Studies on the bioenergetics of certain terrestrial isopoda

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STUDIES ON THE BIOENERGETICS OF CERTAIN TERRESTRIAL ISOPODA

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A thesis presented in candidature for the degree

of Doctor of Philosophy

by

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Introduction

Ecology has been defined by Odum (1962) as the "study of the structure and function of ecosystems". He indicated that much attention has been devoted to the structural or descriptive approach, whereas few studies of the function of ecosystems have been attempted. Odum (1962) further states that by structure he meant: a) the composition of the biological community, including species, numbers, biomass, life history and distribution in space of populations, b) the quantity and distribution of abiotic materials such as nutrients and water, and c) the range or gradient of conditions of existence, such as temperature and light. Function was defined as: a) the rate of biological energy flow through the ecosystem i.e. rates of production plus rates of respiration, b) the rate of biogeochemical cycling e.g. nutrient flow, and c) biological or ecological regulation.

The structural or descriptive approach therefore, serves only to describe the existence of organisms, and materials in the ecosystem. Odum (1962) and Macfadyen (1964) have indicated that, although biomass in different ecosystems may be widely different, the energy flow produced may be very similar. Strict comparisons of numbers alone are therefore of limited use when one wishes to fully understand the working of ecosystems. The functional approach,

whereby rates of energy flow per unit area of habitat per unit time are measured for various organisms, will enable strict comparisons to be made both within and between ecosystems.

The energy flow models constructed by Odum (1962, 1963) and Macfadyen (1964) indicate that in an open water marine ecosystem the important food chain appears to be the grazing one, whereas in a forest ecosystem the detritus food chain appears to be the more important of the two. Early bioenergetic studies dealt with aquatic ecosystems, and although Bornebusch published his now classic study in 1930, it was not until the publication of Golley's (1960) study, that serious attention was paid to the terrestrial ecosystem. The reason for this was due in part to the supposedly simple structure of the aquatic ecosystem, as opposed to the complexity of the terrestrial one. Currently, increasing attention is being paid to the role of terrestrial animals in promoting energy flow through ecosystems. Most of the terrestrial animals already studied belong to the relatively simple grazing food chain. The detritus chain has a more heterogeneous collection of organisms than the grazing one, the commonest groups being the large decomposers (Lumbricidae, Isopoda, Diplopoda); the small decomposers (Collembola, Orobatei, Enchytraeidae); and the microorganisms such as Protozoa, Fungi and Bacteria. Macfadyen (1961, 1964) has suggested that

microorganisms can account for as much as 90 percent of the energy flow through an ecosystem. If this assumption is correct, the question arises as to the role of the large and small decomposers in a detritus food chain.

Before the present study began, no single species of a type designated by Macfadyen (1963) and others as "large decomposers", had been studied in all its life stages to determine its role in the breakdown of litter, and its contribution to the total energy flow of a woodland ecosystem. As part of a woodland ecosystem study in Durham, the two isopods Oniscus asellus.L. and Porcellio scaber. Latr. (large decomposers in the detritus food chain) were chosen to obtain such information.

The equations commonly used for the measurement of energy flow are those defined by Slobodkin (1962), and Wiegert (1964). These equations employ different symbols to describe the same parameters, and may be applied to whole ecosystems, species population, or single individuals. Slobodkin's (1962) terminology expressed in its simplest form is:-

I	=	R	+	Y
Energy of assimilation		Energy of respiration		Energy of growth and reproduction

Wiegert's (1964) formula encompasses the components of Gibb's free energy equation, and may be expressed as:-

ΔH	=	$T\Delta S$	+	ΔF
Food energy assimilated		Energy dissipated as heat of respiration		Energy used for growth and reproduction

ΔH represents the energy income, $T\Delta S$ the energy lost as heat from the system (unavailable or bound energy), and ΔF the energy staying in the system (available or free energy). Energy flow is represented by R+Y or $T\Delta S + \Delta F$. Quantification of these expressions in conjunction with biomass data, permits the energy budgets of ecosystems, species populations, or single individuals, in terms of energy flow per unit area of habitat per unit time, to be calculated.

Attempts to solve the equation for whole ecosystems have been made by Odum and Odum (1955); Odum (1957); and Teal (1957). However, it is difficult for one person to perform all the tasks necessary for a whole ecosystem approach. Most workers have restricted their studies to the evaluation of the whole equation for simple food chains, species populations, or the study of one parameter of the whole equation. The individual parameter most often studied is $R, (T\Delta S)$ for terrestrial invertebrates, as it represents the greatest

proportion of total energy flow. These restricted approaches are valuable, for as information is obtained, albeit gradually, a synthesis of the total energy flow of the ecosystem will be made. Attempts to solve the whole equation for simple food chains or species populations have been made by:- Richman (1958); Odum and Smalley (1959); Slobodkin (1959); Golley (1960); Smalley (1960); Englemann (1961); Kuenzler (1961 a.b.); Teal (1962); Odum, Connell and Davenport (1962); McNab (1963); Golley and Gentry (1964); Mann (1964, 1965); Wiegert (1964, 1965); Paine (1965); Petrides and Swank (1965); and Saito (1965). Measurements for R(T S) have been made by:- Nielson (1961); Phillipson (1962, 1963); Berthet (1963); O'Connor (1963); and Ito (1964).

The present study attempts to solve the whole equation for the two isopod species Oniscus asellus and Porcellio scaber. For a complete energy flow study the rates of assimilation, respiration, body and reproductive growth, and the calories they represent must be determined. Measurements of numbers and biomass, and death rates will enable the above data to be expressed in terms of energy per unit area of habitat per annum. It was not possible to obtain the population data for the two species in the time available, therefore the rates obtained for assimilation, respiration, and growth, are presented as 'best estimates', thus facilitating the calculation

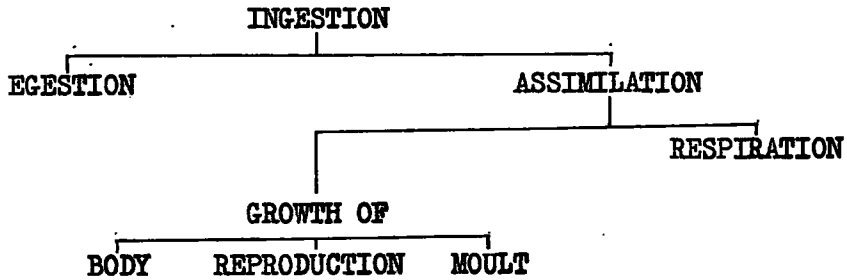
from biomass data, when available, of the rate energy flow per unit area of habitat per annum.

Energy of assimilation may be calculated according to the equation:-

Energy of assimilation	=	Energy of ingestion	-	Energy of egestion

$I_{(\Delta H)}$

Energy of respiration R or $T\Delta S$, and energy of growth and reproduction Y or F, may be measured directly. The independent measurement of all three parameters of the energy flow equation enabled two estimates of energy flow to be presented i.e. $I_{(\Delta H)}$ or $R_{(T\Delta S)} + Y_{(\Delta F)}$. Thus a double check is available, enabling the accuracy of the results obtained to be ascertained. The complete energy budget of each species may be presented in the following manner:-



As body growth, reproductive growth, and growth by moulting were to be separately measured Slobodkin's (1962) terminology may be expanded to:-

$$I = R + Y1 + Y2 + Y3$$

Y1 = body; Y2 = reprod.; Y3 = moult

Since the study began Saito (1965) has presented data for the energy flow of the isopod Ligidium japonicum in a warm temperate ecosystem. The biomass data presented by Saito plus the 'best estimates' obtained in the present study are used to compare the roles of Ligidium japonicum, Oniscus asellus, and Porcellio scaber in promoting energy flow through different woodland ecosystems.

SECTION 1

Investigations to determine the energy assimilated (I or Δ H) by Oniscus asellus L. and Porcellio scaber Latr.

General Introduction.

Detailed accounts of assimilation rates of terrestrial invertebrates are few. Auzou (1955) studied the isopod P.scaber; Gere (1956a) the isopod Protracheoniscus politus; and (1956 b, c and d. and 1957) the caterpillar Hyphantria cunea; Odum and Smalley (1959) and Smalley (1960) the grasshopper Orcheliumum fidicinium; Phillipson (1960 a. b.) the harvest spider Mitopus morio; Odum, Connell and Davenport (1962) the herbivorous Orthoptera Melanopus femur-rubrum, M.biliteratus, and Oecanthus nigricornis; Hartenstein (1964) the isopod O.asellus; Waldbauer (1964 a.b.) the tobacco hornworm Protoparce sexta; Wiegert (1964) the spittle bug Philaenus spumarius; and (1965) the grasshopper populations in old field and alfalfa field ecosystems; Hubbell, Sikora and Paris (1965) the Isopod Armadillidium vulgare; and Wieser (1965) the isopod P.scaber.

The determination of assimilation rates (I or ΔH) by the different life stages in the field, according to the equation Assimilation = Food ingested - Faeces produced, is a difficult task. Experiments under as near natural conditions as possible were made

by enclosing animals, so that the food not eaten and the faeces produced by them during the course of an experiment could be ascertained. However, possible experimental errors were centered around the fact that the rates of assimilation might vary with the type of food eaten. To reduce any errors associated with varying assimilation rates, it was felt that information was needed concerning the preferred foods of each of the isopod species, before any measure of assimilation could be made. The methods used and the results obtained, form the content of Chapter 1.

The most preferred foods as shown in Chapter 1 were then used in experiments to investigate the rate of assimilation. To calculate this rate for each life stage of O.asellus. and P.scaber. it was necessary to measure the rate of food ingestion and faeces production. Initially the intention was to carry out these experiments during the winter and summer months, so that a seasonal comparison could be made. Owing to a shortage of time and a lack of animals in the winter months, only the rate of faeces production was determined. The methods used and the results obtained in this winter study are presented in Chapter 2.

The rates of ingestion, egestion and assimilation of the known preferred foods were obtained in the summer experiment. The methods used and the results obtained form the basis of Chapter 3.

Wieser (1965) is the only author to have presented assimilation data for a 'large decomposer' (P.scaber) in all its life stages. The present study rectifies this situation for O.asellus. The experiments with P.scaber were being made before Wieser's (1965) account appeared, thus the results obtained proved useful for comparative purposes. The results given in Chapters 2 and 3 were used to calculate a 'best estimate' of energy assimilated (I or ΔH), for both the isopod species, thus facilitating the calculation, from biomass data, of the annual energy assimilated per unit area of habitat by any population of O.asellus or P.scaber. The methods used and the results obtained form the content of Chapter 4.

Chapter 1.

Food preference of *Oniscus asellus* and *Porcellio scaber*.

Introduction.

Many statements are to be found in the literature concerning the omnivorous habits of isopods: Theobald (1904); Pierce (1907); Collinge (1915); Howard (1940); Heeley (1941); Hatchett (1947); Beerstecher et al (1954); Bakker (1956); Brereton (1956); Gere (1956 a); den Boer (1961); Dunger (1962); Paris (1963); Beyer (1964); Hartenstein (1964); Hubbell, Sikora and Paris (1965); Paris and Sikora (1965); Wieser (1965); and Saito (1965). However, only Paris, studying *Armadillidium vulgare* has attempted food preference experiments. Paris' work is important because he conducted preliminary experiments to eliminate foods not eaten in the field. For those foods most readily eaten, he was able to list a table of preference by conducting laboratory experiments where the numbers of individuals feeding on each food were compared. The food which was most frequently visited (dead *Picris* sp. leaves) was assumed to be the one most commonly eaten in nature.

In the present study, food preference investigations were of three kinds:-

1) Preliminary studies with O.asellus to eliminate the foods not eaten.
2) The determination of the order of food preference of O.asellus in the laboratory.
3) The determination of the order of preference of O.asellus and P.scaber under near natural conditions.

1. Preliminary studies with O.asellus.

Methods:

A modification of the methods employed by Paris (1963) was used. Forty different food items and two hundred individuals of all size ranges of O.asellus were collected in the vicinity of Durham City. The foods consisted of recently killed animals, and fresh and decaying plant materials, which collectively represented most of the potential foods available to the isopod. A disc of each plant food, 4 cms in diameter was cut with a cork borer, and introduced into a 60 x 60 x 5 cm metal tray, the bottom of which was covered with damp filter paper. The recently killed potential animal foods were placed individually in the tray. Two hundred O.asellus were then introduced into the tray, the top of which was finally sealed with a sheet of glass. After 24 h. the isopods were removed and the percentage of each food item eaten was estimated by eye.

Results:

The eight foods most readily eaten were assumed to be the preferred ones. Table 1. summarises the results obtained.

Table 1: Foods most readily eaten by O.asellus when allowed to feed for 24 h on 40 of the most commonly occuring foods in the habitat.

Food item	% consumed
Dead Thistle (Onopordum sp) leaves	90
*Dec Sycamore (Acer sp) leaves	90
Dead Nettle (Urtica sp) leaves	85
Dec Oak (Quercus sp) leaves	80
Dec Chestnut (Castanea sp) leaves	80
Dec Beech (Fagus sp) leaves	5
Fallen log bark	2
Bark + Pleurococcus	1

* Dec = Decaying

An indication of the preference is given by the various percentages consumed, and it is clear that dead and decaying plant material was most readily eaten. It is possible that only a small proportion of the two hundred animals were responsible for the removal of the foods, therefore further experiments to determine the numbers of animals actually feeding during the course of the experiment were made.

