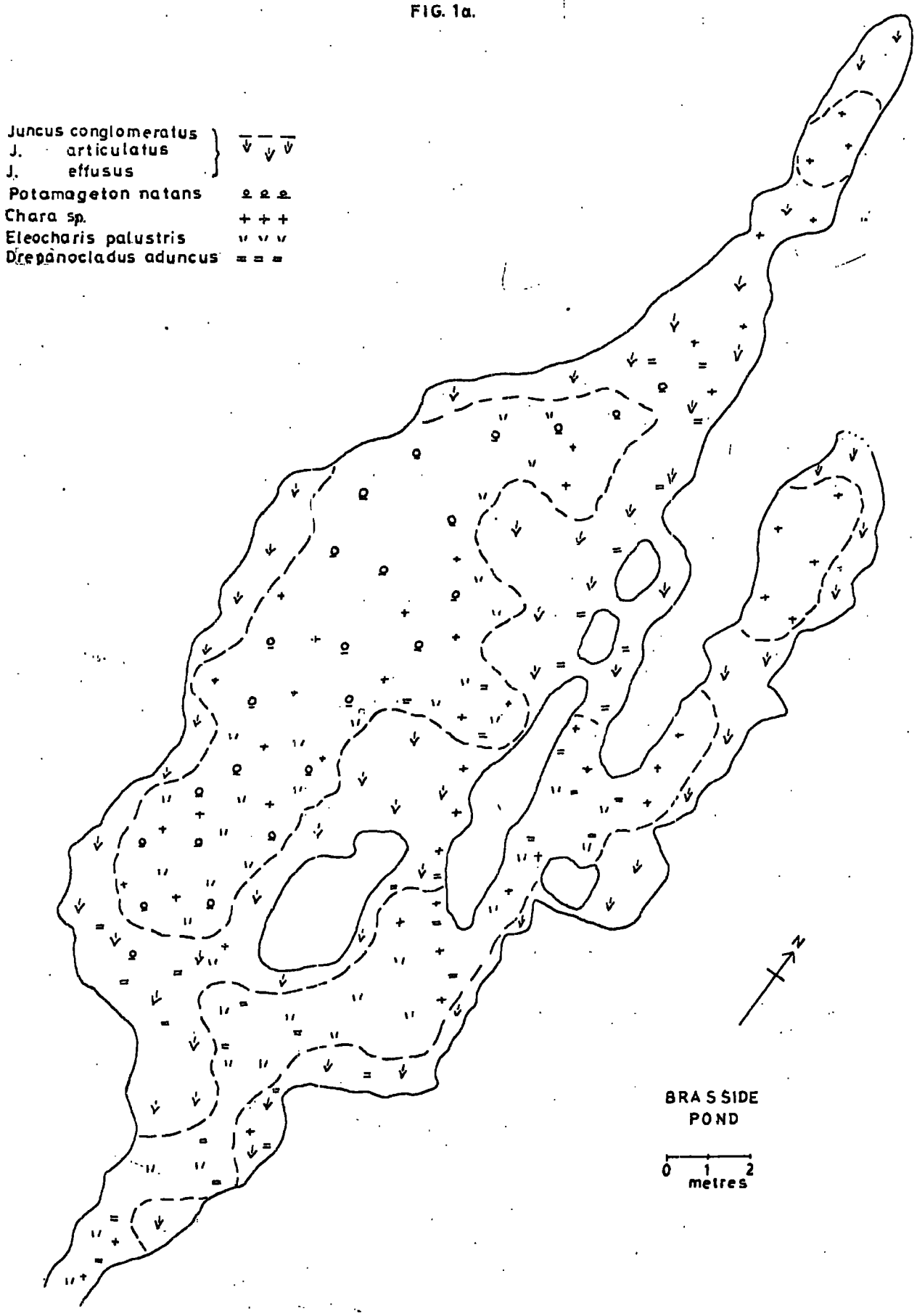
No study of the ecological energetics of a fresh water mollusc has, to the author's knowledge, been reported in the literature to date; although Paine, (1965) has given an excellent account of such a study in the marine mollusc Navanax inermis (Cooper) and Smalley, (1959) made a study of Littorina irrorata, a saltmarsh dweller.

The present work is an attempt to assess the contribution of a population of Planorbis (Tropodiscus) planorbis (L.) (Macan, 1960) to the energy flow in a small pond near Durham City. The work was carried out between December 1966 and July 1967.

Study Area.

The study area, (Pond A in Morphy, 1966) is one of a series of water bodies known as Brasside Ponds, which are situated approximately 3 kms. ($2\frac{1}{2}$ miles) north east of Durham City, (map reference NZ 45/290452). They lie at 70 metres (200 ft O.D.) in a depression approximately 0.8 hectares (2 acres) in extent, which is an old brick workings abandoned in the 1930's. The workings are in laminated clays. Morphy, (1966) noted that Pond A carried a high population of Pl. planorbis, whereas six of the remaining eight ponds contained no individuals of this species.

FIG. 1a.


Juncus conglomeratus
J. articulatus
J. effusus
Potamageton natans
Chara sp.
Eleocharis palustris
Drepanocladus aduncus
BRASSIDE POND
0 1 2
metres

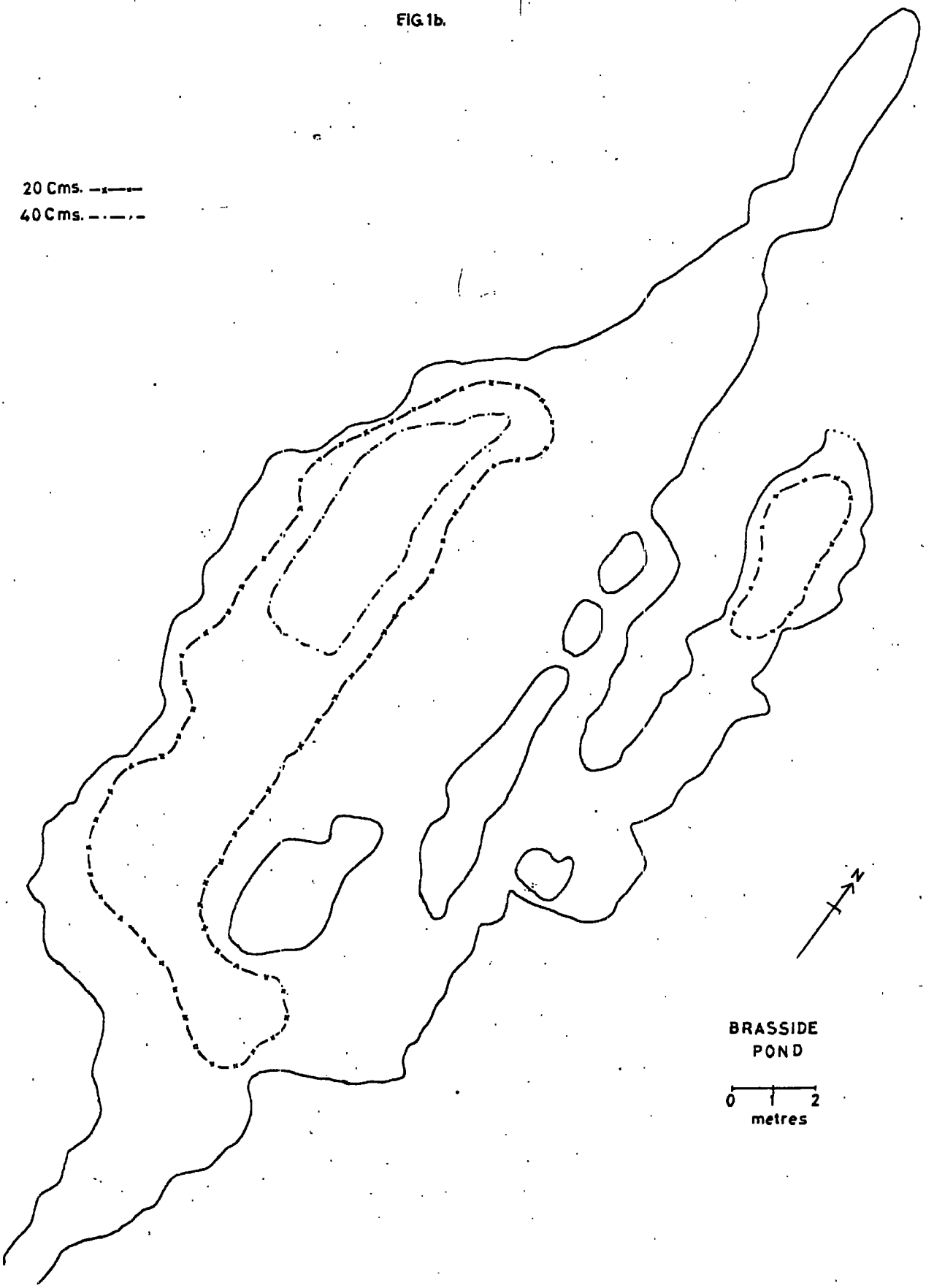
Pond A is the most north easterly of the group and is the largest in surface area. It lies in an isolated depression, within the main depression, which has no inflow except for seepage and rainfall. The southerly part of the depression is marshy and has small sheets of water and one fairly well defined channel that connects with the main part of the pond, which lies at the north end. The channel dries to pools in drought and though Pl. planorbis occurs in it, it was decided to arbitrarily confine the study to the main part of the pond as delimitated in figure 1., because of the difficulty of sampling and estimating the size of a widely fluctuating body of water. This main part of the pond shall be referred to as the study area herein after. The study area has an outflow from the north easterly arm, that connects with the main drainage system for the area. It only runs after very heavy rain. To this extent, the population of snails studied, is not strictly isolated.

The study area has a total surface area of 220 square metres, the bottom of the pond is rough, irregular and of bare clay, where it is not vegetated. The contours for 20 cm. and 40 cm. depths are shown in figure 1.b. The maximum depth recorded was 65 cms.

The principal vegetation was distributed as shown in figure 1.a.

Juncus conglomeratus L.
Juncus effusus L.
Juncus articulatus L.
Potamogeton natans L.
Eleocharis palustris (L.) Roem. Schult.
Drepanocladus aduncus (Hedw.) Warnst.

FIG. 1b.



Chara sp.

In addition, there were the following species :

Lemna trisulca L.

Myosotis sp. (L.)

Epilobium parveflorum. Schreb.

Equisetum sp. L.

Marchantia polymorpha L.

Lemna was common among the Juncus spp. and anywhere where it was sheltered. Myosotis, Epilobium and Equisetum grew up in the spring in the shallow marginal waters and Marchantia occurred in the north westerly arm of the study area. Potamogeton and Eleocharis grew up in April and transformed the open part of the study area into a vegetated one. This would presumably cut down the effect of wind on the study area.

Planorbis planorbis L.

Planorbis (Tropodiscus) planorbis (L.) (Macan 1960) belongs to the family Planorbidae, which is in the suborder Basommato phora, order Pulmonata. Pl.planorbis has a shell coiled in one plane. Its' shape is plane on the underside and convex on the upperside with a sunken columella. There are five whorls, each partially enclosing the preceding one, with a reduced keel on the lower margin. In the smaller individuals, the shell is smooth and semi translucent brown; in the larger ones, it is opaque brown, rougher and thicker. The species is said to have a 18 mm. maximum breadth (Macan,1960) but specimens larger than 13 mm. were never found in the study area. Pl.planorbis is hermaphrodite and both self - and cross - fertilisation have been recorded (Bondesen, 1950). It has a vascularised mantle cavity for gaseous exchange and haemoglobin in its' blood. It browses

on algal epiphytes with a radula and there are no records of it having preferred macrophytes to browse over, or of it consuming macrophytes in the field (Boycott, 1936). Janus (1965) noted that it preferred areas of vegetation and calm waters. It produces mucus for locomotion, but, as it is in water, this is probably a smaller production, than in terrestrial snails.

Methods.

Because of the limited time available for study, it was decided to concentrate on:

a) The total population at monthly intervals.
b) The size distribution at monthly intervals.
c) Bodily growth over the period of study.
d) Bomb calorimetry.
e) Oxygen consumption of different size classes at different seasons.
f) Pond temperature measurements.

it was hoped to use the above data to quantify the equation:

Assimilation = Respiration + Production.

for the population of Pl.planorbis in the study area as follows: the monthly samples give an estimate of the total population at monthly intervals and thereby permit estimates of natality and mortality within the population. Size class distribution within the population as shown by the monthly samples would allow production in terms of bodily growth to be calculated and bomb calorimetry can be used to convert the biomass data to energy units. The measurement of oxygen consumption at different seasons and for different size classes can be used to estimate population respiratory metabolism over

the period of study and the pond temperature data relates this to conditions in the field. Using an oxycalorific value, the respiratory loss can be expressed as energy units. The sum of production and respiration should equal the assimilation of the population.

a. Estimate of total population.

The total snail population of any area has never been estimated (Hairston et al., 1958). Snails present a problem to sampling, because of their vertical distribution; they may be in the surface layer of the mud, clinging to the vegetation at any level in the water column or in the surface film. The methods used in sampling fall into three broad categories. First, quadrat methods such as the ring samples, where the snails within a quadrat are counted directly. Hunter (1953) used a similar principle by sampling a unit surface area of rock. Pesignon et al (1958) considered this only practicable and reasonably accurate in less than 5 cms. depth of water and for snails larger than 2.5 mm. It is certainly not practicable for thick vegetation. Second, there is a variety of grabs and samplers, such as the Ekman grab and tube sampler (Garnett and Hunt, 1965) which sample both mud and vegetation; the latter, theoretically, includes the whole water column, though I would have thought the diameter was so small that the disturbance caused by lowering it would nullify this advantage. Third, there are net methods for comparative results, where either a constant surface area or constant volume is sampled with a pond net. Duncan (1959) used this on Physa fontinalis (L.). The first two categories satisfy the conditions necessary for attempting to make a total population estimate, but the first is inapplicable and it was decided that the second would be too destructive to the vegetation

in such a small pond and would alter the ecosystem so much as to make the study meaningless.

In this study, sweeping by means of a pond net over a constant surface area was the method of sampling used. In December, the study area was divided into two subsections; one, the open subsection, was more than 20 cm. deep and there was little vegetation except for a Chara mat and a little Potamogeton and the other, the closed subsection, which was less than 20 cm. deep and had Juncus spp. and, or quantities of benthic vegetation. The study area was divided into $4m.^2$ areas and the sampling sites were chosen using a list of random number for each of the two subsections i.e. a form of stratified random sampling. The sampling was done using a fine pond net 0.33 m. wide. This was passed six times across a metre of bottom, so that there were three sweeps in either direction and the first and last sweep passed through the water column, if it were deeper than the net. This only applied in the open subsection. The samples usually contained mud, some benthic vegetation and Lemna, if present. The speed of sweep was kept as constant as possible. The sample collected was emptied into an enamel dish and the net washed into it, before the sample was taken back to the laboratory. There the snails were sorted, first by going through the vegetation and then by flooding the sample in a shallow dish, when the snails came to the surface. This gave complete extraction, as far as could be assessed, until July when very small snails were present. The snails were measured to the nearest 0.25 mm. across their maximum breadth, using mm. graph paper. In any one month, all the snails were measured as it was found that size class distribution varied markedly in different samples, which made taking only a subsample for measuring to obtain the size class distribution less reliable. The snails and vegetation were returned to the sampling areas the following day. The depth of water and

vegetation for each sampling site was noted. This was repeated at monthly intervals between January and July.

During January, February and March, the above procedure was slightly modified as an attempt was made to get a total estimate of numbers per sampling area so that the comparative results from the samples could be used for estimating total population. In December, a sample of snails was marked and released in a known area. A week later, a series of samples were taken at known distances from the point of release. This showed that the snails had not moved more than 1 m. in the time interval. Further it was found that cellulose paint adhered satisfactorily to the shell, if this was first cleaned of epiphytes and dried. The preliminary experiments in the laboratory to show this, were later confirmed in the field, where, after a month marked individuals could still be captured. A more quantitative evaluation was possible in growth cultures in the field, where few individuals lost their marks.

In January, sampling was done as described above and all the snails collected were marked and scattered randomly in the actual areas from which they were collected. Three days later, they were resampled and the numbers of marked to unmarked individuals found for each area. This simple mark and recapture was repeated in February but, as recapture percentages were so poor, it was decided to make a prolonged mark and recapture study in March, so that a Jackson (Andrewartha, 1961) negative and positive analyses could be done on the results. The procedure was the same except that marking was done on three days and recapturing done on three days and different marks were used on each day, so that the date of marking of recaptured individuals on successive days was known. The results from this were no more satisfactory than before, so it was decided to abandon mark and recapture and increase the number of samples per month.

b. The size distribution at monthly intervals.

The size distribution for each month was found from the data collected above.

c. Bodily growth over the period of study.

Bodily growth estimates for the population were found from the above data. Also an attempt was made to measure the bodily growth of individuals experimentally in the field. A representative sample of the size classes present in January were measured, marked individually and placed in the pond in galvanised mesh containers covered in muslin. These were immersed so that an air space was left and a selection of vegetation included. About fifteen snails were put in each container, which was 25 x 25 x 15 cm. Thus the snails were experiencing similar conditions to those snails free in the study area. The cultures were examined at fortnightly intervals, the snails measured and any dead ones replaced.

In June, when egg masses were found, some were collected and kept in petri dishes in the laboratory with some vegetation at about 19^{o}C. The size at hatching and the growth for the next six weeks were measured. These snails were supplemented in numbers by newly hatched ones found in the study area, which were similarily kept in the laboratory. Bodily growth was eventually expressed in terms of energy units using the conversions that were found as outlined in the next section.

d. Bomb calorimetry and size-weight conversion.

The individuals used for size-weight conversion determinations were also used in determining the calorific value of snail tissue and were treated as follows. A winter estimation was made in February and March, when snails were collected,

measured, the excess moisture removed and then weighed to the nearest 0.01 mg. on a Mettler balance. Following weighing, they were killed in boiling water, removed from their shells and dried in weighed metal foil for 48 hours at 60°C and weighed again to get dry weight. The unbroken shells were also dried and weighed, but some of them had to be broken to remove the tissues. The above procedure was repeated in June and July for a summer estimation, except no shell weights were obtained. The dried material was stored in a desiccator till July, when the calorific values were determined.

