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The population dynamics and bioenergetics of the isopod Asellus aquaticus L. in a small freshwater pond

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The population dynamics and bioenergetics of the isopod

Asellus aquaticus L. in a small freshwater pond

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Contents

INTRODUCTION

It is a fundamental concept of ecology that a minute fraction of the solar energy flows through the living organisms of the earth's ecosystems. Many ecologists believe that the study of this energy flow gives a deep insight into the dynamics and organization of nature.

Early attempts to investigate energy flow were concerned with whole freshwater ecosystems (e.g. Teal 1957, H.T. Odum 1957). Because of the prodigious amount of work involved, however, assumptions were frequently necessary. In an attempt to provide more reliable data later workers concentrated on smaller units such as single species populations (e.g. Phillipson 1963, Weigert 1965), and it was hoped that information for whole ecosystems could be synthesised from the more accurate individual studies. However, in no case was a freshwater invertebrate field population examined, and so the possible sources of error in the earlier, more extensive, studies were never investigated. The present study is an attempt to rectify this situation in part; and to this end a population of the freshwater isopod <u>Asellus aquaticus (L.)</u> was studied between November 1966 and August 1967.

Since a detailed knowledge of the animal's life cycle is a prerequisite for bioenergetic studies, the present investigation may be conveniently divided into two major parts. The first is concerned with an examination of the population dynamics, including the life cycle, whilst the second deals with the physiological processes affecting energy flow through the population.

THE STUDY AREA

The population of A. aquaticus * inhabits one of a system of freshwater ponds (pond C, Fig.1) located near the village of Brasside (Nat.grid.ref.NZ 45/290452). The village lies at a distance of two miles to the north-east of Durham City. The pond basins were man-made and resulted from clay diggings which were discontinued some 20 to 30 years ago. The excavations have since filled with water and now support a rich and varied flora and fauna (Morphy 1965).

Pond C covers an area of 124 sq.metres and reaches a maximum depth of 1.6 metres. These dimensions, as gauged from monthly visits to the pond, remained almost constant throughout the period of study.

* The species was identified by using the Freshwater Biological Association scientific publication No.19. Key to Crustacea : Malacostraca.

Fig. 1.   The study area - Brasside pond system.

Labels within the figure: H, A, I, L, A₁, G, Track, F, C, E₁, E, D, E₂, B, Stream, N., Scale, 0, 100ft.
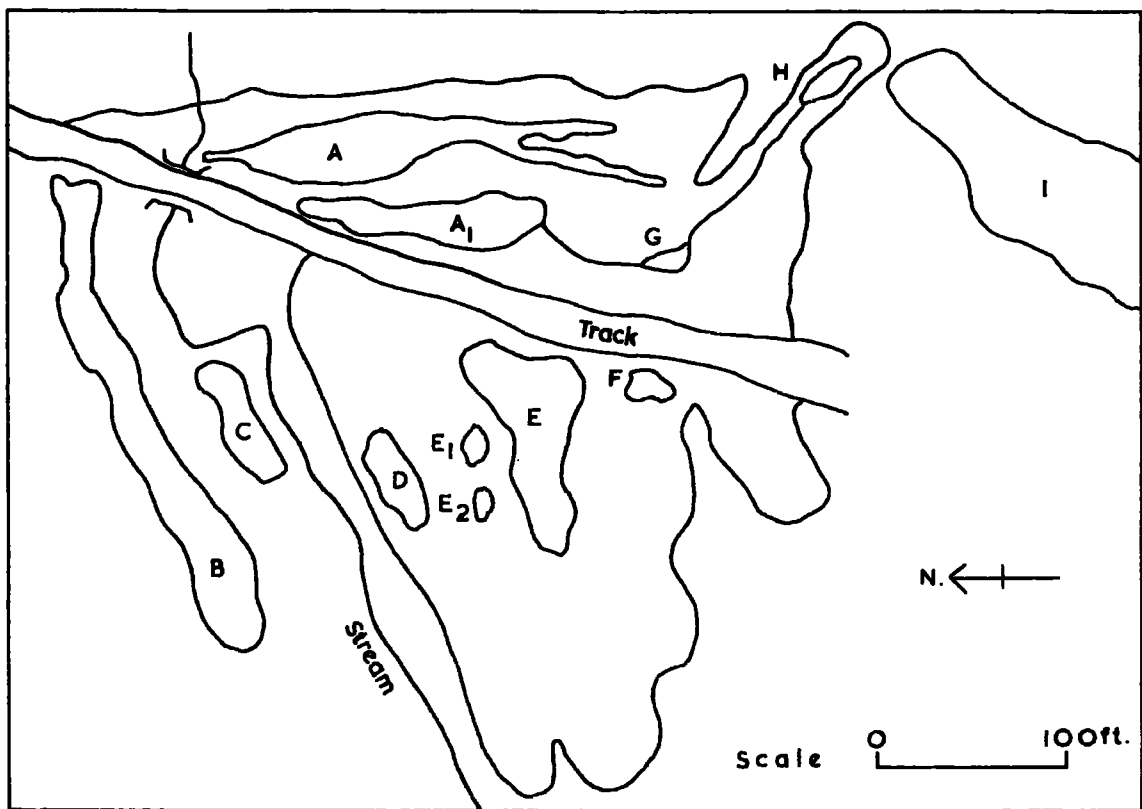
BRASSIDE POND SYSTEM   (After Morphy 1966)

Figure 2 is a plan of pond C showing the plant zonation. A marginal zone of <u>Juncus effusus L.</u> is occasionally interspersed with <u>Salix nigricans Sm.</u>, whilst a narrow band of <u>Alisma plantago-aquatica L.</u> lies to the inside of this and surrounds a large central area of <u>Potamogeton natans L.</u> A few shoots of <u>Typha latifolia L.</u> are evident within the zones described.

THE POPULATION DYNAMICS

Before a study of the energy flow through a population can be attempted, one must have detailed knowledge under two headings. Firstly, one requires a thorough under-standing of all features of the animal's life cycle, and, secondly, one must show how the population changes in size throughout the year.

<u>(i) The life cycle of A. aquaticus in Brasside pond</u>

(a) Size-structure of the population throughout the period of study.

<u>Method</u>

The life cycle of <u>A. aquaticus</u> was studied by taking monthly samples from the pond.

A pond net of sufficiently fine mesh (24 meshes/cm), to retain all sizes of <u>A. aquaticus</u>, was used to remove animals from all the vegetational zones and all depths of the pond. The catch was washed into a white tray

Fig. 2.   Plan of study pond (C) showing the plant zonation.

PLANT ZONATION
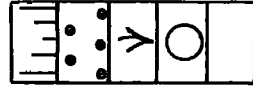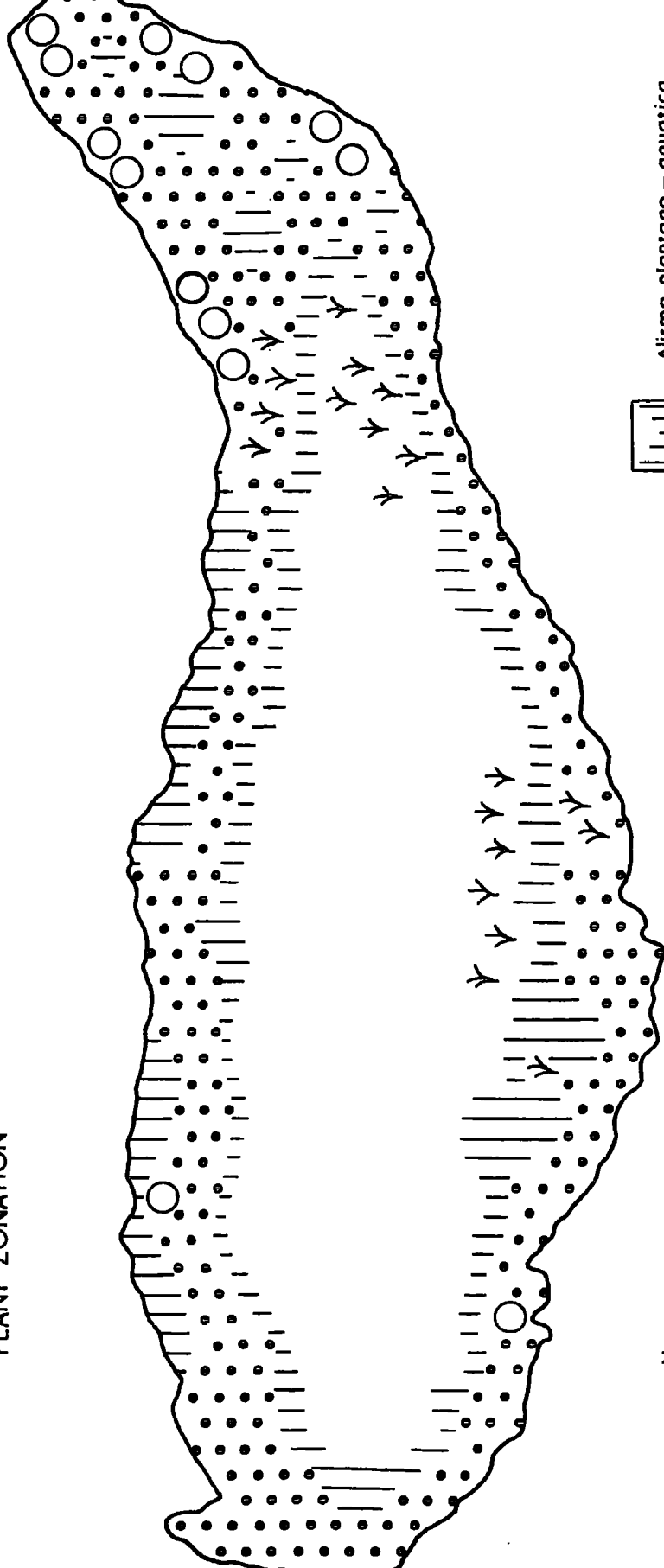
Alisma plantago—aquatica
Juncus effusus
Typha latifolia
Salix nigricans
Potamogeton natans

N ←
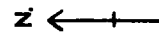
and as many predators as possible removed. The samples were then transferred to glass jars and transported to the laboratory for sorting.

The larger pieces of vegetation were examined individually under a dissecting lens and the animals removed. The water and smaller fragments of plant material were examined a few ccs at a time in a petri-dish. The use of a dark background, oblique illumination, and a lens, rendered even the smallest animals easily visible.

The length of each individual was determined. The live animals tended to assume a position with the back arched antero-posteriorly which made it difficult to measure them accurately. This problem was solved by overturning the animal and gently resting a microscope slide (or coverslip for the smaller individuals) on top of it. The entire length of the animal's dorsal surface thus remained in contact with the substratum. It was then superimposed on squared millimetre graph paper and its length determined using a low-power binocular microscope. The animals were measured to the nearest 0.5mm below, measurement being taken between the base of the antennules and the mid-point of the end of the abdomen (Fig.3).
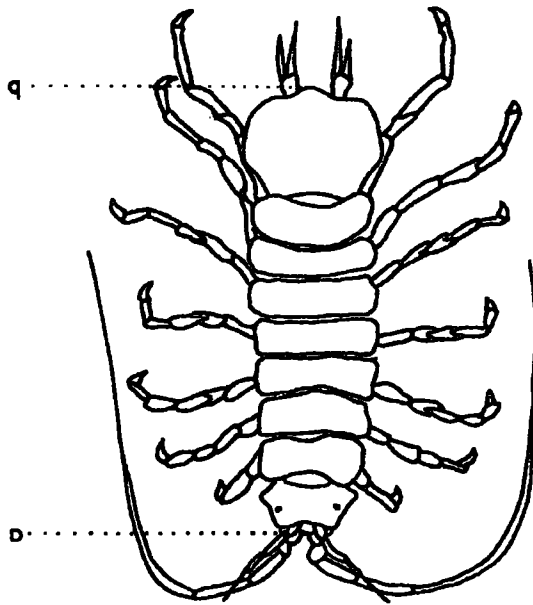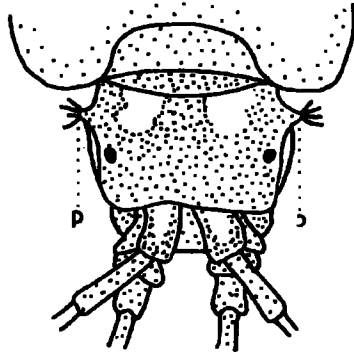
Fig. 3.   Drawings of a whole individual and the

head of Asellus aquaticus.   Length measurements

were taken between points a and b whilst measurements

of head width were taken between points c and d.

After measurement those animals longer than 3mm
were sexed. The sexing of individuals smaller than
this was found to be difficult and unreliable.

After this procedure was completed, all the animals
were returned to the pond to minimize interference with
the habitat.

Results

The results were grouped into 1mm size-classes and
plotted as size/frequency histograms, each size-class
being expressed as a percentage of the total sample
(Fig.4). The life-history of A. aquaticus in Brasside
Ponds was deduced from a number of observations drawn
from these data.

At the beginning of the study in November the
population was bimodal with one peak at 3mm and the
other at 8-9mm. Some growth occurred, especially in
the larger animals, during December and January.
Although the bimodality remained, there was a slight
suggestion that the animals distributed about the longer
length mode showed a further sub-division with a peak at
10mm and another at 12mm in January.

Animals in pre-copula were found for the first time
in the January sample, this being consistent with the
appearance of ovigerous females in February. The
percentage of ovigerous females in the sample increased

SIZE/FREQUENCY DISTRIBUTION.

Ovigerous females.

Nov. n=103.

Dec. n=88.

Jan. n=108.

Feb. n=63.

Mar. n=39.

Apr. n=42.

Length—mms.

May.

n= 93.

Jun.

n=143.

Jul.

n= 61.

Aug.

n= 49.

70
60
50
40
30
20
10

30
20
10

20
10

40
30
20
10
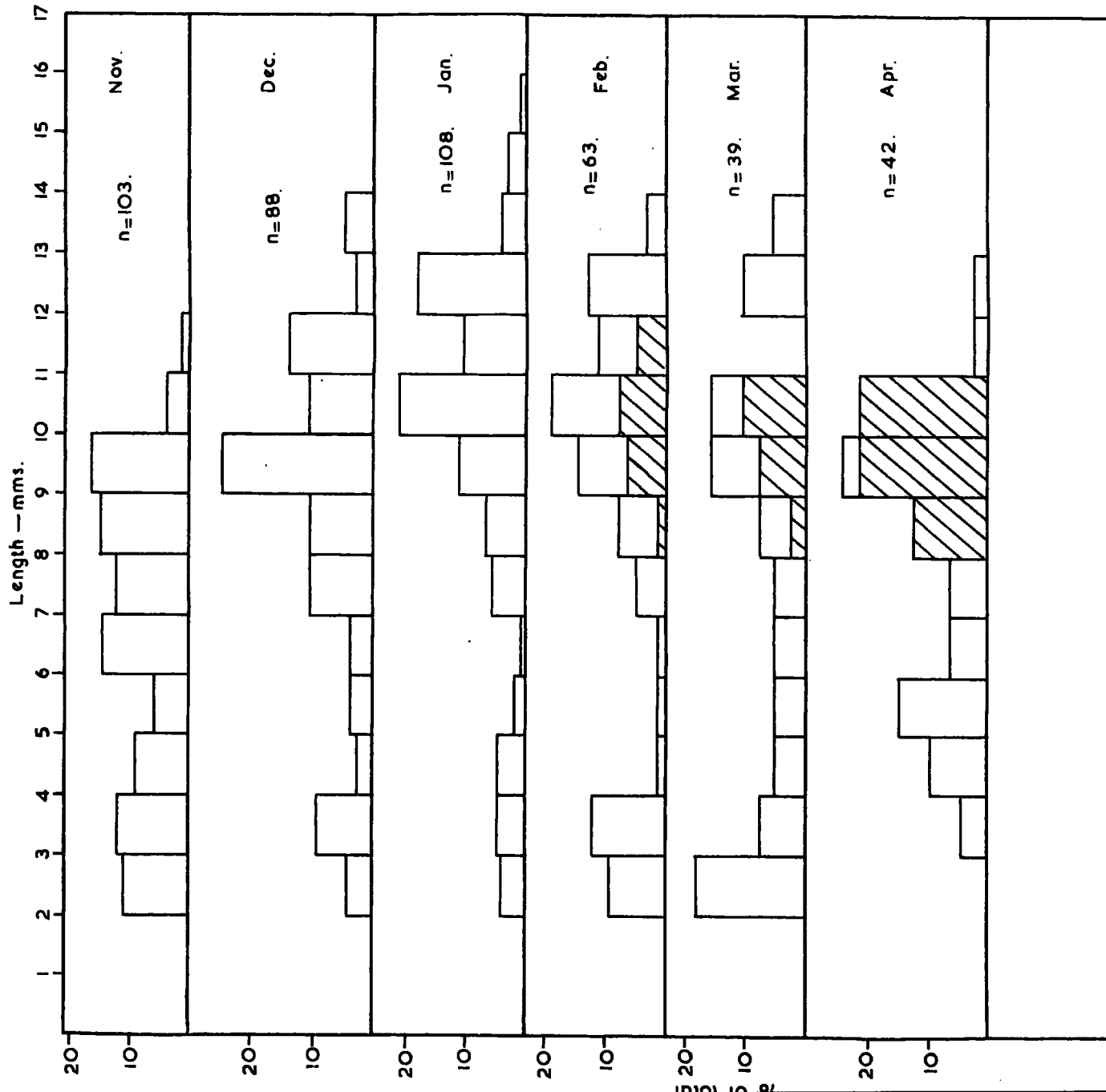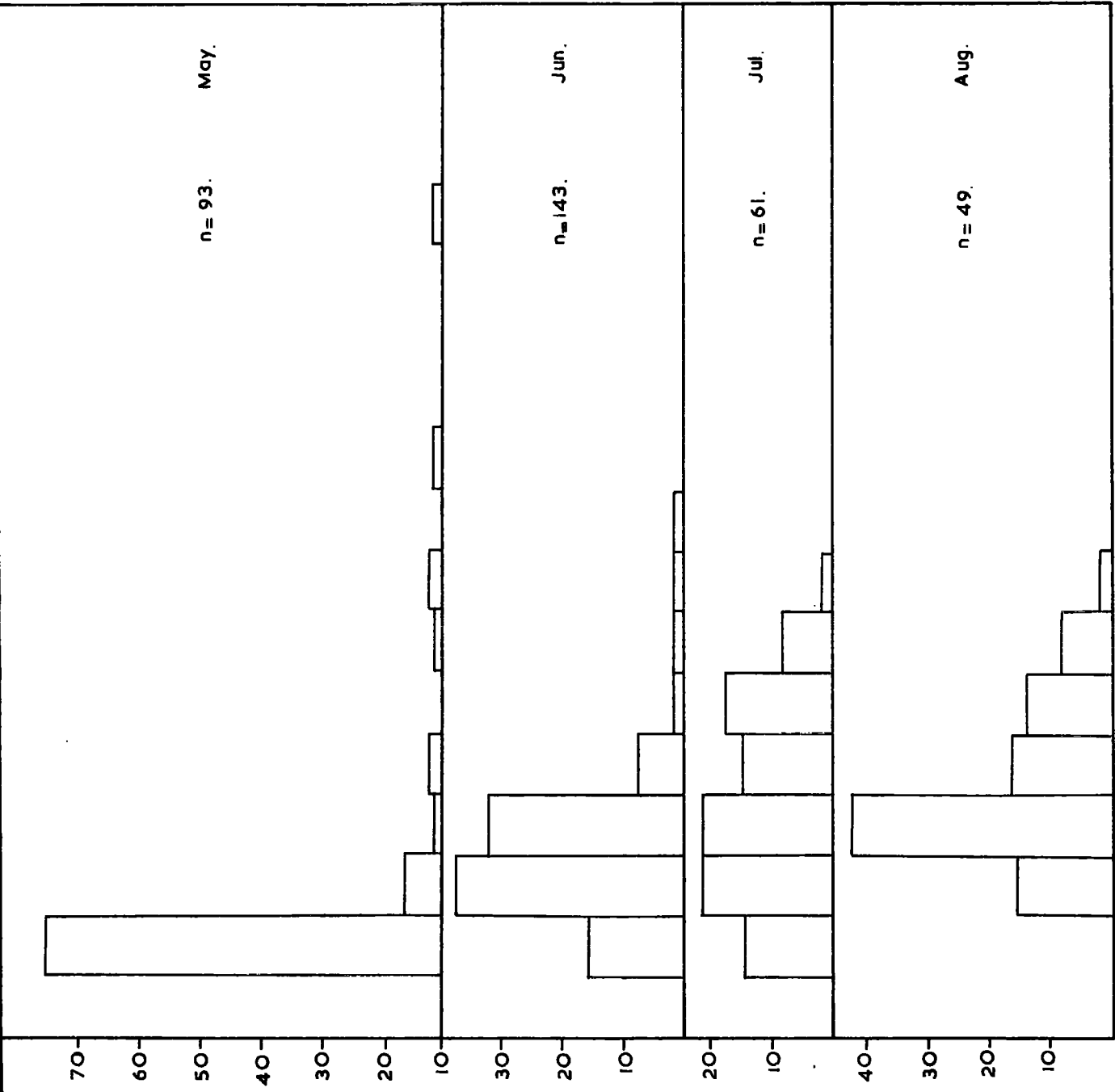
through March to April, and at the same time the 14mm