2. Food preference of O.asellus in the laboratory.

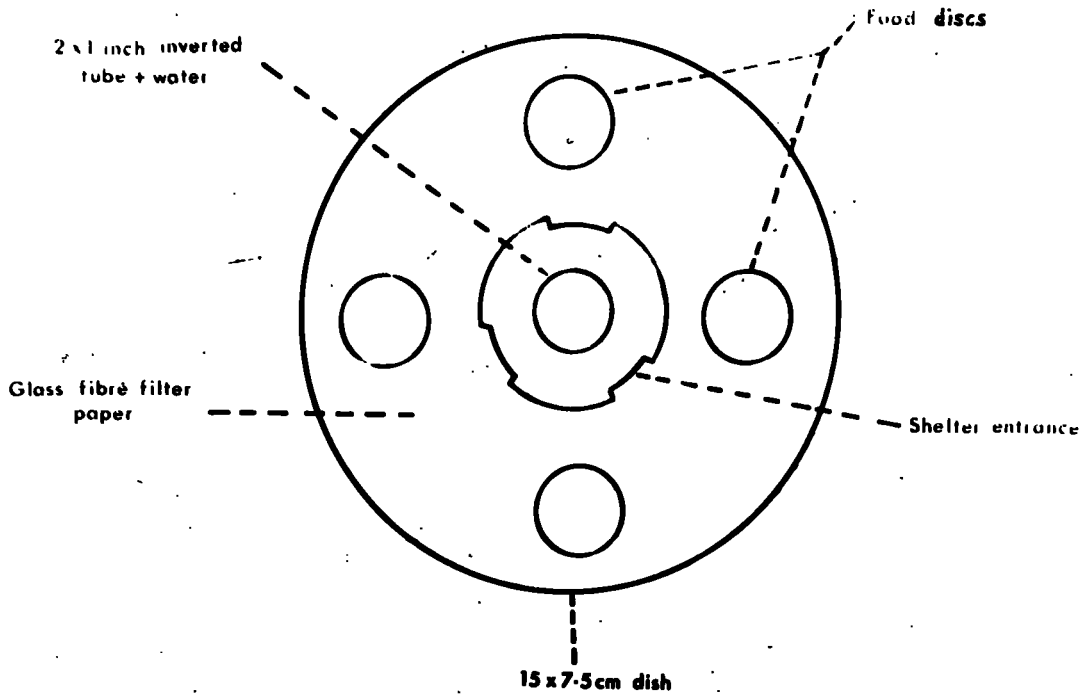
Methods:

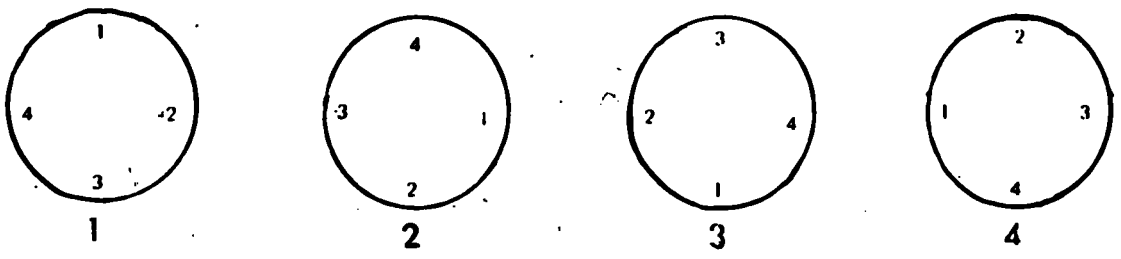
Individual O.asellus of all size ranges were collected in the field and brought into the laboratory. The foods which were shown by the earlier experiment to be most readily eaten were collected and cut into 3 cm discs. Feeding chambers were prepared, the basic layout of which is shown in Fig. 1a. Each feeding chamber consisted of a crystallising dish 15 x 7.5 cm, on the bottom of which glass fibre filter paper was placed, and kept damp by an inverted 2 x 1" tube filled with water. Glass fibre filter paper was considered necessary in that isopods eat normal filter paper, and this activity could have influenced food preference determinations. The shelter which surrounded the 2 x 1" tube was made from the lid of a pill box of 6 cm diameter, and entrances were cut to facilitate movement of the experimental animals into and out of the shelter. Shelters were considered necessary as Bakker (1956) noted that without them P.scaber tended to remain feeding on the food all day, which is contrary to their daytime habit of hiding under stones, log bark, and in crevices. Each chamber was sealed with a 6 x 6" glass lid which enabled RH to be maintained at >95%.

Fig.1.

(a) The Layout of a typical feeding chamber

(b) Arrangement of feeding chambers in the food preference experiments so that light coming from a certain direction would affect all foods equally.


2 x 1 inch inverted tube + water
Food discs
Glass fibre filter paper
Shelter entrance
15 x 7·5cm dish


1
4
2
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3
1
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2
3
2
4
1
3
2
1
3
4
4

The eight chosen foods were divided into two groups of four (see Table 2). Discs of each of the four foods in the group were placed equidistant around the perimeter of the feeding chamber. Four replicates were used for each group of foods, and these were orientated in the manner shown in Fig. 1b. This ensured that light coming from a certain direction would affect all foods equally, thereby reducing potential errors if the animals happened to congregate on food unaffected by the light. Twenty-five animals were introduced into each dish and allowed to feed for 24 h. During this time hourly counts were made of the numbers feeding on each food. Counting at night was facilitated by the use of a torch masked with a yellow filter. At the end of the 24 h. feeding period the animals were removed and the results analysed as follows:-

a) The numbers of isopods observed feeding on each food at each hourly observation were summed and divided by the number of replicates, thus giving the mean number per chamber seen feeding on each food during the 24 h. feeding period.

b) The percentage of food eaten in 24 h was estimated by eye.

Table 2 shows a summary of the results obtained.

Table 2: *O.asellus:* The mean number per chamber observed feeding on a given food during a 24 h period, and the percentage of each food eaten per 24 h.

Experiment 1	Mean no feeding	% eaten
Dec Sycamore (*Acer* sp) leaves	33	65
Dead Nettle (*Urtica* sp) leaves	24	75
Dead Thistle (*Onopordum* sp) leaves	23	80
Bark + *Pleurococcus*	8	1
Experiment 2		
Dec Oak (*Quercus* sp) leaves	25	50
Dec S. Chestnut (*Castanea* sp) leaves	20	40
Fallen log bark	12	3
Dec Beech (*Fagus* sp) leaves	8	2

A further 24 h experiment was made on five of the foods to obtain an order of preference for the most readily eaten foods. The foods used were decaying Sycamore leaves, dead Nettle leaves, dead Thistle leaves, decaying Sweet Chestnut leaves, and decaying Oak leaves. The methods and experimental set up were similar to the previous experiment, but five foods instead of four were placed in each feeding chamber. The results are shown in Table 3. It is clear that dead and decaying plant material is most preferred,

Table 3: O.asellus: Final order of food preference as shown by the laboratory experiments, showing the mean number per chamber feeding per 24 h on the five foods most readily eaten.

Food item	Mean no. feeding	% eaten
Dead Thistle (Onopordum sp) leaves	35	85
Dead Nettle (Urtica sp) leaves	32	75
Dec. Sycamore (Acer sp) leaves	32	75
Dec. Oak (Quercus sp) leaves	20	40
Dec. S. Chestnut (Castanea sp) leaves	18	25

dead Nettle, dead Thistle, and decaying Sycamore leaves being the most preferred of all the foods offered. Maximum feeding occurred during the hours of darkness, little or no feeding being observed during the day when the animals sought refuge under the shelters.

The above method was thought to have certain limitations, for example hourly counts over a 24 h period were tedious, and the experiment had to be made under laboratory conditions which may not have reflected the field situation. The combined effect of removing the feeding chamber lids, and the prolonged use of the torch light when counting during the night, tended to disturb the animals, and in some cases the animals moved from the food on which they were

feeding before counting took place. Therefore a more sophisticated technique involving an automatic camera, which removed the burden of regular observation, and enabled the experiments to be conducted under near natural conditions was employed.

3. An automatic camera device for food preference and activity studies, under near natural conditions.

Automatic camera devices were used by Pearson (1960 b) and Cowardin and Ashe (1965) to record animal activity. The value of an automatic device is that once the apparatus is set up and the experiment begun, continuous observation by the experimenter is eliminated, and a permanent photographic record is given which may be analysed at a later date. The present apparatus was designed for the specific purpose of determining, with the minimum of interference:-

a) the number of animals feeding on the foods most commonly occurring in the habitat of both O.asellus and P.scaber, thereby determining an order of food preference.
and

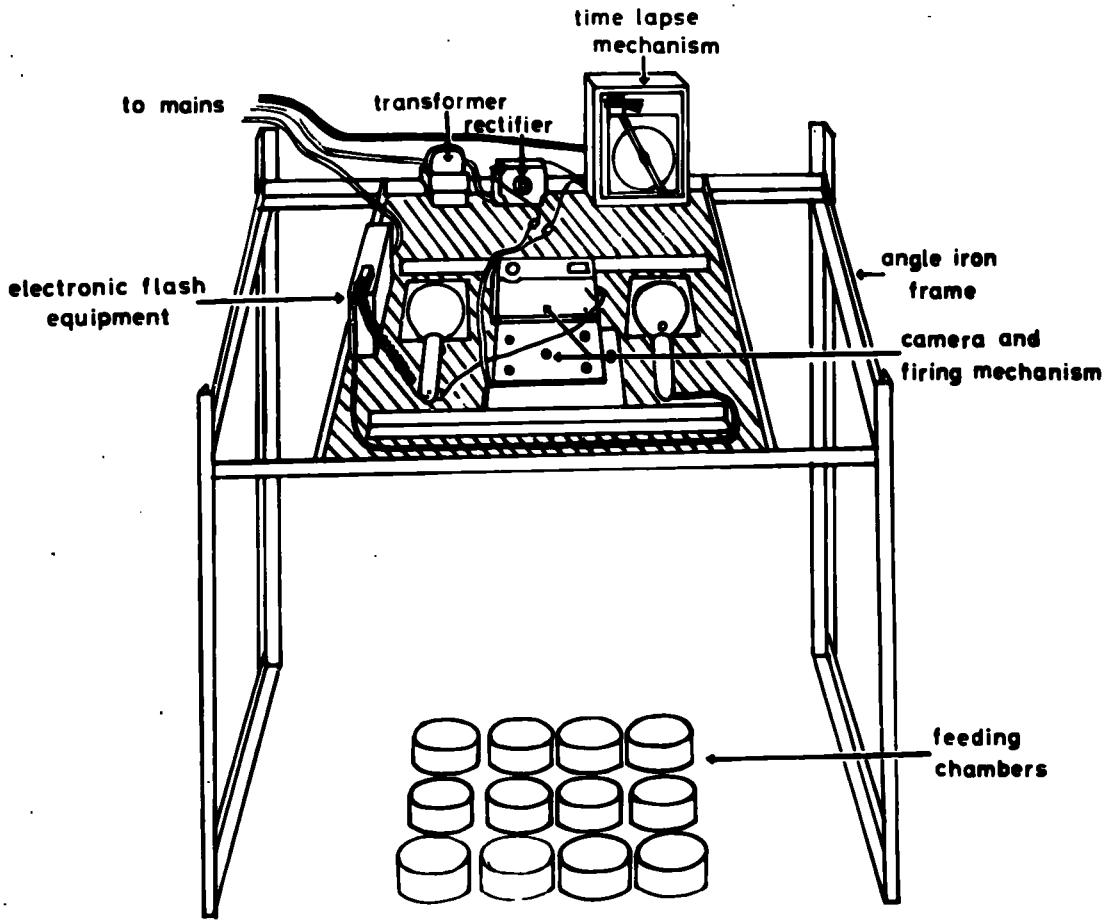
b) the feeding activity patterns of the two species whereby the percentage of animals active at a given time during a diel could be determined.

Fig. 2 shows the assembled apparatus and Figs. 3a and 3b show the individual components. It can be seen from Fig. 3b that a Prakti 35 mm. fully automatic camera was mounted firmly on a reinforced hardboard frame. The camera shutter release mechanism was connected by means of a strong wire to a lever operated by a solenoid, also firmly mounted to the frame. A clock mechanism (Fig. 3a) operated from the mains via a transformer and rectifier, set to activate the solenoid once every 30 minutes ensured that the camera operated at regular intervals throughout a given period of time, normally 24 h. This assemblage was placed on an adjustable frame of angle iron which had previously been erected in the Zoology department insectary, where a mains supply was available, and the temperature and light conditions approximated to those in the field. Feeding chambers were placed at ground level beneath the camera as shown in Fig. 2.

The transformer - rectifier output to the time lapse clock mechanism and solenoid was 6 volts D.C., whereas the coupled flash mechanism operated on a full mains supply of 240 volts A.C. In operation the steel disc attached to the time lapse mechanism revolved, moving the pointer towards the open strip contact X (Fig. 3a). The pointer closed the contact and completion of the

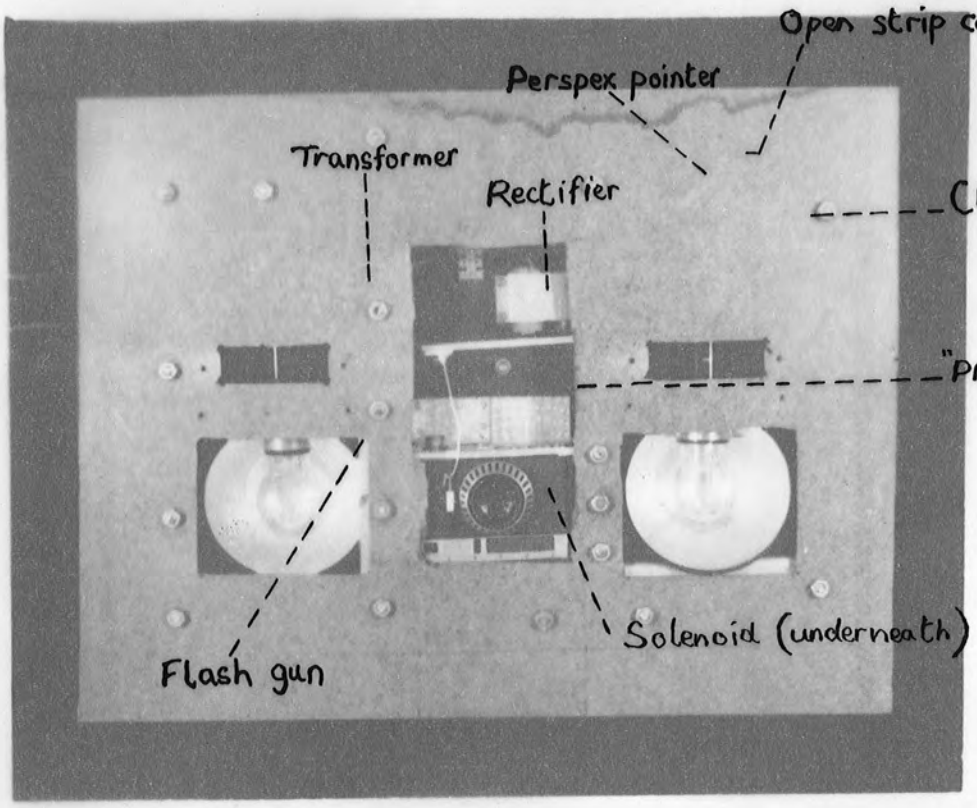
Fig.2.