The calorific value was determined using a micro bomb (Phillipson, 1964). The dried material in the different size classes, for both summer and winter, were ground to a fine powder and compressed into pellets, weighing between 3 and 18 mg. These were stored in a vacuum oven at 60°C till just before they were combusted, when they were transferred to a desiccator to cool to room temperature. First the bomb was calibrated using benzoic acid pellets of known calorific value. The procedure for this and for the actual material was the same and was as follows: a platinum pan was weighed to the nearest 0.0001 mg., a pellet was placed on it and it was rapidly reweighed, as tissue pellets take up moisture as soon as they are exposed to the atmosphere. The pan was then inserted in a cup in the head of the bomb and a platinum wire attached across two terminals to complete the firing circuit . The wire was bent to make good contact with the pellet and hold it in place. The head of the bomb was screwed into the base and the value on the head opened. The bomb was then filled with oxygen to 30 atmosphere pressure, the valve closed and the bomb tested for leaks in water. It was then placed within a copper ring, which lies in close contact with the thermocouples which record the temperature of the bomb. The contact in the base of the bomb now was in connection with a mercury contact below and this completed the

firing circuit. when a second contact was clipped to the terminal on top of the bomb. The bomb was heated by hand till a temperature gradient was recorded by the recording potentiometer. Then the bomb was enclosed by an insulated cover to prevent draughts affecting it and the mains switched on. The firing circuit was charged for 10-15 seconds before the recording potentiometer started to reverse, so that one could ignite the pellet just before it did reverse and when there was no heat being gained or lost from the bomb. The deflection in microvolts on the recording potentiometer was noted. Eight determinations were made on the benzoic acid to calibrate the bomb and, if possible, three determinations were made for each mm. size class in both winter and summer. No determination was made of ash content of the material.

e. Oxygen consumption.

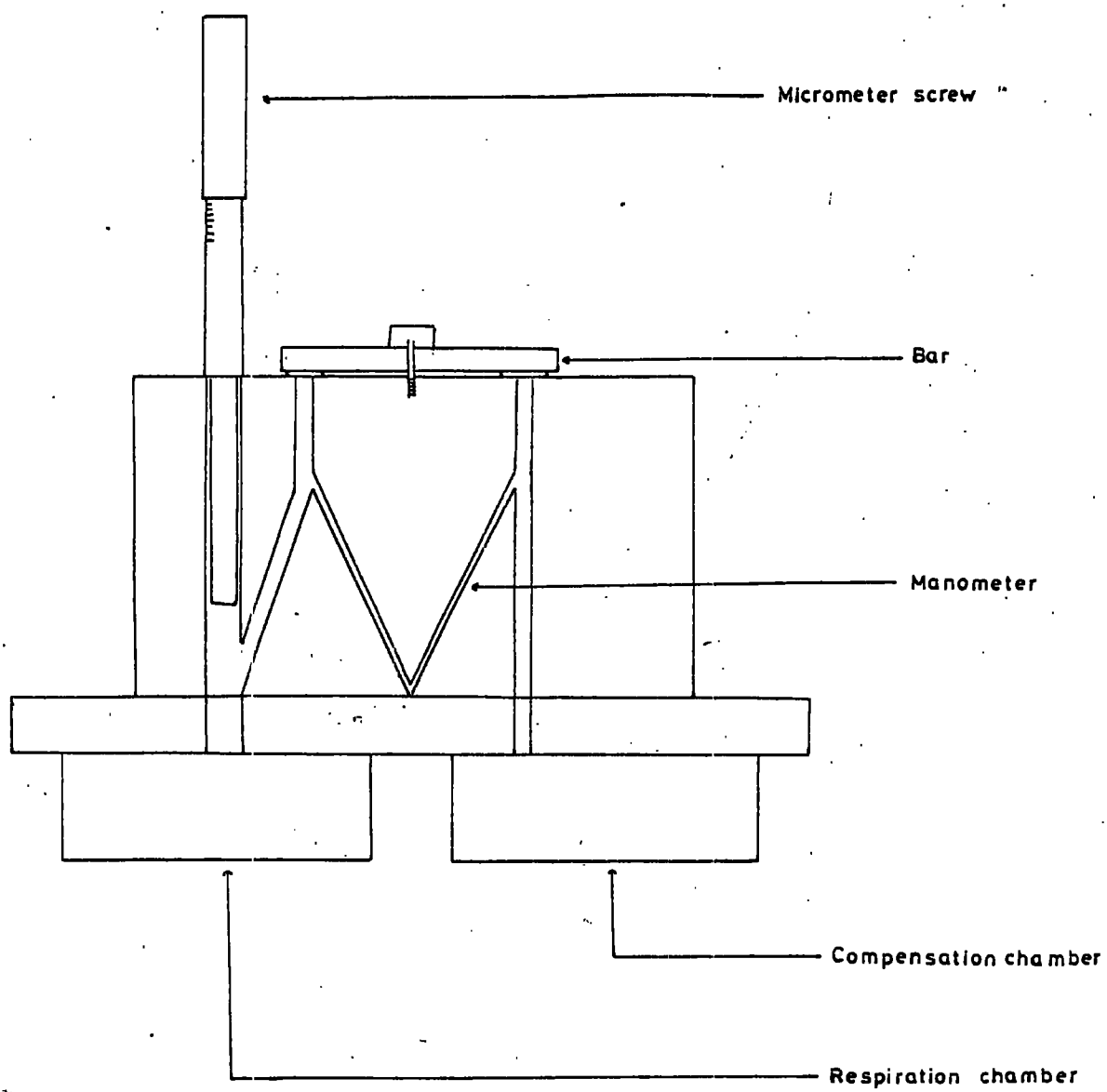
Pl. planorbis is a pulmonate and so uses a vascularised mantle cavity for gaseous exchange. Sometimes, in small individuals, the mantle cavity is filled with water but usually it contains a bubble of air. In warm weather, it is noticeable that the snails frequently come to the surface to renew the air and this applies particularly to larger individuals. Thus Pl. planorbis presents a problem in measuring its' oxygen consumption as one has to consider it either as an air breather entirely or as a water respirer. Berg (1959) used a polarographic method to determine oxygen consumption and so forced the pulmonates to have water-filled mantle cavities. In the present study, the choice lay between the Winkler method, which would give similar conditions for the snails as in Berg's work, or using a constant pressure apparatus in which oxygen consumption is measured in a saturated atmosphere. This

method was used by Spenser Davies (1966) on Patella spp., also molluscs, with consistent results, so it was decided to try this method on Pl.planorbis, the assumption being that a saturated atmosphere would be equivalent to the conditions in a bubble of air inside a mantle cavity.

The Spenser Davies' constant pressure respirometer is shown in figure 3. It is made of perspex. Two chambers of 150 ml., one the respiration chamber and the other the compensation chamber, are screwed into a base and connected to each other by a manometer. The manometer, also, connects at either end with the top of the apparatus. These external openings can be closed simultaneously by screwing down the bar with rubber pads. The respiration chamber has a second connection with the top of the apparatus, which contains a rod of known diameter, that can be moved up and down by a micrometer screw. This alters the volume of the respiration chamber, and the distance through which it moves is measured and the conversion factor from distance to volume is known. The manometer fluid is paraffin stained with Sudan III.

The apparatus was set up as follows: two containers with equal quantities of soda lime were placed one in each of the chambers to absorb carbon dioxide. In winter, five to eight snails and in summer two to four snails depending on size were dried of excess moisture and placed in the respiration chamber. Each lot of snails were approximately the same size. Then, six drops of hot water were placed in each of the two chambers to ensure a saturated atmosphere. Care had to be taken to ensure the water did not come into immediate contact with the snails. The apparatus was then assembled and placed in a water bath, so the chambers were completely covered. The temperature of the water bath was recorded at every reading.

FIG 3


Micrometer screw
Bar
Manometer
Compensation chamber
Respiration chamber

The apparatus was left open for the first two hours, so that the chambers could equilibrate with the temperature of the water bath and the snails could settle down after handling. Then the chambers were closed. During the next two hours readings were taken frequently and the manometer levels adjusted when necessary. This period was necessary as immediately after closing the apparatus there often were anomalous changes in volume in the respiration chamber. After this initial two hour period, readings were taken at about twelve hour intervals for the next forty eight hours in order to obtain a mean oxygen consumption for twenty four hours. At the end of the experiment, the snails were measured and weighed for total and dry weight as outlined above. The dry weight was not found for the winter results. The snails for respiration were collected from the study area and either used directly or stored in dishes in an incubator at the temperature at which the oxygen consumption was to be measured. As there was no constant temperature bath available, tap water was used and the temperature during each experiment noted. This gave respiration results in the three sets of results for February, May and July that were over a small temperature range. In addition to the above results, two experiments were carried out using a micro-Winkler method as a check on the results obtained with the constant pressure apparatus.

f. Pond temperature measurements.

A temperature integrator described by Berthet (1960) was used in this study. The mean temperature in the study area was measured at monthly intervals from December till June and fortnightly in June and July. The change in interval was necessitated by the mode of action of the integrator. The method depends on the fact

that, at constant pH. , the rate of inversion of a sucrose solution is proportional to temperature. In fact the relationship is not exactly direct but Berthet considers that, as this applies to all chemical processes, the mean obtained, which is slightly higher than the true mean, is of greater ecological application.

The sucrose solution is made up with buffer, so it has a pH. of approximately 1.21. This solution, with a little formaldehyde to sterilise the solution and to prevent bacterial and fungal interference, was put in 10 cc. tubes with tightly fitting polythene tops. These were further sealed with vaseline. The tubes were immediately put in a freezing mixture in a vacuum flask to stop inversion, and taken to the field. Two tubes were placed just below the surface, one in the vegetation and one in the open, and two tubes at 25 cm depth, in the study area. The remaining tubes were taken back to the laboratory and two placed in a 15^{o}C and two in a 5^{o}C. constant temperature rooms and two determinations were made of the initial degree of rotation using a polarimeter. After either a month or a fortnight (see above) the tubes in the field were replaced at the same time of day, and taken back to the laboratory in the freezing mixture. The degree of rotation in the field tubes and the constant temperature tubes was determined. From the constant temperature results, the constant for pH. 1.21 in the equation was recalculated for the actual solution's pH. and with this, the integrated mean temperature in the study area over the period could be calculated using Berthet's equations.

Results.

a. Estimate of total population.

FIG.5.

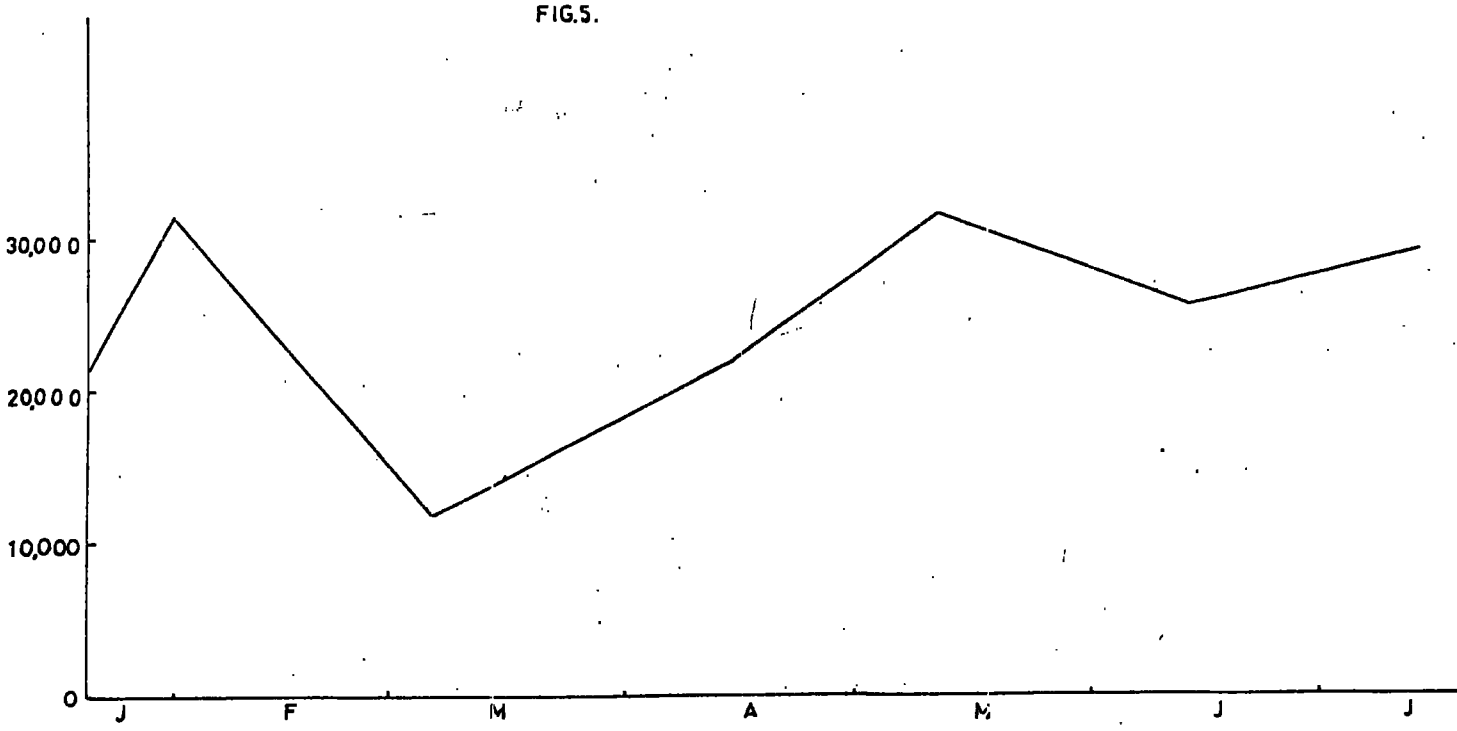


FIG.4.

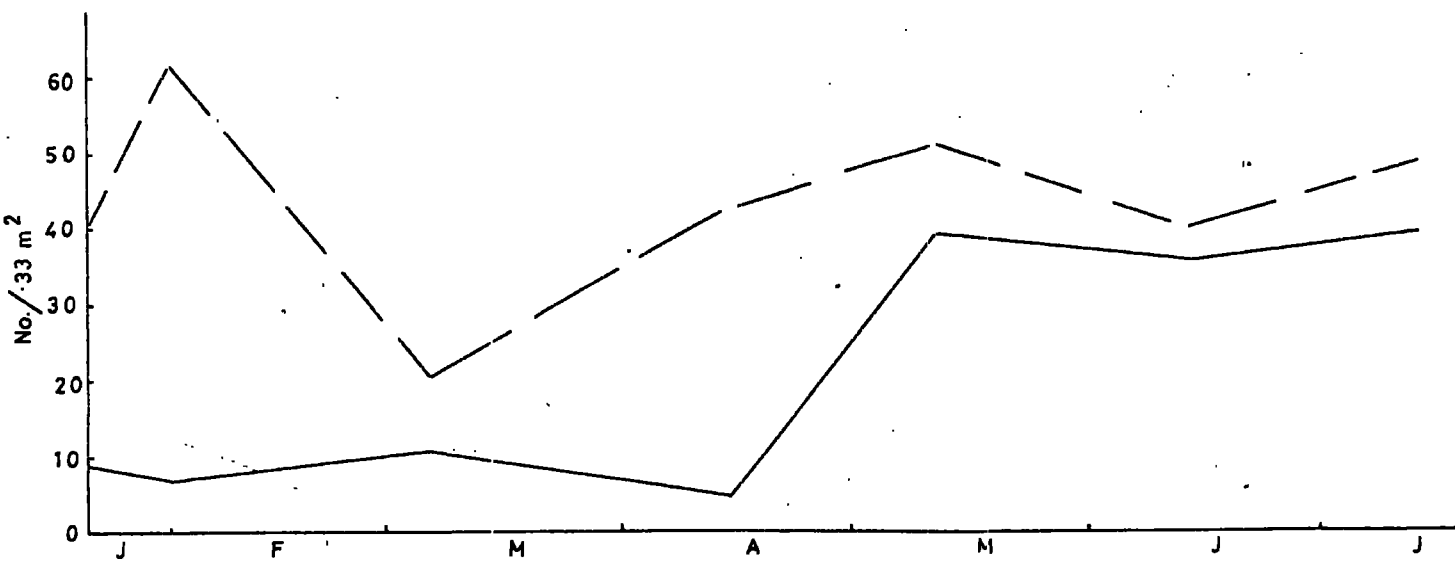


Table 1. gives the results obtained by net sweep sampling.

Table 1.

Date	Subsection	No. of samples.	Mean no./0.33m^2	Mean no./ m^2
Jan.20th	Open	2	9	27.0
	Closed	6	40.5 ± 20.6 S.D.	121.5
Jan.31st	Open	4	6.75 ± 42 "	19.3
	Closed	8	61.1 ± 21.1 "	183.3
March.6th	Open	2	10.5	31.5
	Closed	10	20.2 ± 10.2 "	60.6
April.14th	Open	6	4.5 ± 3.5 "	13.5
	Closed	14	42.5 ± 30.7 "	127.5
May.11th	Open	6	39 ± 21.7 "	117.0
	Closed	14	51 ± 18.4 "	153.0
June.13th	Open	8	35.4 ± 17.4 "	106.0
	Closed	18	40 ± 23.4 "	120.0
July.13th	Open	8	39 ± 25.6 "	117.0
	Closed	12	48.7 ± 18.4 "	146.1

Figure 4 shows the mean number /0.33 m^2 / month plotted for each of the two subsections over the period of study. Note the consistently low numbers in the open subsection until April after which month they attained a similar level to those in the vegetated areas. This rise in numbers was concurrent with the growth of Potamogeton and Eleocharis in the open area. The numbers in the closed subsection were between four and six times those in the open except in March, when an exceptionally low number was obtained. An increase in number of samples per month did not markedly decrease the standard deviations.