and 15mm size-classes disappeared.

The May sample revealed a remarkable change in the

structure of the population. The two modes present in

April were lost and a new one appeared at 1mm. This was

due to the influx of a large number of newly-hatched

individuals, and coincided with the loss of most of the

ovigerous females. Only a few remnants of the 1966-67

population remained.

The newly-hatched individuals showed rapid growth,

but animals were found in the 1mm size-class through June

into July because of a continued influx of juveniles into

the population. By August, however, breeding has ceased

and all animals had grown out of the 1mm size-class.

(b) Sex ratio

At each monthly sampling the sex of all individuals

longer than 3mm was recorded. Figure 5 shows how the

numbers of males, expressed as a percentage of the total

above 3mm, varied throughout the year.

The sex-ratio was maintained at approximately 1:1

until January. Following this, however, a progressive

and very marked decline in the percentage of males in the

population was observed. This continued until May when

the population rapidly reverted to the 1:1 ratio.

SEX RATIO

Males as % of total

60 —
50 - - - - - - - - - - - - - - - - - -
40 —
30 —
20 —
10 —

        Dec   Feb   Apr   Jun   Aug
N= 92   85   108   63   39   42   22   27   26   29
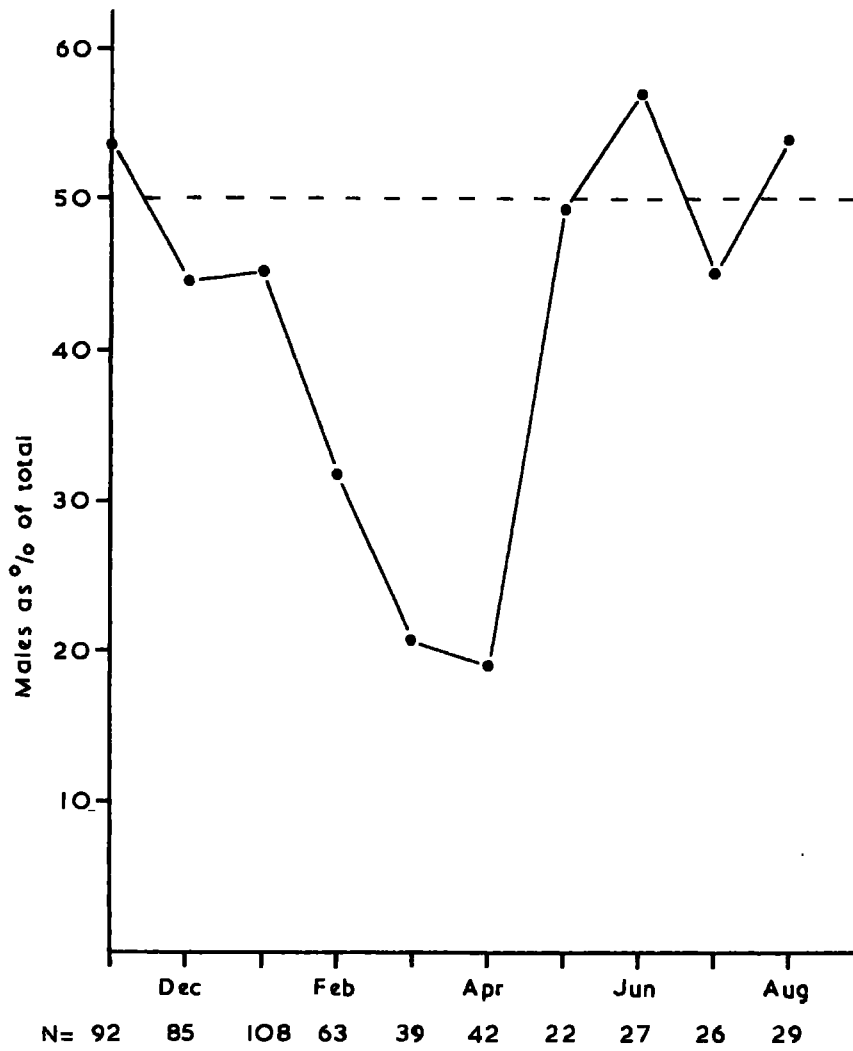
Fig. 5. The sex ratio. The numbers of males present in the monthly samples are expressed as a percentage of the total population above 3 mm in length.

Since no recruitment into the population could have occurred between January and April, the decline in percentage of males must be explained by one of two alternatives. Firstly, the mortality rate in males may have been greater than in females, resulting in a rapid change in the sex-ratio, or, secondly, some difference in the behaviour of the two sexes may have caused an apparent change in the sex-ratio, and the only reasonable example of this is that the males burrowed deep into the mud leaving the females above it. Examination of samples containing mud during the months February to May eliminated the latter alternative, and so it was assumed that differential mortality rates were responsible for the uneven sex-ratio. This is in agreement with the conclusions reached by Steel (1961) whilst investigating the life-history of A. aquaticus.

The disappearance of the 1966-67 population and the birth of the new individuals caused the sex-ratio to return to 1:1 in May.

(c) Growth rate in males and females

The collection of biomass data will be described below, but it will be useful to discuss growth in general terms at this point. Figure 6 shows the change in wet weight per individual expressed as a percentage of the previous month's mean weight per animal. The graph was

VARIATION OF GROWTH RATE
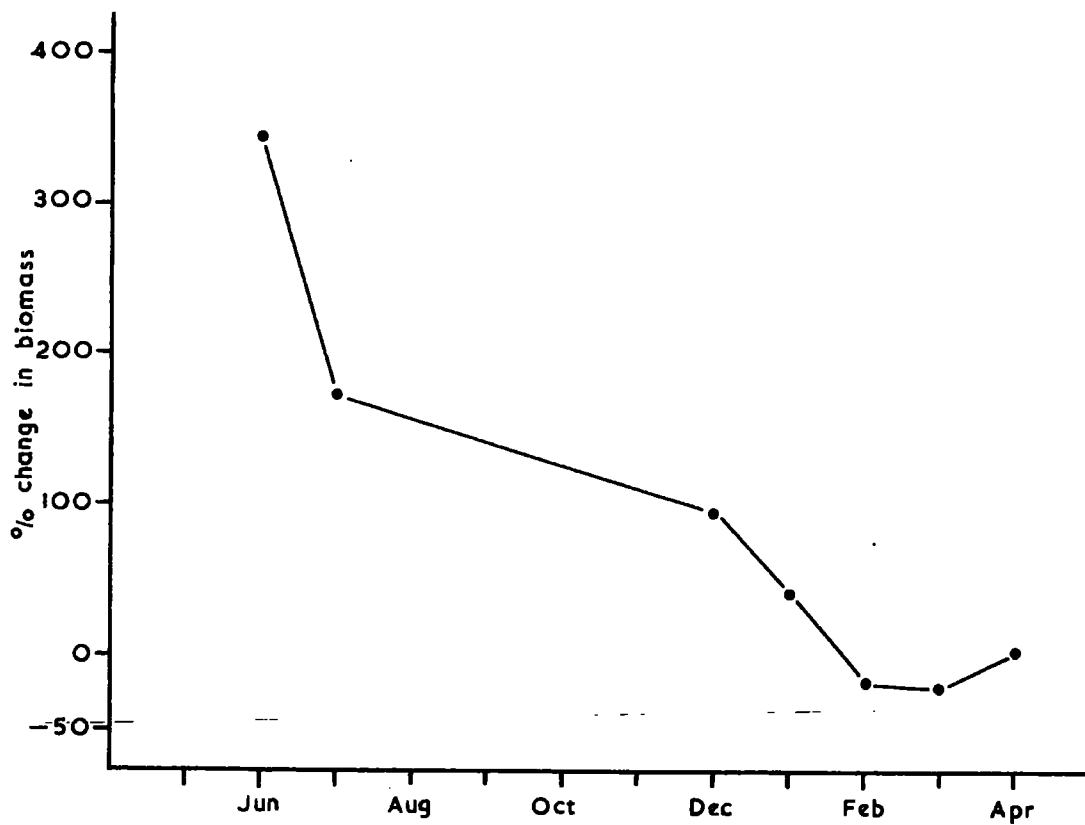
Fig. 6.   The change in mean wet weight per

individual expressed as a percentage of the

previous month's mean weight per animal is

plotted against time.

constructed by combining data for the 1966-67 and

1967-68 populations although the value for June was

calculated ignoring the remnants of the old generation

(see later for explanation).

It can be seen that soon after birth the growth rate

was very high, the mean wet weight per individual being

quadrupled between the May and June sampling dates despite

dilution of the population by very small, newly-hatched

animals. Some growth occurred right through to January,

although the rate declined. The apparent decrease in

the mean wet weight of animals in February and March

(indicated by minus values in Fig.6) was due to a

relatively higher death rate in larger animals. This

was probably linked with the change in sex-ratio noted

above (Fig.5).

It was found, however, that the rate of growth was

not equal in males and females. Figure 7 shows data

collected in February, and compares the length/frequency

distribution for the whole population with the distribution

of the males and females treated separately. Despite the

fact that the male mortality referred to above had proceeded

to some extent, the bimodality of both the male and female

histograms is very strongly emphasized. These data show

that the mode for the larger males lies at 12mm whilst

that for the larger females is found at 9mm. The sex-

ratio data (Fig.5) shows that both sexes hatched

Length — mms.

% of total

Total pop'n.

Males

Females

Ovigerous females
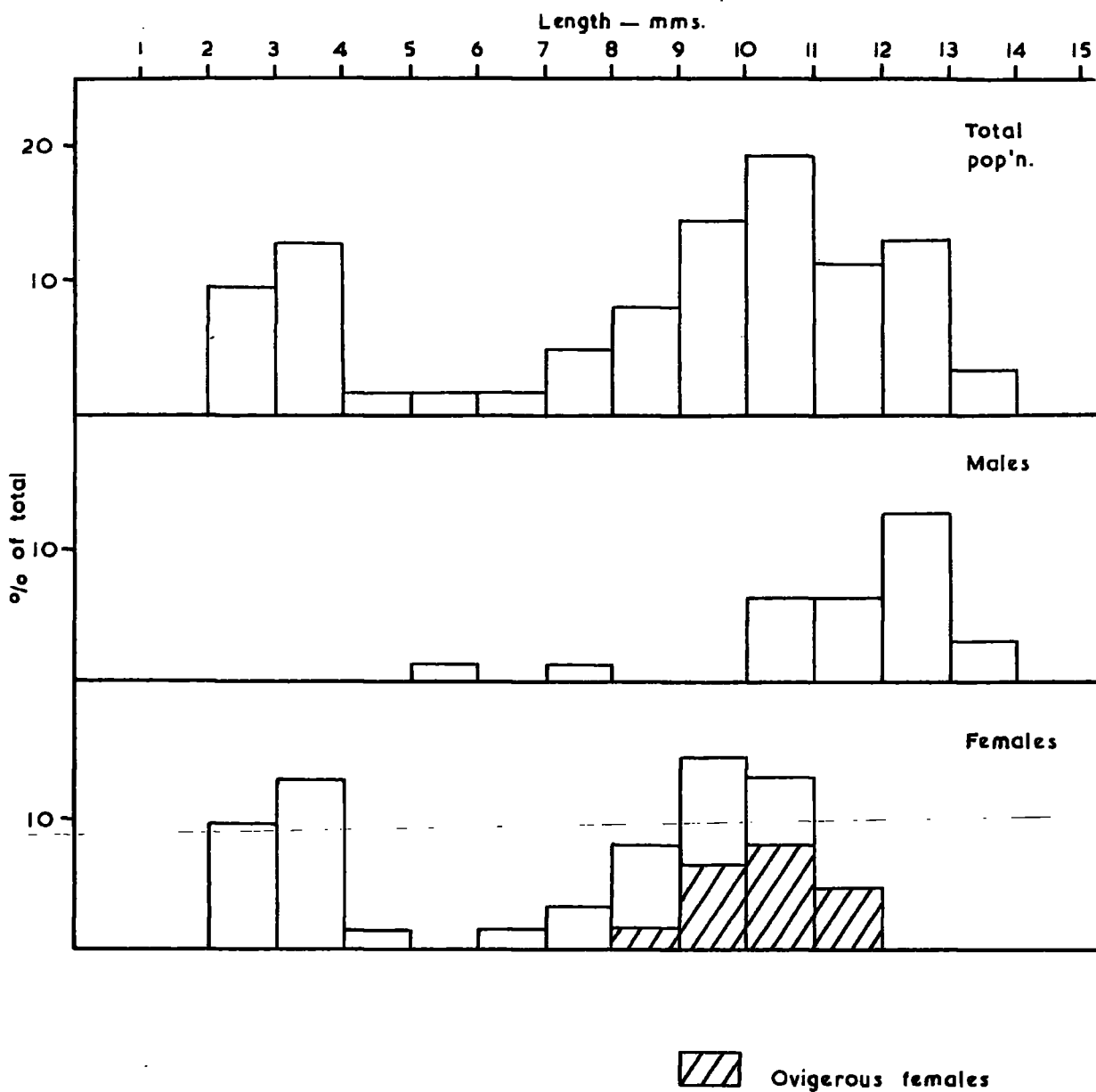
Fig. 7.   Length/frequency histograms for males,

females, and the whole population in February are

compared.   The numbers of males and females in

each size class are expressed as a percentage of

the totøal number of animals present.

simultaneously and thus the length difference must be explained by a higher growth rate in males. The females never make up this difference since the largest female found was11mm and the largest males were 4mm longer.

Figure 8 shows biomass data discussed below (p.27) and emphasizes further the higher growth rate of males. For reasons described below (pp.10,27) the graph is concerned only with those animals distributed about the higher of the two modes possible for each sex. The mean wet weight of these animals is shown plotted against time for the period between the beginning of the study and the time of high male mortality. The graph shows that despite identical hatching times the production of males, in the form of body tissues, was much greater than that of females.

It is probable that this differential between the male and female growth rates is responsible for the partial sub-division of the larger size classes described above for the months December to March (Fig.4). The longer length sub-mode will be largely composed of males whilst the smaller will be predominantly females (see Fig.7).