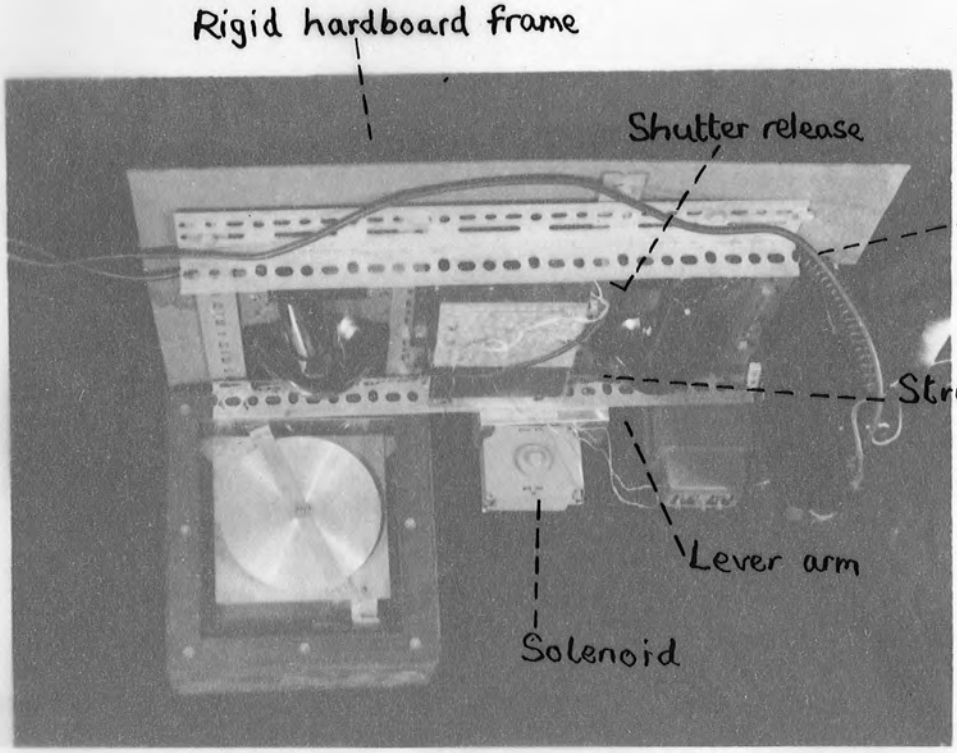
The automatic camera device, complete assembly.


time lapse
mechanism
to mains
transformer
rectifier
electronic flash
equipment
angle iron
frame
camera and
firing mechanism
feeding
chambers

(a) Individual components of the automatic camera device, as viewed from above.

(b) Automatic camera device, ventral view of the rigid hardboard frame.


Open strip contact X
Perspex pointer
Transformer
Rectifier
Clock mechanism
"PRAKTI" 35mm camera
Flash gun
Solenoid (underneath)


Rigid hardboard frame
Shutter release
Flash gun
Strong wire
Lever arm
Solenoid

circuit activated the solenoid which pulled the lever towards it, which in turn operated the shutter release mechanism and the coupled electronic flash. The film was automatically wound on after each exposure. With the time lapse clock mechanism still in operation the pointer moved past the contact X which sprung back to its position of rest, thus breaking the circuit, and inactivating the solenoid. The lever was pulled from the solenoid by the shutter release mechanism. This procedure was repeated every 30 minutes.

Preliminary experiments showed that the best photograph definition was obtained using Kodak Plus X film at a camera to feeding chamber distance of 3'6". It was observed that the animals were not disturbed when the flash operated, therefore no filters were needed. The animals were made more easily distinguishable by painting a small spot of white cellulose dope on the dorsal surface. At a camera to feeding chamber distance of 3'6" it was possible to recognise all the animals feeding in twelve 15 x 7.5 cm feeding chambers, or one 60 x 60 x 5 cm metal tray. The feeding chambers were almost identical to those used in the earlier food preference studies (Fig. 1), however condensation on the glass lids affected the picture quality, therefore the lids were discarded. In the absence of glass lids the water level in the 2 x 1" tubes fell rapidly, and it was found that 6 x 1" inverted tubes, the bottoms

of which were drilled out, required topping up only once every 12 h.

Preliminary experiments for food preference.

In view of the new method being employed to determine food preference it was decided to repeat the study of foods which were eaten and those which were not.

Methods:

Owing to the large numbers of foods to be simultaneously tested, eight metal trays 60 x 60 x 5 cm were used as feeding chambers. The bottoms were covered with glass fibre filter paper each being marked with a grid of 49 squares. Nine 6 x 1" inverted tubes, each surrounded by a shelter and filled with water, were placed one per square in each tray to maintain RH >95%. A band of stictite was applied 1 cm below the rim of each tray, to prevent escape of the experimental animals. Forty food items were collected as previously described, 4 cm discs of the plant material were cut and each disc placed at random, one per square on the grid. The freshly killed food animals were placed together on the remaining square. One hundred isopods marked in the usual manner were introduced into each tray, there being four replicate trays for each of the two isopod species. Eight separate 24 h. runs were carried out.

As the isopods took several hours to settle after being introduced into the trays, they were allowed to become accustomed to the trays overnight. At 0730 h. GMT the following morning the overnight foods were replaced, and the camera set to take the first photograph at 0800 h. GMT. At the end of 24 h. the experiment was ended and the isopods removed.

Results:

Analysis of the film and the food remains showed that O.asellus and P.scaber attempted respectively 24 and 26 of the forty foods offered. The results are summarised in Table 4. Due to the shortage of P.scaber in the field, no further experiments were conducted to determine food preference of this species. However, the mean number feeding on each of the foods, at each observation during the 24 h. feeding period was determined, and the percentage of each food eaten was determined by eye. The eight foods most readily eaten are shown in Table 5, where it can be seen that dead and decaying litter is most preferred. The food preference of O.asellus was investigated in more detail.

Table 4: A list of the foods most commonly occurring in the habitat which were attempted by the two isopod species O.asellus and P.scaber. (* indicates food attempted)

	O.asellus	P.scaber
Dead Beech (Fagus sp) leaves	*	
Dec. Beech " " leaves	*	
Dead Oak (Quercus sp) leaves	*	*
Dec. Oak " " leaves	*	*
Dead H. Chestnut (Aesculus sp) leaves	*	
Dec. H. Chestnut " " leaves	*	
Dead Chestnut (Castanea sp) leaves	*	*
Dec. S. Chestnut " " leaves	*	*
Fresh Sycamore (Acer sp) leaves		*
Dead Sycamore " " leaves	*	*
Dec. Sycamore " " leaves	*	*
Fagus bark + Pleurococcus	*	*
Acer bark + Pleurococcus	*	*
Quercus bark + Pleurococcus	*	*
Castanea bark + Pleurococcus	*	*
Aesculus bark + Pleurococcus	*	*
Fresh Bryophyta	*	*
Assorted Fungi	*	*
Fresh Nettle (Urtica sp) leaves		*
Dead Nettle " " leaves	*	*
Dead Bracken (Pteridium sp) leaves		*
Dec. S. Chestnut (Castanea sp) husks	*	*
Fresh Thistle (Onopordum sp) leaves		*
Dead Thistle " " leaves	*	*

Table 4 (continued)

	O.asellus	P.scaber
Fresh grass leaves and stems		*
Dec. " " " "	*	*
Fresh Bramble (Rubus fruticosus) leaves		*
Soil	*	*
Fallen log bark	*	*
Rotten inside of fallen log	*	*

Table 5: P.scaber: Order of food preference as determined by an automatic camera and showing the mean number of animals recorded feeding on each preferred food during a 24 h. experiment, and the percentage of food eaten.

Food item	Mean no. feeding	% eaten
Dead Thistle (Onopordum sp) leaves	166	90
Dec. Sycamore (Acer sp) leaves	126	80
Dead Nettle (Urtica sp) leaves	115	75
Dec. Oak (Quercus sp) leaves	66	50
Dec. S. Chestnut (Castanea sp) leaves	62	30
Fallen log bark	43	3
Dead S. Chestnut (Castanea sp) leaves	41	10
Dead Sycamore (Acer sp) leaves	38	10

Final food preference experiments on O.asellus.

Methods:

The 24 foods attempted by O.asellus were divided into eight groups of three foods per group. Four replicates were made for each group. In this way two 24 h. experiments with the aid of the automatic camera accommodated all the groups. 3 cm discs were cut in the usual manner. Discs of each of the three foods in a group were placed equidistant around the perimeter of the feeding chamber. Twenty-five marked individuals were introduced into each feeding chamber, and allowed to feed and settle overnight. Freshly cut discs were offered at 0730 h. GMT the following morning and the camera set to take the first photograph at 0800 GMT. At the end of each 24 h. experimental period the individuals were removed and the film developed.

Results:

Table 6 shows a summary of the results obtained, listing the mean number of animals per chamber feeding on each food for the 24 h. experimental period. In groups 1, 2 and 3 the dead Nettle, dead Thistle and decaying Oak leaves were completely eaten by 0400 h., therefore the numbers actually recorded feeding on these

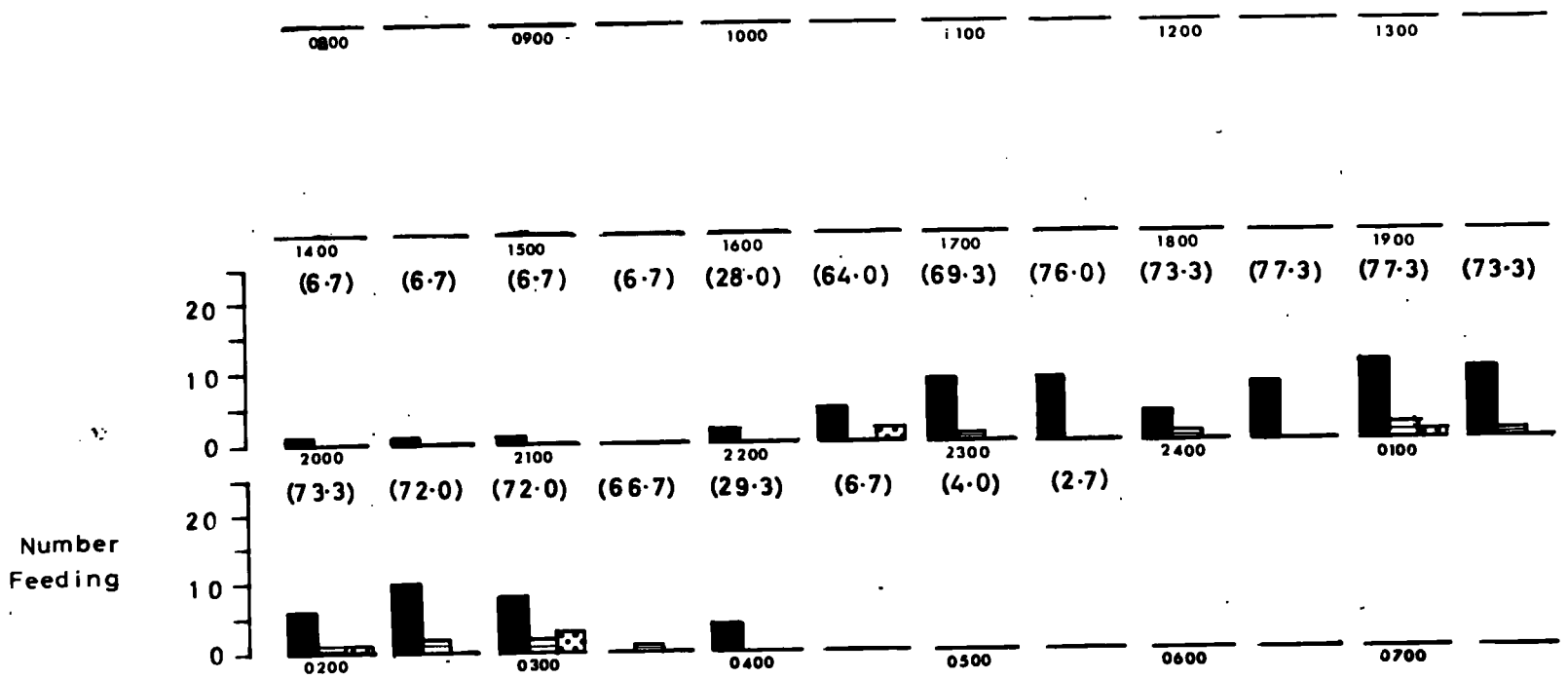
foods may be considered a minimum estimate over the 24 h. period. Figs. 4 - 11 show histograms of the mean numbers per chamber feeding on each food, and the percentage of animals active (i.e. out of the shelters) at half hourly intervals during the 24 h. experimental period.

The most preferred foods (marked 'P' in Table 6) from these eight groups were used in further experiments, and were divided into two groups of four foods each. Four replicates were made for each group. The apparatus and experimental procedure was as described previously, with the exception that the animals were allowed to feed for a continuous period of 48 h., so that activity could be determined for two consecutive 24 h. periods.

The observed order of food preference for O.asellus is shown in Table 7. It is clear that dead Nettle (Urtica sp) and dead Thistle (Onopordum sp) were more preferred. Of the foods found all the year round in the habitat, decaying Oak (Quercus sp) and decaying Sycamore (Acer sp) leaves were most preferred. The results thus obtained were in general agreement with those obtained in the previous laboratory experiments, but give a more accurate estimate of preference because potential errors were minimised.

O.asellus:

Histograms showing the mean number of animals per chamber feeding on each food, and the percentage of animals active at half hourly intervals during a 24h. experimental period.



24h Food preference experiment July 13/14th 1965.