Table 2. The calculated total population of Pl.planorbis in the study area, by sweeping with a pond net.

Table 2.

Date	Estimated no.in Open, 55 m^2.	Estimated no.in Closed, 165 m^2.	Estimated total no.in Study Area.
Jan.20th	1,485	20,048	21,533
Jan.31st	1,059 ± 693 S.D.	30,245 ± 10,445 S.D	31,304 ± 11,138 S.D
March.6th	1,733 ± 83 "	9,999 ± 5,024 "	11,732 ± 5,107 "
April.14th	743 ± 578 "	21,038 ± 15,197 "	21,781 ± 15,774 "
May.11th	6,435 ± 3,581 "	25,245 ± 9,108 "	31,680 ± 12,689 "
June.13th	5,841 ± 2,871 "	19,800 ± 11,583 "	25,641 ± 14,454 "
July.13th	6,435 ± 4,213 "	24,107 ± 9,108 "	30,542 ± 13,321 "
July.13th	Corrected for 3.9% recruitment		29,351 ± 12,802 "
July.13th	Recruitment in July		1,191

The recruitment percentage in July is probably too low as the sorting method was not reliable for snails in the smallest size classes. For this reason, the July estimate was corrected, so that the 1967 generation did not occur in the population estimates. Figure 5 shows, in graphic form, the above results using the corrected July number. There is no consistent decline apparent in the estimated total populations, despite the fact that mortality must have occurred between February and July. As recruitment did not occur until July, and has been corrected for in that month, the result for February, which was similar to those obtained for May to July, must be a lower proportion of the true population than for these months, because of mortality. For this reason, the mean of the last three months was taken as an estimated mean total population for the summer. This

estimated mean total population, which is 28,747 ± 13,315, does not represent the accurate number present in the study area but, at best it represents a number fairly close to the true population for this time and at worst is a gross underestimation.

Mark and recapture.

Table 3. The results obtained from simple mark and recapture in January and February.

Table 3.

Month	No. recaptured : no. marked		No. /m^2 estimated
	Open	Closed	
January	0:3	3:19	817
	0:5	1:13	1,861
		1:3	603
		1:14	2,394
February	0:13	6:35	210
	0:8	3:34	984
	0:2	2:75	4,275
	0:4	3:56	2,240
		2:66	1,485
		20:44	403
		11:84	756

There was a thin film of ice in the February recapture which could have been responsible for consistently low numbers collected in each sampling area. The proportion of marked animals recaptured in the majority of cases was too small to put much weight on the no./m^2 calculated. Where recaptures were more than 10% of those marked, the

mean no. /m^2 calculated is 558 snails while in those were the recaptures were less than 10% the mean no./m^2 is 2,206. Using the former figure a total population estimate of 92,070 is obtained, if one ignores the open area. However, as only five out of twenty areas sampled meet the 10% recapture requirement the above calculation cannot be taken as a reliable total population estimate for January and February.

Table 4, shows the mark and recapture data for the March experiment.

In this series, the percentages of marked animals recaptured were, on the whole, even poorer. Areas 3 and 4 and 7 and 8 (see table) were very similar pairs in depth and vegetation and were quite close together so, as these had the best recapture figures, the pairs were combined and Jackson's calculations, as in Andrewartha (1961), were done on the data.

Table 5. The estimates of total population per m^2. using Jackson's positive and negative calculations.

Table 5.

Area	Jackson's Positive	Jackson's Negative
3, 4	4,098/m^2.	1,001/m^2.
7, 8	2,183/m^2.	711/m^2.

Jackson's positive calculation allows a correction for natality or immigration into the area during the period of sampling, while Jackson's negative calculation allows for mortality or emigration from the area. As no natality was occurring and as mortality could be considered negligible over the twelve day period of sampling,

Table 4.

Section.	No. sampled / sampling occasion.				No. marked / sampling occasion.			No. recaptured / Sampling occasion and occasion of marking.					
	1st	2nd	3rd	4th	1st	2nd	3rd	1st	1 - 2		1	2	3
Open													
1	10	9	3	5	10	9	3	0	0	0	0	0	0
2	11	5	6	5	11	5	6	0	0	0	0	0	0
Closed													
3	19	36	33	29	19	35	29	1	1	3	2	4	3
4	28	51	23	31	28	50	18	1	1	4	1	1	2
5	13	25	15	12	13	25	13	0	0	2	0	4	2
6	11	25	11	5	11	20	6	5	3	2	0	0	1
7	33	31	29	9	33	29	21	2	1	7	1	0	0
8	33	16	13	6	33	14	12	2	1	0	0	0	0
9	31	22	10	13	31	20	9	2	0	1	1	0	0
10	21	25	7	14	21	25	6	0	0	1	0	0	0
11	4	1	1	4	4	1	0	0	0	0	0	0	0
12	9	8	10	4	9	8	9	0	0	1	0	0	0

it is immigration and emigration, that is corrected for in this case. The four - and three-fold differences in the estimates by the two methods is too large to be allowable as experimental error, so mark and recapture was abandoned.

b. The size distribution at monthly intervals.

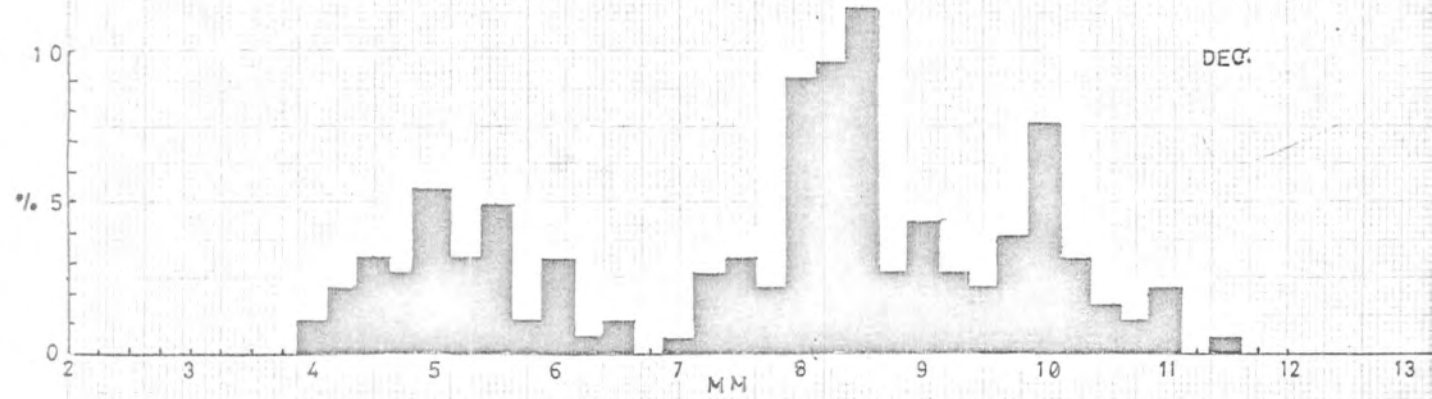
Figure 6. shows the percentage frequency of snails plotted in 0.25 mm. size classes at monthly intervals, from December to July. The poly modal distribution, shown by the histograms, was analysed for each month by Harding's (1949) method using probability paper. This showed a distinct bimodal distribution until July when, though one can still see the two groups in the histogram, the analysis does not separate them. In July, recruitment appeared for the first time but the histogram is unlikely to show the true size class distribution for this group, because of the unreliability of the sorting for very small individuals in a sample.

The large size class group shall be called the 1965 generation, the small size class group the 1966 generation and the July recruitment the 1967 generation in the following sections. The assumption inherent in the above divisions is justified in the next section and in the discussion.

c. Bodily growth over the period of study.

Growth cultures in the field failed to produce meaningful results. Initially the mortality was very high and later, when mortality was down to 10%, no significant growth was ever demonstrated. The cultures were discontinued in June. Therefore no comparison between mean growth rate for the two generations and the individual growth rate in the different size classes is possible.

FIG. 8.


DEC.
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12
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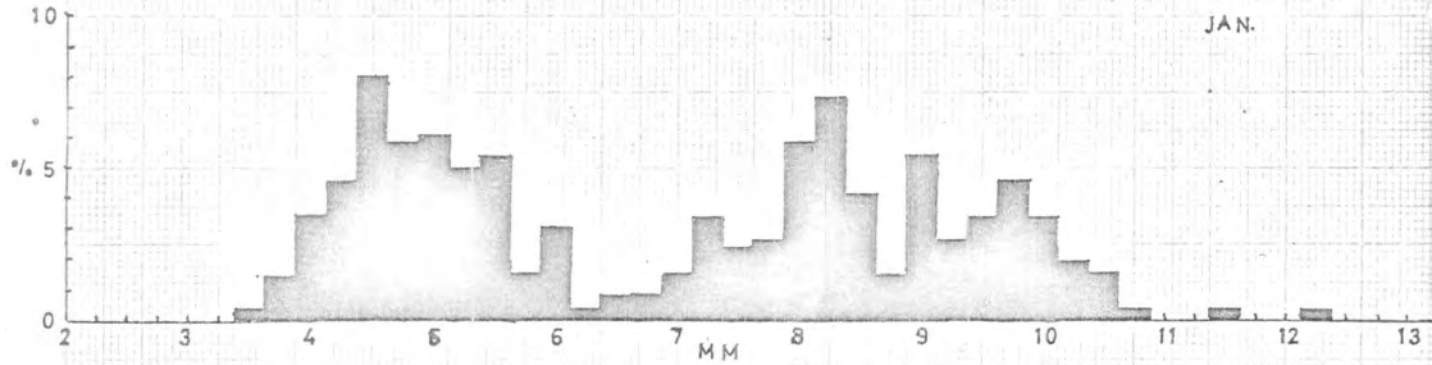
MM


JAN.
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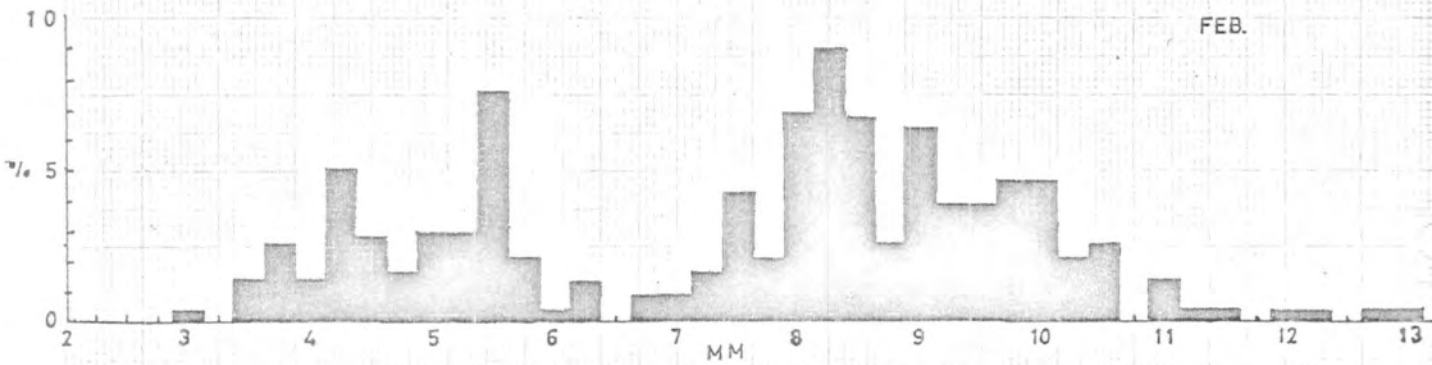
MM


FEB.
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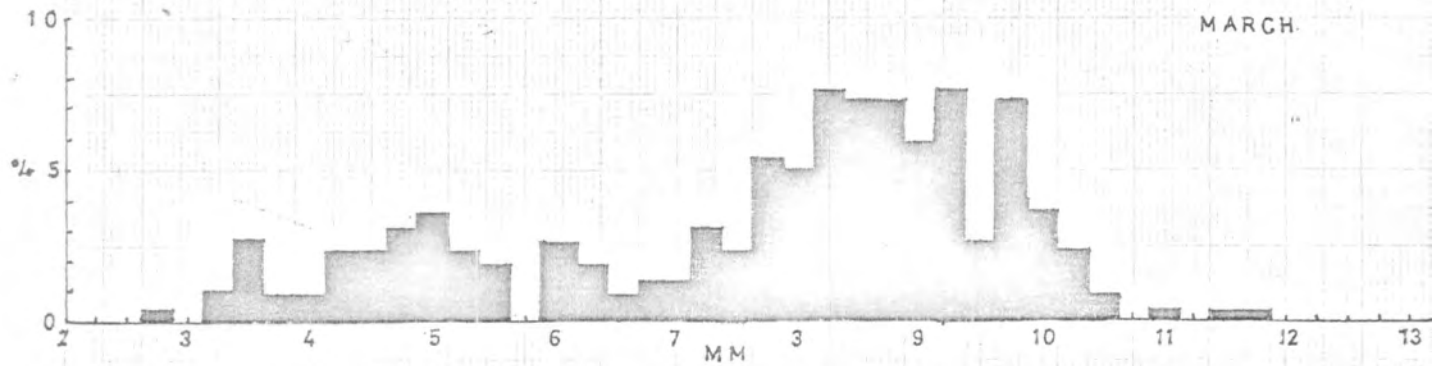
MARCH.
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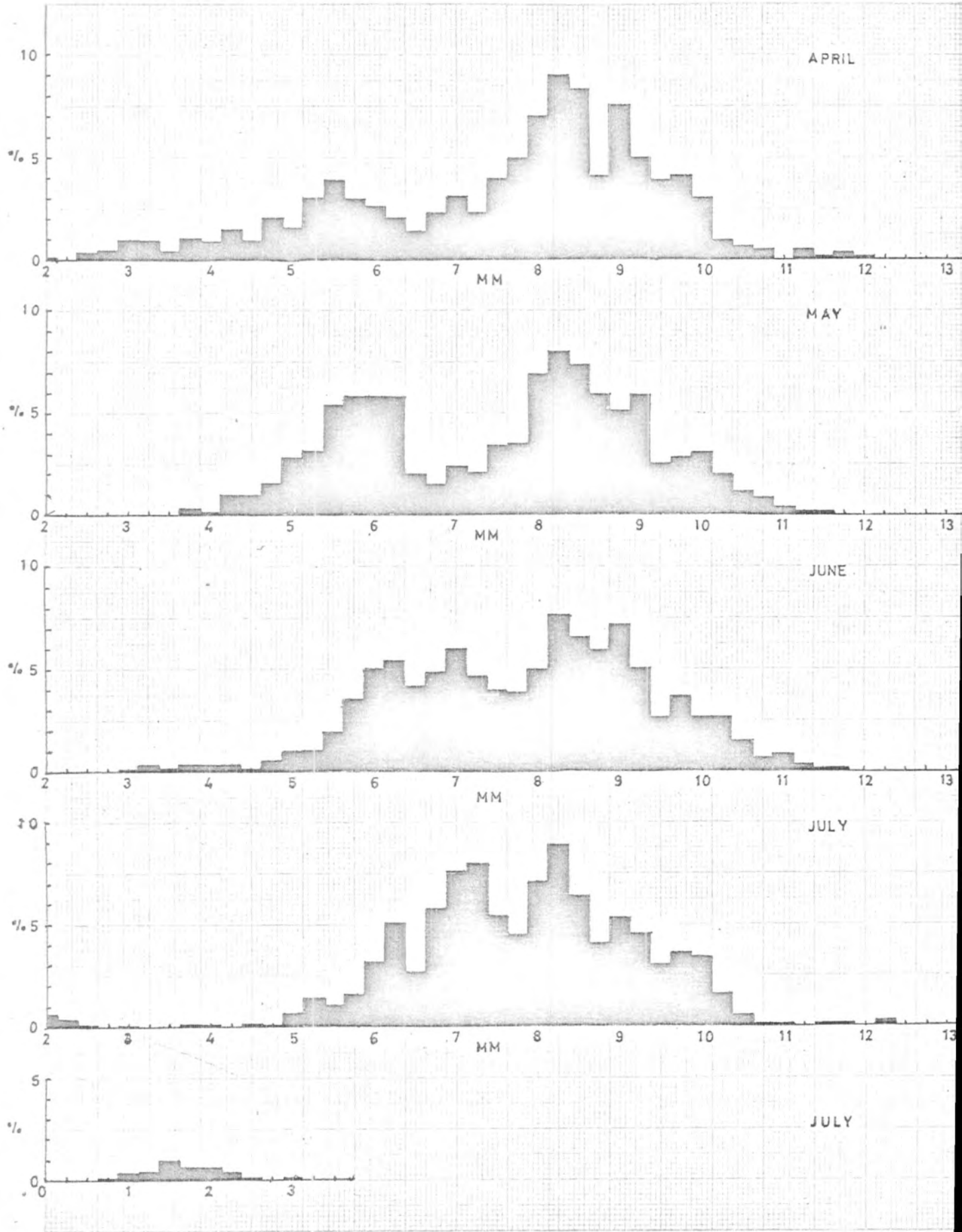
APRIL
MAY
JUNE
JULY
JULY
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12
13
1
2
3

From the size frequency distribution for each of the months, the mean size of the 1965 and 1966 generations were found using Harding's analysis. In July, this method could not be applied and the mean sizes of the two generations were estimated by judging the proportions in the histogram by eye. Therefore the results for this month may not be reliable. From the mean size, the bodily growth for each monthly period was calculated as increase in breadth/week. The bodily growth was also estimated, from the size/weight conversion, as increase in total weight/week in order to see if increase in breadth gave a satisfactory picture of growth. For comparison between the two generations the size or weight increase was also expressed as percentage increase per unit size or unit weight.

Table 6. The bodily growth for each monthly period for each generation expressed both as increase in breadth and increase in total weight per week.

Table 6.