(d) Summary of the life cycle

Using the data given above, it is possible to explain most of the events in the life cycle of A. aquaticus in Brasside Pond. Only one point is without explanation, and that is the change from monomodality of the population during May-August to the bimodality of the months November-
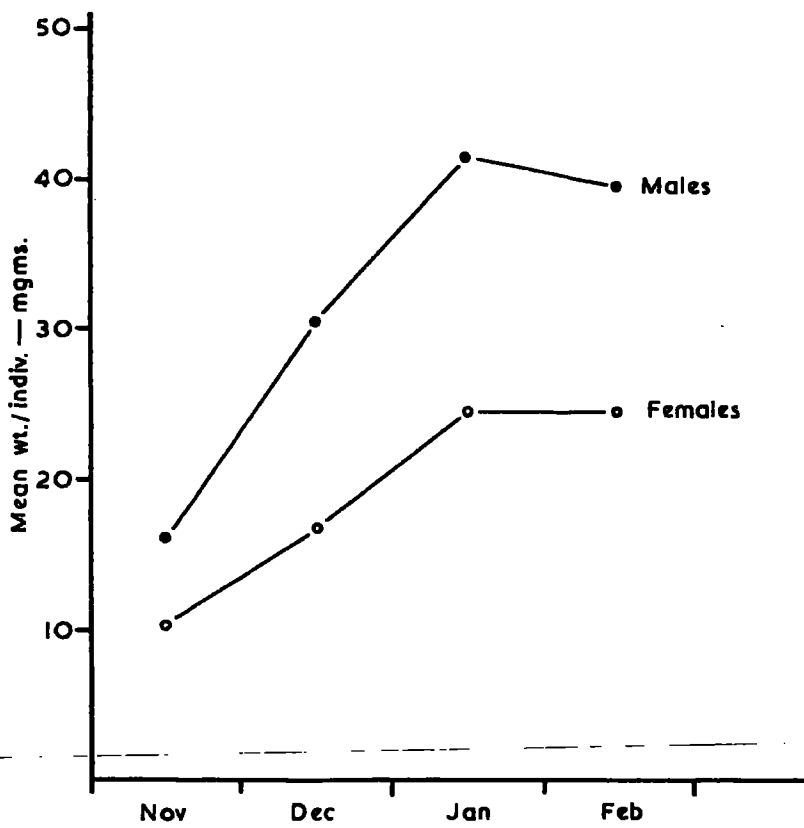
Fig. 8.   The mean wet weight per individual

for males and females is plotted against time.

The graph deals only with animals of generation

I (see text).

April. Unfortunately, the period of transition, September and October, was not covered by the present study. The observations described, however, differ only in detail from the life-histories of other members of the genus and from A. aquaticus in other habitats, thus one can find an explanation in the work of other authors (e.g. Steel 1961). It transpires that the juveniles born in the period May-July, after a period of rapid growth, begin to breed for a brief period in September. Animals may breed when only 3.5-4mm in length. This breeding activity was not detected in the first sample of this study (November). However, it is probable that the production of such a second generation towards the Autumn gave rise to the bimodality of the population.

One may now give a brief synopsis of the life-cycle. During the main breeding season of May-July the first generation of the year is born, and these animals form the major part of the population for the year. The animals grow quickly and then breed to produce a second generation in September and October, this being numerically smaller than the first. Growth continues slowly throughout the winter, but the males produce more biomass than the females (Fig.8). In January the first generation commences breeding for the second time, the males dying soon after

copulation. This male mortality gives rise to the fluctuations in sex-ratio (Fig.5) and also to the apparent decrease in mean wet weight per individual in February and March (Fig.6). The ovigerous females live on to release their broods in April, May and June, but soon after this is accomplished these and the rest of the over-wintering animals die also. Only a few live into June, and by July all have died.

(ii) The variation in population density throughout the year

The actual number of A. aquaticus present in the pond is obviously a factor of great importance in determining the energy flow through the population. Unfortunately a detailed investigation of this parameter is very time-consuming and does not lend itself to a short-term study. Because of its great importance, however, an attempt was made to examine this factor. The study resulted in what was considered to be a reasonably accurate estimate of the variation in population density throughout the year.

The problem was studied in two stages. Firstly, a standard sampling technique was adopted so that the relative changes in the population density could be followed from month to month; and secondly, an absolute determination of the numbers of A. aquaticus/m^2 was made in order to calibrate the standard sampling technique.

Method

A standard sampling procedure with a pond-net was carried out at monthly intervals. A standard sweep consisted of one horizontal movement of a square-sided net through 150cm of water and vegetation, such that a volume of $0.883/m^3$ was sampled.

The catch from each sweep was screened for predators, returned to the laboratory, and sorted as described above, each sweep being treated separately. The numbers of A. aquaticus caught with each sweep were counted and the results are presented below (page 14).

It was found that sweeping with a pond-net was causing considerable disturbance to the ecosystem, and for this reason the number of samples taken each month was kept to a minimum. Thus 18 samples per month were considered to provide a balance between accurate population size estimation and minimal environment disruption. These samples were not taken at random but at definite sites marked out in the different vegetation zones at the beginning of the study. This was designed to facilitate the comparison of catch size from month to month, despite the necessarily small number of samples taken.

Between 13-19th July an attempt was made to estimate the numbers of A. aquaticus/m^2 in the pond. Insufficient time precluded the possibility of examining the population density

in all the vegetation zones, and so it was decided to
concentrate on the large central area of Potamogeton where
it was judged that most of the animals were situated.

The absolute population size determination was made
with the aid of a large sampling device.   This consisted of
a wooden framework covered with polythene sheeting so as to
form an open-ended tube of square cross-section.   Four strips
of steel plate were fixed round the perimeter of one end in
order to form a cutting edge which protruded beyond the end of
the tube.   The structure was 2 metres long and 0.5 metres along
each side of the square.

In use, the sampler was dropped upright into the pond
and forced down so that the steel edge cut through roots and
debris to become firmly embedded in the substratum.   Thus a
column of water and Potamogeton beneath an area of $0.25/m^2$ was
effectively isolated from the rest of the pond.   A. aquaticus
does not swim but walks along the substratum, and use was made
of this fact in removing all the animals from the isolated
column of water.   All the vegetation was cropped from inside
the sampler and carefully placed, together with the animals on
it, in plastic dishes.   Any animals were carefully brushed
from the inside walls of the tube and sufficient time allowed
for them to sink to the bottom of the column.   A square-sided
pond-net was used to skim off the top layer of ooze within the
sampler, and this, together with the vegetation, was returned to

the laboratory for sorting as described above.   Using the

procedure described, it was reasonably certain that the great

majority of the A. aquaticus present in the column were

captured.

The sampler was then transferred to another part of

the Potamogeton and the procedure repeated.   All the samples

taken were from a column of water 160cms deep and, since the

central area is of approximately uniform depth, it follows that

data collected in this way may be applied to the whole area of

Potamogeton.

Sorting of the material collected was found to be

very time-consuming, and thus the number of samples taken was

strictly limited.   Of the four samples returned to the laboratory,

one was lost, and the remaining three gave numbers of A. aquaticus

which were in close agreement with one another and within the

range expected from a consideration of the standard sweeping

data (Table 1).   It was thought, therefore, that despite the

limited sampling programme, a reasonably accurate estimate of

the numbers of A. aquaticus/m^2 had been achieved.   The results

are presented below.

Results

The mean number of A. aquaticus caught per sweep was

calculated for each standard sampling date and plotted against

time (Fig.9).   By plotting the mean of samples taken from all

areas and depths of the pond it was possible to obtain an

Fig. 9.   The mean number of animals caught per standard sweep ($\pm$ S.E.) is plotted for each month of the study.

Calibration of the standard sweeps made in July permitted all data to be expressed as the change in numbers/m^2 with time (see Table 1 and text for further explanation).
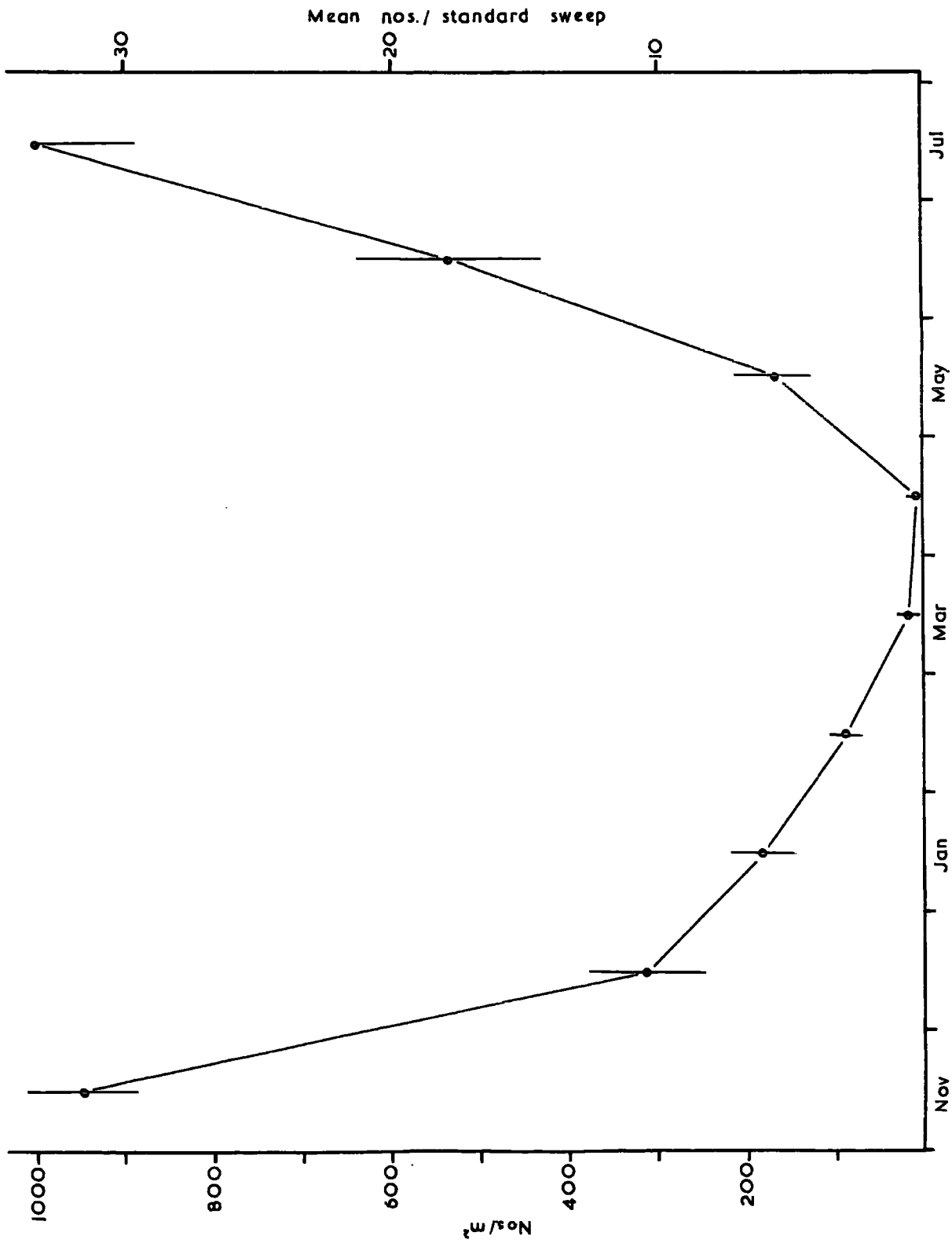
estimate for relative changes in population density which appeared to be unaffected by local migrations of animals within the pond as no pronounced effects of this nature were detected. Figure 9 demonstrates how the numbers per standard sweep showed progressive and very marked changes throughout the period of study.

Table 1 shows the results of the absolute population size determination made in July with the aid of the tubular sampler :

Table 1.

Sample	No./m^2
1	1068
2	816
3	1100
Mean	994.6

These data were used in conjunction with the standard sweeping data given above to calculate the population size density throughout the year. For this purpose it was assumed that the catch of 33.1 individuals per sweep in July was equivalent to a density of 1000 animals/m^2. The results are shown in Figure 9.

It can be seen that at the start of the study in November the population density was very high, but these numbers were rapidly depleted and almost reached the level of total extinction in April. Following this, however, the population size increased rapidly, and this coincided exactly with the

appearance of juveniles in the population (Fig.4).   Although
it was not studied quantitatively, the production of so many
young points to the high fecundity of the few females which
remained in April.

THE PHYSIOLOGICAL FACTORS AFFECTING ENERGY FLOW

The study of bioenergetics is based on the principles
of thermodynamics, the first of which may be stated as :   energy
may be transformed from one form into another, but is neither
created nor destroyed.   Thus for any animal we can write :

$$\text{Chemical energy ingested} = \text{Chemical energy assimilated} + \text{Chemical energy of faeces}$$

This is the first of two equations which are commonly used by
bioenergetics workers, the second being :

$$\text{Chemical energy assimilated} = \text{Chemical energy of growth} + \text{Energy utilized in maintenance metabolism}$$

The energy of growth is that energy which is required
for the synthesis of the complex molecules of which animal
tissues are composed.   In arthropods this includes the energy
used in the production of exoskeletons, part of which are
periodically cast as exuviae.

The energy of maintenance metabolism refers to that
energy expended by the numerous physiological processes which
summate to form the routine daily metabolic activity which the

animal must carry out to continue its existence. Examples
of these activities include the production of hormones,
enzymes, and the energy dissipated by muscular contraction.

These equations may be applied to an individual
or to a group of animals, and thus by solving one half of the
second equation and relating it to population density estimates,
one may calculate the total energy flow through the population.
The present study was designed to estimate the energy utilized
in growth and the energy dissipated by maintenance metabolism.

Direct observation of the population will give a
figure for growth.However the energy of maintenance metabolism
must be estimated indirectly. Fortunately, the different
components of the latter factor may be treated collectively
since each ultimately derives its energy from the same source,
namely the biological oxidation of complex compounds. Since the
oxidation process requires oxygen, it is only necessary to
estimate the oxygen consumption of the population to permit the
calculation of the energy dissipated by maintenance metabolism.

Thus the energy utilization by A. aquaticus may be
studied under three headings; the energy utilized in growth
of the population, the energy of growth lost in exuviae
production, and the energy dissipated by respiration.

1. The energy utilized in growth of the population.

Biomass and energy units.

Biomass production involves the utilization of

energy. However, the amount of biomass produced by an
organism gives no real indication of the amount of energy
which has been used in its manufacture, because the energy
required per unit weight varies with the animal and from
part to part within the animal. Thus the student of energy
flow and energy transformations finds little use for biomass
as a comparative unit. It has become customary to express
production in terms of energy units, and because all forms of
energy can be converted completely to heat, but not completely
to any other form, the calorie is now recommended for comparative
purposes. Thus the bioenergetics worker refers to biomass in
terms of the energy required in its synthesis or the energy it
would yield on complete combustion, both expressed in calories.
In this way the production and utilization of biomass of every
nature is readily comparable.

In order to conform to this custom the estimation
of population growth must fall into two parts; firstly, the
calculation of the biomass produced by the population, and
secondly, the determination of the calorific value of
A. aquaticus tissue so that the biomass produced can be
expressed in calories.

The biomass production was calculated by following
the increase in length of an individual and converting this
to biomass by determining the relationship between length and
live weight. The figure obtained was then multiplied by the

number of animals exhibiting length increase to obtain the

biomass production by the whole population.

The various stages in this exercise are discussed

below.

a) <u>The increase in length of individuals and the numbers</u>

<u>exhibiting this increase</u>

In order to obtain these data it was first necessary

to estimate the numbers of animals/m^2 present in each size

class on each monthly sampling date, and the information

enabling this estimation to be carried out was derived from

the population dynamics study discussed above. For reasons

given below (pp.2226, it was also necessary to treat the males

and females separately in the calculations. The required data

were conveniently obtained by multiplying the monthly absolute

population densities (Fig.9) by the appropriate percentages of

the population present in each size class, the sexes being

treated separately. These percentages were obtained from the

raw data used in the construction of Figure 4, and the data

for February shown in Figure 7 are examples of those used in

the present calculations, the results of which are presented

in Table 2.

The increase in length of individuals can be

calculated from the shift in the size classes represented in

the population with time, as shown in Table 2, and the numbers

of animals exhibiting length increase at any time in the year

can be obtained directly from the same source.

The present study was able to cover ten months of the year. However, it was thought that an estimate of the energy flow through the population for one whole life cycle was more informative and of much greater interest than an estimate for an incomplete life cycle. For this reason the data were examined and deemed to be sufficiently detailed to permit an informed prediction of the course of events during the two months not covered by this investigation. Thus the data in Table 2 for September and October is extrapolated rather than observed data, and in subsequent calculations the results for this period and the rest of the year will be presented separately. A figure for the total energy exchange per annum may be obtained by summing these results.

b) The length/live weight relationship

The relationship between length and live weight was examined to allow the length increase shown in Table 2 to be expressed in terms of biomass production.

Method   On five occasions animals were selected for weighing. After length measurements were taken as described above, the live-weights were determined by removing all excess moisture from the surface of the animals with filter paper and weighing to the nearest 0.1mgm. In order to maintain accuracy with the smaller animals, several of the same length were weighed together and thus a mean value was obtained.

Results   Although determinations were made in five months,
the results obtained were so similar that all were combined
and are shown in Figure 10.   The constancy of the weight/length
relationship throughout the year has been demonstrated in other
isopods (e.g. Phillipson & Watson 1965).

For the purpose of calculating the biomass production,
a double logarithmic transformation was carried out on the data.
Figure 11 shows the logarithm of live body weight plotted against
the logarithm of body length.   This and all subsequent regression
lines were fitted by the method of 'least squares'.

Although no significant difference was found between
the weights of males and females of comparable size, those of
ovigerous females were found to be consistently higher.   For
this reason these data were treated separately (Figure 12),
and the distinction between females and ovigerous females was
made in Table 2.

The mean wet weights of animals in each size class
were calculated from the regression lines in Figures 11 and 12,
and are presented in Table 3.

The data contained in Table 3 are used to calculate
the energy utilized in population growth (section (e) below.

Wet wt. — mgms.