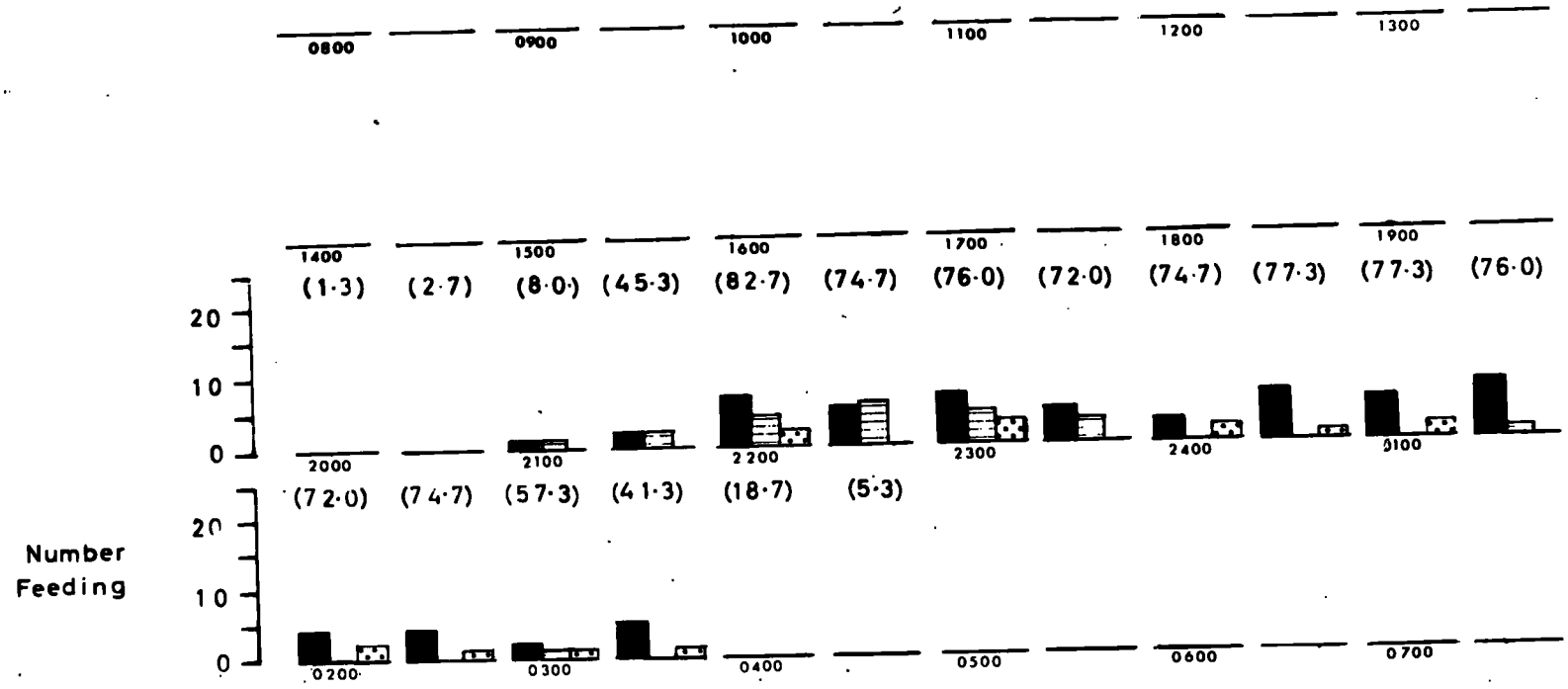
Dead Thistle leaves

Sycamore bark + Pleurococcus

Dead Horse Chestnut leaves

Temp:- Max: 18°C; Min: 11°C.
Grass Min: 10·5°C.

Hours of darkness: 2030-0400

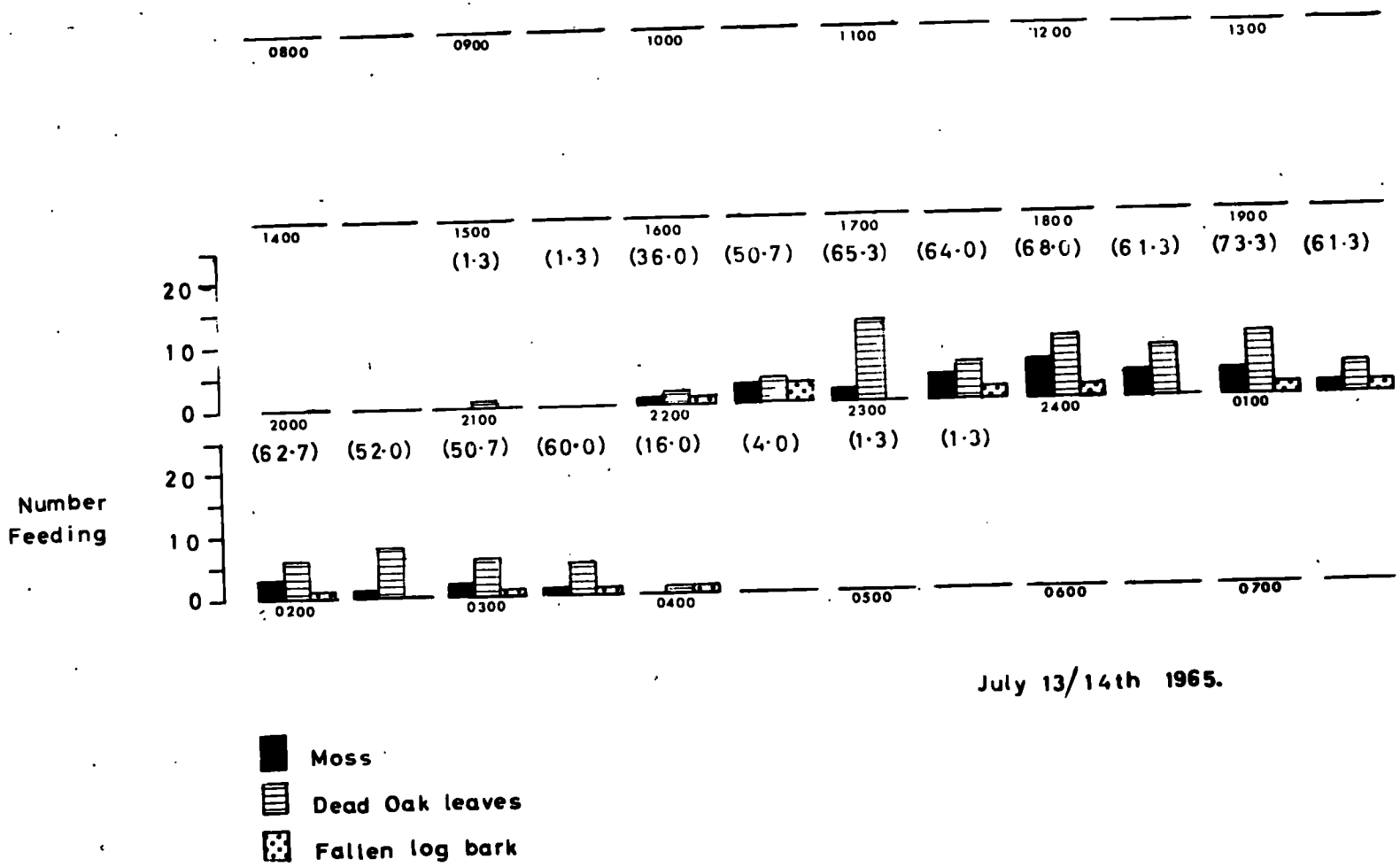


24h. Food preference experiment July 13/14th 1965.

Dead Nettle leaves

Decaying Sweet Chestnut husks

Beech bark + Pleurococcus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(1·3)
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(50·7)
(65·3)
(64·0)
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(61·3)
(73·3)
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(62·7)
(52·0)
(50·7)
(60·0)
(16·0)
(4·0)
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(1·3)
Number Feeding
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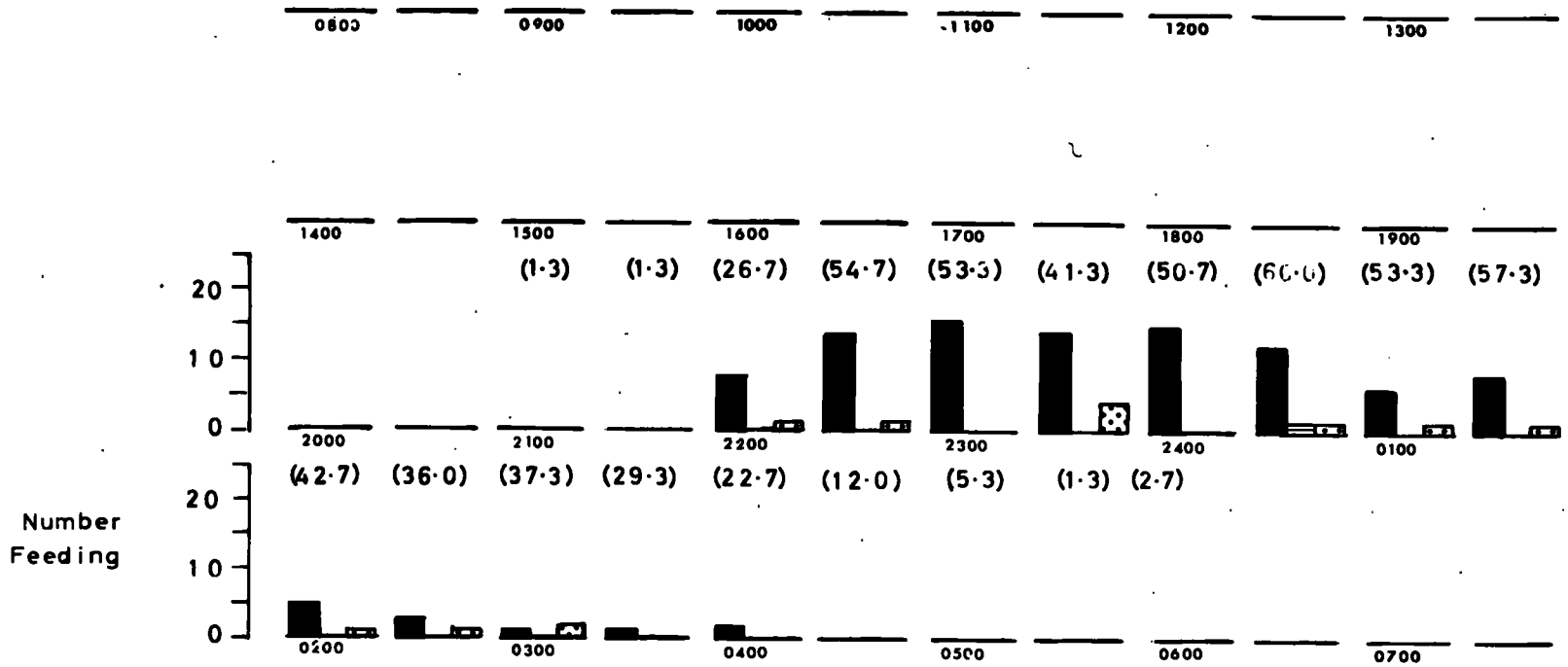
0500
0600
0700
July 13/14th 1965.
Moss
Dead Oak leaves
Fallen log bark

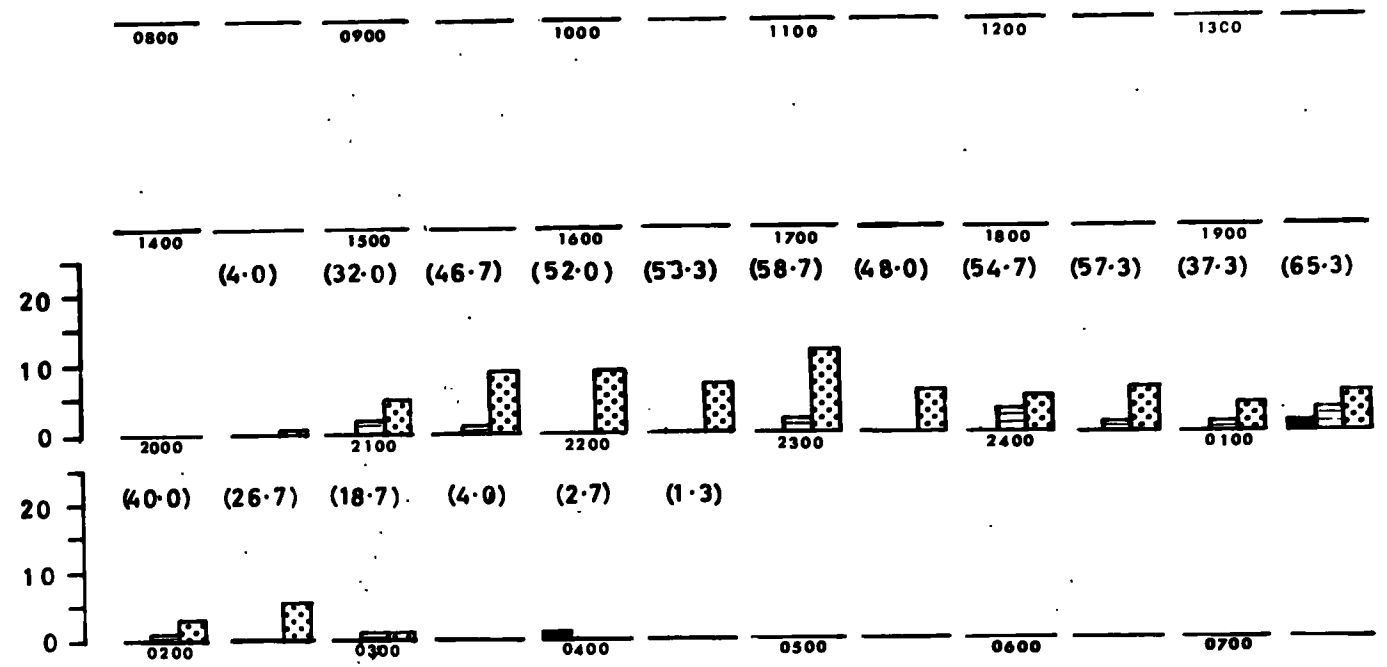


July 13/14th 1965.

Decaying Sweet Chestnut leaves

Soil

Assorted Fungi



24h Food preference experiment July 19/20th 1965.

Rotten inside of fallen log.

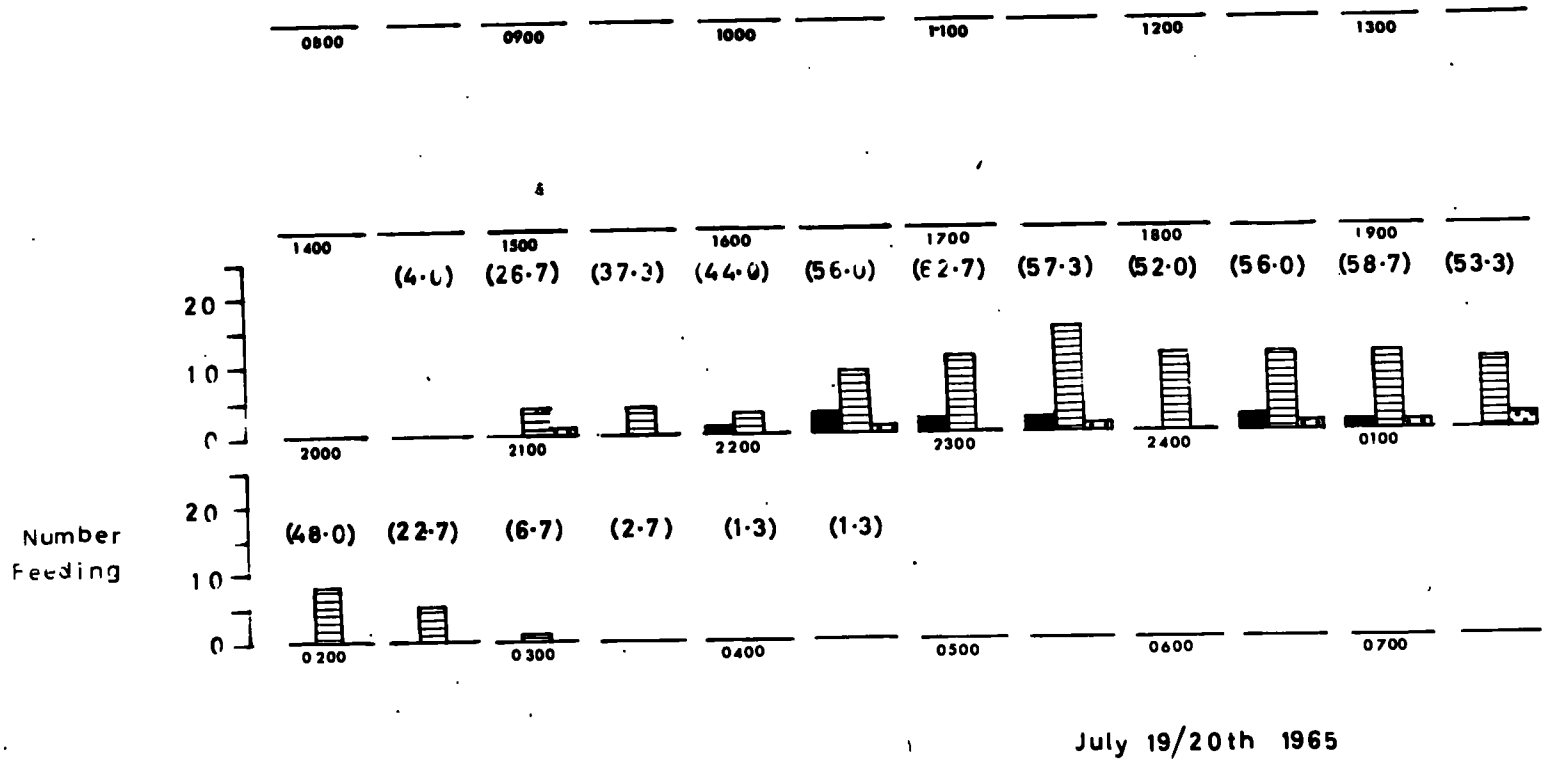
Oak bark + Pleurococcus.