Generation	Jan.-Feb	Feb-March	Mar-April	April-May	May-June	June-Jly
	mm./week	mm./week	mm./week	mm./week	mm./week	mm./week
1965	0.19	-0.11	0.009	0.065	0.03	0.00
	2.28%	-1.25%	0.1%	0.77%	0.35%	0%
1966	0	-0.04	0.108	0.113	0.16	0.075
	0%	-0.8%	2.37%	2.19%	2.9%	1.18%
	mg./week	mg./week	mg./week	mg./week	mg./week	mg/week
1965	3.17	-1.67	0.13	2.01	0.65	0
	6.67%	-2.78%	0.24%	3.6%	1.04%	0%
1966	0	-2.22	0.76	1.11	1.74	0.94
	0%	-2.2%	6.8%	7.1%	8.83%	3.37%

Expressing the growth as weight gives a similar pattern to that obtained using size except in the 1966 generation in April-May when size shows a decrease in growth rate while weight maintains the small steady increase in growth rate. From the table and considering the percentage increase in total weight, the following can be inferred: in January - February, the growth in the 1965 generation was so high it was suspect, especially as there was no growth in the 1966 generation. In February, there was an anomalous decrease in growth rate in both generations, which is probably an arte fact: March had an exceptionally low total sample population, which might explain it. In March - April, the 1966 generation had a high growth rate which, because of the apparent decrease in growth in the preceding month, was probably too high and then there was a slight increase in the growth rate till June. The decrease in rate in July could either be a genuine slowing down of growth but might be just a result of the method used to obtain the mean size for this month. The 1965 generation, over the same period, had a slower rate of growth in March - April which rose to a maximum rate in May (but considerably lower than for the 1966 generation) and decreased in June and July. The decline to zero of the growth over June and July might be explained by a higher mortality in the largest individuals after breeding.

The growth of the 1967 generation was found in the laboratory.

Table 7 summarises the results, from the laboratory growth cultures, for growth of the 1967 generation, between June 20th and August 6th.

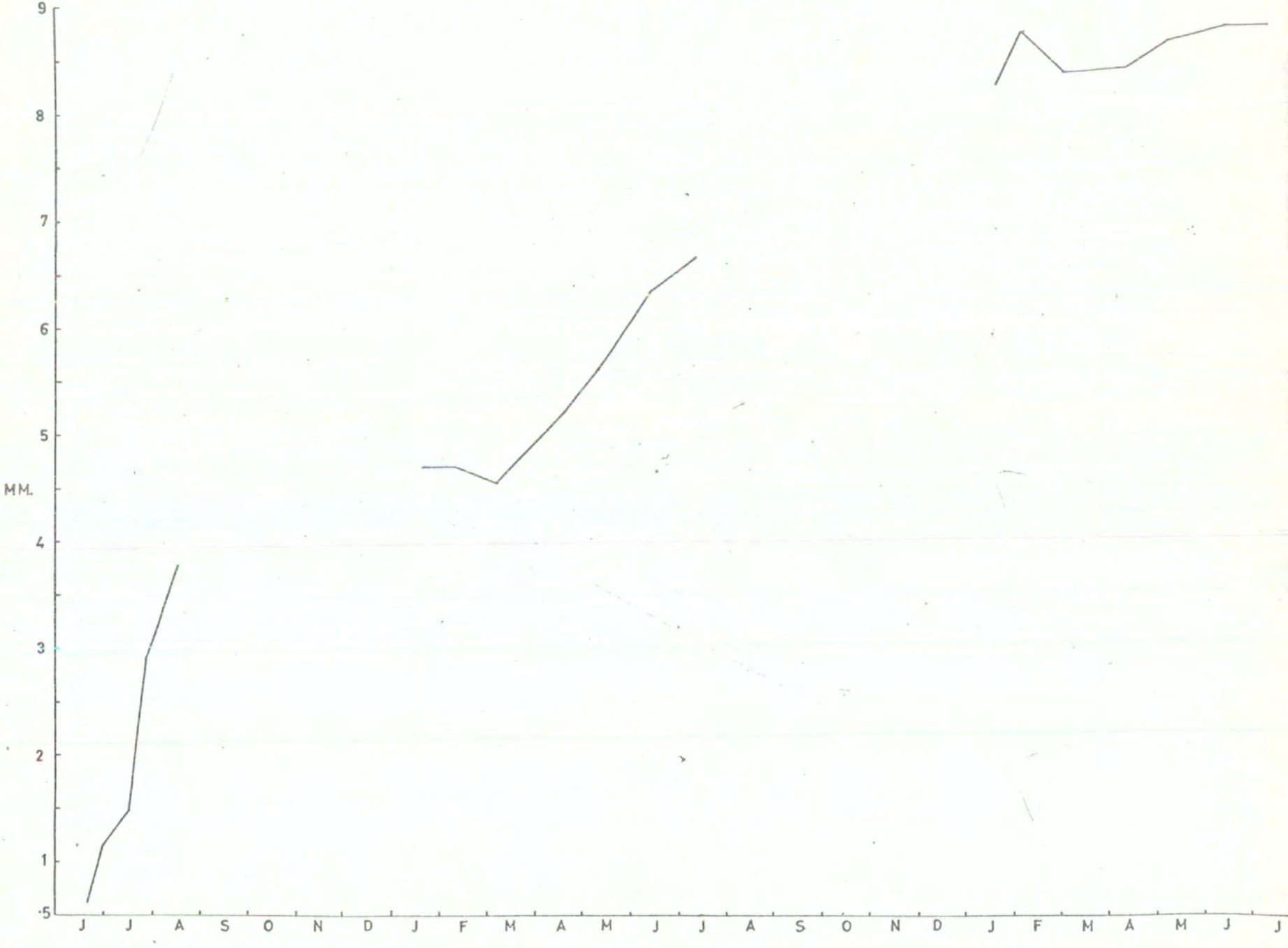
Table 7.

Weeks	0	1	2	3.5	6
Size in mm.	0.605	1.22	1.48	2.875	3.8
Increase in size/ week	0	0.538	.26	0.977	0.357
% growth/week	0	88.5	21.3	66.0	12.4

These results could only be expressed in terms of size, because there was no size-total weight conversions for these size classes. The percentage rate of growth per week showed a very high one in the first week but by the sixth it had dropped to four times that of the 1966 generation. The results were compiled from only ten individuals, as a number of the cultures looked unhealthy and inactive so were omitted. Thus, probably, the results show too high a growth rate compared to what would be found in the field. However, by August 20th snails between 3 and 4.5 mm. could be found in reasonable numbers in the study area.

Figure 7 shows the mean size of the three generations at each sampling occasion plotted as if the three generations represented the growth patterns over a life of twenty six months of one generation of snails. This shows graphically that, if one assumes no growth over the Winter throughout the life of the snails and that therefore growth would cease in late September or October, then the rates of growth over the rest of the year are such as to be compatible with raising the mean size in spring of one group to the mean spring size of the next group. The growth for the first summer is rapid at first and then slows, as if it were the second half of a sigmoid curve. Growth in the second summer

FIG. 7.



is apparently sigmoid and in the third summer, there is no definite pattern, probably because of mortality. For the above reasons, the use of the term generation for the two groups in the histograms is justified.

d. Size/weight conversion.

In order to express the data for bodily growth and standing crop as dry weights of tissues and to relate the oxygen consumption of individuals to the tissue dry weight, it was necessary to find the size/total live weight and size/tissue dry weight relationships.

Included in the data specifically collected to estimate the above conversions, were data collected on size/total live weight and size/dry weight of tissues from respiration experiments.

Figure 8 shows the relationship between size in terms of maximum breadth and total live weight, during winter 1966/67. The two lines were drawn in by eye. The graph might also have been drawn as a curve with the point of inflexion approximately where the intersection of the two lines is. The line for the smaller size classes corresponds approximately with the size range of the 1966 generation (from 3.5 mm. - 6.75 mm.) and shows that the relative increase in weight per unit increase in size was greater in the 1966 generation than in the 1965 generation, which is represented by the second line.

Figure 9 shows the situation in summer 1967. The two parts of the graph remain but are less well marked, and the division is at about 7.5 mm. which corresponds approximately with the point of overlap of the ranges of the two generations in summer. The relationship between size and total live weight that changed was in the 1966 generation. Despite this change, the actual total live weights for the 1966 generation in winter and summer for each size class are similar as the two lines intersect

FIG. 8

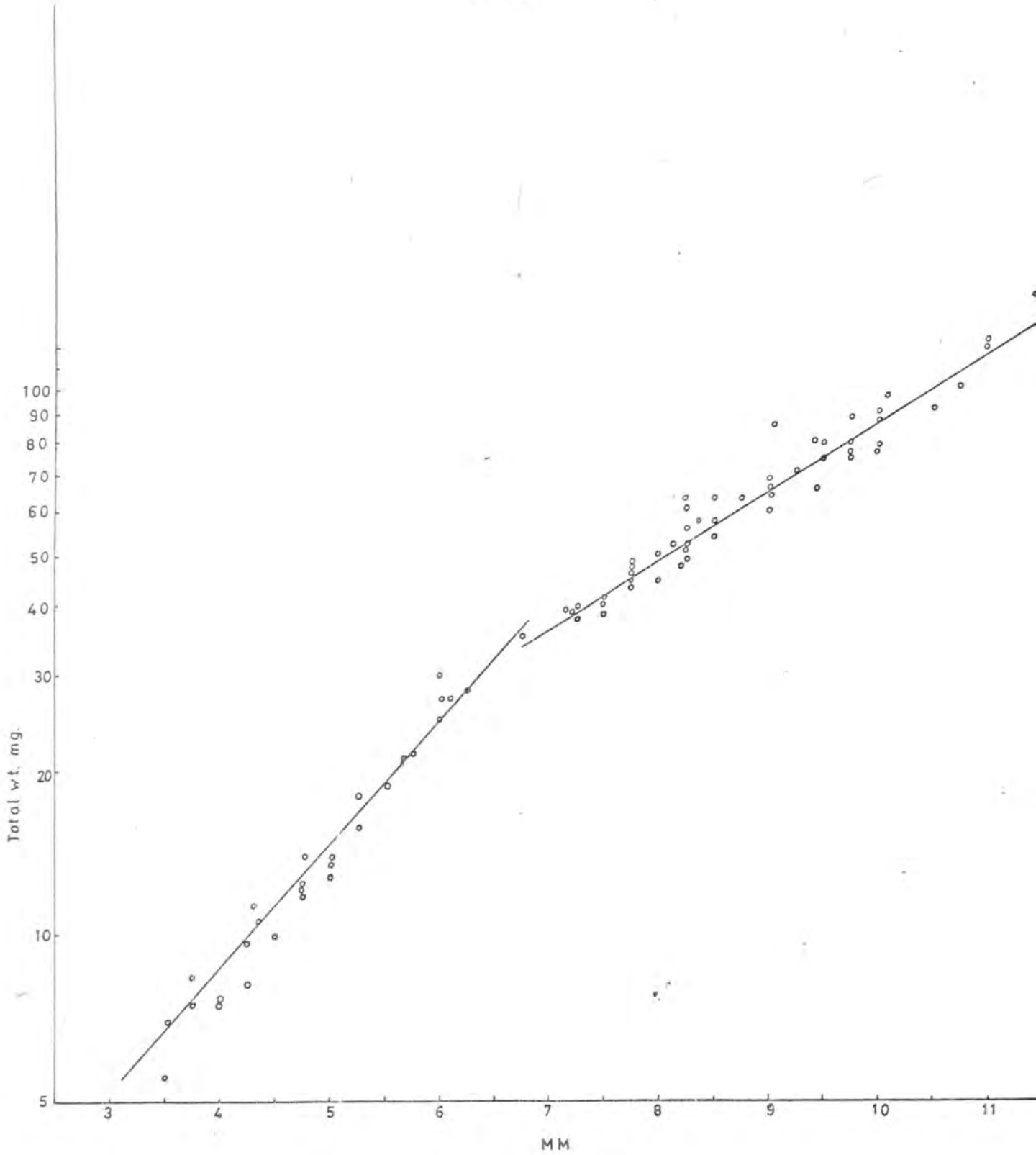
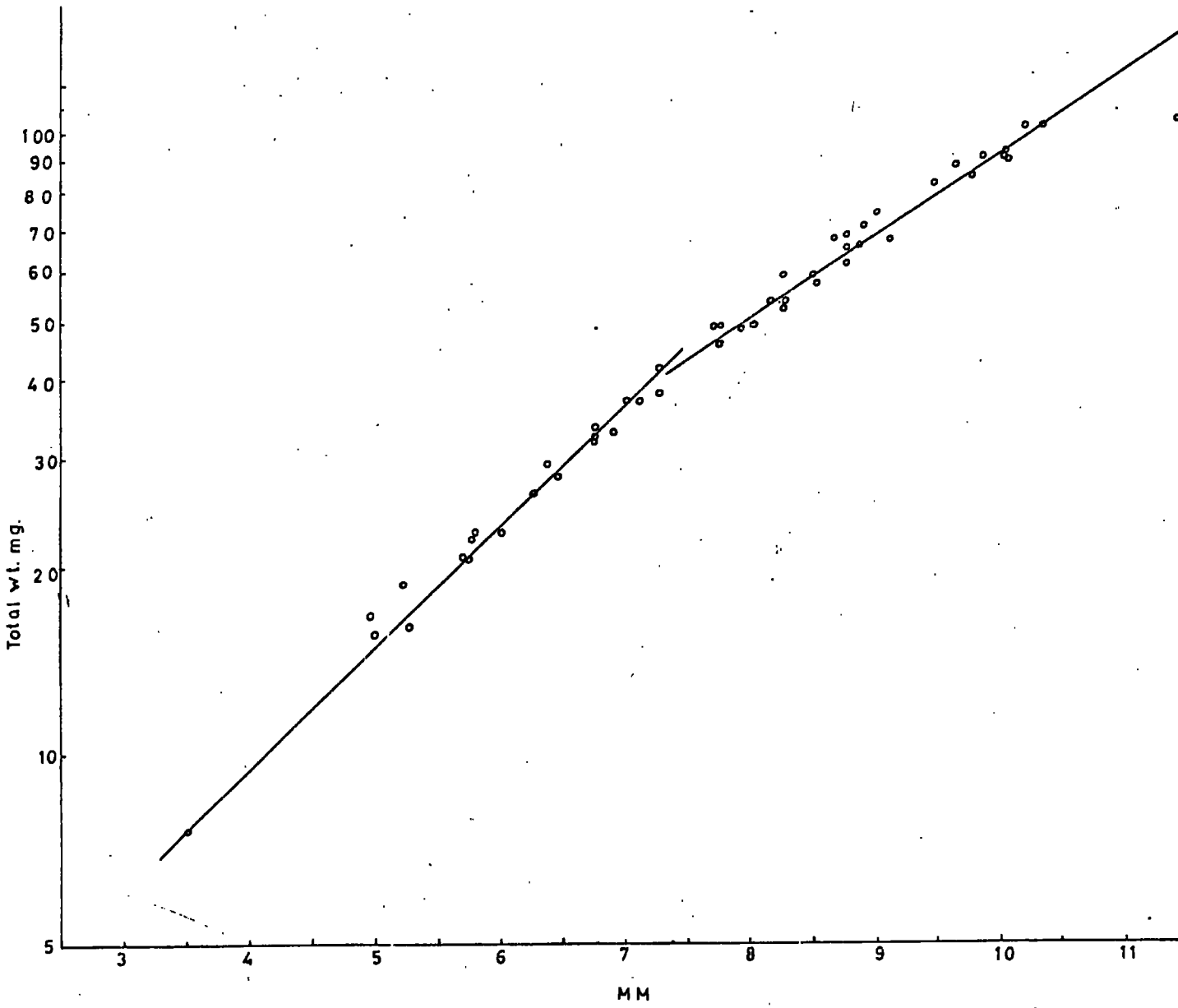


FIG.9.



about the midpoint of the generation's size range. In the 1965 generation, where the relationship between total live weight and size over the size range remained similar, the summer weights were consistently higher for each size class than in winter.

Figure 10 shows the winter relationship between breadth and shell weight. The regression line for the points was calculated using the method of least squares and a regression coefficient of 0.998 obtained. The excellent fit of points to the regression line does not indicate a possible double relationship and, if one also considers the results from figure 11., then the differences found in the two generations in figures 8 and 9 would appear to lie in the water content of the tissues.

Figure 11 shows the winter and summer relationship between size and dry weight of tissues. The least squares regressions, for both seasons, were calculated. The regression coefficients for winter and summer are 0.98 and 0.82 respectively. The slope for winter is 0.13 and for summer 0.114 and the regression lines intersect at 10.5 mm. This means that, in the smallest individuals there was a considerably higher dry weight of tissues in summer than in winter but as the size of the individual increased this difference progressively decreased until, in the largest individuals there was no marked difference between the weights in the two seasons.

Table 8 is a summary of shell weight, total live weight in winter and summer and dry weight of tissues in winter and summer in relation to size measured as maximum breadth.

This table shows the conversions used in the sections on respiration and the energy budget.

FIG. 10.