50

40

30

20

10

    ×   Gravid females

    ●   Females

    ○   Males

    +   Unsexed

1 2 3 4 5 6 7 8 9 10 11 12 13 14

Length — mms.
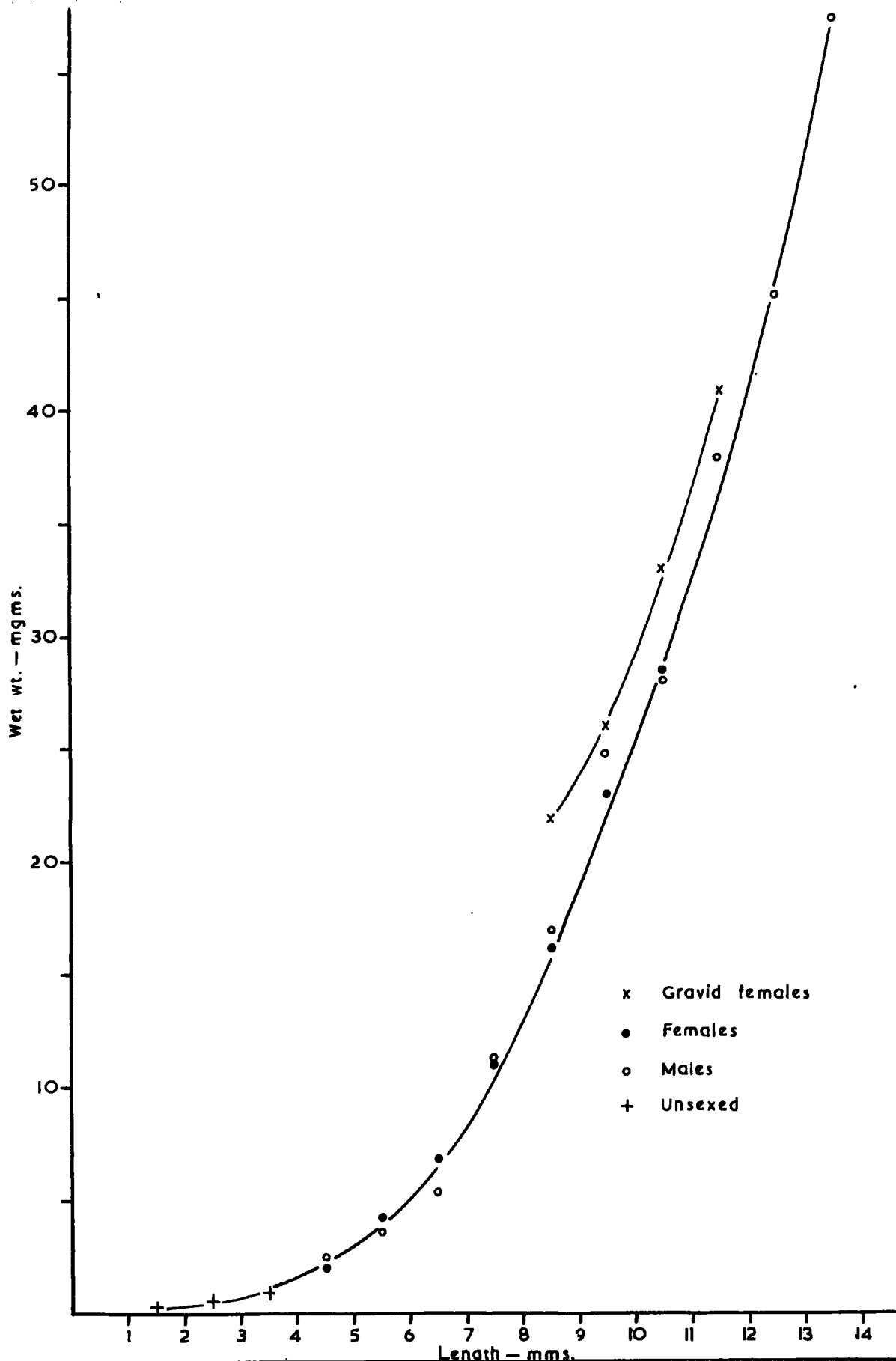
Fig. 10.   The relationship between length

and live weight in <u>Asellus aquaticus</u>.
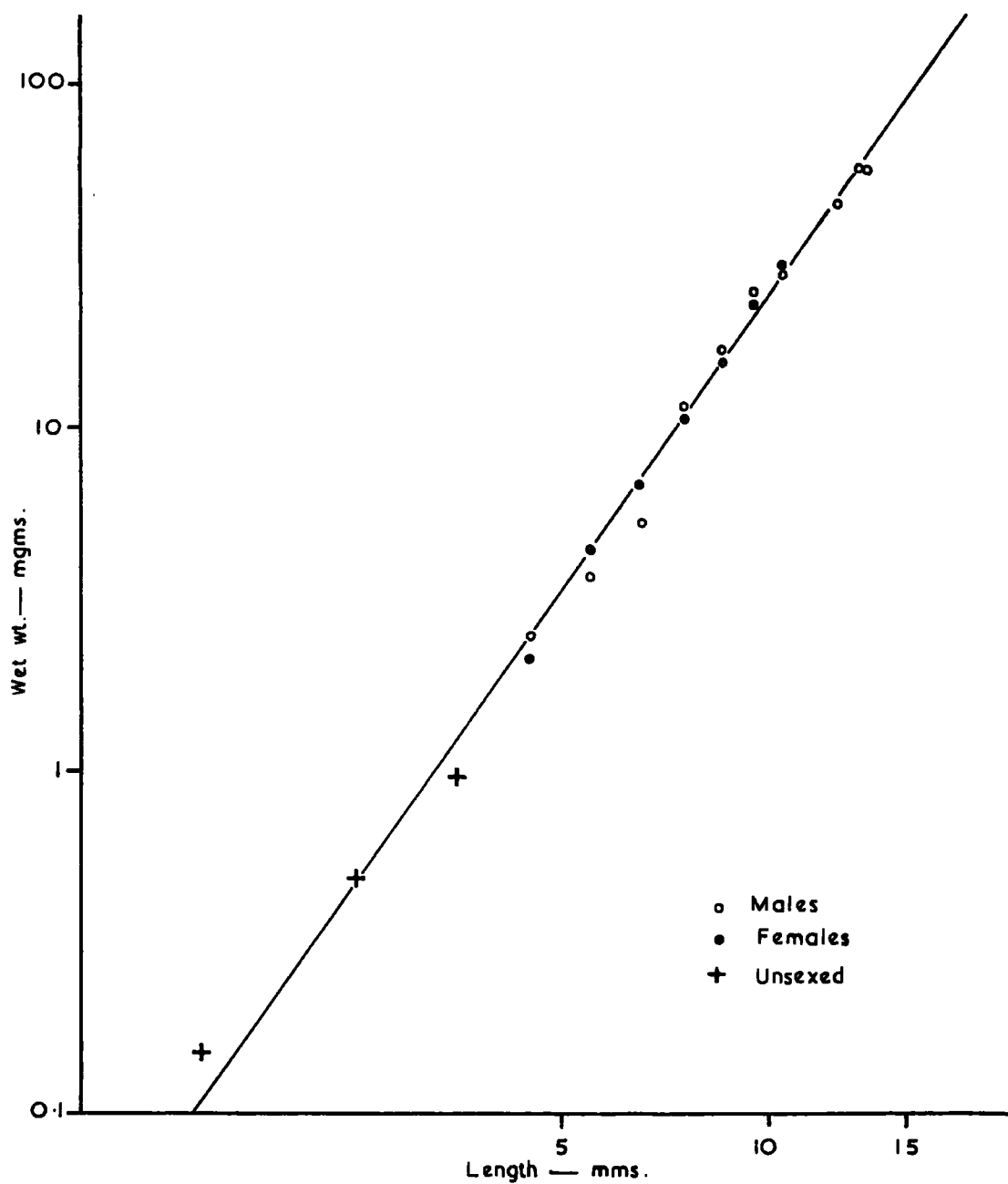
		1	2	3	4	5	6	7
May	M	62.6	13.8	0.9				
	F	62.6	13.8	0.9				
Jun	M	41.2	102.9	86.1	26.2			
	F	41.2	102.9	86.1	15.0			
Jul	M	85.1	123.0	123.0	37.8	75.6	56.8	18.5
	F	85.1	123.0	123.0	132.4	132.3	37.9	-
Aug	M	-	97.8	257.4	122.3	98.1	73.8	-
	F	-	97.8	257.4	74.2	73.5	24.6	12.0
Sep	M	89.4	34.6	72.8	190.5	85.9	81.9	62.0
	F	89.4	34.6	72.8	190.5	85.9	81.9	62.0
Oct	M	49.1	87.3	52.7	49.7	127.5	73.6	76.7
	F	49.1	87.3	52.7	49.7	127.5	73.6	76.7
Nov	M		51.1	55.9	27.7	18.6	83.6	27.8
	F		51.1	55.9	55.4	36.9	55.7	92.5
Dec	M		7.1	14.2	-	-	3.5	3.5
	F		7.1	14.2	7.1	10.6	7.1	28.3
Jan	M		3.4	4.2	-	-	-	3.4
	F		3.4	4.2	8.3	3.4	1.6	6.8
Feb	M		4.2	5.6	-	1.4	-	-
O.F.	F		4.2	5.6	1.4	-	1.4	4.2
Mar	M		1.6	0.7	-	0.5	-	-
O.F.	F		1.6	0.7	0.9	0.5	0.9	0.9
Apr	M		0.2	-	-		0.2	0.2
O.F.	F		0.2		0.4	1.2	0.2	0.2
May	M				-	-	1.8	1.8
	F				3.6	-	-	1.8
June	M					-	7.5	3.8
	F					7.5	-	3.8

GENERATION II

Table 2. The numbers of males, females and ovigerous females/m^2
It will be noted that, although the present study cover
of the 1967-68 cycle, in this table all the data have b
was followed in order to facilitate discussion, and doe
population during the study period.

8	9	10	11	12	13	14	15 mms
14.8	1.7						
14.8	1.7						
72.0	17.0	3.2					
72.0	17.0	3.2					
83.6	148.2	37.2	8.6				
55.8	9.3	-	-				
37.1	31.8	22.3	35.4	7.1	14.2		
24.8	46.0	9.6	7.1	-	-		
-	6.7	11.7	3.4	31.9	6.7	5.1	1.6
11.8	13.4	35.2	15.1	-	-	-	-
1.2	-	5.6	5.6	11.3	2.8		
4.7	7.1	4.3	-	-	-		
1.2	5.6	7.1	4.2				
-	-	0.5	-	1.9	0.9		
0.9	1.4	0.5	-	-	-		
0.5	1.4	1.9					
-	1.4	1.9					
-	0.2	-	0.2	0.2			
1.0	-	-	-	-			
-	-	-	-	-	1.8		
-	1.8	-	-	-	-		
-	-	3.7					
7.5	-	-					

GENERATION I

ent in each size class at the monthly sampling dates.
he later part of the 1966-67 cycle and the earlier part
considered to refer to one life cycle. This procedure
t affect the value obtained for energy flow through the

M - MALES
F - FEMALES
O.F. - OVIGEROUS FEMALES

Fig. 11.   Animal length is plotted against live

weight - logarithmic scale - regression line

(y = 2.8407x - 1.4574, where x = length and
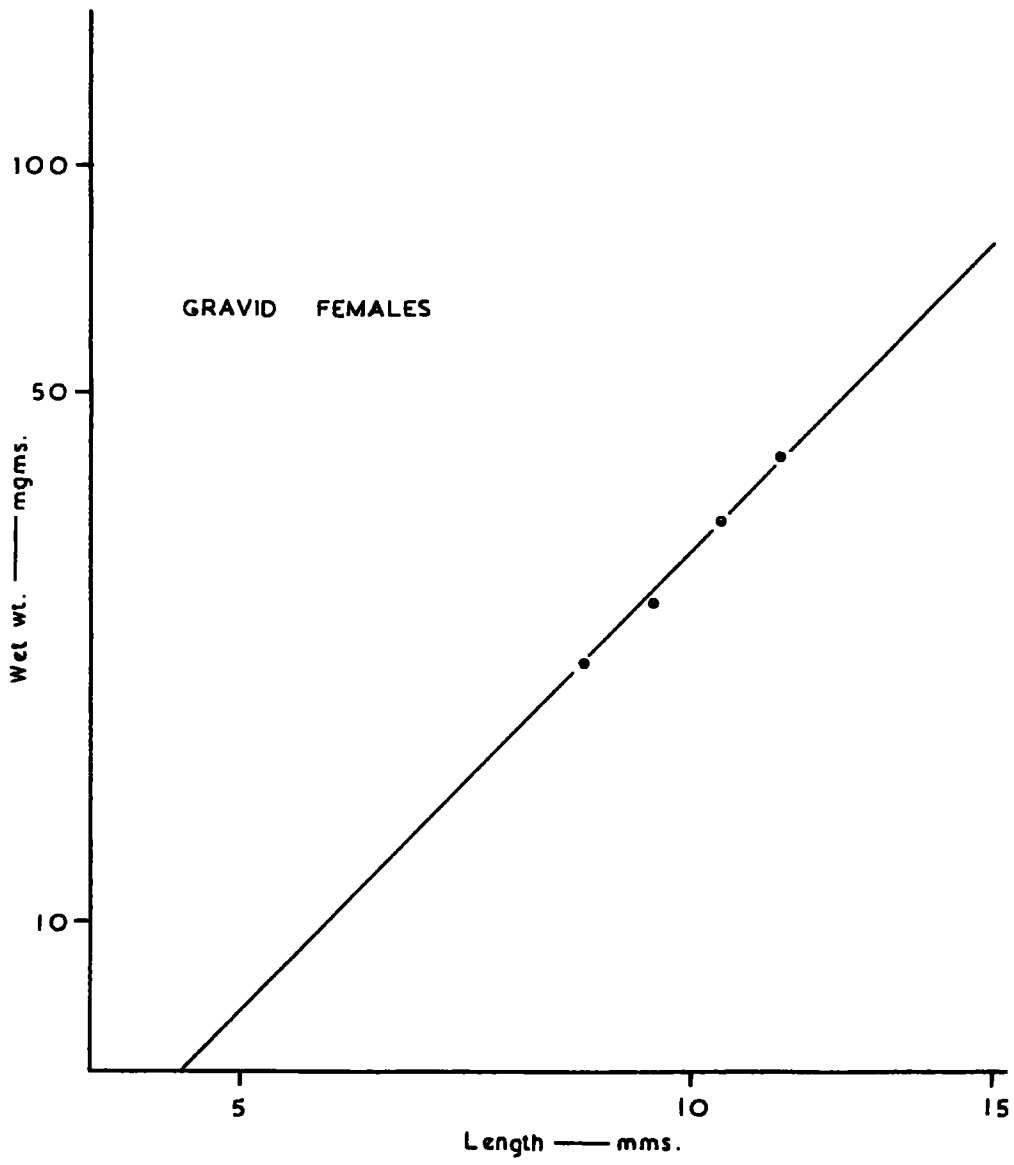
y = wet wt.).

Fig. 12. The length of gravid females is plotted against live weight - logarithmic scale - regression line ($y = 2.0208x - 0.5388$, where x = length and y = wet. wt.).

Table 3.   Length/wet weight conversion data.

Size class	Mean wet weight - Mgms	
- mms	Males & females	Ovigerous females
I - 2	0.11	-
2 - 3	0.47	-
3 - 4	1.23	-
4 - 5	2.50	-
5 - 6	4.42	-
6 - 7	7.11	-
7 - 8	10.68	-
8 - 9	15.23	21.84
9 - 10	20.89	27.35
10 - 11	27.76	33.48
11 - 12	35.95	40.24
12 - 13	45.56	-
13 - 14	55.67	-
14 - 15	69.47	-
15 - 16	83.90	-

c) <u>The calorific value of A. aquaticus tissue</u>

      The calorific value of A. aquaticus tissue was
determined and used to express the biomass production in
calories. This value was obtained directly by using the
oxygen microbomb calorimeter described by Phillipson (1964).

<u>Method</u>   Animals of all sizes and sex were collected, dried
and stored separately during the period of study. This
material was pressed into pellets weighing approximately
10 mgms and dried for 48 hours in a vacuum oven at $60^{o}C$.
The calorific value of each was then determined using the
bomb calorimeter.

      A pellet of the material under test was weighed
to the nearest 0.001 mgm and sealed in the microbomb.
After oxygen had been admitted to a pressure of 30 atmospheres,
the pellet was ignited by discharging a condenser across a
platinum wire in contact with it. The heat released on
combustion was detected by a ring of thermo-couples on which
the bomb rested, the change in potential produced being
monitored by a recording potentiometer. The calorific value
of the tissue was then calculated from the potentiometer
deflection observed, after the bomb had been calibrated by
burning a substance of known calorific value. Benzoic acid
was used for the calibration.

<u>Results</u> The values obtained are recorded in Table 4.

Table 4. The calorific value of <u>A. aquaticus</u> tissue

Males		Females	
Length mms.	Calorific value K.cals/gm dry wt.	Length mms.	Calorific value K.cals/gm dry wt.
13	2.208	9	2.578
11	2.881	9	3.759
10	2.811	8	3.830
9	2.671	7	3.702
8	2.737	6	3.125
8	2.365	6	3.332
8	2.781	5	2.826
7	3.354	4	3.231
6	3.040		
5	2.808		
4	2.844		

Examination of the data revealed a significant difference in the calorific value of male and female tissue, females having a much higher value than males.   The respective means obtained ($\pm$ S.D.) were :

Males   - 2.773 $\pm$ 0.289 K.cals/gm dry wt.

Females   - 3.298 $\pm$ 0.423 K.cals/gm dry wt.

The difference between the means ($\pm$ S.E. of difference)

= 0.525 $\pm$ 0.173 K.cals/gm dry wt.

This difference is probably due to the relatively large quantity of high calorific value reproductive material carried in the ovary or brood pouch of the females, and it is unlikely that this difference applies to juveniles.

Males and females were separated in Table 2 to enable the appropriate calorific values to be applied.

d) The ratio of live weight to dry weight

The biomass data shown in Table 3 are live weight values, and this permitted the animals to be returned to the pond in order to minimize interference with the population. The calorific values, however, were necessarily expressed in K.cals/dry weight gm.   It was necessary, therefore, to establish the ratio between live weight and dry weight so that the calorimetry data could be applied to the biomass data available.

Method   A number of the over-wintering animals were taken from the pond and their live weights determined as described above.   They were then dried for 48 hours in a vacuum oven at 60°C and allowed to cool in a dessicator before re-weighing. This procedure was repeated on a sample of animals from the population in the summer months.