Decaying Sycamore litter.

Temp:- Max: 20°C; Min: 8°C.
Grass Min: 5·5°C.

Hours of darkness: 2030-0400

Figures in parentheses = % animals active.
All times G.M.T.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(44·0)
(56·0)
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(58·7)
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2100
2200
2300
2400
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Number Feeding
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(22·7)
(6·7)
(2·7)
(1·3)
(1·3)
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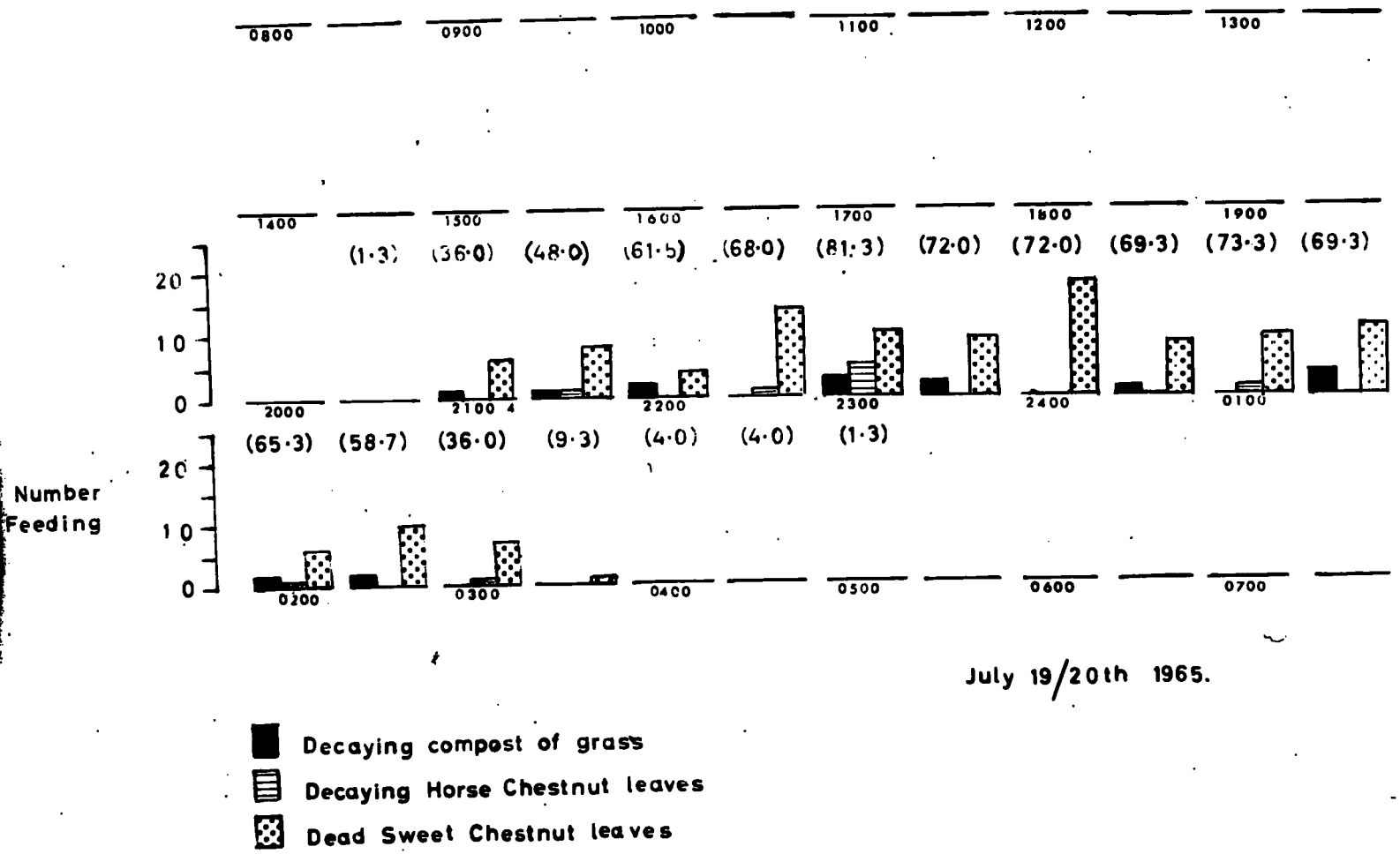
0400
0500
0600
0700
July 19/20th 1965
Sweet Chestnut bark+Pleurococcus
Dead Sycamore leaves
Decaying Beech leaves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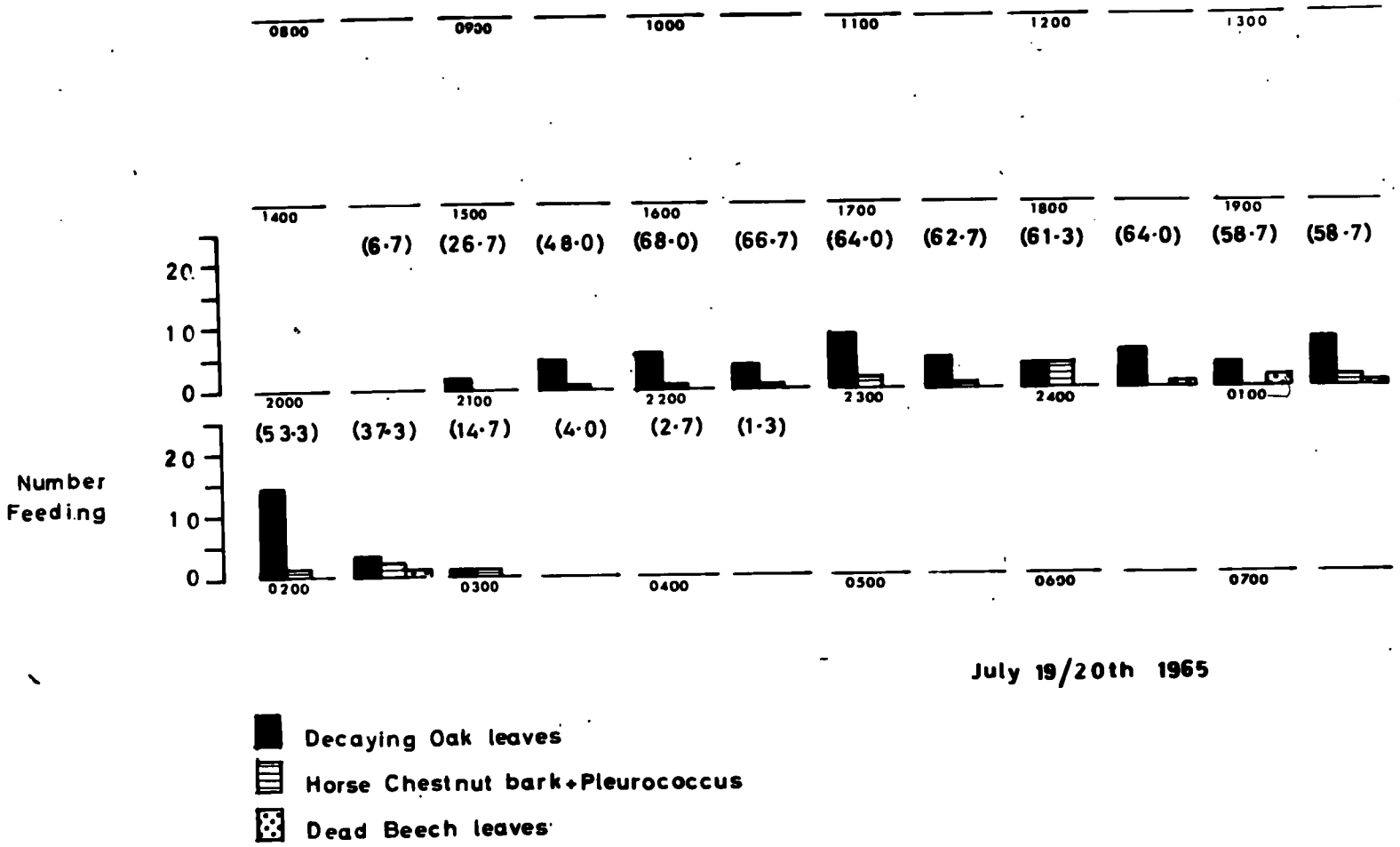
(65·3)
(58·7)
(36·0)
(9·3)
(4·0)
(4·0)
(1·3)
Number Feeding
20
10
0
0200
0300
0400
0500
0600
0700
July 19/20th 1965.
Decaying compost of grass
Decaying Horse Chestnut leaves
Dead Sweet Chestnut leaves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(53·3)
(37·3)
(14·7)
(4·0)
(2·7)
(1·3)
Number Feeding
20
10
0
0200
0300
0400
0500
0600
0700
July 19/20th 1965
Decaying Oak leaves
Horse Chestnut bark+Pleurococcus
Dead Beech leaves

Table 6: *O. asellus:* Mean numbers per chamber feeding per 24 h. on 24 food items.

Group	Food item	Mean no. feeding	
1	Dead *Urtica* leaves	66	P
	Dec. *Castanea* husks	25	
	Fagus bark + *Pleurococcus*	15	
2	Dead *Onopordum* leaves	89	P
	Acer bark + *Pleurococcus*	11	
	Dead *Aesculus* leaves	7	
3	Dec. *Quercus* leaves	69	P
	Aesculus bark + *Pleurococcus*	10	
	Dead *Fagus* leaves	5	
4	Dec. *Acer* leaves	80	P
	Quercus bark + *Pleurococcus*	16	
	Rotten inside of fallen log	2	
5	Dec. *Castanea* leaves	105	P
	Assorted Fungi	13	
	Soil	1	
6	Dead *Acer* leaves	103	P
	Castanea bark + *Pleurococcus*	12	
	Dec. *Fagus* leaves	7	
7	Dead *Castanea* leaves	116	P
	Dec. grass leaves and stems	18	
	Dec. *Aesculus* leaves	10	
8	Dead *Quercus* leaves	85	P
	Fresh Bryophyta	33	
	Fallen log bark	16	

Table 7: Order of food preference of O.asellus as determined by an automatic camera and showing the mean number per chamber feeding on each preferred food during a continuous 48 h. experimental period.

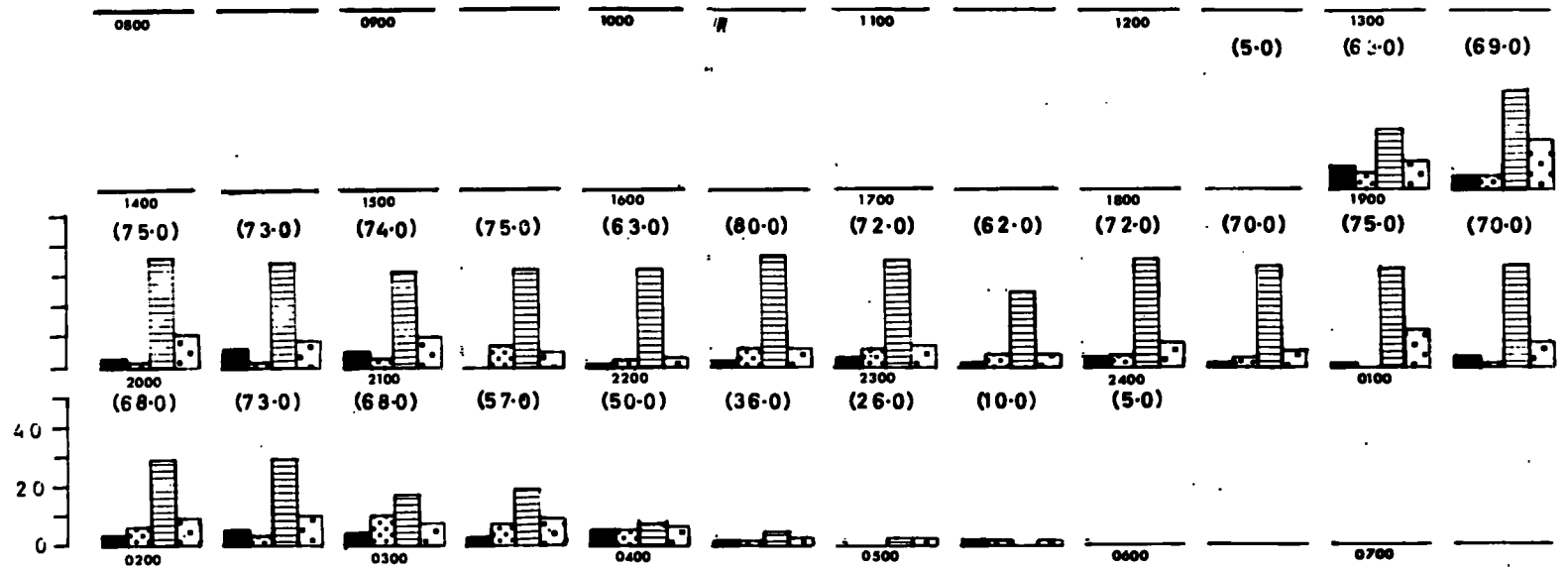
Food item	Mean no. feeding
Dead Nettle (Urtica sp) leaves	1096
Dead Thistle (Onopordum sp) leaves	712
Dec. Oak (Quercus sp) leaves	503
Dec. Sycamore (Acer sp) leaves	260
Dec. S. Chestnut (Castanea sp) leaves	234
Dead Sycamore (Acer sp) leaves	213
Dead S. Chestnut (Castanea sp) leaves	135
Dead Oak (Quercus sp) leaves	113

Figs. 12 - 15 show histograms of the numbers feeding on the experimental foods and the percentage of animals active at each observation during the continuous 48 h. period. It is clear that activity followed a regular pattern, and can be related to the hours of darkness. With the onset of darkness the animals began to appear from the shelter; their feeding activity reached a maximum approximately 1½ h. after dusk. This maximum was maintained until 2 - 3 h. before dawn when the animals began to return to the shelter.