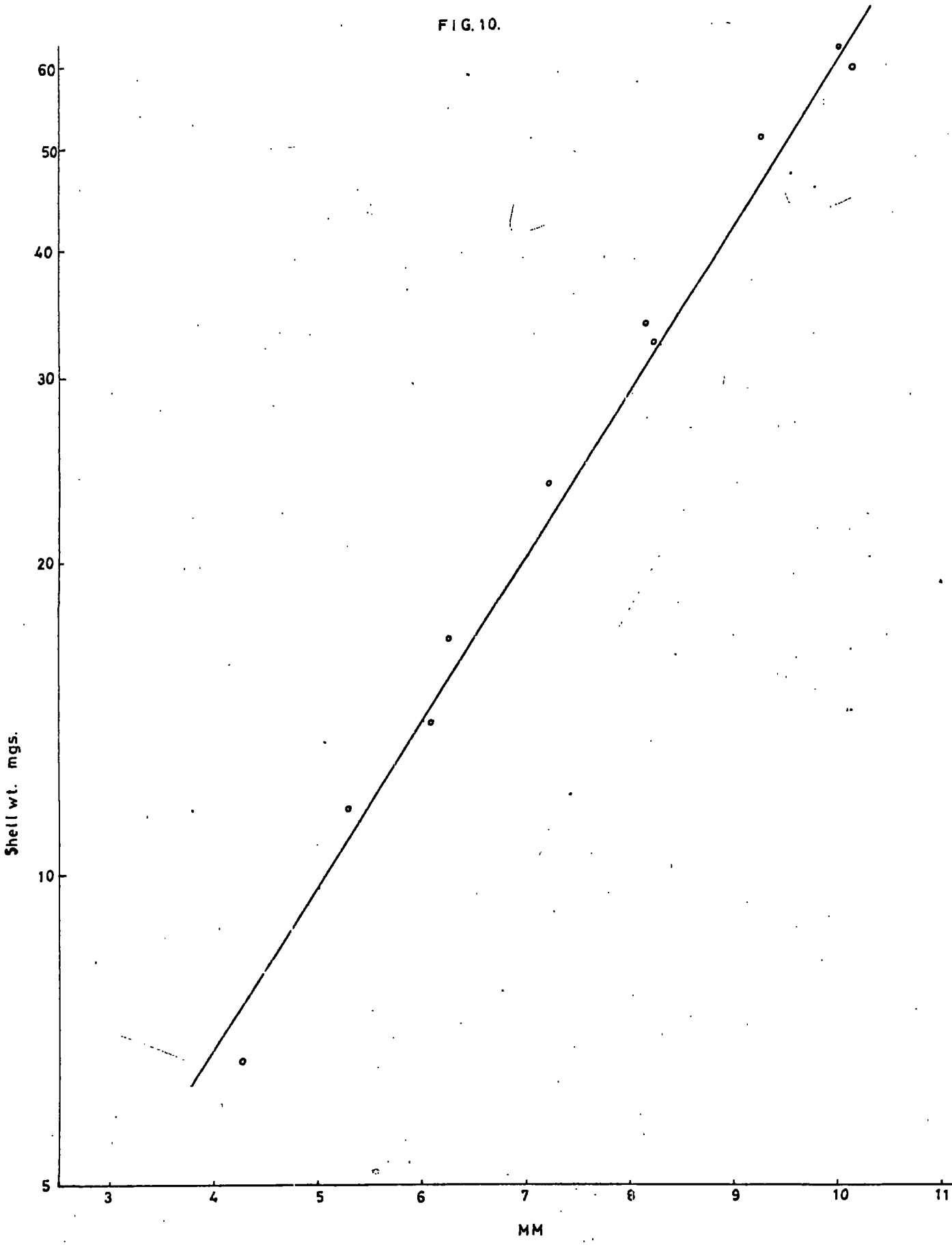


FIG. 11.

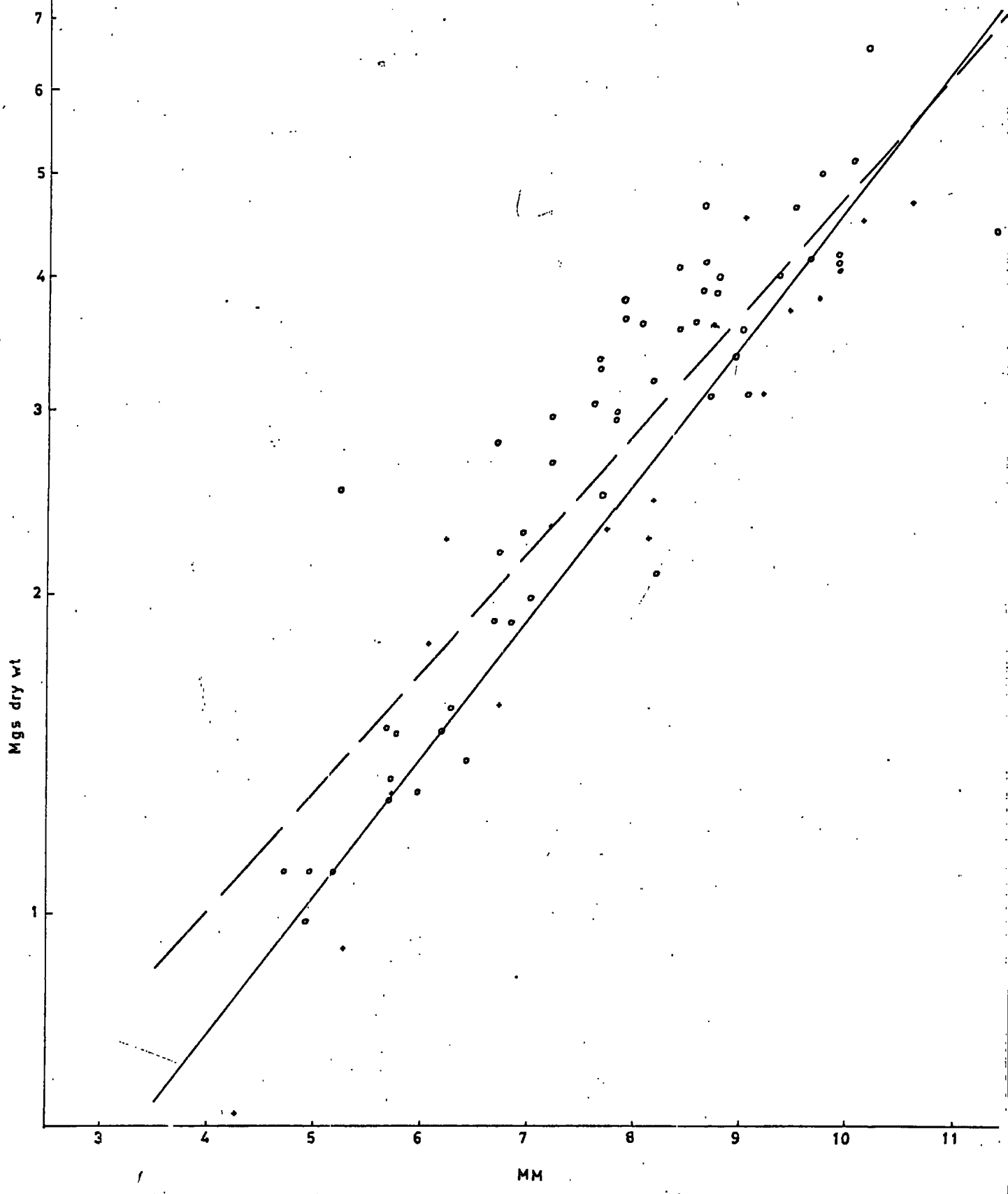


Table 8.

Size (mm.)	3.5	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5	9	9.5	10	10.5	11	11.5
Winter shell wt. (mg.)	5.6	6.7	8.1	9.7	11.6	14	16.8	20.2	24.3	29.2	35.2	42.3	50.8	61.1	73.5	88.3	106.2
Winter total live weight (mg).	6.4	7.8	10.8	14.3	18.7	24.6	32.4	36.4	42.2	48.4	55.6	64	73.5	84.1	96.6	110.9	127.4
Summer total live weight (mg.)	7.5	9.4	11.9	15	18.8	23.7	36.4	36.4	42.4	49.6	57.5	66.8	78.5	90.2	106.4	125	146.2
Winter dry weight of tissues (mg.)	0.66	0.77	.89	1.04	1.2	1.4	1.62	1.88	2.19	2.55	2.97	3.44	4.0	4.62	5.4	6.3	7.27
Summer dry weight of tissues (mg.)	0.88	1.0	1.1	1.3	1.48	1.69	1.93	2.2	2.51	2.86	3.26	3.72	4.24	4.85	5.48	6.28	7.13

d. Bomb calorimetry.

Figure 12 shows the mean calorific value for mm. size classes for winter and summer plotted as Kcal./gram dry weight of tissues against size class. The value for the 4-5 mm. class is only one determination using a pellet of less than 5 mg. so cannot be considered reliable. Otherwise there is no detectable consistent trend either within one season or between seasons.

Figure 13 is the calorific values calculated for each pellet plotted against pellet size. This shows pellets below 5 mg. weight gave a consistently lower calorific value than those between 5 and 17 mg. and as this could not be related to any characteristic of the material e.g. a particular size class, it was decided to exclude them from the calculations on the grounds that the experimental technique was not valid below 5 mg.

Table 9 shows the mean calorific values for the 1966 and 1965 generations in winter and summer, the mean value for the total winter and total summer results and the mean total value for all the results.

Table 9.

Season.	Grouping.	Calorific value Kcal./gram tissue dry weight.	Standard Deviation	Standard Error of Mean.
Winter	1966 gen. 5-6 mm.	3.2626	-	-
	1965 gen. 6-10 mm.	3.8276	0.6147	0.1705
	Both " 5-10 mm.	3.7870	0.6114	0.1634
Summer	1966 gen. 5-8 mm.	3.5730	0.3927	0.1756
	1965 gen. 8-12 mm.	3.7700	0.6490	0.1957
	Both " 5-12 mm.	3.7087	0.5867	0.1467
Summer and Winter	Total. 5-12 mm.	3.7454	0.5990	0.1094

FIG.12.

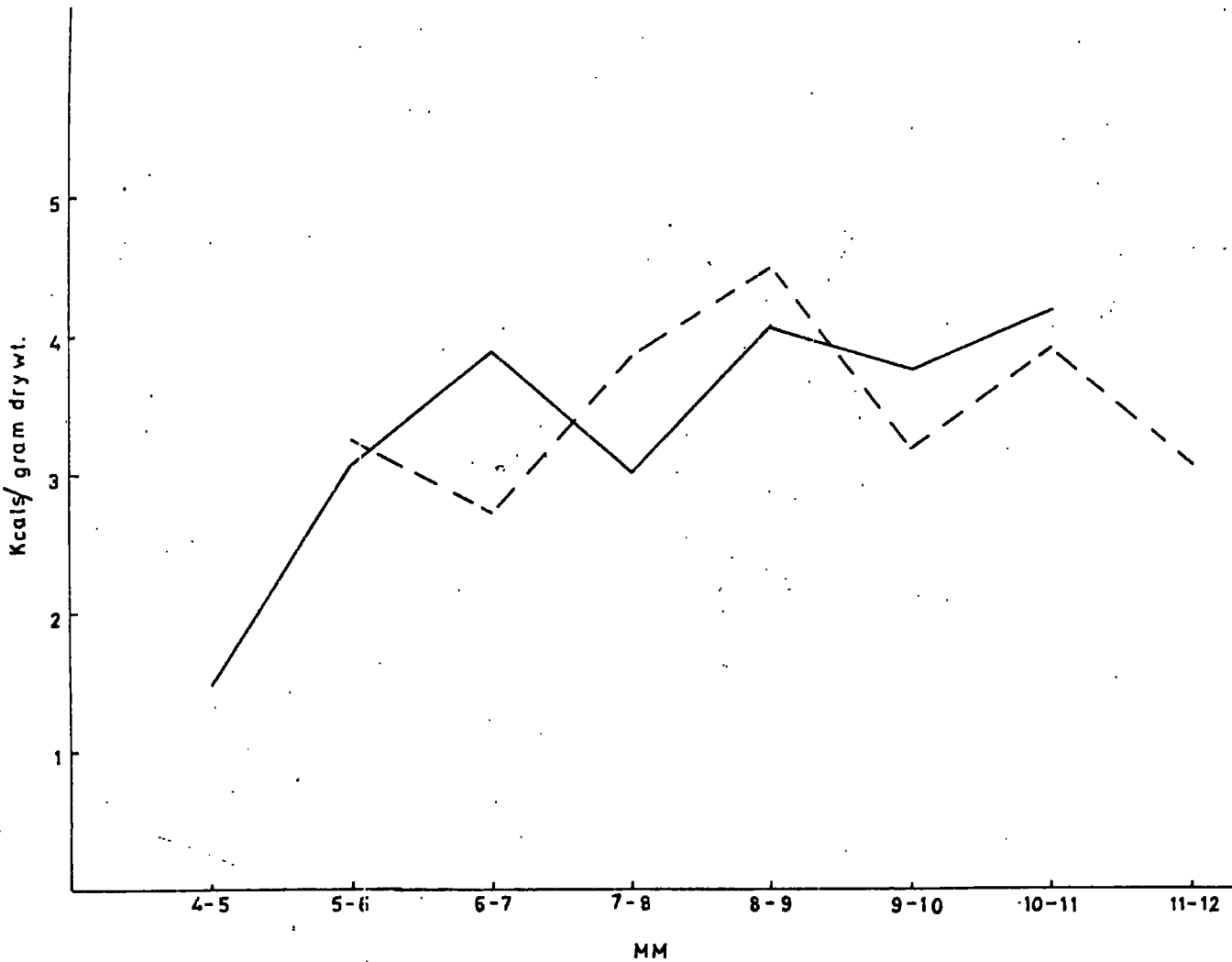
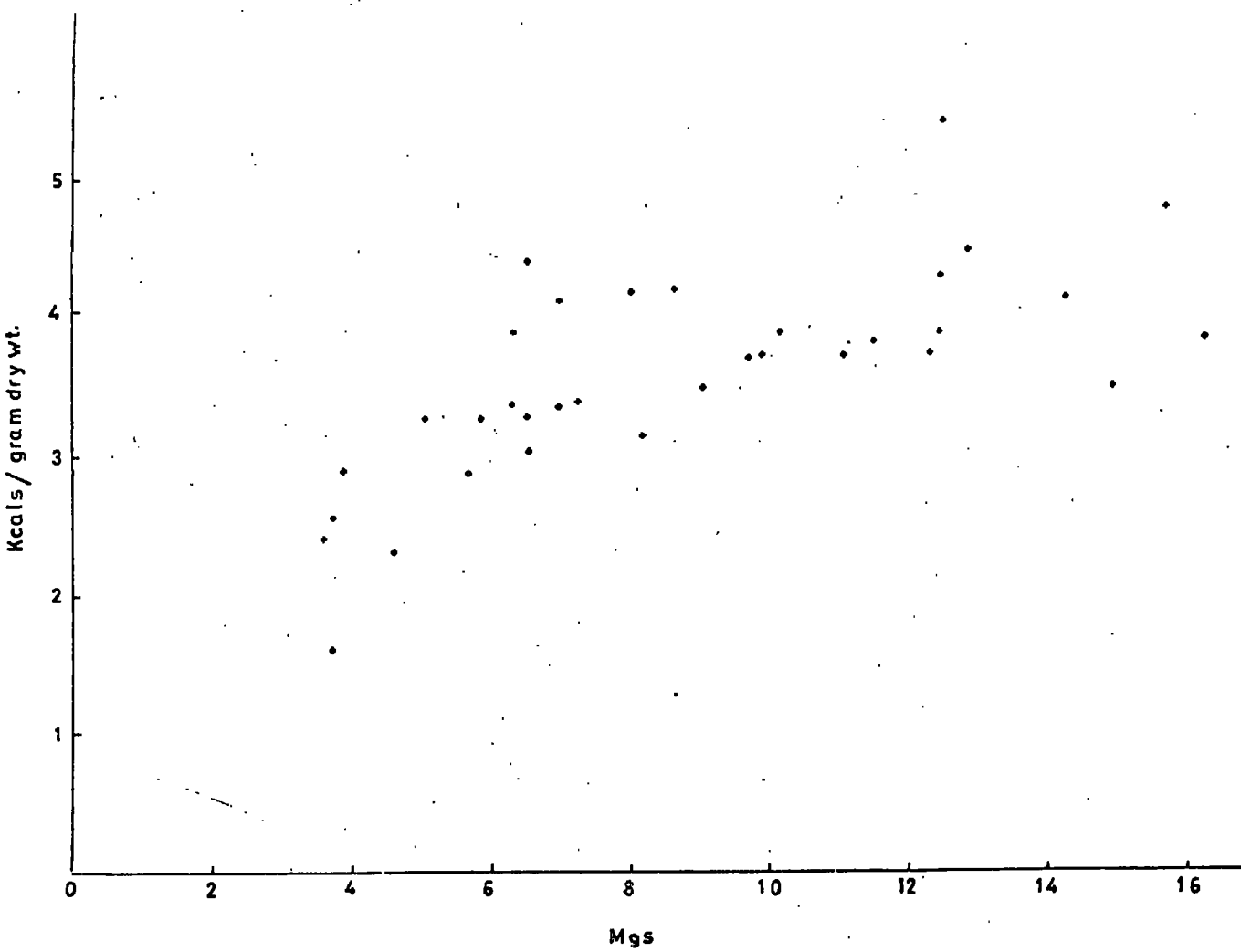


FIG. 13.



The results from the summer and winter 1965 groups were compared using the Student "t" test. The result, $t = 0.0761$, $n = 1$, showed the difference was statistically not significant. Similarly the difference between the two generations in summer was not statistically significant. Therefore the results were combined, thirty in all, and the mean calorific value of 3.7454 ± 0.599 Kcal./gram dry weight of tissue used in the energy budget to convert biomass data into energy units.

e. Respiration.

The check results, obtained using the micro Winkler method, fell within the range found using the constant pressure apparatus, so were included in the final results.

Figure 14 shows the respiration results for February and early March, at a mean temperature of $6.2^{o}C$, as oxygen consumption per individual per day plotted against total live weight. The least squares regression was calculated and gave a coefficient of 0.91.

Figure 15 shows the respiration results for May and July at $10.78^{o}C$. and $14.73^{o}C$. respectively. The oxygen consumption per individual per day was plotted against dry weight of tissues. The regressions were calculated and gave coefficients of 0.83 for the former and 0.72 for the latter.

Table 10 is a summary of the temperature conditions at which the experiments were carried out and gives the regression equations.

FIG.14.