Results   Statistical analysis revealed no significant difference between the ratio of live weight to dry weight in males, females, winter or summer animals.   The mean value obtained ($\pm$ S.D.) was :

$$0.217 \pm 0.023$$

e) <u>The calculation of the amount of energy utilized in</u>

   <u>growth of the population</u>

Three major factors may act on the population
between successive sampling dates, and these are growth,
mortality and natality. Many bioenergetics studies have
been carried out on animals in which the hatching period was,
or was assumed to be, of limited duration (e.g. Smalley 1960.),
and in these cases the extent to which natality and mortality
had occurred was easily gauged from the change in population
size between successive sampling dates. However, Phillipson
(1967) has pointed out the difficulties involved in studying
an animal which breeds more than once in its life-cycle and
in which new individuals are introduced into the population
over a prolonged period, for under these conditions the
difference between successive population sizes cannot be
held to be an estimate of either natality or mortality since
it results from the interaction of both. In addition, such
a population must necessarily be composed of individuals of
two or more generations in which the pattern of growth,
natality and mortality would almost certainly differ.

It can be seen, therefore, that a different approach
to that used for an animal with a simple life-cycle is
required if the growth of the population of <u>A. aquaticus.</u>
is to be estimated. Only one attempt to study a population
of this type is on record, and that is a contribution by

Saito (1965) in which he studied the terrestrial isopod
Ligidium japonicum in a temperate forest ecosystem. The
method used in the calculation of the biomass production
in this study is a modification of that used by Saito.

When no natality is occurring, the biomass
production by a population between time t_1 and t_2 is given
by Saito's formula :

$$N_t \; x \; \frac{\Delta W}{t} \quad \pm \quad \frac{\Delta N}{t} \; x \; \frac{\Delta W}{t} \; x \; \frac{1}{2}$$

where N_t = population size at t_2,

$\dfrac{\Delta W}{t}$ = mean weight increment per individual between
t_1 and t_2,

$\dfrac{\Delta N}{t}$ = number of mortalities between t_1 and t_2,

and the $\frac{1}{2}$ is based on the assumption of a constant mortality
rate between t_1 and t_2.

The first part of the expression gives the production
by the survivors at t_2 and the second gives the production by
those animals which died between t_1 and t_2. By extending and
modifying this basic idea one may calculate the production by
all fractions of the _A. aquaticus_ population.

An essential feature of the method used by Saito
is the ability to distinguish different age-classes within
the population, and in _A. aquaticus_ this was done on the

basis of size-distribution. The size of an animal was, therefore, taken to be an indication of its age. This enabled the two generations to be separated; a necessary step in view of the differences in their patterns of natality, growth and mortality. To facilitate discussion, the generation born between May and July will subsequently be referred to as generation I, and the other as generation II. The ability to age an animal was also necessary in order to distinguish newly-hatched individuals from the rest of the population.

During the months when births are absent, the mortality may be observed directly. However, Table 2 shows that natality occurred for five months of the year, and therefore one requires an alternative method for calculating the mortality during this period. Figure 13 shows a survivor-ship curve for the population between November and April, the period during which mortality was not masked by natality. The logarithm of the number of survivors/m^2 was plotted against time, and it represents a single logarithmic transformation of some of the data presented in Figure 9. The result is a line which coincides with that designated as type II by Deevey (1947), and is also very similar to that obtained by Saito for _Ligidium japonicum_. Therefore, one can conclude that the population of _A. aquaticus_ experienced a constant mortality rate; and since Figure 4 shows that the histograms maintain a fairly constant outline which may be
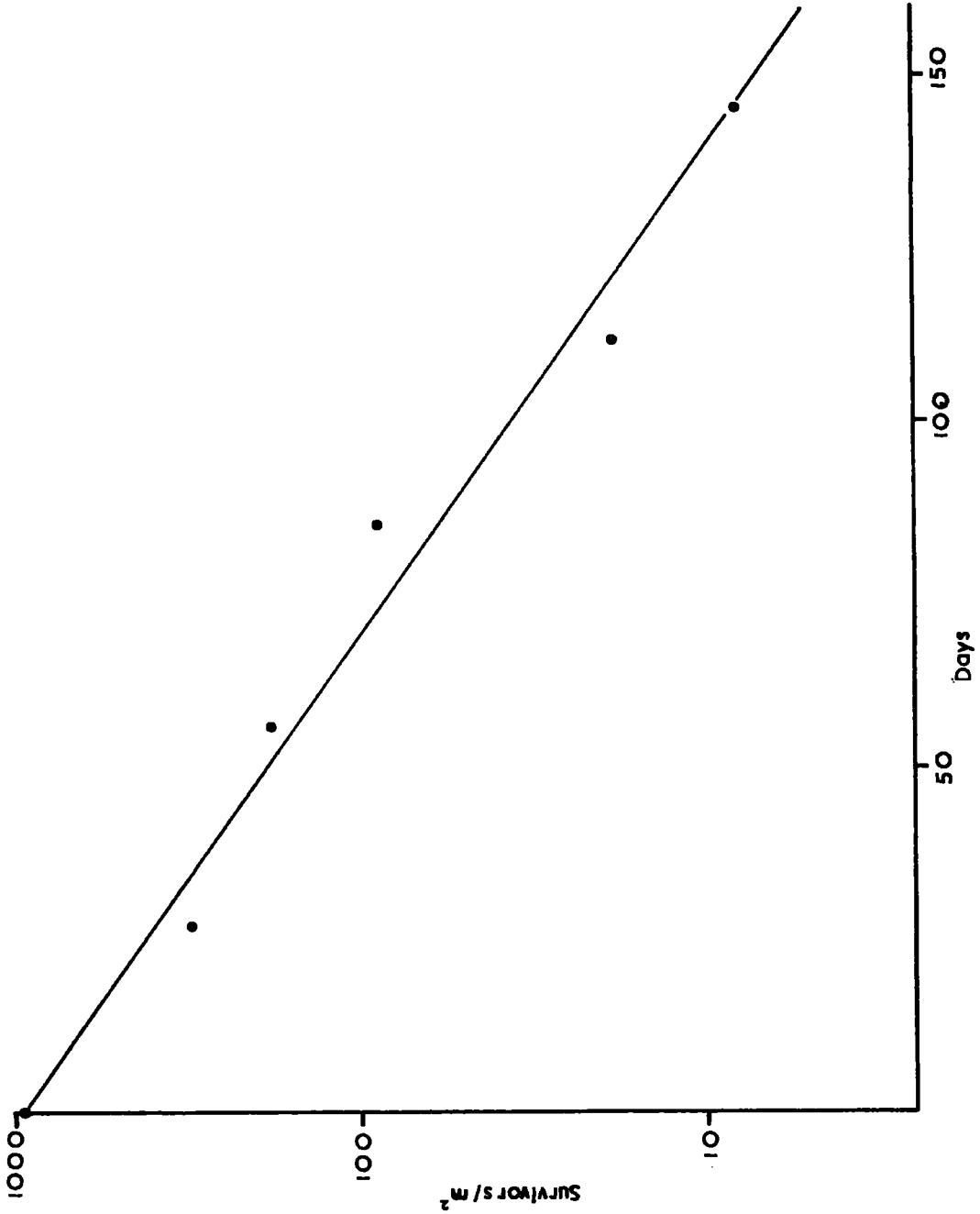
Fig. 13.   The number of survivors/m^2 is

plotted against time - semi logarithmic

plot - regression line ($y = 0.0141x +$

2.978, where $x =$ days and $y =$ survivors/m^2).

followed from month to month, the constant mortality rate

must have applied equally to all size-classes.   (The male

mortality during the short period following January copulation

is probably an exception to this observation.)   Thus, given a

constant mortality rate, the number of mortalities which

occurred during the natality period may be calculated from

the slope of the line in Figure 13.

The constant mortality rate was not unexpected,

and the possible reasons for this will be discussed below

(page 49).

N_t and $\underline{\Delta W}$, the remaining factors in the expression

given above may be ^{t} calculated directly from the data in

Tables 2 and 3.

For the purpose of calculating the biomass production

the population was considered to be composed of sixteen

categories of individuals :

The males of generation I –

(i)   present at t_1 and surviving to t_2

(ii)   present at t_1 but dying before t_2

(iii)   hatching after t_1 and surviving to t_2

(iv)   hatching after t_1 but dying before t_2

– the remaining 12 categories were given by considering the

females of generation I and both sexes of generation II.

By using Saito's formula the biomass production was

calculated for the categories represented in each of the

sampling intervals throughout the year, and the results

obtained are presented graphically in Figure 14.

Both generations reached a peak of secondary production late in the year, but the graph emphasizes the great difference in the contributions each generation makes to the total biomass production by the whole population.

Figure 14 also shows an interesting irregularity in the production by generation I during the period July - August, and a possible explanation of this will be discussed below (page 49).

Table 5 shows the calculation of the annual biomass production taken to completion. The separate totals for males and females are multiplied firstly by the live weight/dry weight ratio (page 26), and secondly by the respective male and female calorific values (page 25).

Table 5. The combined biomass production of generations I and II expressed in calories.

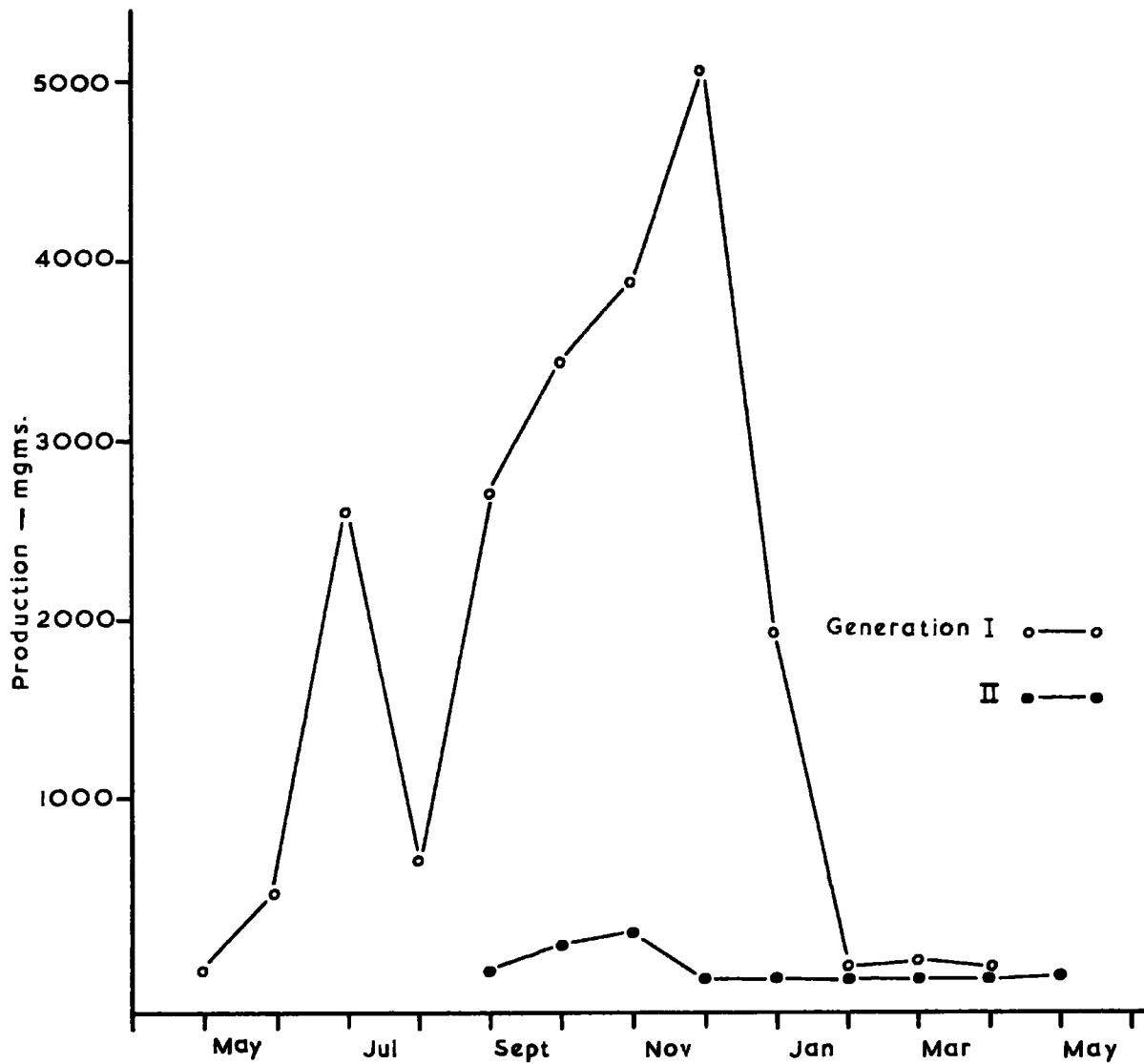|		Total production mgms live wt.	Total production mgms dry wt.	Production K.cals.
Nov.22nd − (	Males	6867.90	1490.0	4.135
Aug.16th (	Females	4132.74	896.9	2.960
Aug.16th − (	Males	6558.30	1423.0	3.950
Nov.22nd (	Females	3990.53	866.0	2.858
			TOTAL	13.903

Fig. 14.   The biomass production during each sampling interval is plotted against time.   The two generations are treated separately.

Therefore the energy utilized in growth during the period Nov. 22nd - Aug. 16th

$$= 7.095 \text{ K.cals/m}^2$$

Energy utilized in growth during the period Aug.16th - Nov. 22nd

$$= 6.808 \text{ K.cals/m}^2$$

Therefore total energy utilization

$$= 13.903 \text{ K.cals/m}^2/\text{annum}$$

One may now proceed to compare this figure with the amount of energy used in exuviae production and maintenance metabolism.

(ii) The energy of growth lost in exuviae production

The calculation used above for the energy utilized in growth does not give the total energy expended. Part of the biomass produced by the animals is deposited as exuviae and so cannot be detected by following the increase in body weight with time. Although insufficient time prevented a detailed examination, it was thought desirable to obtain an approximate estimate of the energy of growth lost by exuviae production.

(a) The number of moults made by each animal

The number of moults required for an animal to reach any given size was determined by using a modification of the "Brooks-Przibram" method for calculating growth rates

(see Kormondy 1959). Brooks was the first to describe how growing arthropods always increase in size by a fixed percentage at each moult. This factor is relatively constant for each species and is approximately 1.25. If the length of an animal at hatching is known, one can calculate the number of moults required to achieve any particular size by repeatedly multiplying the animal length by the growth factor until the desired size is reached. Thus the number of multiplications gives the number of moults required.

METHOD

The growth factor was determined for <u>A. aquaticus</u> by maintaining animals in the laboratory and measuring head-widths before and after moultings. The head-width was measured between the points C and D shown in Figure 3, by using a low-power microscope fitted with an eye-piece micrometer. A reading was taken only if both reference points were in focus simultaneously. The difference in width before and after moulting was used to calculate the growth factor, which in turn was used to estimate the number of moults required to achieve any given size.

RESULTS

The 9 results obtained gave a mean figure ($\pm$ S.D.) for the growth factor of 1.200 $\pm$ 0.0083.

Using this value it was estimated that a female requires 11 moults to reach maximum size whilst a male requires an additional 2 moults.

b) **The weight of the exuviae produced at each Moult**

METHOD

A number of animals were maintained in the laboratory until they moulted. The exuviae produced were carefully collected, dried for 48 hours at $60^{o}C$ in a vacuum oven, and weighed to the nearest 0.001 mgm. The head-width was measured before and after the moult.

RESULTS

Figure 15 shows the results in graphical form, the exuvial weight in mgms, having been plotted against the mean of pre- and post-moult head-widths.

The mean weight of the exuviae produced at each of the moults calculated above was computed from a regression of the logarithm of exuvial weight on the logarithm of mean head-width (Fig. 16).

c) **The determination of the calorific value of exuviae**

METHOD

Collections of cast exoskeletons were made over a long period, sufficient being obtained for one determination with the micro-bomb calorimeter.