O.asellus:

Histograms showing the mean numbers per dish feeding on the foods preferred in previous experiments (Table 6; Figs.4-8), and the percentage of animals active at half hourly intervals during a 48h experimental period.

Sept 23rd



48h Food preference experiment Sept 23/25th 1965.

Dead Oak leaves

Dead Sweet Chestnut leaves

Dead Nettle leaves

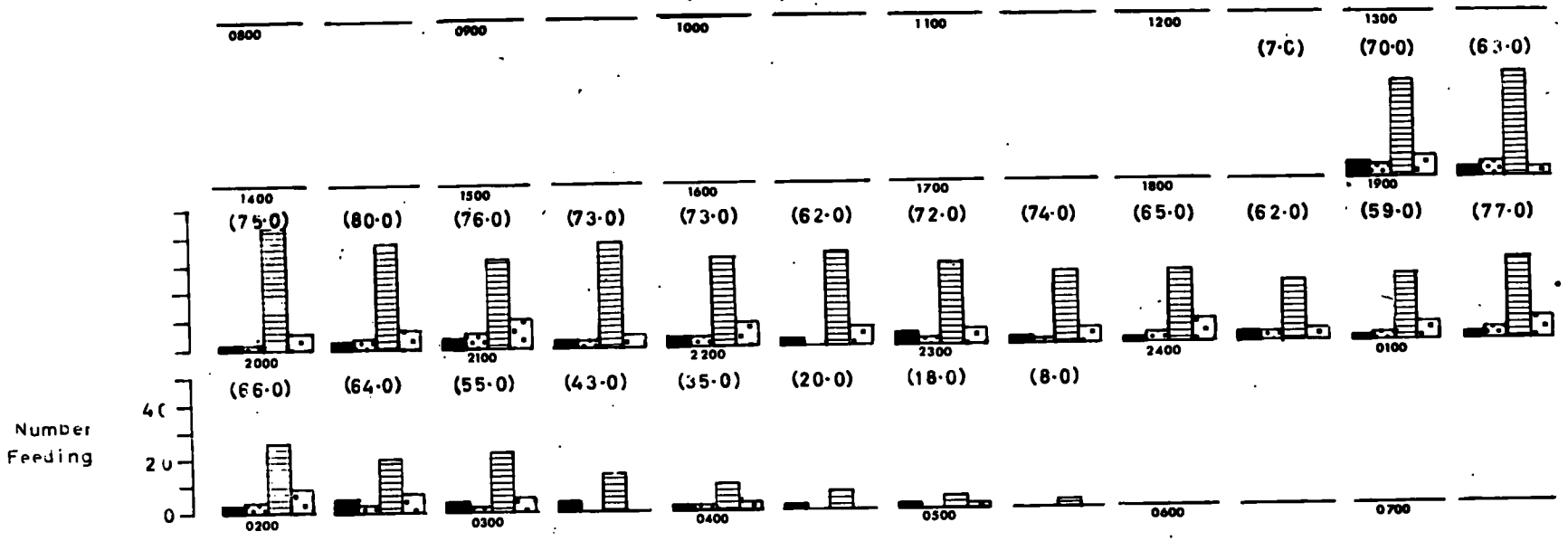
Decaying Sycamore leaves

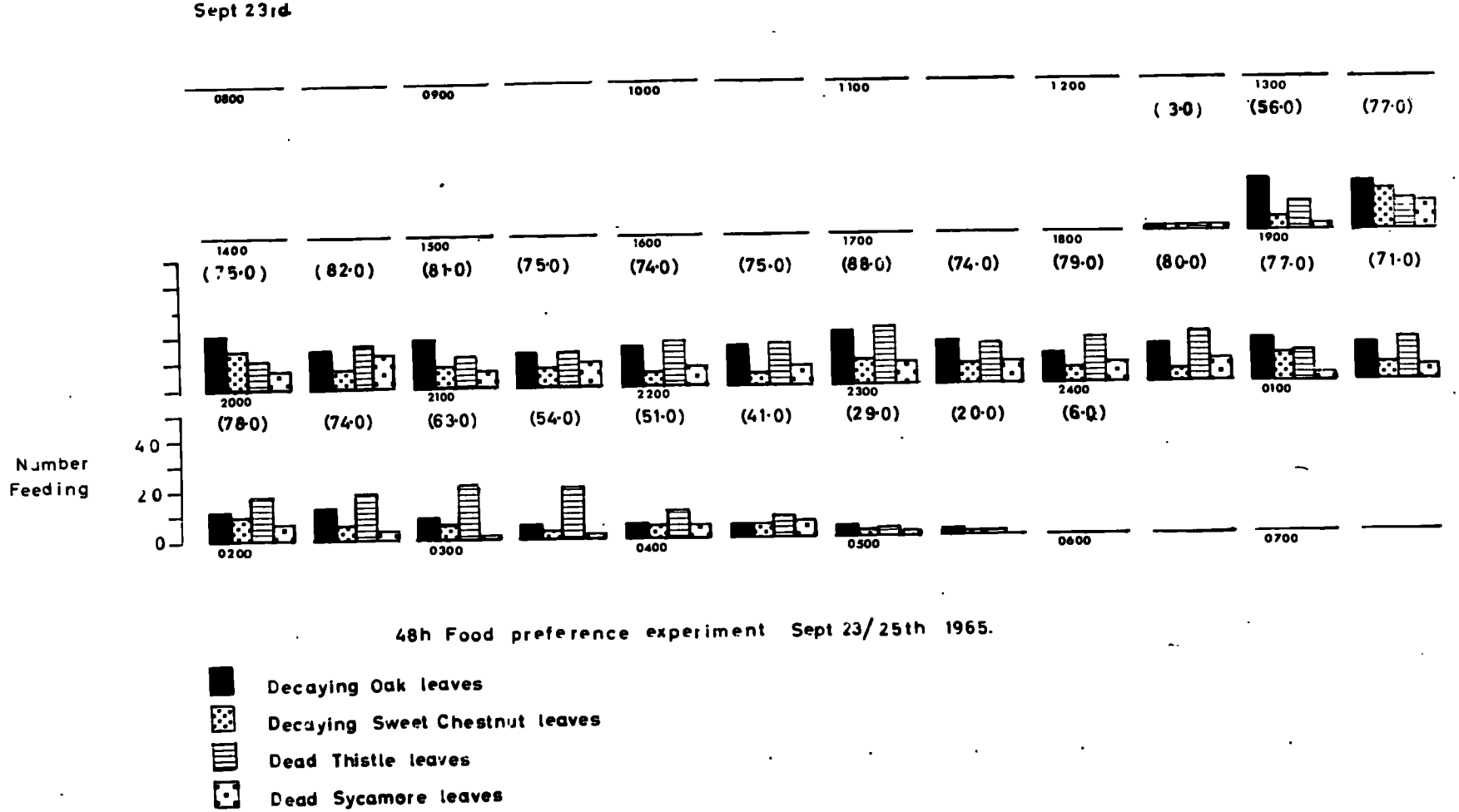
Temp:- Max: 17 °C; Min: 8 °C.
Grass Min: 4·5 °C.

Hours of darkness: 1800-0600

Figures in parentheses = % animals active
All times G.M.T.

Sept 24th cont[d].

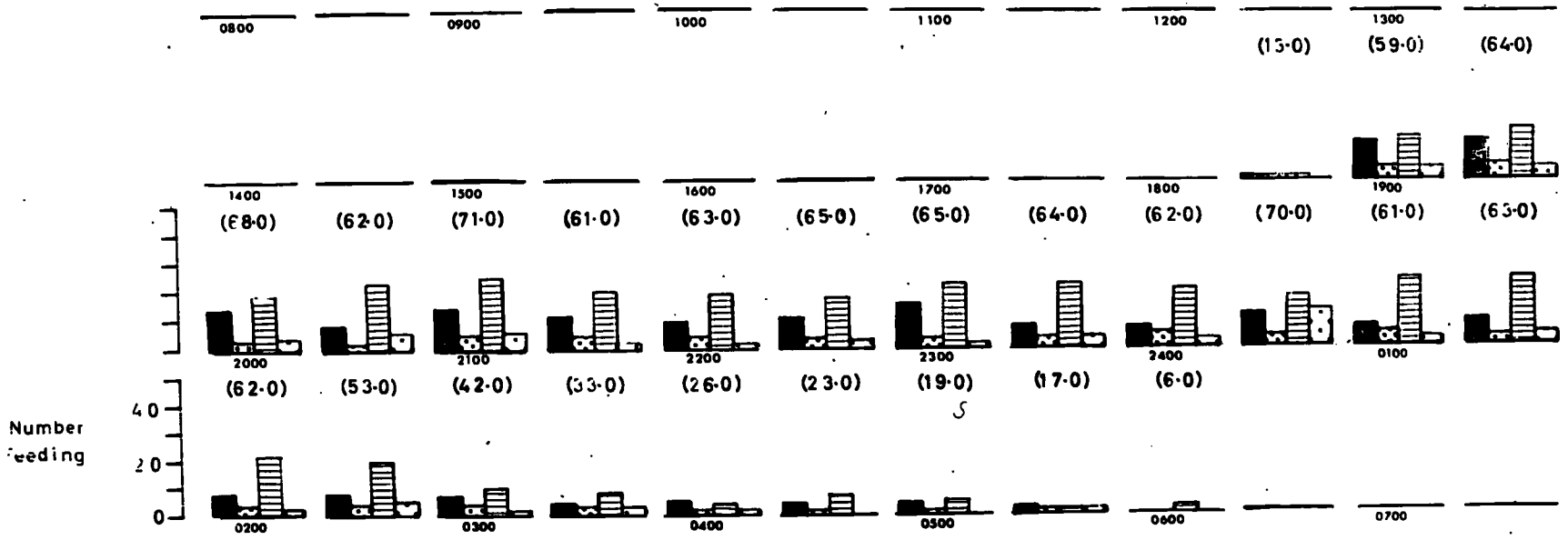




48h Food preference experiment Sept 23/25th 1965.

- Decaying Oak leaves
- Decaying Sweet Chestnut leaves
- Dead Thistle leaves
- Dead Sycamore leaves

Sept 24th cont[d].



As stated in the general introduction, knowledge of the preferred foods facilitated the design of further experiments to determine the rate of assimilation (I or ΔH).

CHAPTER 2.

The rates of egestion during the winter season for the two isopods Oniscus asellus and Porcellio scaber.

To determine I (assimilation), data is required to satisfy the equation:-

Food assimilated = Food ingested - Faeces egested

The present chapter presents data for faeces production under near natural conditions during the winter season for both species.

Methods.

10 x 1 cm. dishes were lined with damp glass fibre filter paper. Into each dish was placed a shelter made from the lid of a 3 cm. diameter pill box, entrances being made in the usual manner. 3 cm. discs of dead Thistle, decaying Oak, and decaying Sycamore leaves were cut, and one disc of each of the preferred foods was placed in each dish. Dead Nettle, the most readily eaten food in the preference experiments was not available at the time of the experiment (December 1964). Individuals of both species were collected in the field and separated into the following size classes:-

0- 3 mm.	Unsexed
3- 6 mm.	"
6- 8 mm.	"
8-11 mm.	Males and Females
11-14 mm.	" " "
14 mm.	" " "

Groups of twenty individuals of the 0-3 mm. group and five of the 3-6 mm. group were introduced into the appropriate experimental dish. This number of indiviuals per dish being chosen so that enough faeces were produced to facilitate accurate weighing. Individuals from all the remaining groups were isolated, one individual per dish. Twenty replicates for each size and sex were considered sufficient to give an accurate measurement of faeces production. In the case of P.scaber only 20 individuals for each of the size groups 8-11, 11-14, and > 14 mm. were obtained and separate experiments for each of the sexes were not made. The dishes were sealed by lids, and each dish numbered according to the size group of the animal or animals present, before placing them in the field. These dishes remained outside for 24 h., and faecal pellets were removed every 6 h. to prevent them being refected. At the end of the 24 h. period the live weight of each animal or group of animals in the case of the 0-3 and 3-6 mm. size groups, was determined. Faecal pellets were vacuum dried at 60°C and weighed on a Cahn electrobalance model M.10.

Results.

Tables 8 and 9 show the results obtained for O.asellus and P.scaber respectively.

Table 8: Mean dry wts. and numbers of faecal pellets produced 24 h. by all life stages of O.asellus. (December 1964) Ranges in brackets.

Size range	Mean live wt. mg.	Mean no. of pellets/ indiv./ 24 h.	Mean dry wt. of pellets/24 h. mg.
0- 3 mm.	1.7 (0.9-5.5)	7.4 (3-15)	0.076 (0.001-0.160)
3- 6 mm.	8.2 (6.3-11.6)	7.8 (4-14)	0.167 (0.04-0.45)
3- 6 mm.	10.2 (7.5-14.4)	7.8 (3-15)	0.262 (0.09-0.82)
6- 8 mm.	14.5 (10.2-18.3)	10.2 (5-23)	0.333 (0.14-0.86)
6- 8 mm.	16.4 (11.0-25.4)	19.3 (7-30)	0.890 (0.40-1.94)
8-11 mm. ♀	35.8 (26.3-42.6)	14.1 (3-38)	1.060 (0.16-2.96)
8-11 mm. ♂	32.0 (25.0-44.3)	15.2 (3-36)	1.180 (0.32-2.78)
11-14 mm. ♀	63.0 (45.4-75.6)	11.1 (3-21)	1.530 (0.26-2.66)
11-14 mm. ♂	64.5 (46.3-78.8	13.1 (3.32)	1.500 (0.24-3.16)
>14 mm. ♀	112.0 (83.6-141.4)	12.0 (4-25)	1.870 (0.68-3.02)
>14 mm. ♂	99.0 (76.4-136.6)	13.0 (5-25)	1.690 (0.54-3.77)

Table 9: Mean dry wts. of faeces produced/24 h. for all life stages of P.scaber. (December 1964) Ranges in brackets.