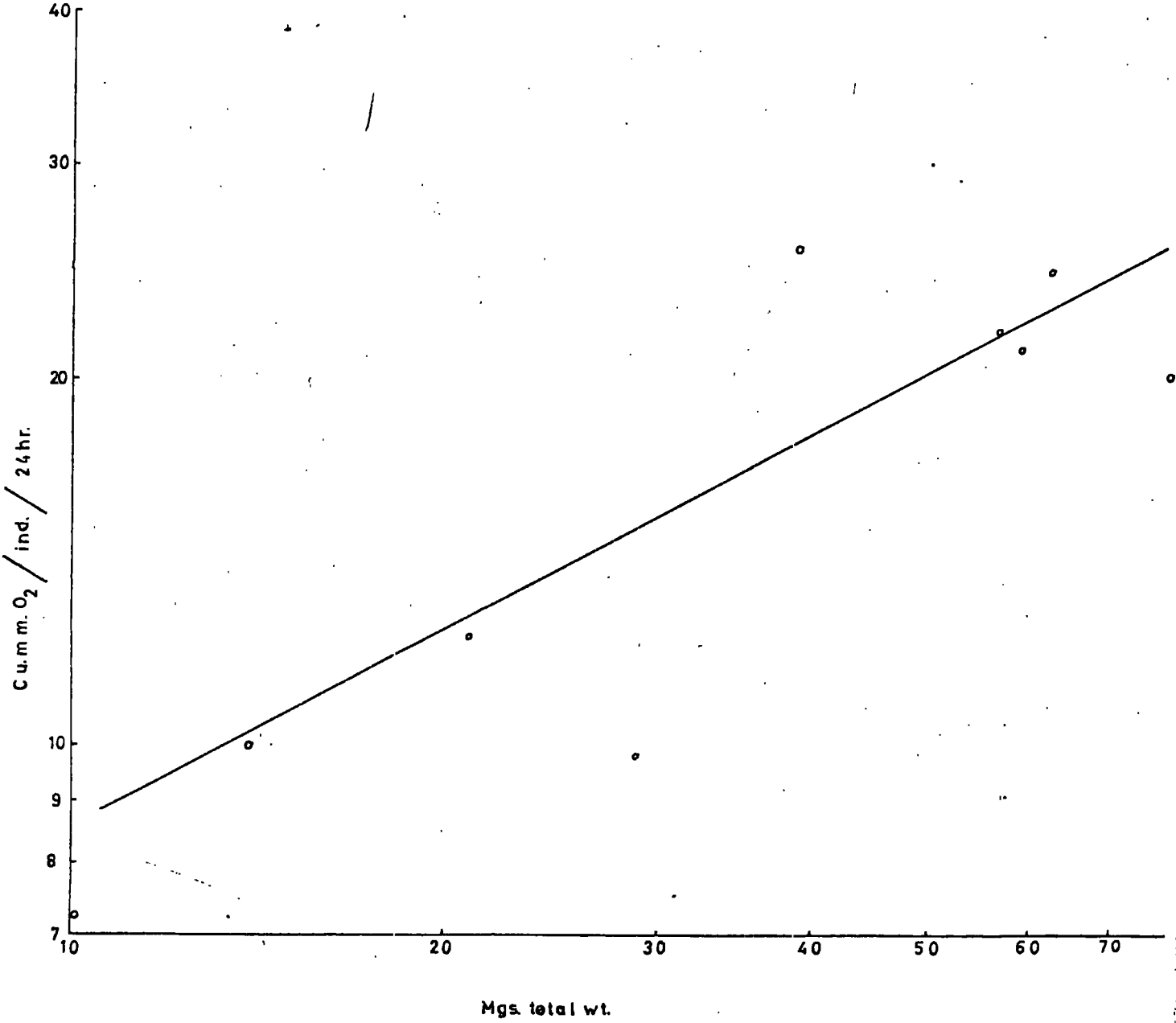


FIG.15.

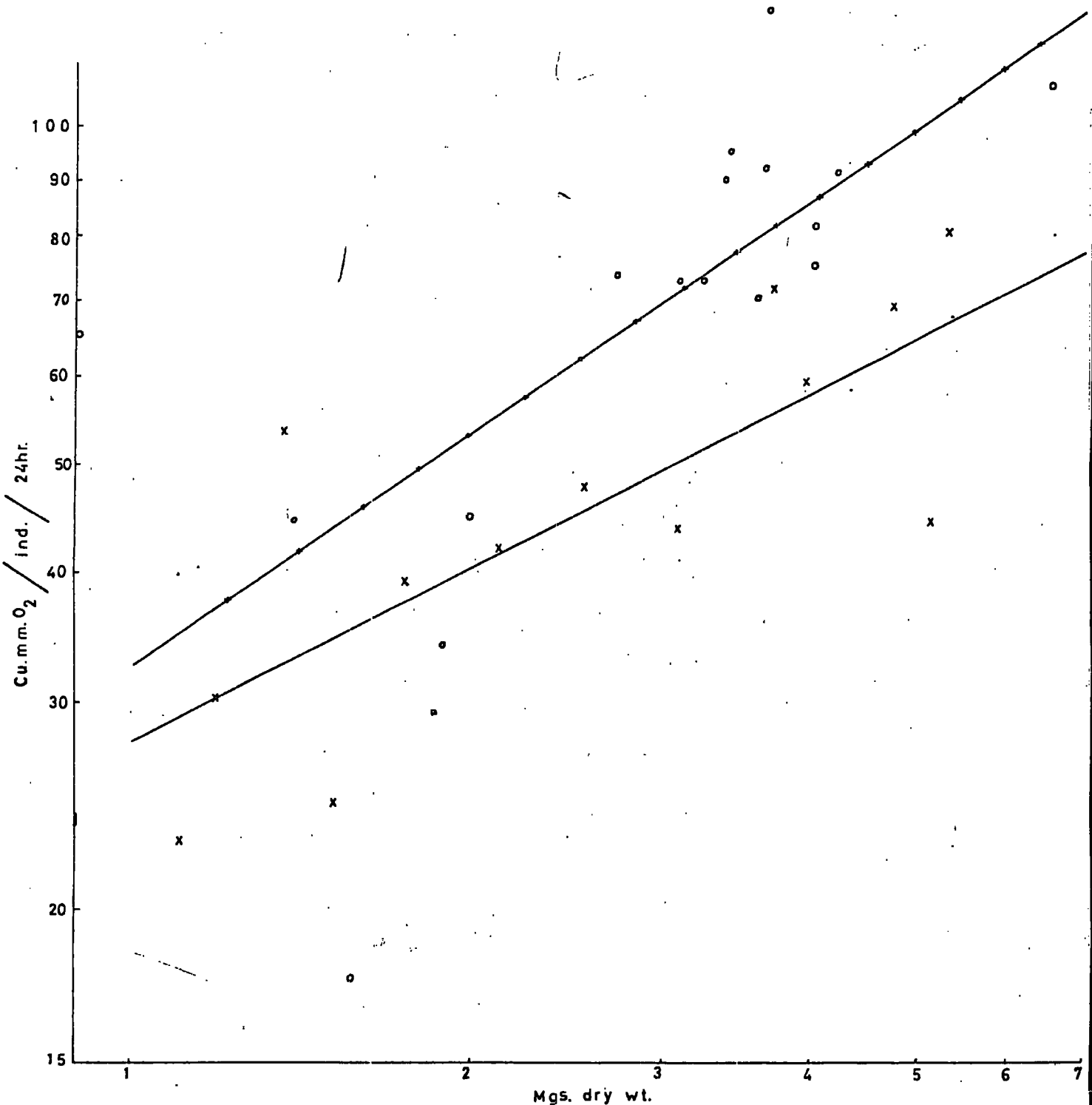


Table 10

Months	Temp. Range	Mean Temp.	Regression Equation
Feb-March	6 - 6.35°C	6.2°C.	$y = 0.5697x + 0.329$, $r = 0.91$
May-June	9.75 -12.58°C	10.78°C.	$y = 0.518x + 1.45$, $r = 0.83$
June-July	13.88 -15.5 °C	14.73°C.	$y = 0.684x + 1.52$, $r = 0.72$

Table 11 gives the oxygen consumption as cu. mm. O_2 per individual per day calculated from the regressions for size intervals of 1 mm. breadth.

Table 11

Temp.	3 mm.	4 mm.	5 mm.	6 mm.	7 mm.	8 mm.	9 mm.	10 mm.	11 mm.
6.2°C.	5.24	6.97	9.67	13.21	16.54	19.45	22.8	26.65	31.33
10.78°C.	24.73	23.25	32.28	36.99	42.4	48.57	55.65	63.86	73.02
14.73°C.	27.85	33.21	39.62	47.42	56.78	67.95	81.32	97.5	116.3

Table 12 shows the relationship between oxygen consumption at different sizes and temperatures: the oxygen consumption at the higher temperature being expressed as a factor of the oxygen consumption at the lower one.

Table 12

Temperatures Lower	Higher	Difference	3 mm.	4 mm.	5 mm.	6 mm.	7 mm.	8 mm.	9 mm.	10 mm.	11 mm.
6.2°C	10.78°C	4.58°	4.7	4.05	3.33	2.8	2.6	2.5	2.4	2.4	2.3
10.78°C	14.73°C	3.95	1.2	1.2	1.3	1.4	1.4	1.5	1.5	1.5	1.6

FIG. 18.

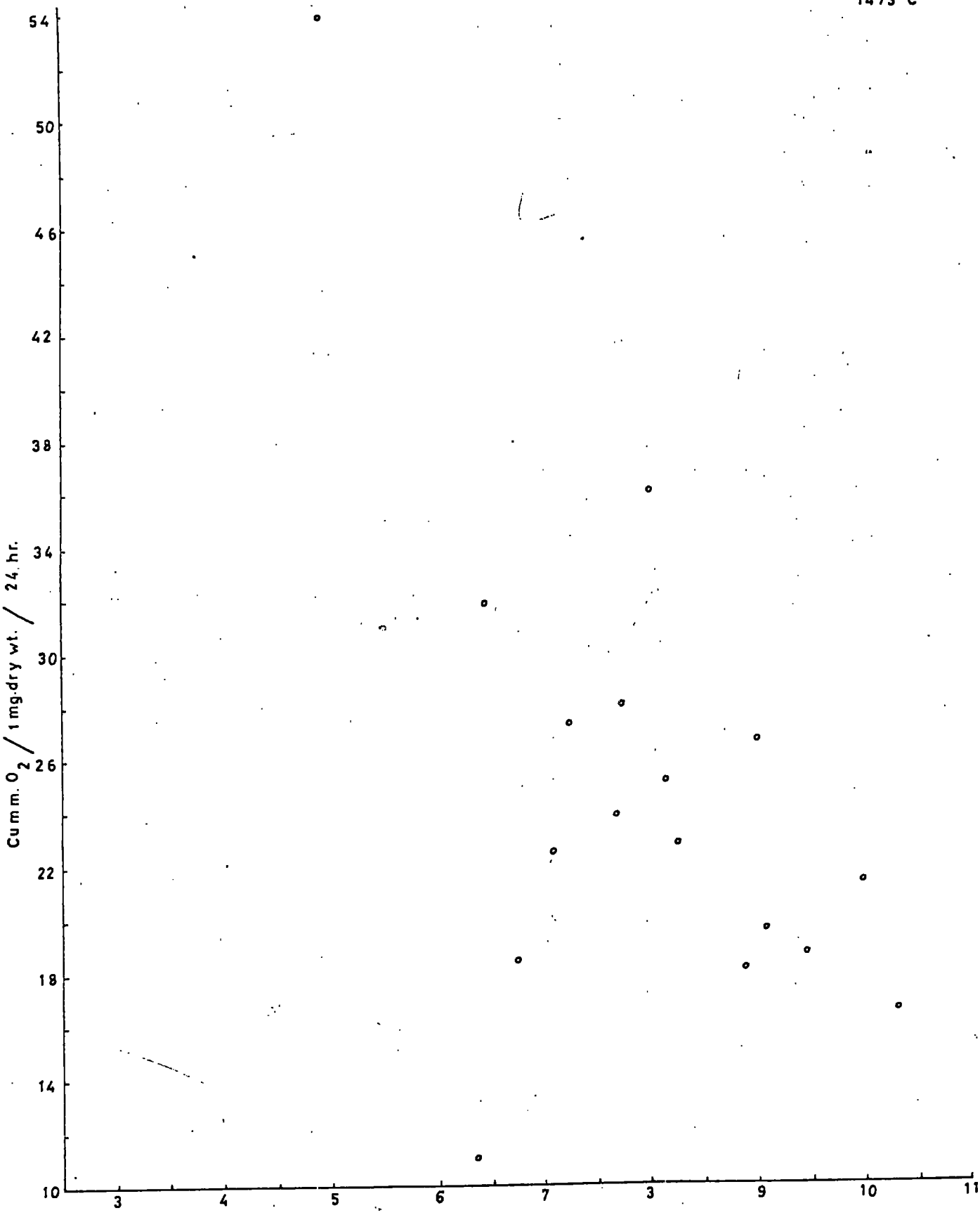
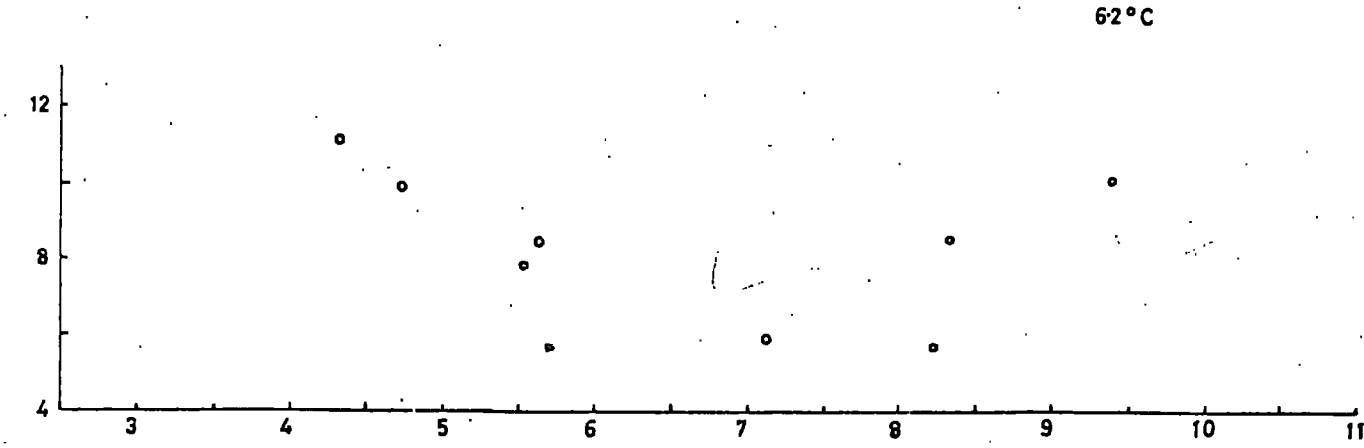

14·73 °C
54
50
46
42
38
34
30
26
22
18
14
10
Cumm. O_2 / 1 mg. dry wt. / 24 hr.
3
4
5
6
7
3
9
10
11

FIG.16.


6·2 °C
12
8
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3
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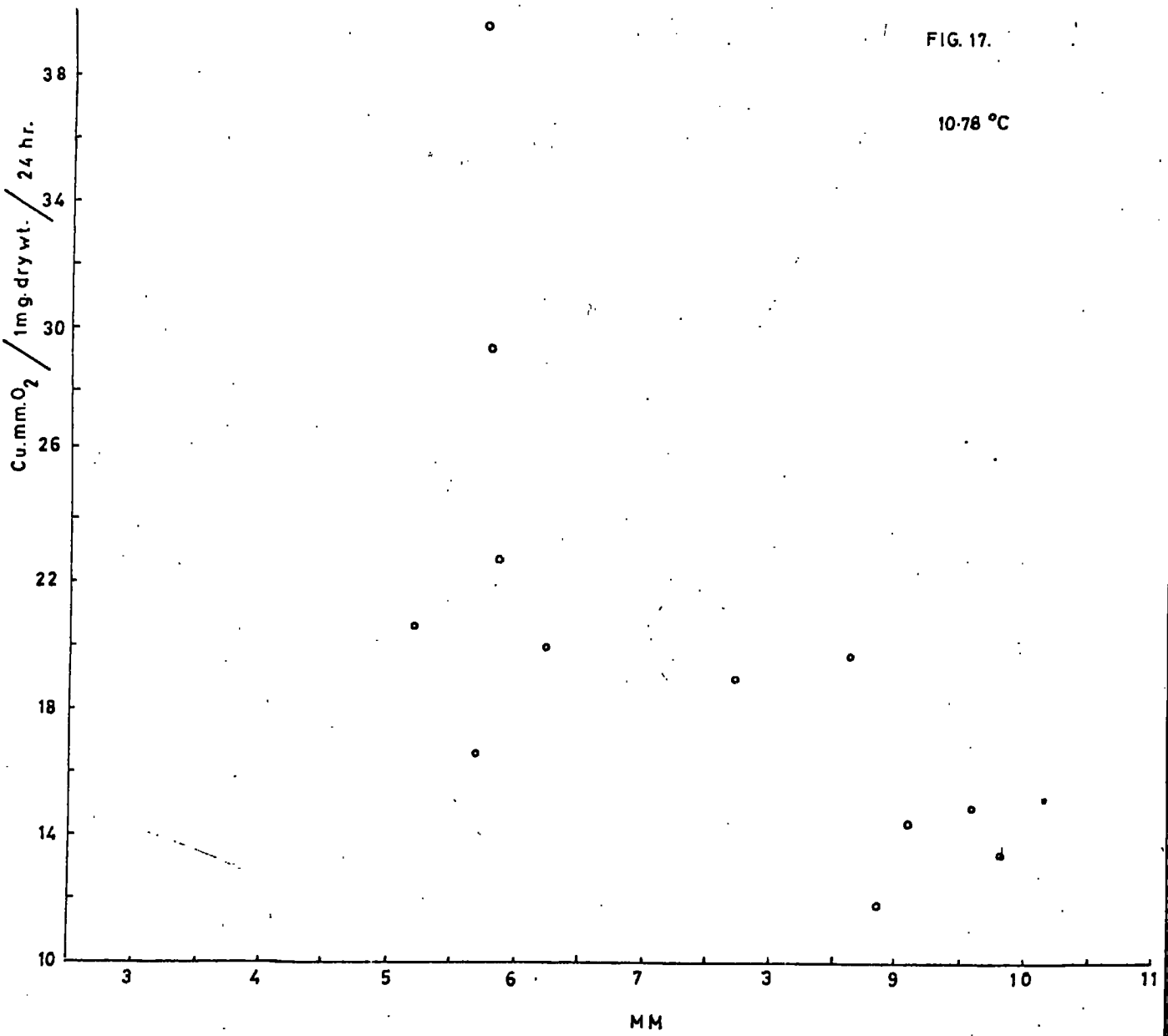
9
10
11

FIG. 17.