The calorific value was determined directly using the calorimetry technique described above.
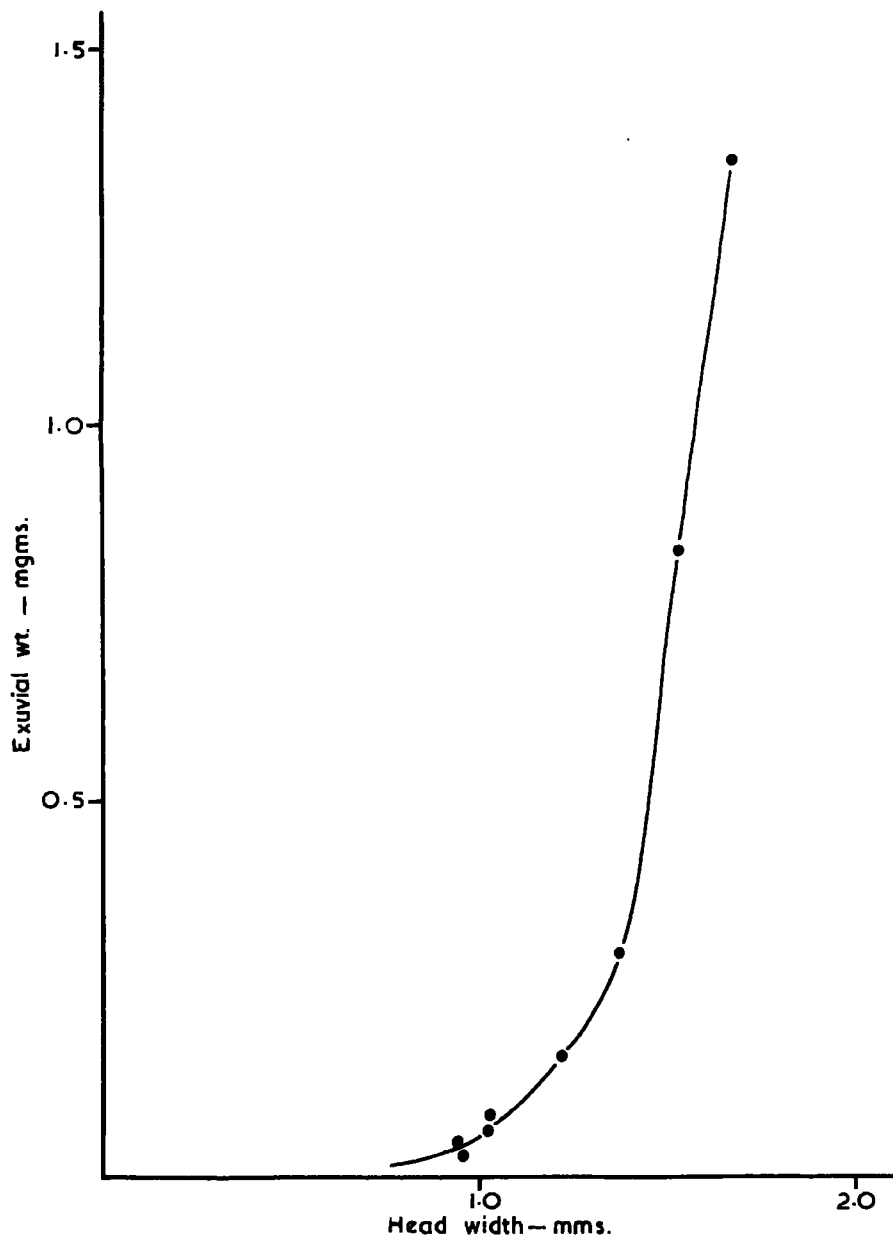
Fig. 15.   The relationship between animal
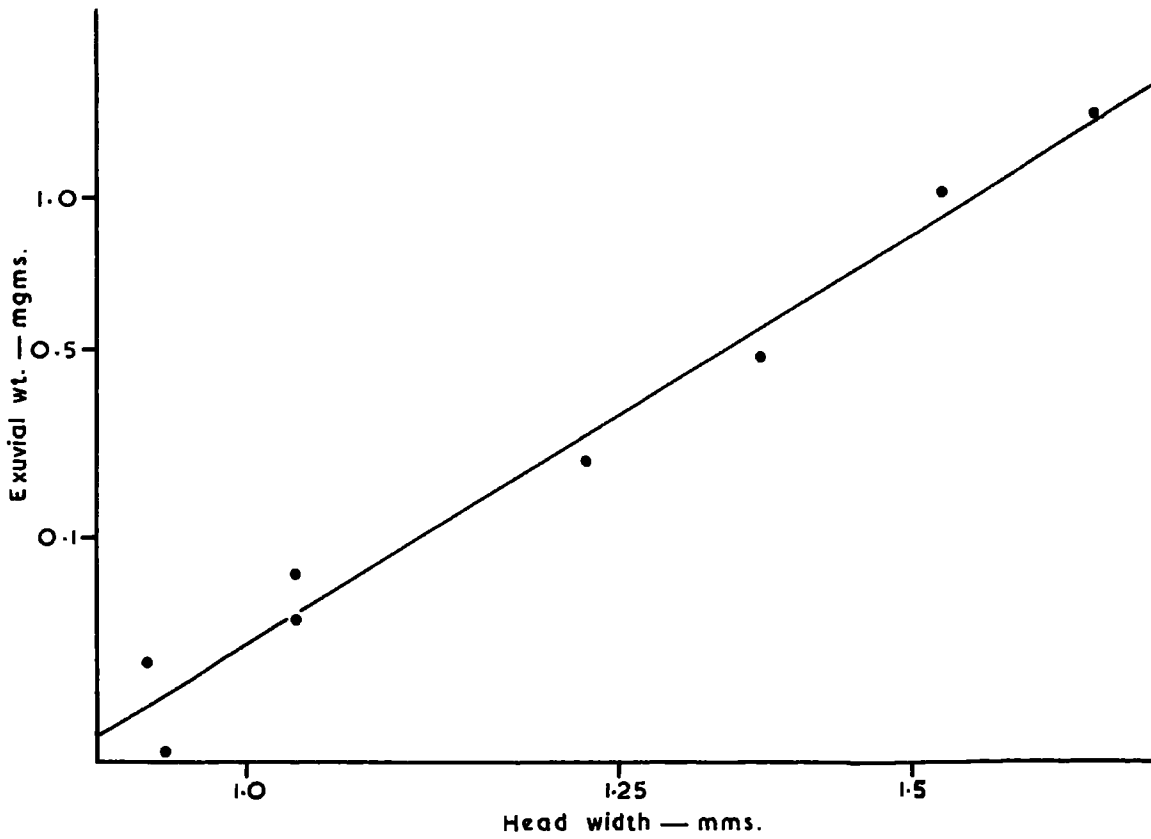size and the dry weight of exuviae produced
on moulting.

Fig. 16.   Headwidth is plotted against dry

weight of exuviae produced on moulting -

logarithmic saale - regreession line (y =

6.179x - 1.284, where x = head width and

y = exuvial wt.).

RESULTS

The calorific value of exuviae was found to be.

0.816 K.cals/gm dry wt.

d) The calculation of the energy used in exuviae production

by the population

The data discussed above were combined and used to estimate the energy of growth deposited in cast exoskeletons.

The total weight of exuviae produced by an individual cannot be determined until after its death. Thus the total exuviae production by the population was estimated by computing the production to date by those animals which died in the first sampling interval, and repeating the calculation for each subsequent sampling interval until the whole population was extinct

The number of mortalities which occurred during each month was calculated from the data in Table 2.

Since it was/established that the mortality rate was the same in each size-class, the exuviae production to date by each mortality was taken to be the same as the mean value per individual calculated for the whole population present at the mid-point of the sampling interval considered. The mean exuviae production per individual was calculated from the moulting data given above and the data in Table 2.

RESULTS

Table 6. The total weight of exuviae produced by those
animals dying in each sampling interval

Sampling interval	Total weight of exuviae produced — mgms dry wt.	
	Generation I	Generation II
May	0.5506	—
June	16.2958	—
July	70.4279	—
Aug.	37.8233	—
Sept.	100.9896	0.8374
Oct.	221.5954	4.5695
Nov.	1136.0566	6.8304
Dec.	526.9387	0.9459
Jan.	494.7153	0.1909
Feb.	272.3343	0.6193
Mar.	26.8565	0.5020
Apr.	13.0274	—
May		
TOTAL	2917.6114	14.4954

Exuviae production by whole population

$= 2.932 \text{ gms/m}^2/\text{annum}$

The calorific value of 0.816 K.cals/gm dry wt. was used to express the exuviae production in calories, and the results obtained were :

Energy used in exuviae production during the period Nov. 22nd - Aug. 16th

$$= 2.094 \text{ K.cals/m}^2$$

Energy used in exuviae production during the period August 16th - Nov. 22nd

$$= 0.299 \text{ K.cals/m}^2$$

Therefore total energy used in exuviae production

$$= 2.393 \text{ K.cals/m}^2/\text{annum}$$

The vast majority of this energy flowed through generation I, only 0.49% having passed through generation II.

One may now proceed to complete the determination of energy flow through the population by evaluating the energy dissipated by respiration.

(iii) <u>The energy dissipated by respiration</u>

Teal (1959) was prompted to write : "the respiration of animals in an ecosystem is the most important single measure of the energy flow through the organisms of that ecosystem". The results of the present study demonstrate the validity of this view.

Currently there is considerable controversy about the effects of acclimatization to varying temperatures on the respiratory rates of animals. Berthet (1963) believed

that acclimatization is not important and, whilst working
on 16 species of oribatid mites, reported Q_{10}s ranging from
2.6 to 5.6.   These he used in conjunction with population
data and annual temperature measurements to calculate the
amount of energy released by respiration per annum.
Phillipson (1963), however, believed that animals may compensate
for temperature changes and thus their respiratory rates do not
change markedly with long-term temperature fluctuations.   He
considers that it may be erroneous to allow for seasonal
temperature change in calculations, and thus applied respiratory
data collected at $16^{\circ}C$ to a species population of the phalangid
Leiobunum rotundum (Latr.) for the whole year.

The method chosen to examine the respiration of
A. aquaticus was designed firstly to show the respiratory
rate of different categories of animals under various
environmental conditions, and secondly, to determine the extent
to which acclimatization affected the respiratory rate.   It was
proposed to combine these data to give figures for the respiratory
rates of different types of individual throughout the year, and
by applying these to the population, to calculate the total
energy dissipated per annum by maintenance metabolism.

a) The respiration rate of A. aquaticus

Method   The principle of the respirometry technique used
was simple.   The animals were placed in a stoppered bottle
full of pond water for the duration of the experiment.   The

oxygen consumption was then calculated as the difference between the oxygen concentration in the water at the beginning and end of the run.   Series of experiments were carried out at three constant temperatures, namely 10°, 15° and 20°C.

A. aquaticus were collected from the pond, measured, sexed and placed in containers of pond water within a constant temperature cabinet preset to the temperature required.   A fluorescent light operated by an automatic switching device gave a 24 hour cycle of alternate light and darkness.   The animals were fed and allowed to acclimatize to the experimental conditions for seven days before respiratory experiments were carried out.

The artificial diel was important since A. aquaticus is nocturnal, its oxygen consumption being at a minimum round about noon (Lang & Ruzickova-Langova 1951).   For this reason respiratory experiments carried out under a constant light regime would lead to incorrect values for the mean oxygen consumption per 24 hours.

The artificial day length was adjusted so that it corresponded to the natural day length which prevailed when the pond was at those temperatures selected for the laboratory experiments.   This required knowledge of the pond temperature throughout the period of study, and the method of obtaining these data is described briefly below.

The respiration of A. aquaticus was, therefore, examined under conditions which were as near natural as possible.

The determinations of oxygen consumption were carried out by placing one or more animals of the same size and sex into bottles full of filtered pond water, the oxygen content of the water being determined chemically at the beginning of the experiments and again 24 hours later.   No food was supplied during this time.   Immediately after the run the animals were dried in a vacuum oven for 48 hours at 60°C and their dry weights determined.

Preliminary experiments were carried out to determine the number of individuals of each size and the bottle capacities required to produce a fall of 15-20% in the oxygen concentration in 24 hours.   In this way the percentage error of the oxygen determinations was maintained at a low level, and the fall in oxygen concentration was not sufficient to affect the respiratory rates of the animals.   The respiration of A. aquaticus is of the 'regulatory' or 'independent' type, the rate being only marginally affected by considerable falls in oxygen concentration (Edwards & Learner 1960).   It is unlikely, therefore, that any error was introduced by allowing the oxygen concentration to fall 20% below saturation level.

By allowing the experiments to run for 24 hours, a mean figure for oxygen consumption at all parts of the diel was obtained, and errors which might otherwise have been

introduced due to the diurnal rhythms of A. aquaticus were
avoided.

The chemical analyses were carried out using the
standard Winkler method.   The use of the Whitney (1938)
modification of the Fox & Wingfield micro-Winkler syringe
greatly facilitated the determinations.   This apparatus
obviated the possibility of any contamination by atmospheric
oxygen and allowed very accurate determinations to be made.

Pond water filtered through a Whatman's No.1 filter
paper was used as the experimental medium.   Thus the animals
were not required to make any abnormal ionic regulatory effort
which might have altered their respiratory rates.

Although the animals were not fed during the
experiments, it has been stated by Edwards & Learner (1960)
that the onset of the respiratory symptoms of starvation
does not occur within 24 hours.   It is unlikely, therefore,
that any error was introduced by starving the animals.

The experimental results are presented following a
description of the method used to measure the pond temperature
throughout the period of study.

b)   The measurement of pond temperature

It was necessary to record the temperature of the
ecosystem for two reasons.   Firstly, so as to be able to
match temperature and day length in the experiments described
above, and secondly, if necessary to permit the application of

oxygen consumption and Q_{10} data to the population for the specific temperature conditions it experienced throughout the period of study.

Method   The technique used was a modification of an idea by Pallmann, Eichenberger & Hasler, as described by Berthet (1960). The principle of the method depends on the fact that a buffered sucrose solution slowly inverts at a rate proportional to the temperature at which it is maintained. Since sucrose isomers are optically active, polarimetric analysis of the solution before and after a period of submergence in the pond enables the water temperature during that period to be calculated.

The sucrose solution used was maintained at pH 1.5 by a HCl/KCl buffer, whilst the addition of formaldehyde prevented the growth of micro-organisms. Small watertight tubes of the mixture were attached to stands positioned in the pond and thus a continuous record of the water temperature during the period of study was possible. The tubes were changed every 3-4 weeks. Because of the practical difficulties involved in maintaining the solution at exactly pH 1.5, the results obtained by theoretical calculations were checked by comparing the sucrose inversion in the field and in 5° and $15^{\circ}C$ constant temperature rooms.

Results   The change in pond temperature throughout the

period of study is shown in Figure 17.

The artificial day lengths decided on the basis of

these data were :

$10^{\circ}C$ -   16.5 hours

$15^{\circ}C$ -   17.5 hours

$20^{\circ}C$ -   17.5 hours

The results of the respiratory experiments

Figure 18 shows the data collected at $10^{\circ}C$.

The oxygen consumption per gm is plotted against animal weight

in mgms.   The results clearly show that the oxygen consumption

per unit weight in small animals is much higher than in large

animals.   This is another point of similarity between

A. aquaticus and other isopods (Phillipson & Watson 1965),

(Edwards & Learner 1960).

Figures 19, 20 and 21 show regressions of the

logarithm of oxygen consumption per individual on the logarithm

of animal weight, the results having been collected at 10°, 15°

and $20^{\circ}C$ respectively.   To facilitate comparison, the three

regressions are given together in Figure 22, and it can be

seen that they are very similar showing no progressive increase

or decrease in respiratory rate with temperature.   On the

evidence provided by this study, therefore, the Q_{10} for

A. aquaticus is 1, and thus its respiratory rate remains

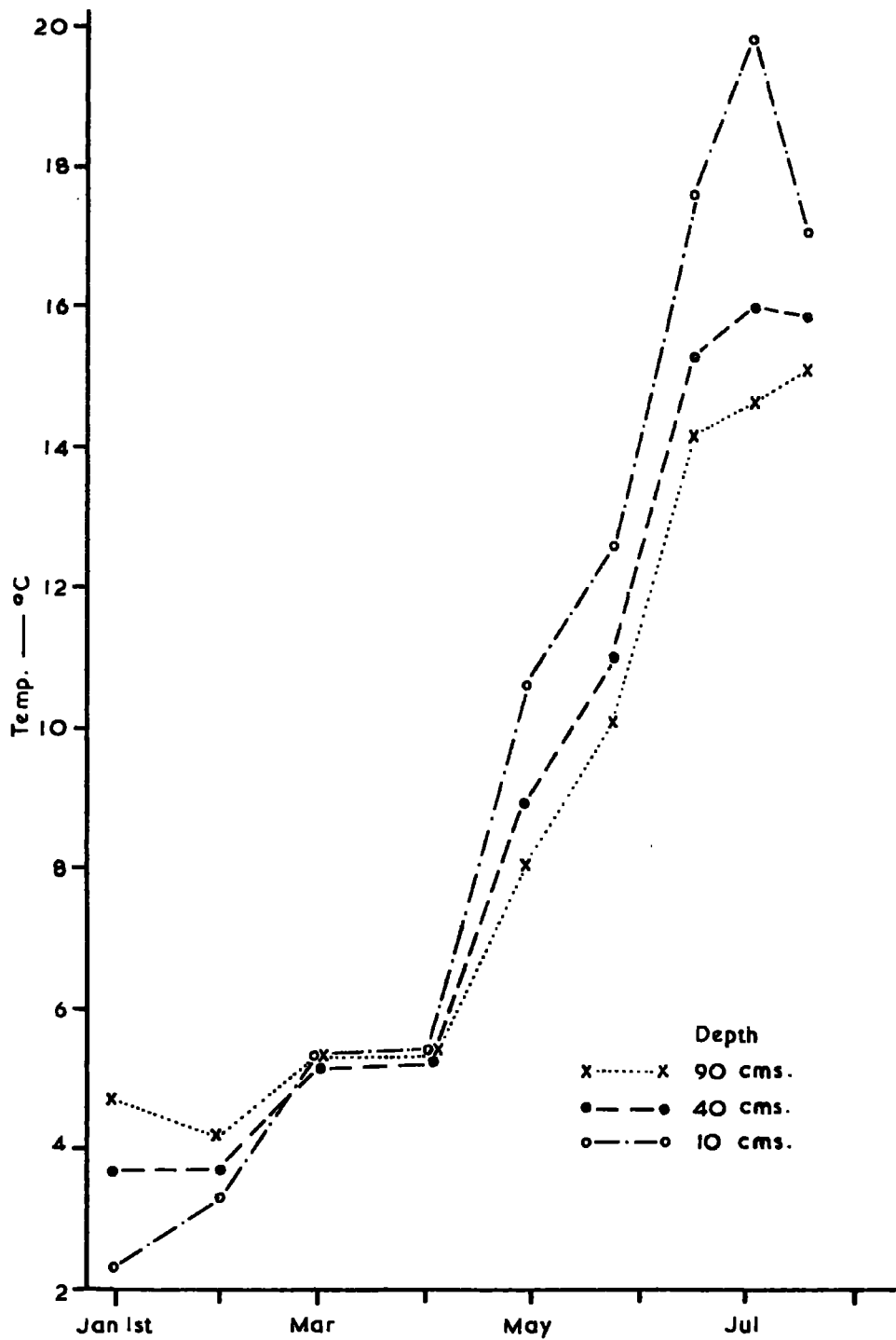unaffected by long-term temperature change.   This makes it