Size range	Mean live wt. mg.	Mean dry wt. of faeces produced/ 24 h. mg.
0- 3 mm.	5.3 (3.6-6.6)	0.151 (0.058-0.336
3- 6 mm.	13.4 (9.9-15.6)	0.349 (0.166-0.663)
6- 8 mm.	14.9 (12.2-17.4)	0.408 (0.220-0.924)
6- 8 mm.	27.7 (22.4-33.6)	0.586 (0.326-1.102)
8-11 mm.	48.0 (41.6-56.6)	0.804 (0.444-1.334)
11-14 mm.	71.0 (60.0-79.6)	0.982 (0.536-1.604)
>14 mm.	91.5 (81.3-106.6)	1.113 (0.533-1.846)

Although there was great variation in faeces production between individuals of the same group, the mean rate of faeces production showed an increase with increasing weight.

A further experiment was conducted in the laboratory at the same time as the above experiments. Males and females of the >14 mm. size group of O.asellus were collected and isolated in petri dishes

provided with the same preferred foods as above. They were allowed to defecate in the laboratory for 24 h., where the mean temperature was 20 ± 5°C. Table 10 compares the results obtained in this experiment with those obtained for the same size group in the previous field experiment.

Table 10: A comparison of the number and dry weights of faecal pellets produced/24 h. by adult O.asellus >14 mm. in length under laboratory and near natural conditions.

Experiment	Sex	Mean live wt. mg.	No. of pellets/24 h.	Dry wt. faeces prod./24 h. mg.
Laboratory	♀	118.9 (85.5-150.6)	18.5 (6-47)	3.600 (0.96-6.44)
Field	♀	112.0 (83.6-141.4)	12.0 (4-25)	1.870 (0.68-3.02)
Laboratory	♂	87.2 (73.0-126.6)	25.4 (9-46)	3.84 (1.04-7.36)
Field	♂	99.0 (76.2-136.6)	13.0 (5-25)	1.69 (0.54-3.77)

It is clear that the laboratory experiment gave much higher rates of faeces production than the field experiment, which emphasises the fact that experiments with isopods performed at laboratory temperatures do not reflect the field situation. It is evident that experiments with these animals should be conducted under as near natural conditions as possible, if the data is to be related to field populations.

CHAPTER 3.

The rates of ingestion, egestion, and assimilation during the summer season, for the two isopods O.asellus and P.scaber.

1. Preliminary experiment for the availability of a marker food.

To obtain accurate information for the assimilation of food by employment of the equation:-

Food assimilated = food ingested - faeces produced,

all of the faeces produced from a known weight of food ingested must be accurately determined. The initial task was to discover a food which gave faecal pellets of a different colour from those normally produced in the field, as this food could then be fed to the animal being studied, and used as a marker. By first offering the marker food, then the preferred food, followed by the marker again, all of the faeces produced from the amount of preferred food eaten, could be easily recognised and collected. Shredded carrot was found to give bright orange faeces and was readily eaten. This food was therefore used as a marker in the assimilation experiments.

2. Ingestion, egestion, and assimilation of foods under near natural conditions.

1) O.asellus

Methods.

Individuals of all size groups were collected in the field

during June 1965, placed in feeding chambers, and allowed to feed on shredded carrot until orange faecal pellets were produced, when it was assumed that all field faecal pellets had been voided. 15 x 7.5 cm. feeding chambers were prepared in the manner described in Chapter 1. The possibility of I varying with the type of food consumed was mentioned in Chapter 1, and to obviate possible errors from this source two of the most preferred, and two of the least preferred foods were offered as food; these were decaying Sycamore leaves, decaying Oak leaves, dead Sweet Chestnut leaves, and dead Oak leaves. The procedure adopted for the determination of assimilation for each animal was as follows:-

The individuals of the 0-3 and 3-6 mm. groups were introduced 20 and 5 respectively, into a feeding chamber for the reasons mentioned in Chapter 2. Individuals of the remaining groups were isolated, one animal per chamber. The live weight of each animal or group of animals (0-3; 3-6 mm.) was determined immediately before each experiment. For a given food, two 3 cm. discs, similar in vein structure, state of decomposition, and texture were prepared. One was vacuum dried at 60°C and the other was offered as food to the animal. The dry weight of the vacuum dried disc was assumed to be equal to the dry weight of the food offered. Each feeding chamber thus prepared was placed in the field and the animals allowed to feed for 24 h. Black faecal pellets were collected every 6 h. to ensure that none were refected or trampled into the filter paper. After

24 h. feeding the food was removed from each chamber and shredded carrot introduced. The experiment was terminated when the first carrot faecal pellet had been produced. The food remains and all the black faeces from each chamber were vacuum dried separately at 60°C and weighed. 354 such experiments were carried out. Assimilation efficiency was calculated as a percentage of the food ingested according to the formula:-

$$\frac{\text{Abs. dry weight assimilated}}{\text{Abs. dry weight ingested}} \times 100 = \text{Percent Assimilated}$$

The dry weight of food ingested by each animal was calculated by the difference in dry weight between the control disc and food remains at the end of the experiment. The dry weight of food assimilated was calculated by the difference in dry weight of the food eaten and the faeces produced. The faeces production data obtained in this summer experiment served as a comparison between the rate of faeces production determined in the winter experiment (Chapter 2)

Results.

a) Assimilation.

Table 11 shows the mean percentage assimilation for all foods and life stages. Fig. 16 shows histograms of the data presented in

O.asellus:

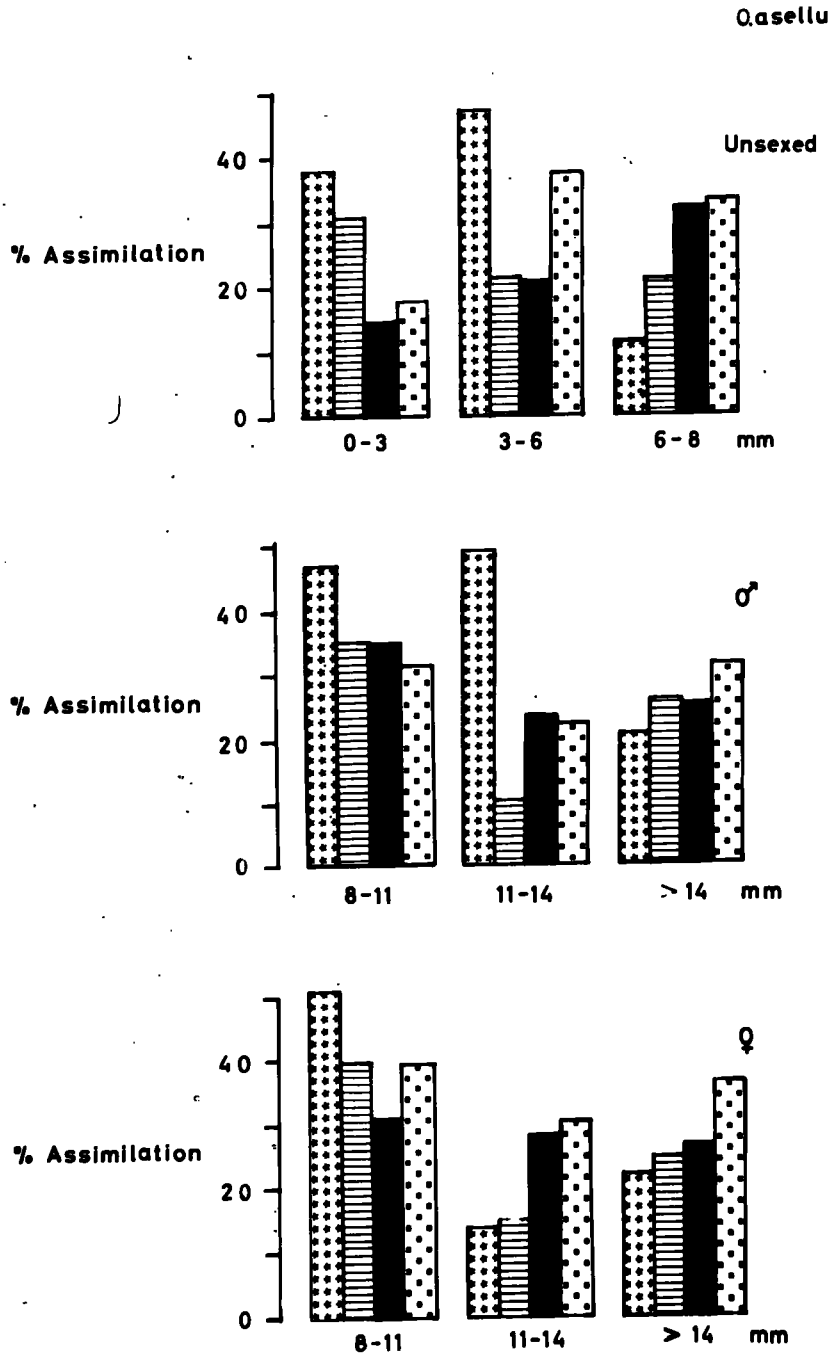
Histograms showing the mean % assimilation of all life stages

Decaying Sycamore leaves

Decaying Oak leaves

Dead Sweet Chestnut leaves

Dead Oak leaves


Oasellus
Unsexed
% Assimilation
40
20
0
0-3
3-6
6-8
mm
♂
% Assimilation
40
20
0
8-11
11-14
> 14
mm
♀
% Assimilation
40
20
0
8-11
11-14
> 14
mm

columns 2 - 5 of Table 11. The ranges show that much variation in assimilation occurred between individuals in all the size groups. Because of this variation the mean percentage assimilation of all the experimental animals in each size group was calculated (see column 6, Table 11). The data thus obtained were tested for significance with the 't' test for small samples, and Table 12 shows the results obtained. The only size group which had an assimilation efficiency (= % assimilation) significantly different from the others was the 8 - 11 mm. group ($p = > 0.05$). The overall mean assimilation efficiency given by the 354 experiments performed, 27.23%, was assumed to be the best possible estimate of assimilation for O.asellus.

b) Rates of Ingestion.

Data on the rate of food ingested were available from two independant experiments:-

1. The present summer experiment, where the amount of food ingested per 24 h. was determined as the dry weight of the food at the beginning of the experiment minus the dry weight of food remaining after 24 h. feeding.

2. The winter faeces production experiments (Chapter 2) where the amount of food eaten (dry wt.) was calculated indirectly from the faeces production data (Table 8), and the percentage assimilation figure of 27.23, according to the equation:-

Food eaten = Food assimilated + Faeces produced.

If food eaten is taken as 100% then the faeces produced must be 72.77% of the food eaten. Knowing the dry weight of faeces produced, simple calculation determined the dry weight of food assimilated. The sum of these two figures (amount assimilated + amount of faeces produced) was assumed to be equal to the dry weight of food eaten.

Table 13 shows the results obtained from experiment 1. Column 7 gives the mean dry weight of food eaten per 24 h. for all the foods used in the experiment. This mean was used to describe the mean rate of ingestion for each size group, as there was such a large variation between the rate determined in each individual experiment. Note that animals tend to ingest more of the decaying material; this was to be expected as the decaying litter was known to be eaten in preference to the dead litter (Chapter 1). The highest ingestion rate in this summer experiment of 2.761 mg/24h. was shown by the 8 - 11 mm. female group.

Table 14 shows the results obtained from the December 1964 faeces production data. Column 5 shows the rate of ingestion for all life stages, and it is clear that the rate of ingestion increases with increasing weight of animal. In this experiment the maximum rate of ingestion was for the >14 mm. female size group, whereas the summer experiment showed that it was the 8 - 11 mm. female size group which gave the greatest ingestion rate.

Table 11: Mean % assimilation for all life stages of O.asellus when fed on 4 different food items.

Size group	Decaying Sycamore	Decaying Oak	Dead Sweet Chestnut	Dead Oak	Mean for each size group
0- 3 mm.	37.64 (16.6 to 82.4)	30.54 (0.1 to 73.9)	14.71 (-104.7 to 83.0)	17.89 (-2.3 to 67.5)	25.19
3- 6 mm.	46.95 (-40.4 to 82.3)	21.14 (0.3 to 56.0)	20.50 (-19.7 to 53.8)	37.25 (-19.9 to 62.0)	31.31
6- 8 mm.	11.20 (-23.8 to 71.5)	20.65 (-10.3 to 52.0)	31.72 (6.0 to 51.0)	32.79 (-9.1 to 65.7)	24.09
8-11 mm. ♀	50.91 (-15.6 to 93.4)	39.76 (1.4 to 84.7)	30.90 (-11.5 to 83.2)	39.44 (-2.0 to 83.7)	40.49
8-11 mm. ♂	46.00 (16.7 to 80.6)	34.03 (2.1 to 85.8)	30.61 (-10.0 to 87.3)	48.24 (-15.1 to 89.4)	39.51
11-14 mm. ♀	13.84 (-20.3 to 35.1)	15.19 (-1.6 to 66.6)	28.31 (-13.3 to 62.1)	30.36 (0.9 to 97.2)	21.41
11-14 mm. ♂	9.74 (-29.4 to 34.3)	22.72 (-15.5 to 89.7)	21.90 (0.2 to 38.7)	27.36 (-13.6 to 79.0)	20.44
>14 mm. ♀	22.16 (0.6 to 77.0)	24.75 (4.4 to 54.7)	26.40 (-47.7 to 83.6)	36.57 (-25.0 to 75.0)	25.80
>14 mm. ♂	20.00 (-27.5 to 77.0)	25.17 (1.2 to 73.0)	24.40 (0.4 to 55.1)	30.84 (-15.0 to 59.5)	24.91

Table 12: Significance of the mean % assimilation of all life stages of O.asellus.

Size group	Mean % Assim.	° of freedom	t	p =
0- 3 mm.	25.19 ± 20.11	39	0.634	None
3- 6 mm.	31.31 ± 24.74	38	1.030	None
6- 8 mm.	24.09 ± 23.08	39	0.850	None
8-11 mm. ♀	40.49 ± 30.22	38	2.705	> 0.05
8-11 mm. ♂	39.51 ± 28.45	38	2.642	> 0.05
11-14 mm. ♀	21.41 ± 23.97	36	1.739	None
11-14 mm. ♂	20.44 ± 24.39	39	1.457	None
>14 mm. ♀	25.80 ± 27.11	39	0.329	None
>14 mm. ♂	24.91 ± 24.74	39	0.586	None

Overall mean assimilation for the 354 experiments performed = 27.23%

Table 13: Mean summer ingestion rate (mg. dry wt./24h.) of all life stages of O.asellus when fed on 4 different food items. Ranges in brackets.