10·78 °C
Cu.mm.O2 / 1mg.dry wt. / 24 hr.
38
34
30
26
22
18
14
10
3
4
5
6
7
3
9
10
11
MM

The mean factor over the whole size range for the temperature difference of 4.58°C was calculated and adjusted to a 5°C difference to give a Q5 of 3.2. This was repeated for the 3.95°C temperature difference to give a Q5 of 1.8. Thus the effect on the oxygen consumption of increasing the temperature between 6°C in February to 11°C in May is almost twice that of increasing it from 10°C in May to 15°C in July. This demonstrates the result of increased metabolic activity associated with growth and reproduction in the first case, where a change of season has occurred while in the second instance there has only been a change in temperature.

Figures 16, 17, 18 show the respiration results calculated as oxygen consumption in Cu. mm. O_2 per mg. dry weight of tissue per day plotted against size in mm. for 6.2°C., 10.78°C. and 14.73°C. The dry weight of tissue for the 6.2°C. group was calculated from the conversion graph (Fig.11). Figure 16 has too few points to show definitely that, the larger individuals have a lower oxygen consumption per unit dry weight of tissue but, this trend is unmistakeable in figures 17 and 18.

f. Pond temperature measurements.

Trouble was experienced with some of the sucrose inversion tubes losing their tops in spring and summer, at the higher temperatures. The April figure and the surface ones for June - July are from other ponds in the Brasside complex.

Figure 19 shows the surface temperature and temperature at 25 cm. depth over the period of study. As no significant difference was found between the two surface and the two surface and the two deep tubes, the mean was taken for each for the graph. The surface was colder from January to March and warmer from June onwards than at 25 cm. This can be correlated with ice on the study area in January and February and in June with hot sunny spells, after a cold May.

FIG. 19.

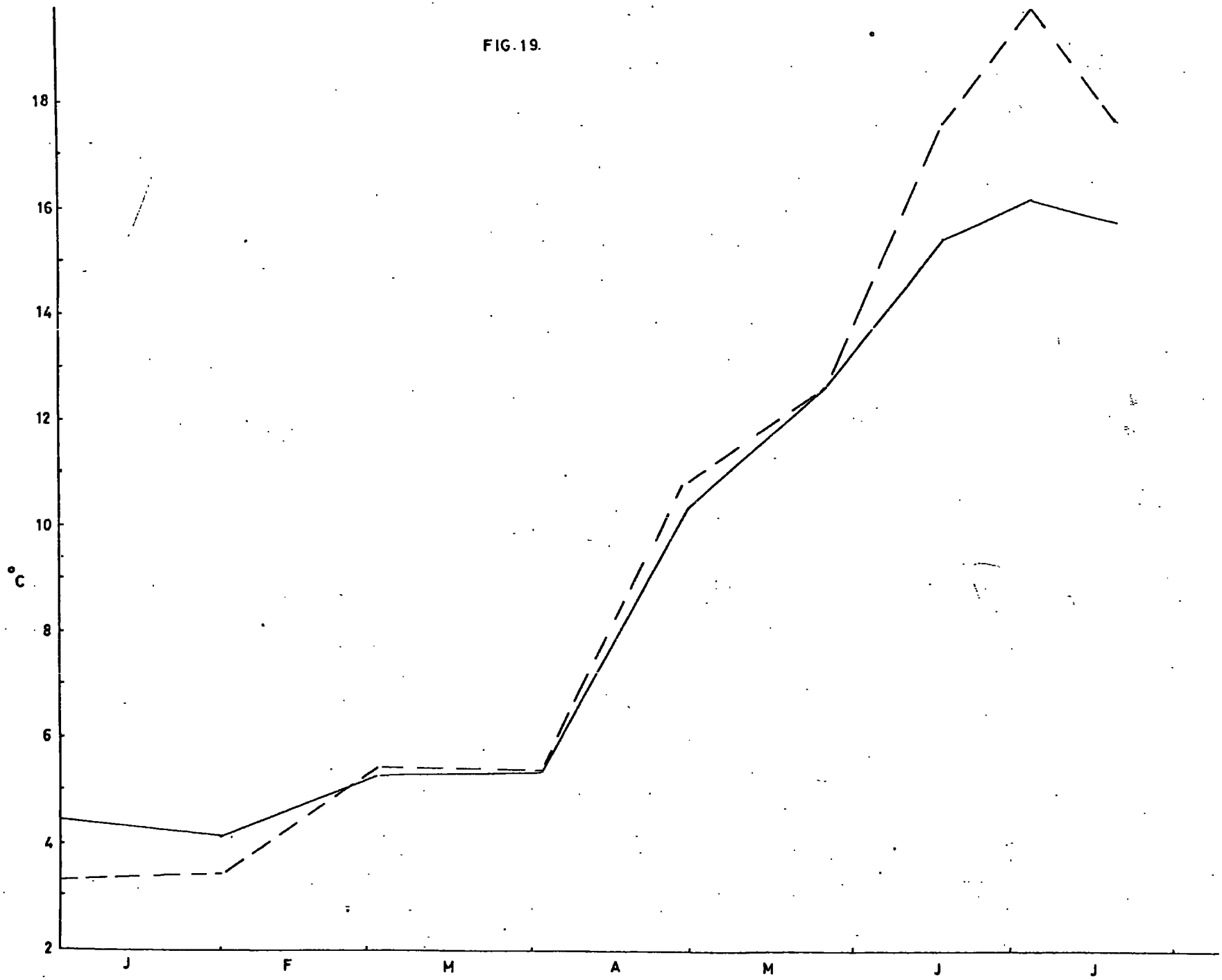


Figure 20 shows the relationship between water temperatures at 25 cm. depth and air temperatures for 1967 as obtained from Durham Observatory, which is 4 Km. to the south west. The water temperatures were consistently lower than the mean air temperatures for January, February and March and 2 - 3^{o}C higher for the rest of the period of study. The 1966 air temperatures are included for comparison.

g. Reproduction.

An attempt was made to estimate the production of the population as a result of reproductive activity and to assess the size range of the breeding population to determine what percentage of the total population were giving rise to this production.

Egg capsules were found on June 8th and newly hatched snails were found in the study area slightly later in the month. This indicates that oviposition, in any intensity, only commenced in late May. Oviposition never occurred in the laboratory, so it was not possible to ascertain the total capsule production per individual.

In July, an estimation of the minimum size of breeding individual, using the development of the oviduct as a criterion for determining it, was tried. From this, individuals down to 5.5 mm. appeared to be in breeding condition. Therefore the majority of the 1965 and 1966 generations were breeding.

Table 13 summarizes the results obtained for size of capsule, no. of eggs per capsule and size at hatching obtained in June and July in the field and laboratory.

FIG. 20.

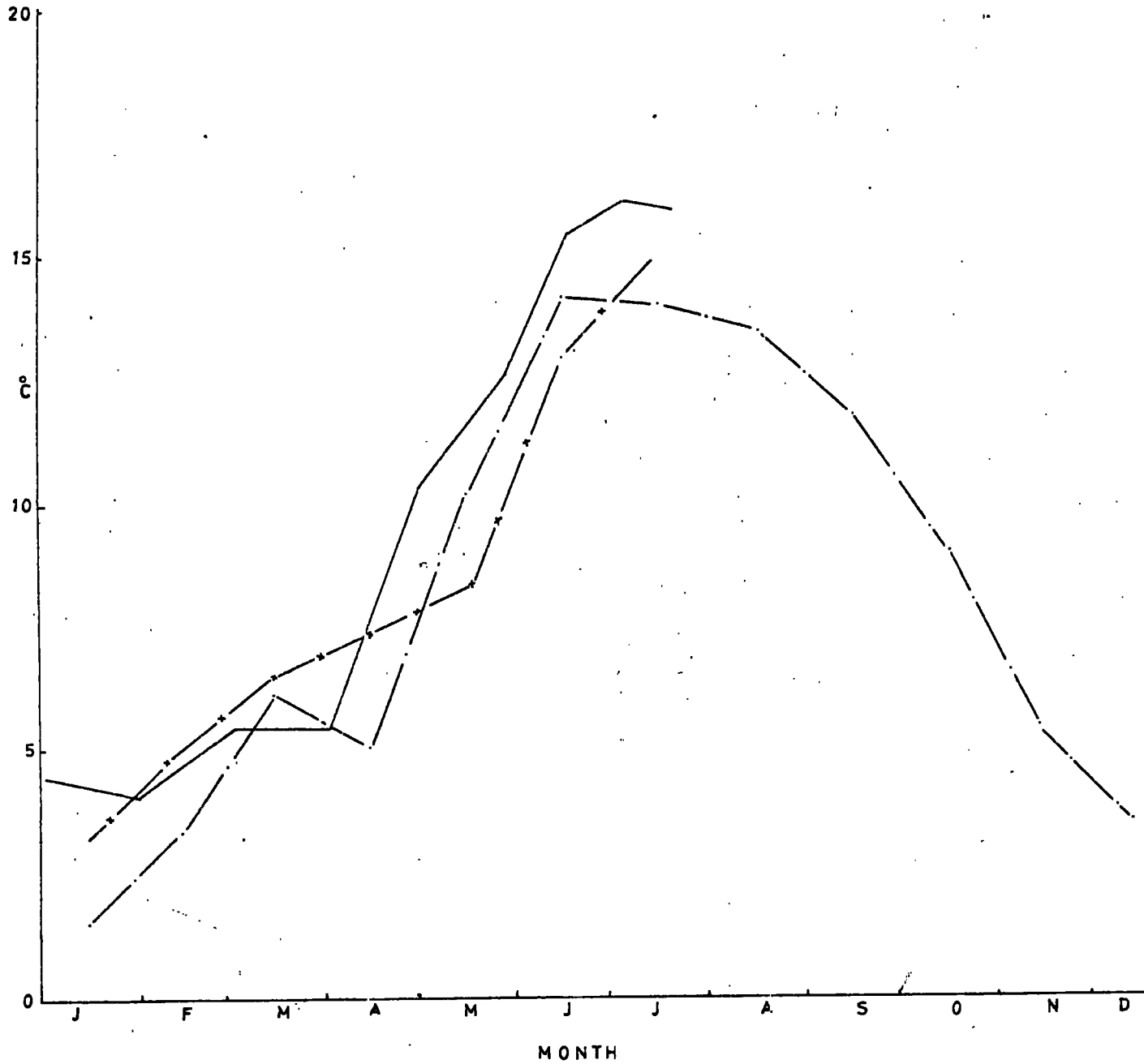


Table 13.

Size of capsule	Mean no. eggs/capsule.	Time for hatching in lab.	Mean size at hatching in lab.
8 mm. (diam.)	8.1 $\pm$ 3.0 S.D.	14 days	0.635 $\pm$ 0.135 S.D

Without an estimation of total capsule production, these results could not be used to quantify reproductive production for the population.

h. Energy budget.

Without a monthly estimate of mortality, it was impossible to follow the month to month changes in the energy flow in the population accurately. It was decided to take the mean total population estimation for summer as calculated in section a. of the results, and use this as an approximation of total population for the study area. Using this number, the standing crop and respiratory loss per day in the study area was calculated for those months that showed the best fit of field temperatures to the laboratory conditions under which oxygen consumption was measured.

Table 14 shows the data used for calculating the standing crop in Kcal. and respiratory loss as Kcal. per day in February, May and July for the study area.

Calorific value of snail tissue = 3.7454 Kcal./gram dry wt.

Oxycalorific value. = 0.005 cal./cu. mm. O_2

Size class.	No.	February. Grams dry wt. tissue	O_2 consumption Kcal./day.
3-4 mm.	1,351	0.8917	0.0414
4-5 mm.	3,191	2.8400	0.1322
5-6 mm.	4,542	5.4504	0.2570
6-7 mm.	733	1.1875	0.0567
7-8 mm.	2,573	5.6349	0.2313
8-9 mm.	7,158	21.2593	0.7530
9-10 mm.	5,376	21.5040	0.6634
10-11 mm.	2,702	14.5908	0.3896
11-12 mm.	604	4.3911	0.1020
12-13 mm.	345	3.3810	0.0695
13 mm.	115	1.3409	0.0251
Total	28,747	82.4716	2.7212

In February: standing crop in study area = 308.889 K cal.

respiratory loss in study area= 2.7212 K.cal./day

∴ The respiratory loss / day = 0.88% standing crop in K.cal.

Size class	No.	May Grams dry wt. tissue	O_2 consumption K.cal./day
3.75 mm.	86	0.0808	0.0117
4-5 mm.	1,092	1.2012	0.1617
5-6 mm.	4,945	7.3186	0.8540
6-7 mm.	4,341	8.3781	0.8600

Continued:

7-8 mm.	3,277	8.2253	0.7439
8-9 mm.	8,049	26.2397	2.0919
9-10 mm.	4,686	19.8686	1.3960
10-11 mm.	1,984	10.8723	0.6752
11.25 mm.	230	1.5364	0.0867
Total	28,747	83.721	6.8811

In May: standing crop in study area = 313.568 K.cal.
respiratory loss in study area = 6.8811 K.cal./day.
Respiratory loss / day = 2.2% standing crop in K.cal.

July

Size class.	No.	Grams day wt. tissue	O_2 consumption K.cal./day
3.75 mm.	29	0.0273	0.0046
4-5 mm.	115	0.1265	0.0203
5-6 mm.	1,409	2.0853	0.3050
6-7 mm.	5,031	9.7098	1.3066
7-8 mm.	7,560	18.9756	2.3496
8-9 mm.	7,934	25.8648	2.9475
9-10 mm.	4,887	20.7209	2.1732
10-11 mm.	1,667	9.1352	0.8835
11-12 mm.	86	0.0613	0.0546
12-25 mm.	86	0.0749	0.0626
Total	28,747	86.7816	10.1075

In July: standing crop in the study area = 325.0318 K.cal.
respiratory loss in the study area = 10.1075 K.cal./day.
Respiratory loss / day = 3.1% standing crop K.cal.

In table 14, the changes in standing crop, expressed in Kcal. from month to month, shows the increase in energy content of the population in the three months as a result of bodily growth within the population. The change in respiratory loss from February to May shows the result of increase in temperature, growth and reproduction on the metabolic activity, while the change in respiratory loss from May - July shows the effect of temperature alone on the metabolic activity.

In order to get an estimate of the energy flow over the period of study, the respiratory loss was calculated for December, January , February and March, using the loss in K cal./day calculated for February. This seemed justified as no growth was occuring over the period and the temperature conditions were similar. The respiratory loss for April and May was estimated using the May figure as growth had started by April and the temperature, 10.78^{o}C, is about the mid one of the temperature range over the two months. The respiratory loss for June and July was calculated using the July estimate, for similar reasons. The respiratory loss was calculated in Kcals./total area and as Kcal./ m^2.

Table 15 shows the respiratory loss for the study area expressed as Kcals./total area and Kcal./m^2 over the period of study.

Table 15.

Months	Respiratory loss K.cal./total area	Respiratory loss K.cal./m^2.
December - March	147.4	0.67
April - May	433.4	1.97
June - July	616.0	2.80
8 months of study.	1,186.8	5.44

As there was no growth over the winter months, the February figure for biomass present in the study area was used as the initial biomass present in December, while the final biomass was given by the July figure. The difference between those two represented the production from bodily growth over the period of study. Therefore production (bodily growth) = 16.14 K.cal for the whole study area or 0.073 K.cal./m^2.

Unfortunately there was no possible estimate for production due to reproduction and the figures, so far given, do not include recruitment for 1967.

Therefore, for the period of study, the quantification of the energy flow equation was as follows:

Food assimilated = Respiratory loss + Production (bodily growth) + Production (reproduction)

= 1,186.8 + 16.14 + P(r) Kcals.

= 1,202.94 + P(r) Kcal./total area of study.

The above equation expressed in terms of energy flow per $m.^2$ is,

Food assimilated = 5.513 + Pr Kcal / m^2.

This result indicates how small a proportion of the energy flow is channelled into bodily growth in comparison to respiratory loss within any population.

Discussion.

Among author's, who have used net sweeps for sampling gastropod mollusc populations, are Duncan (1959), who was only trying to estimate size frequency distribution changes with time and not changes in numbers, and Morphy (1966) who used them in the same study area as the present one. He obtained consistent results with repetitive sampling at two fixed stations over his period of study.

His highest numbers were in December and these declined to a low level in February where they remained until recruitment commenced in July. In the present study, the results from net sweep sampling demonstrated that the method was not satisfactory for reflecting total population changes with time. The probable explanation lies in the behaviour of the snails themselves. In winter, when temperatures were low, the snails were not active and tended to bury themselves low in the benthic vegetation or in the mud, and so a smaller proportion were captured with the net than in summer. In summer, because of the higher temperatures, there was less oxygen dissolved in the water and the snails were more active, so, in order to satisfy their metabolic requirements, they had to come to the surface more frequently. Also, with the growth of vegetation in spring, there was a greatly increased surface area to browse over. The changes in numbers in spring in the open subsection could be directly correlated with the growth of Potamogeton and Eleocharis in this area. This meant that, not only was there an increased browsing surface area but, the vegetation also provided a route to and from the surface for air exchange. The effect of temperature was particularly obvious on the two occasions during mark and recapture sampling, when there was thin ice on the pond. On both occasions, low mean numbers per sample unit were obtained relative to numbers on previous ice free days in the same month. The net may also not sample the differently vegetated areas equally efficiently. Particularily low numbers were recorded in March but, as March and February were very similar in temperature, it is not likely that the low numbers could be explained on grounds of temperature. March was very windy and there was wind on the sampling day, which was not the case in February. As the study area is shallow, the effect of wind will be appreciable at all depths and this would discourage the snails surfacing or actively moving in lose vegetation. The more consistent results for May, June and July can be explained by the fact, they were all collected on calm, warm days and the vegetation cover was much more similar for these months.