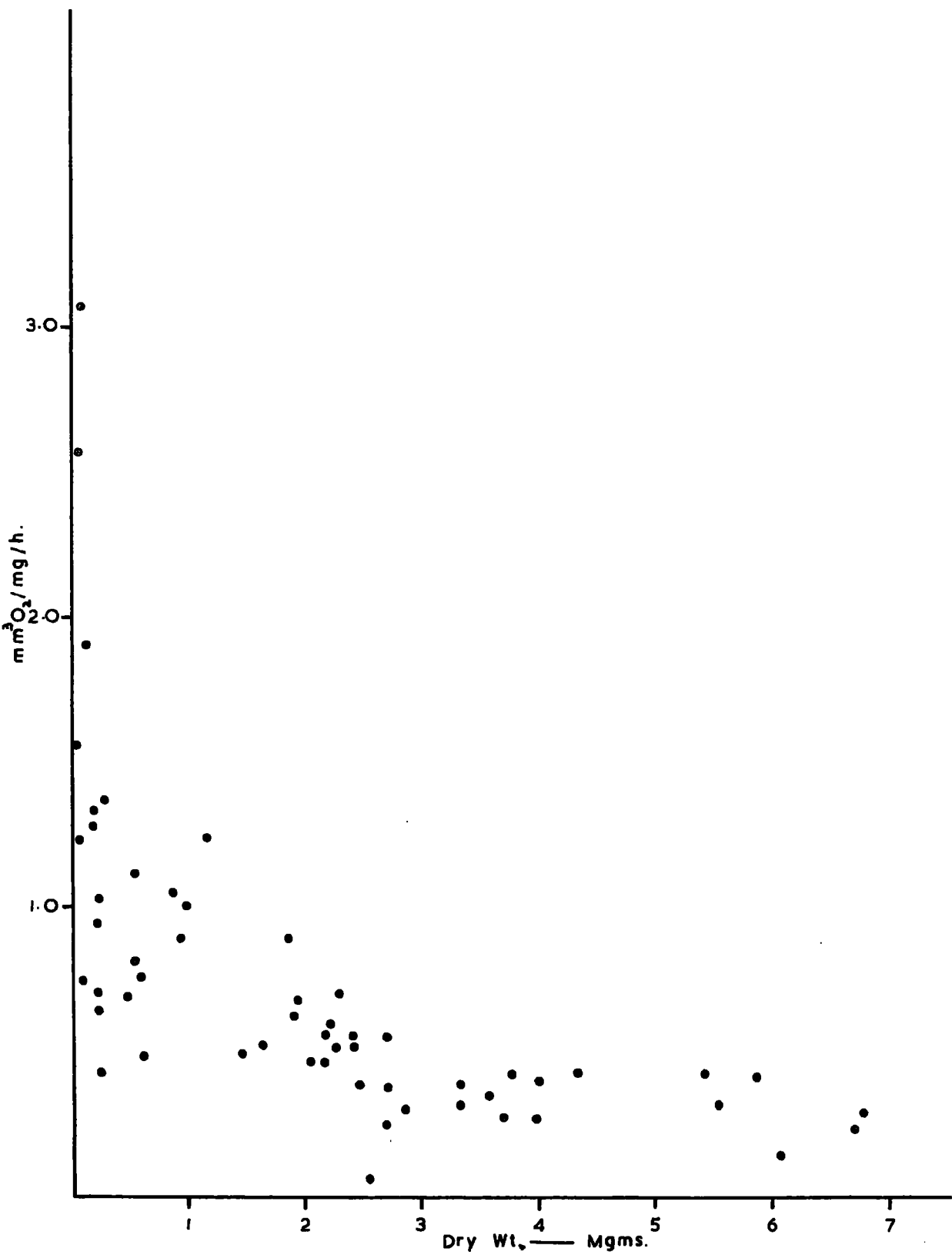Fig. 17.   The variation in pond temperature
throughout the period of study.

Fig. 18. Oxygen consumption per unit weight.
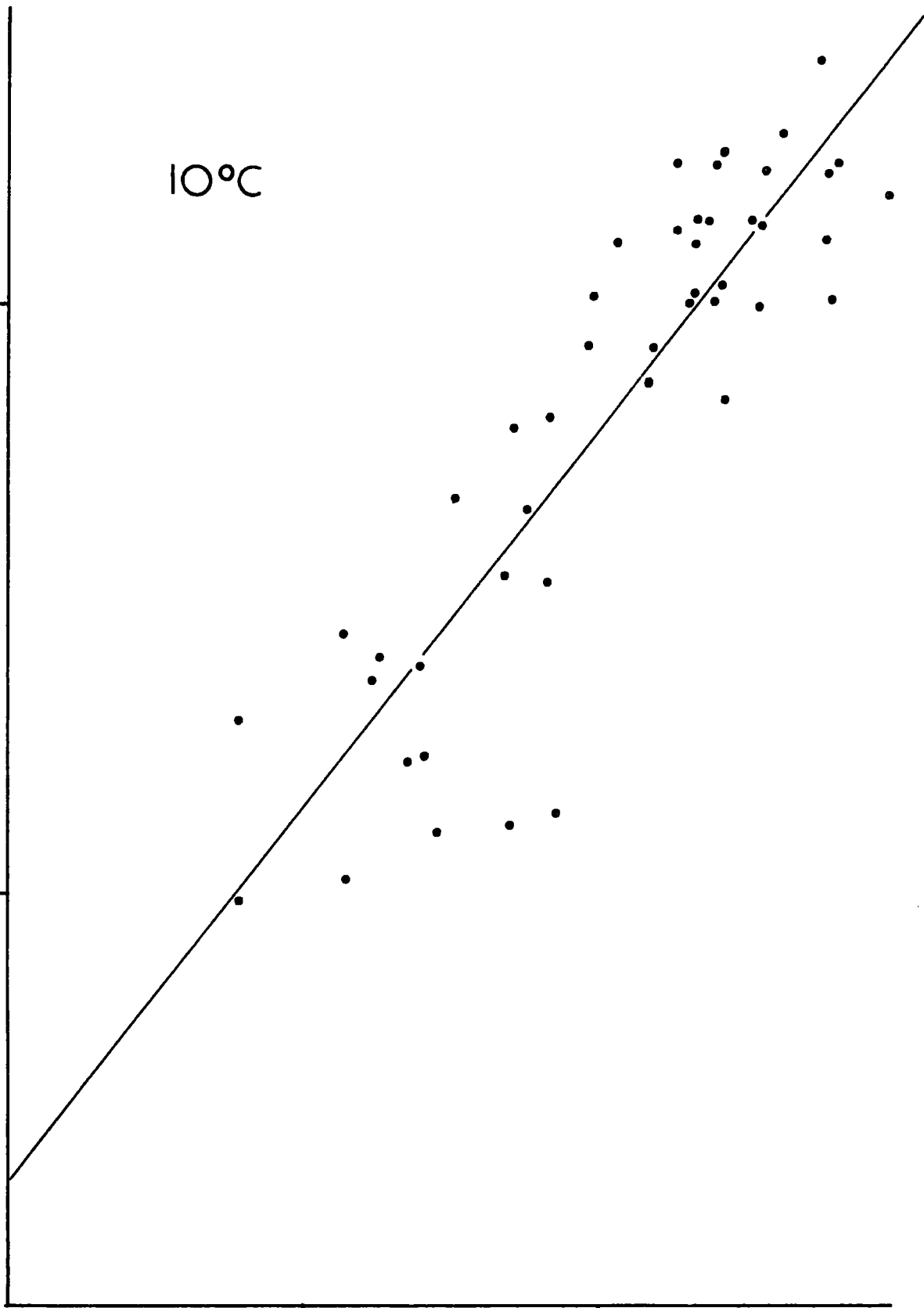Data collected at 10°C.

Fig. 19. Oxygen consumption per animal per unit time - logarithmic scale - regression line ($y = 0.6314x - 0.2168$, where x = dry wt. and y = oxygen consumption). The data were collected at $10^{\circ}C$.

Fig. 20. Oxygen consumption per animal per unit time - logarithmic scale - regression line ($y = 0.6890x - 0.1147$, where x = dry wt. and y = oxygen consumption). The data were collected at 15°C.

20°C

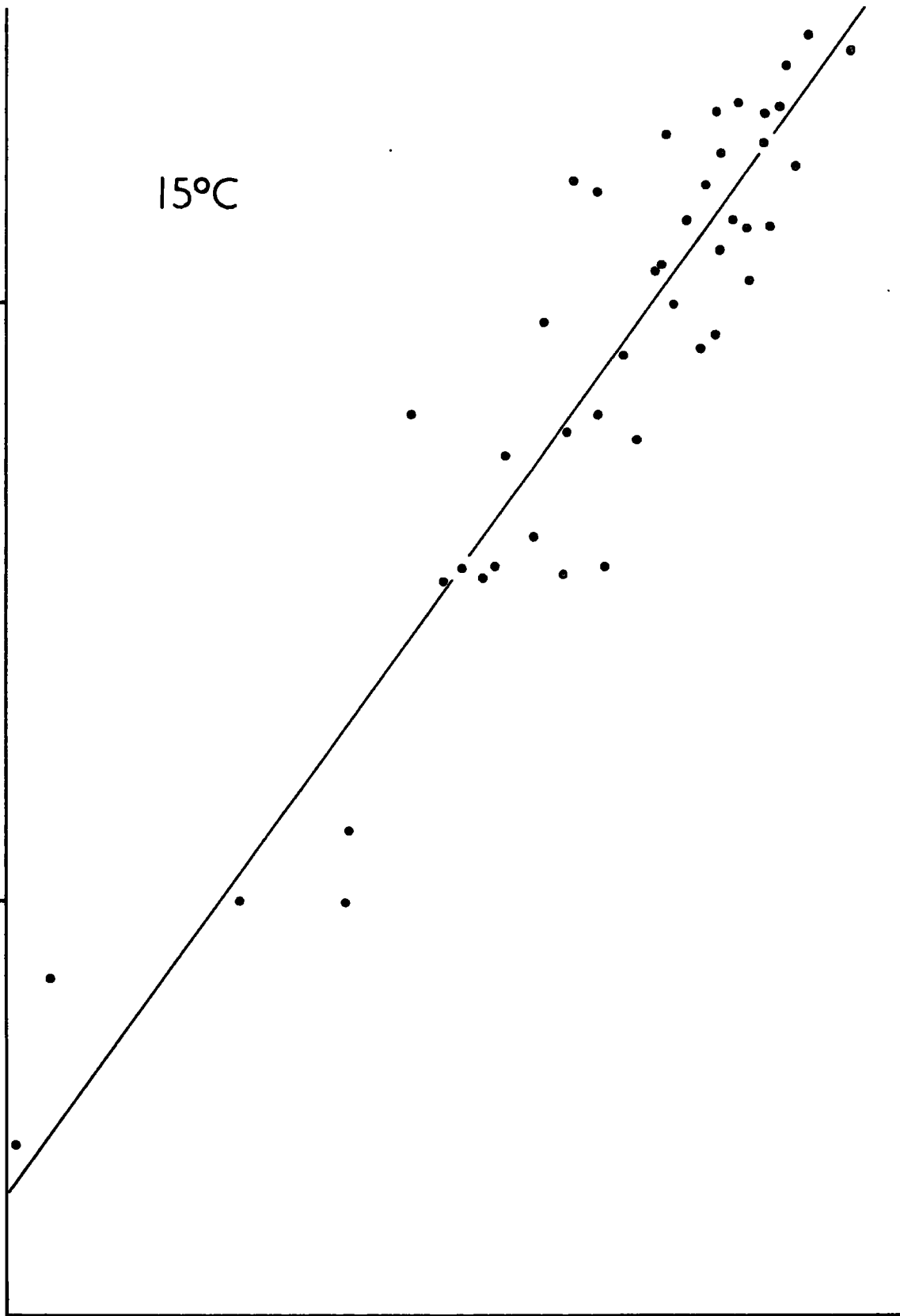mm³O₂/indiv./h.
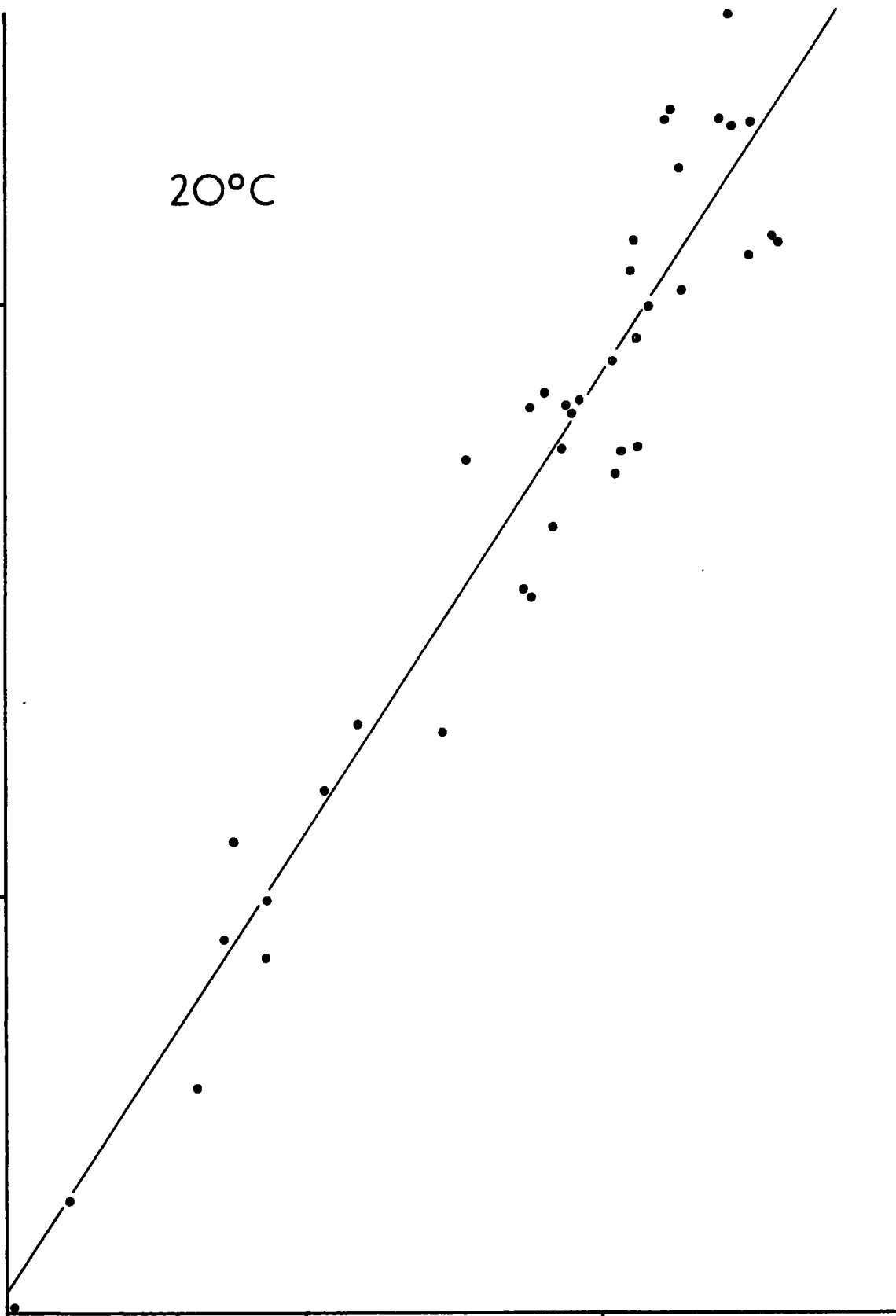
0.1   1.0

Dry Wt.—Mgms.

Fig. 21.   Oxygen consumption per animal per

unit time - logarithmic scale - regression line

($y = 0.7647x - 0.1307$, where x = dry wt. and

y = oxygen consumption).   The data were collected
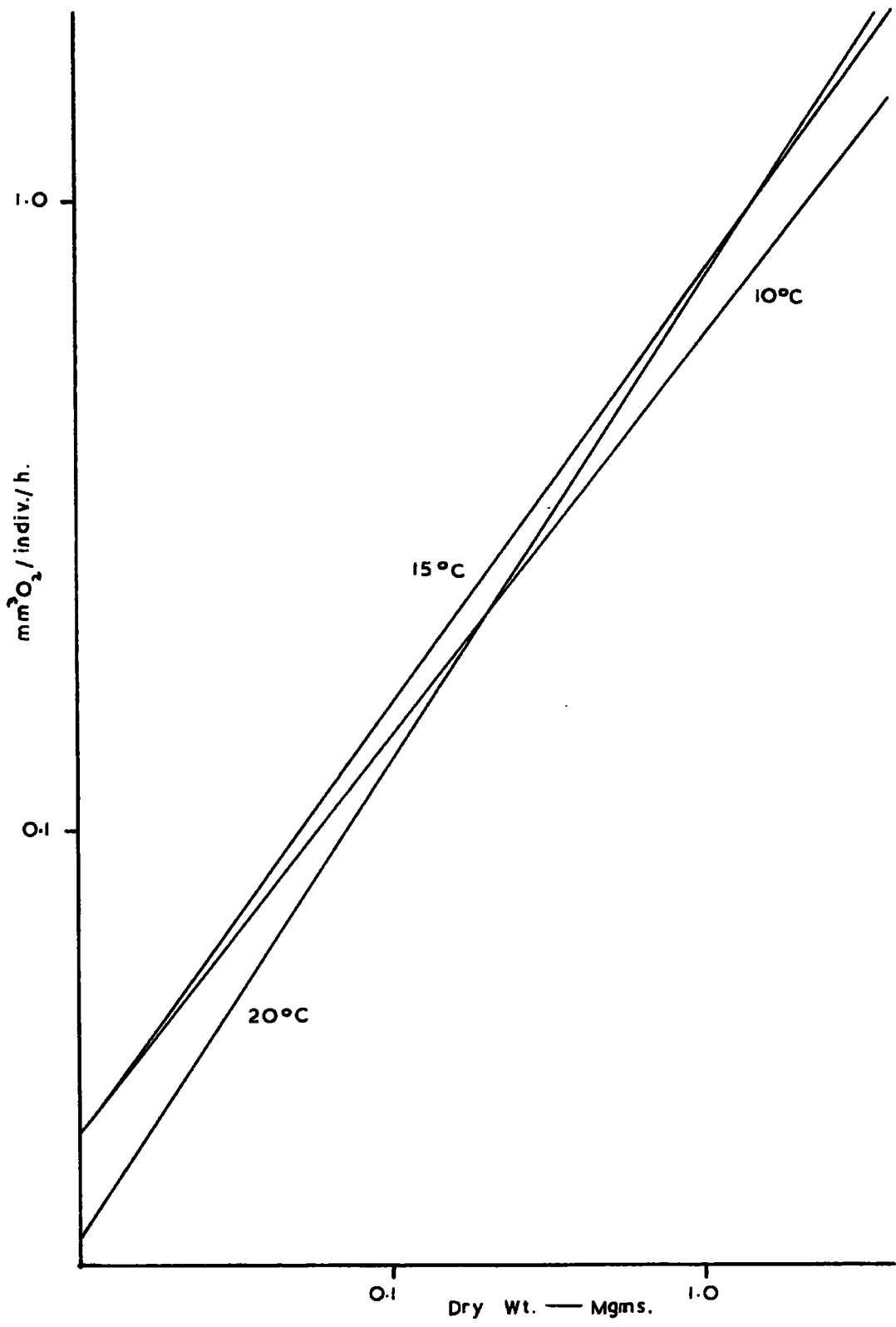
at 20°C.

Fig. 22. Regression lines for oxygen consumption

per animal per unit time at three different

temperatures are compared.

unnecessary to compensate for seasonal temperature variation
when calculating the oxygen consumption of the population.

For the purpose of calculating the respiratory energy
loss by the population, a regression was calculated for all
results regardless of the temperature at which they were
collected. No difference in the respiratory rates of males
and females of comparable size was detected, and the results
for ovigerous females (Figure 23) did not show a significant
difference from those of the rest of the population.

c) The calculation of the energy dissipated by population
respiration

It was proposed to calculate the energy dissipated
via respiration by multiplying the total quantity of oxygen
consumed during one population life-cycle by the appropriate
oxy/calorific coefficient.

Using the data in Table 2, Figures 22 & 23, the mean
oxygen consumption per individual was calculated for the
animals in each of the 16 categories discussed above for each
month of the study. After multiplying the values obtained by
the numbers present in each category, it was possible to
calculate the total quantity of oxygen consumed by the population
in each month. The results obtained are presented graphically
in Figure 24.

Figure 24 emphasizes the great disparity between
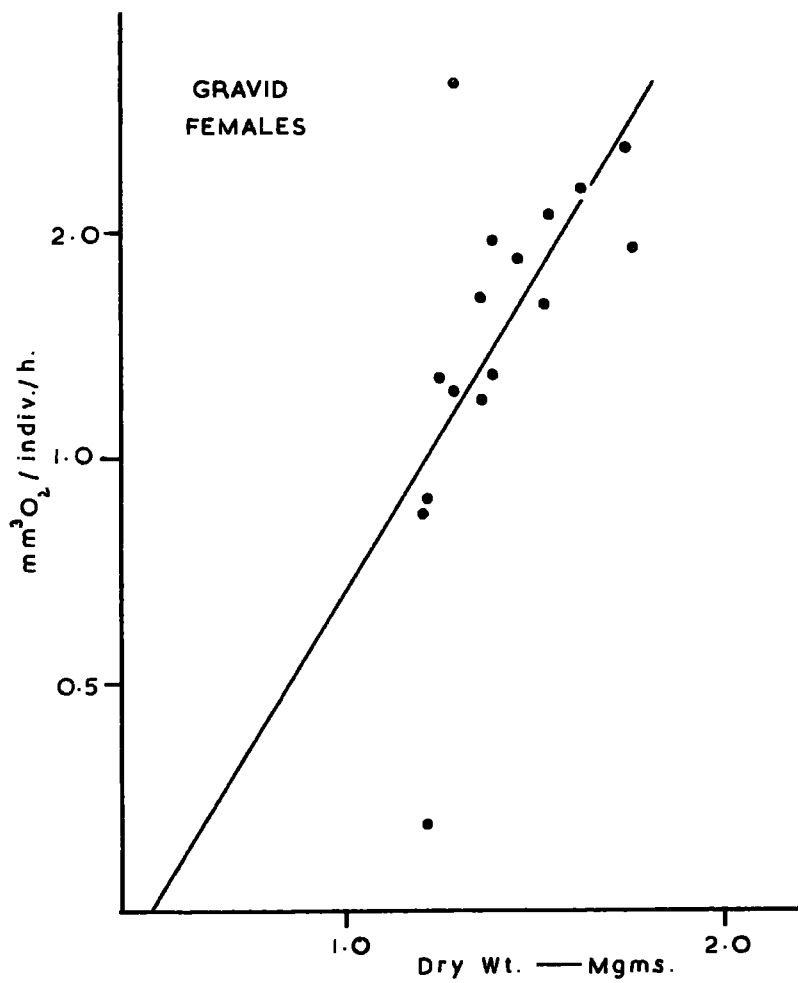the importance of the two generations. Generation II is

Fig. 23.   Oxygen consumption per ovigerous

female per unit time - logarithmic scale -

regression line ($y = 0.8107x - 0.1712$, where

x = dry wt. and y = oxygen consumption).
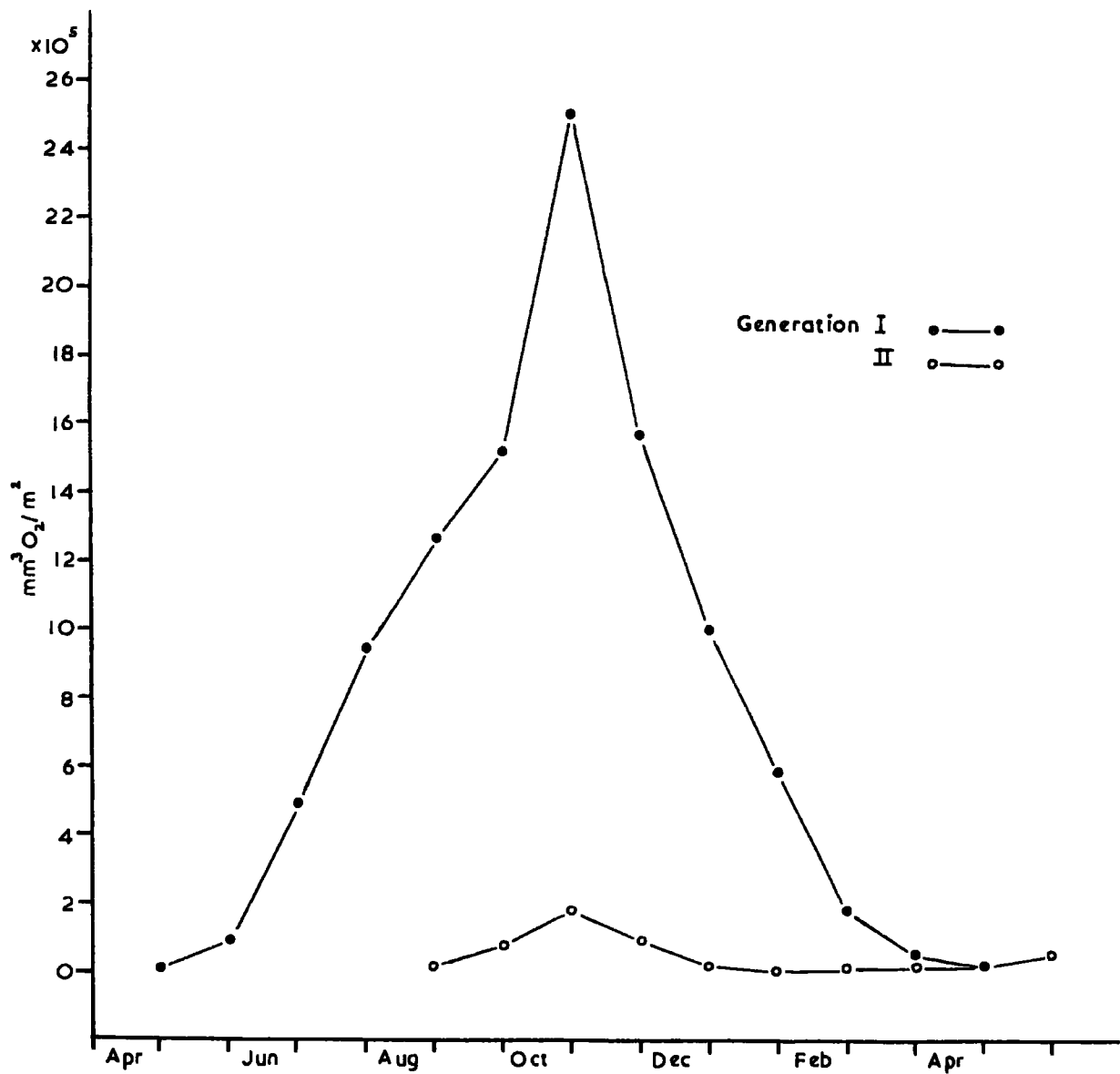
Fig. 24. The quantity of oxygen consumed by
the population during each sampling interval
is plotted against time. The two generations
are treated separately.

responsible for only a very small percentage of the total oxygen consumed.

Insufficient time precluded the possibility of determining the oxy/calorific coefficient during the present study; however, Ivlev (1934) gives 1 ml O_2 = 4.76 cals for this species, and these data were used in the present calculations.

Therefore, energy utilized in maintenance metabolism during the period November 22nd - August 16th

$$= 24.56 \text{ K.cals/m}^2$$

Energy utilized in maintenance metabolism during the period August 16th - November 22nd

$$= 26.50 \text{ K.cals/m}^2$$

Total energy utilized in maintenance metabolism

$$= 51.06 \text{ K.cals/m}^2/\text{annum.}$$

The relative importance of respiration as a pathway for energy flow through the population may be illustrated by drawing up an energy budget.

Energy budget

The results presented above constitute a full description of the fate of the energy which entered the population.   The total energy assimilated by the population may be calculated by summing the different parameters discussed.   Therefore one may write :

Energy assimilated = Energy used in growth + Energy used in

exuviae production + Energy used in

maintenance metabolism.

= 13.903 + 2.393 + 51.060

Therefore total energy assimilated = 67.356 K.cals/m^2/annum.

This figure may help to describe the precise role of A. aquaticus in its ecosystem.

Discussion

a) <u>Population dynamics</u>

It is interesting to consider the cause of the male mortality during the period January to April which gave rise to the unequal sex ratio (Fig. 5). A number of old males were maintained in the laboratory and in cages submerged in the pond. Most of these animals did not die after copulation but lived on until May or June, indeed two individuals began to regenerate lost limbs. These findings suggest that external factors, perhaps predation, play a part; however, no explanation of the mechanism responsible for the differential susceptibility to predation in males and females can be offered.

Predation is in evidence in connection with another feature of the population dynamics. Figure 9 shows the very heavy mortality experienced by the population between November and April, this amounting to approximately 60% per month. This is undoubtedly due in the main to predation since the pond contains large populations of newts, carnivorous caddis larvae, coleopteran larvae and adults, carnivorous hemipteran nymphs and adults and odonatan nymphs, all of which were observed to take <u>A. aquaticus</u>.

Figure 4 and Table 2 show how there are two distinct breeding periods since no newly hatched individuals enter the population in August. This contrasts with the findings of Steel (1961) who demonstrated that <u>A. aquaticus</u> in the River

Thames, although showing two peaks of breeding, produced new individuals continuously throughout the summer.   A possible explanation is that, due to the high predation rate, insufficient ovigerous females remained for the Brasside population to exhibit a continuous breeding season.   In other words, if the times of hatching show overlapping normal distributions about the two modal hatching dates, then the population will show a continuous breeding season;   under heavy predation, however, only those females destined to hatch young close to the modal dates are present in sufficient numbers to leave survivors, and hence the population exhibits two distinct breeding seasons.

Reference to Fig. 4 and Table 2 will also reveal that very few if any of generation II succeeded in breeding. It is probable that this also may be attributed to the high predation rate, for had the mortality not been so great, many of generation II may have grown through the summer and contributed to the breeding later in the year.

b)   The physiological factors affecting energy flow

The method used for the calculation of biomass production in this and Saito's study is, in fact, a combination of methods already used by other workers on animals with simpler life-histories. Smalley (1960), for example, used a

regression of numbers on time to calculate the mortality rate of a grasshopper population, whilst Wiegert (1964) distinguished newly-hatched meadow spittle-bugs in order to allow for a prolonged period of recruitment into the population. The survivorship curve (Fig. 13) is an important part of this calculation, and its interpretation is of interest. It means that an individual's expectation of further life neither increases nor decreases with age. This is precisely what one would expect of most populations subjected to heavy predation, since factors such as an animal's natural life-span are unable to exert their effects. The slope of the line is dependent on the severity of the predation.

Figure 14 shows that the production during July did not follow the general trend but appears to have been much lower than expected. This, in turn, means that the animals did not show the expected increase in length. One possibility is that the production during July was primarily gonad and gamete development, and thus did not express itself as increase in body length. The fact that the irregularity occurred shortly before the birth of the second generation tends to reinforce this view. If this explanation is correct, then the figure for July production must be considered an under-estimate.

The use of the "Brooks-Przibram" law provided a simple and rapid method for estimating the energy lost in

exuviae production. Teal (1957) examined a population of
A. militaris (Hay) as one component of his whole ecosystem
study but did not calculate moulting losses. He considered
that the error would be less than 10% of the total energy
flow, and in this he seems to have been justified since the
results of the present study on A. aquaticus give a figure of
only 3.6%.

The respiratory experiments demonstrated that
A. aquaticus has a Q_{10} value of 1, its respiratory rate thus
remaining unaffected by temperature change provided that it is
allowed to acclimatize. Edwards and Learner (1960) report a
Q_{10} of 1.5 for this species after a short period of acclima-
tization (24 hours). Sprague (quoted in Edwards and Learner
1960) allowed A. intermedius to acclimatize for 7 days and
gives a value identical to that obtained for A. aquaticus in
the present study. It seems, therefore, that it is unneces-
sary to compensate for temperature changes when calculating
the annual respiratory loss for species of Asellus. It is
probable that this principle applies to other genera; however,
since temperature change may or may not induce a change in an
animals rate of activity, the acclimatized Q_{10} value should be
established for each species studied.

One feature which is often used as the basis of
comparison between different species is the relative propor-
tions of the assimilated energy which the animals use for

growth and maintenance metabolism. In the present study
75.8% of the assimilated energy was dissipated by respira-
tion. Teal's (1957) whole ecosystem study includes data
for A. militaris which gave a value of 82.3%, the two values
thus showing quite good correlation. Figures for the genus
Asellus seem to correspond with data given for other inverte-
brates. Engelmann (1966), for example, gives 80% for oribatid
mites, whilst Phillipson (1967) working on the terrestrial
isopod Oniscus asellus (L.) found it to be 75%.

The large range of values in Figs. 14 and 24 serves
to emphasize the necessity of studying population bioenergetics
over a period of at least one full life-cycle. The data
presented show how the relatively short period August 16th –
November 22nd accounted for a large percentage of the annual
energy flow. Although the ratios discussed above would have
remained almost unchanged, had compensation for this short
period not been attempted, the result for total energy flow/
annum would have been a gross under-estimate.

Figure 4 indicates that generation II accounted for
more than 30% of the total number of animals in the population
(data for November), and yet Figs. 14 and 24 show that these
individuals were responsible for only a minute fraction of the
total energy flow. This suggests that the numbers present, or
even biōmass present, is not a reliable index of an organism's
importance in the economy of an ecosystem; study of the energy

flow through these individuals, however, is thought to provide a more accurate assessment.

In the eventuality of data becoming available for other species populations within the pond it will be possible to state in precise terms the role played by A. aquaticus in the ecosystem considered. In the absence of these data, however, it is still possible to gain a general indication of the importance of this species. The Mayfly Cloeon dipterum (L.) and A. aquaticus are the only two macro-herbivores of importance in the pond. Cloeon dipterum is only slightly affected by predation, and thus a large proportion of its production is exported from the pond at emergence (Clennell 1967). A.aquaticus, however, must form the primary food source of most of the predators in the pond, although it is difficult to be certain until the energy flow through the planktonic fractions of the food-chains has been determined. If A. aquaticus does indeed occupy a central position in the economy of the pond then it follows that the detritus food-chains must be well represented in this ecosystem. It may be that the types of food chain present characterize the three major groups of ecosystems. Marine situations may consist almost exclusively of grazing food-chains; terrestrial ecosystems may use detritus food chains as the major energy pathway; whilst freshwater systems may occupy an intermediate

position with the actual percentage importance of each path-
way varying with the individual ecosystem.

The body of information gained by bioenergetic
studies is increasing, and it is hoped that in the near
future predictive hypotheses may be drawn from it. It is
important that we should understand the fundamental laws
acting on our natural ecosystems, for this may point the way
to ensuring that our agricultural ecosystems produce food
with maximum efficiency. Such considerations will obviously
become of even more importance if the present trend in human
population increase continues.

Summary

1. A study was made of the dynamics and bioenergetics of a population of the isopod <u>Asellus aquaticus</u> (L.) in a fresh-water pond between November 1966 and August 1967.

2. The size class distribution, sex-ratio and growth rates were investigated throughout the period of study and used to deduce the life history of the population considered.

3. The change in population density was examined and found to vary between $1000/m^2$ in July and $8.2/m^2$ in April.

4. Growth was calculated from changes in biomass from month to month and expressed in calories using calorific values determined directly by bomb calorimetry. An estimated 13.903 K. cals./m^2/ annum were used in growth. The growth rate was found to differ in the two sexes and to vary with season.

5. Laboratory moulting experiments were carried out and the results used to calculate the energy deposited in exuviae by the population. This amounted to 2.393 K. cals./m^2/ annum.

6. Respiration rates and the respiratory Q_{10} were determined by laboratory experiments. An oxy/calorific coefficient of 4.76 cals./O_2 cc. was used in the calculation of the energy dissipated by maintenance metabolism of the population, and this was estimated at 51.06 K. cals./m^2/ annum.

7.   The growth, moulting and respiratory data were combined
and used to draw up an energy budget for the population.
From this it was calculated that the total assimilation
amounted to 67.356 K. cals./m^2/ annum, this being equal to
the total energy flow through the population.

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