Mark and recapture was used on a snail population by Eisenberg (1967) to estimate the total population of Lymnaea elodes say in pens of 5 yds.^{2} area. He records that consistent results were obtained but that other estimates indicated that the method was not suitable for the pen populations so he changed to a destructive total population estimate method. In the present study, mark and recapture was also found to be unsatisfactory for estimating total population. This poses the question of whether, the basic assumptions for the use of mark and recapture are valid for a snail population or whether, the experimental procedure was at fault. The basic assumptions in a mark and recapture study are as follows: one, that the marked individuals redistribute themselves at random within the time between marking and resampling; two, that no animals move in or out of the area in the time interval; three, that mortality for marked and unmarked individuals is equivalent or negligible and; four, that there is no bias in the method of sampling that favours either marked or unmarked individuals within the population. As sampling was by net, all the possible subdivisions of the population, marked and unmarked, should have been sampled without bias but there is the possibility that the handling caused different behaviour in the marked individuals, as the time interval was only three days. The snails were scattered randomly in the sample area, so had only to achieve random distribution in the vertical plane in the time. The small time interval was to reduce movement in and out of the sample area, between marking and recapturing, and because of the possibility of this being a reason for the poor recapture percentages, the March series of mark and recapture were made to allow for it. The results of this series did not demonstrate anything convincingly. One source of error, though, was observed; if it were windy when snails were returned to the area, a few might be caught in the surface film and blown away before they could sink. Lastly there was the possibility that the proportion marked was too small to give reasonable results,

as theoretically 10-15% of the population to be estimated, should be marked. The poor results could well be the fault of the method of sampling for reasons already discussed, in which case the other factors are of lesser importance. The conclusion is that, though mark and recapture for snail populations is attractive in theory, it has not, as yet, been applied satisfactorily.

The results from the sample population at the beginning of February and the total population calculated from part of the recapture data show that the former was a third of the latter. Despite the unreliability mentioned above, this at least indicates that the sample total population is far too low. Without the month to month changes in total population, an estimation of mortality could not be made over the period of study. Even with few predators, there must be an overwinter mortality so there should be a decline in true numbers between February and May as recruitment did not appear until July. Eisenberg (1967) estimated a mortality of 93-98% in newly hatched individuals of Lymaea elodes. The recruitment in July is probably too low (see section a. of the results) but, if Eisenberg is correct, it indicates a very high production of eggs in numbers. Thus mortality in snails probably approaches a Deevey (1947) type III curve. However, Hunter (1961b) notes that in a number of fresh water snails, there is a heavy post breeding mortality. Despite the uncertainty of knowing the relation between the present population estimate and the true population, for the purpose of estimating an energy budget a mean sample total population in summer was taken as an approximation.

Haskin (1954) reviewed the methods of age determination in molluscs and concluded that size frequency distribution could only be used satisfactorily, if it was checked by marking individuals, because of the possibility of there being more than one generation in the year and the amalgamation of older

age groups, when the numbers were small and growth rates slower. The results from the size frequency histograms indicated in this study, that there were two overlapping groups, throughout winter and spring. The groups were separated using Harding's analysis for polymodal distributions, which assumes a normal distribution for size frequency within a group. Considering the growth rates obtained in this study and the length of the period of ~~our~~ ovi-positioning, it is unlikely there was more than one generation in a year. The possibility that there is more than one generation in the largest group cannot be completely discounted.

Boycott (1936) states that the life span of Pl.planorbis is 9-15 months. Morphy (1966) decided that the life span for this population of Pl.planorbis was 20 months and only one breeding season. Hunter (1961) concluded that, in many species of fresh water snails, there was a considerable intraspecific variation in life span, season of breeding and minimum size of breeding individual between different populations. This means that extrapolation of results from one population to another may be completely unjustifiable. This makes Morphy's results very interesting, as they indicated a considerable difference between 1966 and 1967 in the same population. He concluded that the 1964 generation died out completely by late February and that, thereafter, the mean size of the population, its structure and numbers remained fairly constant until July. He associated the heavy mortality with the severe conditions in late 1965/early 1966. This could account for the heavy drop in numbers but would not explain the time of dying of the oldest generation. A possible explanation of the different results obtained, lies in the methods of sampling used. Morphy used fixed stations while stratified random sampling was used in this study.

If size frequency distributions were plotted for different sampling sites in any one month, there was often considerable divergence from the mean distribution for the whole pond. The anomalous results for growth in the early months of the present study, could be accounted for by this, as fewer samples were taken initially. If Morphy is correct, either the large group in 1967 can only be 1965 generation snails. The conclusion from this study is that the life span is at least twenty six months for Pl.planorbis in Brasside pond.

Duncan (1959) correlated onset of growth in a population of Physa fontinalis with an increase in air temperature above $7^{o}C$, while Hunter (1961) found no winter growth in a population of Planorbis albus until April. Morphy (1966) came to the conclusion that growth continued in Pl.planorbis throughout winter, despite the adverse weather conditions. The results in 1967, which was warmer over the winter period than in 1966, indicated that there was either very slow growth rates or none until April, though the growth results over the winter months were not completely consistent. The onset of growth could be correlated with the rise in air temperature in April. From April to July, the growth rate in the 1966 generation was considerably higher than in the 1965 generation. The latter could be an artefact caused by the dying off of the largest individuals after breeding but, this seems unlikely to be the complete reason, as no snails larger than 13 mm. were found in the study area, while the maximum size for the species is 18 mm (Macan 1960). This indicates that, possibly, environmental factors are reducing growth rate in the snails so that 18 mm. cannot be reached before they die. Other possible explanations of reduced growth rate have been advanced. Hunter (1961) in a Physa sp. population reckoned that growth rate in the larger individuals was reduced because of the relationship between increase in metabolic requirements and area of respiratory surface with increasing size, but as larger Pl.planorbis were to be found in a neighbouring pond,

this seems unlikely in this case. Eisenberg (1967) came to the conclusion that food shortage was a limiting factor in his population. This shortage was meant to be a lack of high class food rather than an absolute shortage, as there was ample macrophytes and detritus present. This is a possibility but it is very difficult to prove. Also it is a fashionable concept in ecology at the present moment.

Duncan (1959) mentions that in Physa sp development of the female reproductive system occurs in spring. This could explain the differences in dry weight of tissue in the size/dry weight conversions for winter and summer in the smaller individuals that had not bred before.

The only other determination of the calorific value of molluscan tissue, known to the author, was that of Paine (1965) on a marine nudibranch. His value of 3.763 $\pm$ 0.166 S.D. K.cal./gram dry weight of tissue is very close to the value of 3.7434 $\pm$ 0.599 S.D. obtained in this study, though the standard deviations in his study was much smaller. On the other hand, he made only five determinations and no attempt was made to determinate variation between size classes or seasons. The results for Pl.planorbis did not show that there was either seasonal or size differences in the value but the variation could have mashed them. To a large extent, variation could be correlated with the size of pellet used. The microbomb is capable of giving consistent results with pellets of 1 mg. but consistent results were only obtained after a considerable period of practising the technique. Therefore, the variation in this case might have been lack of practise. A common source of variation is if the ignition is done when the bomb is not in temperature equilibrium and so is either gaining or losing heat. Careful scrutiny of the recording potentiometer graphs, however, did

not indicate inconsistencies in the firing point. A second source of error is in weighing the pellet as it takes up moisture as soon as it is exposed to the atmosphere. This probably accounted for some of the variation. Lastly there is the possibility that small pieces of shell might have been accidentally included in the material. As the combustion of calcium carbonate is endothermic this would result in too low a result for the weight of pellet.

Hunter (1953) came to the conclusion that all snails, when subjected to handling and in shallow water in the laboratory, became air breathers while this was not always the case in their natural habitat where they might have a water - filled lung or a permanent bubble of gas, that was never renewed and acted as a physical gill. This might invalidate the assumption made in this study that the use of an apparatus, which made the snails respire in a saturated atmosphere, resembled the conditions in the mantle cavity. However in this study area, the water is shallow and most snails observed, except for a few small 1967 generation snails, had their mantle cavities air filled. Also observations of snails coming to the surface to exchange air were made. If,at low temperatures, the snails used the bubble of air as a gill, this does not invalidate the original assumption. It is concluded, therefore, that for this Brasside population of Pl.planorbis, the method used for measuring the oxygen consumption was at least as realistic as a method that forced the snails to be submerged with water filled mantle cavities.

None of the figures for respiration in the literature are for Pl.planorbis. Berg (1959) used a variety of pulmonates, and the closest, phylogenetically, was Lymaea peregra. At 18^{o}C., an individual of 120 mg. live weight (minus shell) had an oxygen consumption of 734 l. O_2 /day. For a Pl.planorbis of about 35 mg. live weight (minus shell) at 14.73^{o}C, the oxygen consumption was 116 l. O_2 /day. Because of the effect of size on

oxygen consumption per unit weight and inter specific variation, the validity of comparing results is questionable.

In this study, the results for each period encompassed a small temperature range. These could have been corrected to constant temperature, using Krogh (1916)'s curve, but the conditions under which Krogh obtained the relationship which was for a basal metabolism, bore no realistic comparison with the conditions under which oxygen consumption of active metabolism was measured in this study, so the results were left uncorrected. For an energetics study, as there is daily variation in temperature in the field, the temperature variation was not important as long as the mean temperature in the laboratory could be related to a mean temperature in the field. During the respiration experiments, the animals were starved but no starvation effect was shown over the 48 hours. Berg (1959) only found starvation effects in two of the species he studied. As the experiments were carried out over more than 24 hours, the oxygen consumption measurements eliminated the effects of variation in oxygen consumption at different times of day. As more than one individual was used in each experiment, this should have reduced intra specific variation between animals of the same size. The results, for the three groups of results, were plotted as mean oxygen consumption per individual per 24 hours against total live weight in winter and dry weight of tissues in the two summer groups, both on log. scales, and the regressions were calculated. Phillipson (1963) criticises this manipulation of the results, on the grounds, that it assumes a linear relationship that is not even proved by a high regression coefficient. An alternative mode of expressing the results is by plotting the oxygen consumption per mg. dry weight of tissues per twenty four hours against size.

The former method was used in estimating respiratory results for the population as it gave a better fit of data.

The results for respiration in the three groups, demonstrated the importance of measuring respiration at different seasons as well as at different temperatures, for energetic studies. The factors calculated for seasonal change were largest in the smaller size classes, which are growing at a faster rate than in the larger size classes; while between May and July when, there is no seasonal change only temperature change, the variation between size classes is much smaller.

The pond temperature measurements show considerable variation between surface and 25 cm. depth at two periods. The winter difference is associated with the presence of ice part of the time, the break down of the difference between April and June is probably a result of the windy spring and cool, wet May. In June, calm, sunny spells caused the reappearance of the divergence. As there was the possibility that the higher temperature at the surface in summer was partly caused by the tubes being temporarily exposed to direct radiation, as a result of fluctuations in the surface level of the pond, the 25 cm. results were used to relate laboratory results in respiration to those in the field. If one considers air temperature to water temperature over the period of study, the former was consistently lower than the latter over winter, and warmer over spring and summer, demonstrating the dampening effect, of even a small water body on temperature fluctuations. The only inconsistency is in April, when the April pond temperature seems rather low compared with the air one. In 1966, the mean air temperature was lower in January February and April and higher in the rest of the months.

Duncan (1959) notes that a generation of Physa fontinalis would breed in one year but not necessarily in another, even if the individuals were similar sizes, so there may be considerable variation from year to year. The estimation of a minimum breeding size of 5.5 mm. in July suggests that the majority of the 1966 generation did breed in 1967. Bondesen (1950) records similar figures for Pl.planorbis, as obtained in this study, for size of capsule, number of eggs/capsule and size at hatching.

The only other estimation of respiratory loss in a gastropod in a fresh water pond, known to the author, is that of Teal (1957) in a constant temperature spring at 12°C. He estimated a 47.3 Kcal./m^2/yr, which could be compared with the May figures in this study at 10.78°C which, if calculated in the same units, give a respiratory loss of 11.81 Kcal/m^2/yr. However, Teal's results were not calculated from data collected for the particular species and there is undoubtedly considerable intraspecific variation. In Odum and Smalley (1959), the respiratory loss of a salt marsh gastropod is given as 246 K.cal./m^2/yr. In a specialised habitat like a salt marsh, the diversity of species is small so the very high respiratory loss/m^2 in this case is probably the result of the major part played by the gastropods in this habitat. In Brasside pond, the conditions are more stable and there is a much more diverse community of animals.

In this study, because of the failure to get an accurate estimate of initial total population or changes in population with time, an accurate quantification of the energy flow equation was not possible. As has been already discussed, the figures used for the mean total population approximation are probably far too low, so the estimation of the contribution of Pl.planorbis to the energy flow in the whole pond will similarily be too low. The

results seem to indicate a fairly small biomass of Pl.planorbis in the study area, but as it shares the role of main with Lymnaea, Asellus and Cloeon, the other numerous species present in this category (see Appendix 1.) it must play an important part in the energy flow at the herbivore level. From the faunal list (Appendix 1.), it can be seen that the number of predators are small so mortality is probably low and the life span is two years. Therefore much of the production of growth and natality will not be released into the energy flow until the snails die and enter the decomposer chains. Thus, the snail is probably not a good direct promoter of energy flow. This is similar to the position found by Negus (1966) in her study of mussels in the Thames. These mussels have few predators except when small, and a long life span. However, animals that only make a small contribution to energy flow directly may do it indirectly. Edward and Heath (1963) concluded that the contribution that earth worms made to the energy flow in the soil was far greater than indicated by the respiratory loss, because of the changes they produced in the soil and material they consumed. In the study area, Pl.planorbis is an important herbivore and browses on algae and epiphytes generally, and so reduces cellulose to fine particles. From observation, they would appear to have a high faecal production and so the snails probably have a low assimilation efficiency, which is a characteristic of herbivores generally. Thus the snail's main contribution may be in reducing cellulose to a form in which it can more readily enter the decomposer pathways.

The snails also produce another source of energy, which so far has not been considered as it did not come into the experiments. They produce a constant flow of mucus for locomotion. This production should be reflected in the respiration figures but, as it leaves the body at once, estimates of bodily growth do not take it into account. For a complete study, the rate of production of mucus would have to be assessed. The rate is presumably directly related to activity so will vary with temperature. This production is a direct contribution of the snails to energy flow.

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Summary.

1. An attempt to quantify the energy flow equation, food assimilated = respiratory loss + production from bodily growth + production from reproduction, for a population of Planorbis planorbis in a small pond near Durham, was made from December 1966 to July 1967.

2. Mark and recapture methods, for estimating the total population of snails, proved unsuitable. The use of net sweep samples over the period of study did not satisfactorily reflect changes in the total population.

3. For the purpose of calculating an energy budget for the population, an approximation to the total population in summer, was taken as 28,747 snails, using the mean of the sample total populations for the summer months.

4. The life span of Pl.planorbis in Brasside pond is, at least, twenty six months.

5. The size/total live weight and size/dry weight of tissue conversions, were obtained.

6. Bomb calorimetry gave a calorific value of 3.7454 $\pm$ 0.599 S.D. K.cal/gram dry weight of tissue. No statistically significant difference was found between seasons or in different size classes within one season.

7. Oxygen consumption was measured in the laboratory, using a constant pressure respirometer, at 6.2^{o}C in winter and 10.78^{o}C and 14.73^{o}C in summer. The results indicated that the change in season, with associated growth and reproductive activity, had considerable effect on increasing oxygen consumptions, in addition to just the temperature effect.

8. The mean water temperatures in the study area were measured over the period of study, using a sucrose inversion temperature integrator, and the results used to relate laboratory conditions to conditions in the field, for oxygen consumption.

9. Oviposition in 1967 occurred between late May and late July and, in July, the majority of the 1966 generation of snails were in breeding condition.

10. The quantification of the energy flow equation, for the population of Pl.planorbis in the study area over the eight months of

study was as follows:

Food assimilated = 1,186.8 + 16.14 + Production from reproduction in K cals.

The role of Pl.planorbis in promoting energy flow in the study area is discussed in the light of the energy flow equation and other possible indirect contributions of the snails.

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Appendix 1.

Faunal List.

The following list records the main species and groups of animals found in the study area.

a. Primary producers.

Hydra sp.

b. Herbivores.

Hydrobia jenkinsi Smith
Lymaea stagnalis L.
Planorbis albus Müller
Planorbis planorbis L.
Asellus aquaticus L.
Cloeon dipterum larva L.

c. Carnivores.

Helobdella stagnalis (L.)
Copepoda.
Coleoptera
Haliplidae
Notonecta glauca
Corixa spp.
Nepa cinerea L.
Odonata larvae
Pyrrhosoma sp.

Coenagrion sp.

Trichoptera larvae

Culcidae

Chaoborus sp.

Chironomids

Newt.

Toad.

Filter feeders.

Pisidium sp.

Cladocera

Copepoda

Gammarus pulex L.

Decomposers. Detritus feeders and scavengers.

Oligochaeta

Trichoptera larva

Chironomids

Diptera pupa and larva

Helobdella stagnalis (L.)

Gammarus pulex. (L.)

From this faunal list, the only species or groups that have been recorded as eating small or large snails are large dragon fly nymphs, dipteran larvae and newts in lab. conditions (all in Eisenberg, 1967), some Trichopteran larvae and Helobdella stagnalis. The other possibility is birds but these must only be passing as the study area is too small for duck to remain. The majority of the snail tissue must eventually pass to the decomposers and scavengers.