Size group	Mean live weight	Decaying Sycamore	Decaying Oak	Dead Sweet Chestnut	Dead Oak	Mean rate all foods
0- 3 mm.	0.69 (0.65-0.73)	0.128 (0.04-0.21)	0.076 (0.03-0.15)	0.034 (0.01-0.08)	0.077 (0.06-0.08)	0.079
3- 6 mm.	7.3 (5.7-8.7)	0.337 (0.12-0.60	0.179 (0.04-0.33)	0.298 (0.06-0.55)	0.262 (0.16-0.44	0.256
6- 8 mm.	16.7 (10.6-19.8)	1.055 (0.20-3.75)	1.347 (0.30-2.23)	1.149 (0.30-2.43)	0.877 (0.22-2.22)	1.082
8-11 mm. ♀	42.7	4.444 (0.40-8.16)	3.413 (0.99-6.32)	1.696 (0.21-3.07)	1.661 (0.51-2.86)	2.761
8-11 mm. ♂	39.4	2.578 (1.20-4.96)	1.554 (0.49-3.48)	1.321 (0.41-2.92)	2.814 (0.40-4.31)	2.047
11-14 mm. ♀	84.7	4.479 (1.94-7.48)	1.972 (0.28-3.52)	1.017 (0.20-2.75)	1.333 (0.38-4.14)	2.296
11-14 mm. ♂	77.0	2.449 (0.20-6.35)	3.624 (0.86-6.78)	2.486 (0.44-5.20)	2.193 (0.44-5.62)	2.687
>14 mm. ♀	142.5	3.986 (0.86-6.64)	3.353 (0.90-6.92)	1.196 (0.30-1.93)	1.400 (0.32-2.30)	2.484
>14 mm. ♂	117.4	3.010 (0.73-6.64)	1.412 (0.24-2.66)	0.896 (0.14-1.71)	2.306 (0.34-5.66)	1.906

Table 14: Mean rates of faeces production, food assimilated, and food ingested (mg. dry wt./24 h.) for all life stages of O.asellus as calculated from the winter faeces production experiment.

Size group	Mean live weight mg.	Mean dry wt. faeces	Mean dry wt. assim.	Mean dry wt. ingested
0- 3 mm.	1.7	0.076	0.028	0.104
3- 6 mm.	8.2	0.167	0.062	0.229
3- 6 mm.	10.2	0.262	0.098	0.360
6- 8 mm.	14.5	0.333	0.124	0.457
6- 8 mm.	16.4	0.890	0.340	1.230
8-11 mm. ♀	35.8	1.060	0.400	1.460
8-11 mm. ♂	32.0	1.180	0.440	1.620
11-14 mm. ♀	63.0	1.530	0.570	2.100
11-14 mm. ♂	64.5	1.500	0.561	2.061
>14 mm. ♀	112.0	1.870	0.700	2.570
>14 mm. ♂	99.0	1.690	0.630	2.320

The data from both the summer and the winter experiments were pooled so that a regression of ingestion rate upon live weight could be calculated. Fig. 17 shows the result of a double logarithmic plot of ingestion rate upon live weight. The straight line was calculated by the least squares method; a correlation coefficient of 0.98 was obtained, and a formula for X on Y of Log X = -1.155 + 0.807 Log Y was calculated.

O.asellus:

Regression of ingestion rate upon live weight. The line is a least squares estimate of the regression.

* From winter faeces production experiment

● From summer assimilation experiment.

0-3 mm size group (summer), live wt 0·69 mg not included.

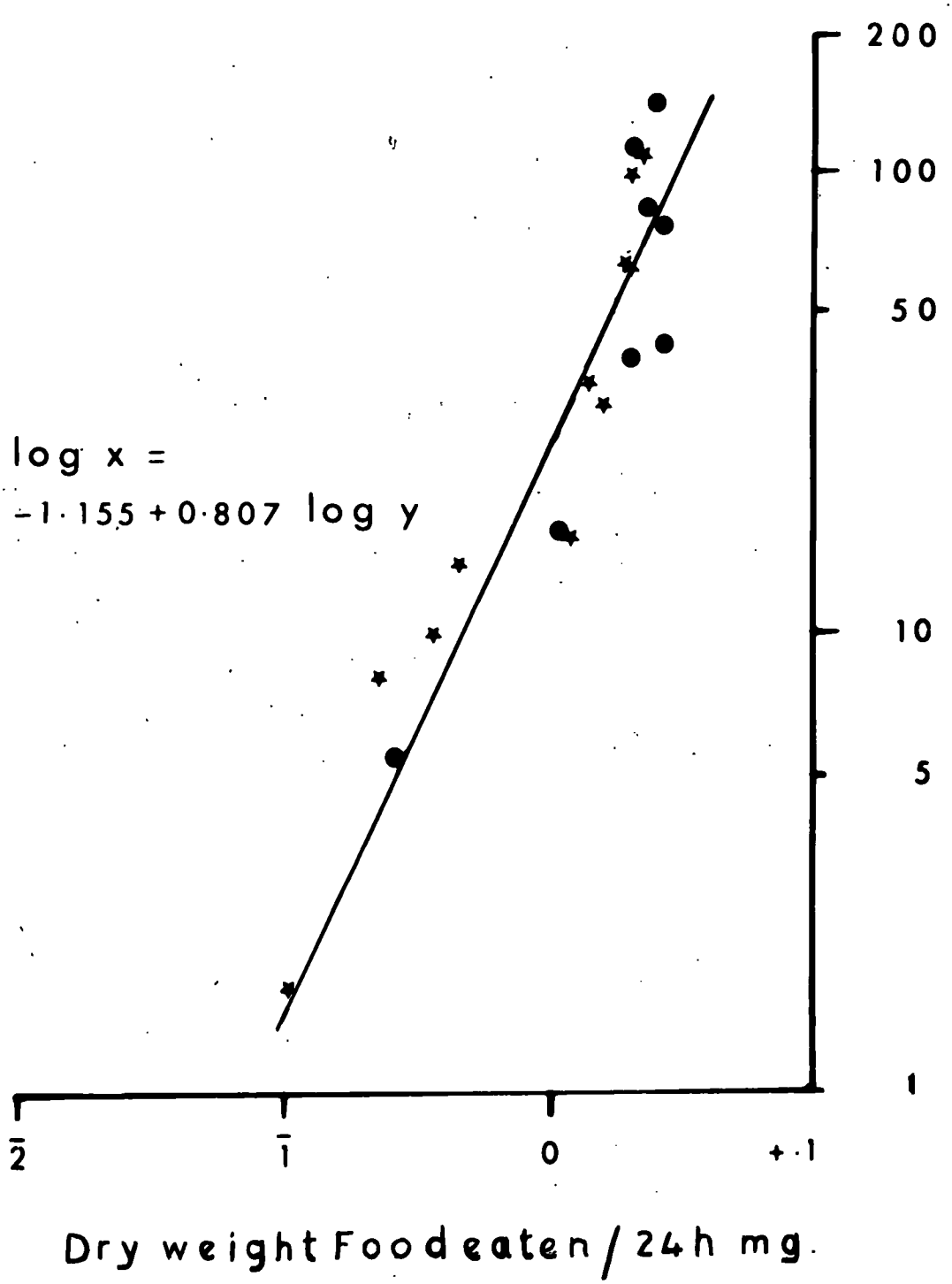

200
100
50
10
5
1
log x =
−1·155 + 0·807 log y
2̄
1̄
0
+·1
Dry weight Food eaten / 24h mg.

Fig.18.

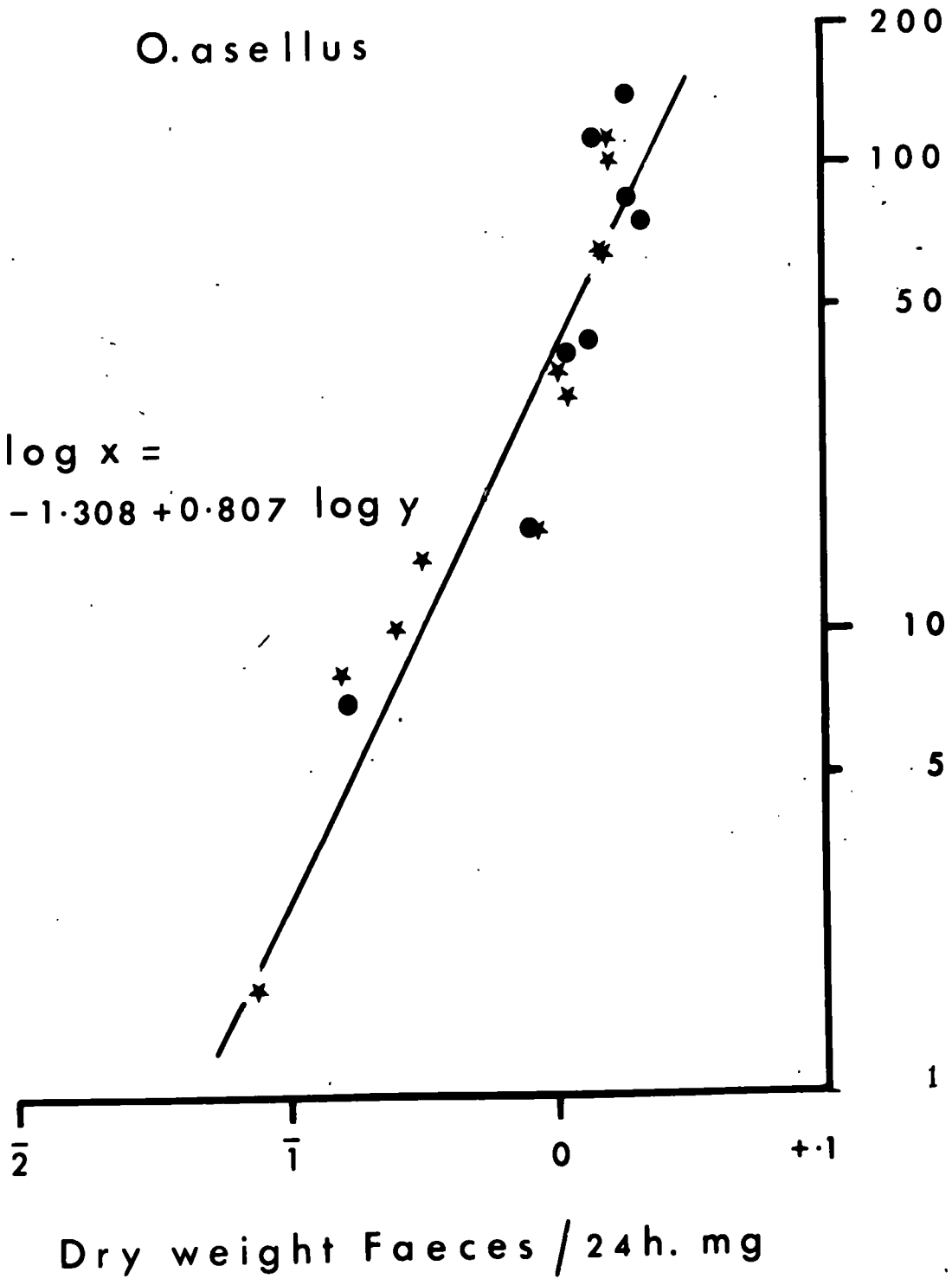
O. asellus:

Regression of egestion rate upon live weight. The line is a least squares estimate of the regression.

* From winter faeces production experiment

● From summer assimilation experiment.

0-3 mm. size group (summer) live wt 0·69 mg. not included.


O. asellus
log x =
−1·308 +0·807 log y
200
100
50
10
5
1
2̄
1̄
0
+·1
Dry weight Faeces / 24h. mg

c) Rate of Egestion.

Column 2 in Table 14, and column 7 in Table 15 show the mean rates of egestion obtained by the two direct measurements of egestion rate, made for all life stages of O.asellus during the winter and summer seasons. The mean rates thus obtained were pooled so that a regression of rate of egestion upon live weight could be calculated. Fig. 16 shows the result of a double logarithmic plot of X (ingestion rate) upon Y (live weight). The straight line was calculated by the least squares method; a correlation coefficient of 0.99 was obtained, and the formula Log X = -1.308 + 0.807 Log Y, was calculated.

2) P.scaber.

1. Introduction and preliminary experiments.

In the previous experiment with O.asellus it was discovered that the initial dry weights of the control and experimental food discs were not always equal. When the control was the heavier of the two, low or even negative results were obtained for the assimilation efficiency, and when it was the lighter of the two, abnormally high results could be given. However, the large numbers of experiments performed tended to cancel out these anomalies, therefore the mean overall estimate of assimilation efficiency given earlier may be considered to be reasonably accurate.

Table 15: Mean summer egestion rate (mg. dry wt./24h.) for all life stages of O.asellus when fed on 4 different food items. Ranges in brackets.

Size group	Mean live weight	Decaying Sycamore	Decaying Oak	Dead sweet Chestnut	Dead Oak	Mean rate all foods
0- 3 mm.	0.69	0.077 (0.02-0.12)	0.049 (0.02-0.07)	0.021 (0.01-0.04)	0.064 (0.01-0.16)	0.053
3- 6 mm.	7.3	0.180 (0.04-0.47)	0.141 (0.04-0.27)	0.199 (0.06-0.45)	0.166 (0.08-0.32)	0.171
6- 8 mm.	16.7	0.877 (0.32-3.41)	1.024 (0.18-1.79)	0.776 (0.35-1.76)	0.602 (0.15-1.95)	0.820
8-11 mm. ♀	42.7	1.594 (0.45-3.07)	1.884 (0.48-4.00)	0.944 (0.18-1.71)	0.808 (0.43-1.40)	1.316
8-11 mm. ♂	39.4	1.392 (0.31-3.20)	0.891 (0.42-1.79)	0.948 (0.09-2.17)	1.278 (0.34-2.97)	1.123
11-14 mm. ♀	84.7	3.835 (1.70-5.95)	1.631 (0.24-2.74)	0.726 (0.18-1.30)	0.893 (0.23-2.27)	1.855
11-14 mm. ♂	77.0	1.899 (0.20-5.82)	3.000 (0.19-6.10)	1.854 (0.37-3.18)	1.516 (0.50-2.51)	2.067
>14 mm. ♀	142.5	3.030 (0.63-5.42)	2.495 (0.86-4.95)	0.809 (0.08-1.30)	0.797 (0.26-1.77)	1.776
>14 mm. ♂	117.4	2.219 (0.50-4.34)	1.003 (0.17-2.50)	0.626 (0.14-1.26)	1.483 (0.33-3.46)	1.333

Clearly, a more direct method of determining the initial dry weight of the experimental food would be preferable to the use of a control. Wieser (1965) used re-wetted dessicator dried Poplar litter for assimilation experiments with P.scaber. Using P.Scaber, an experiment was designed to compare the palatability of preferred foods which had been dessicator dried and subsequently re-wetted.

Methods.

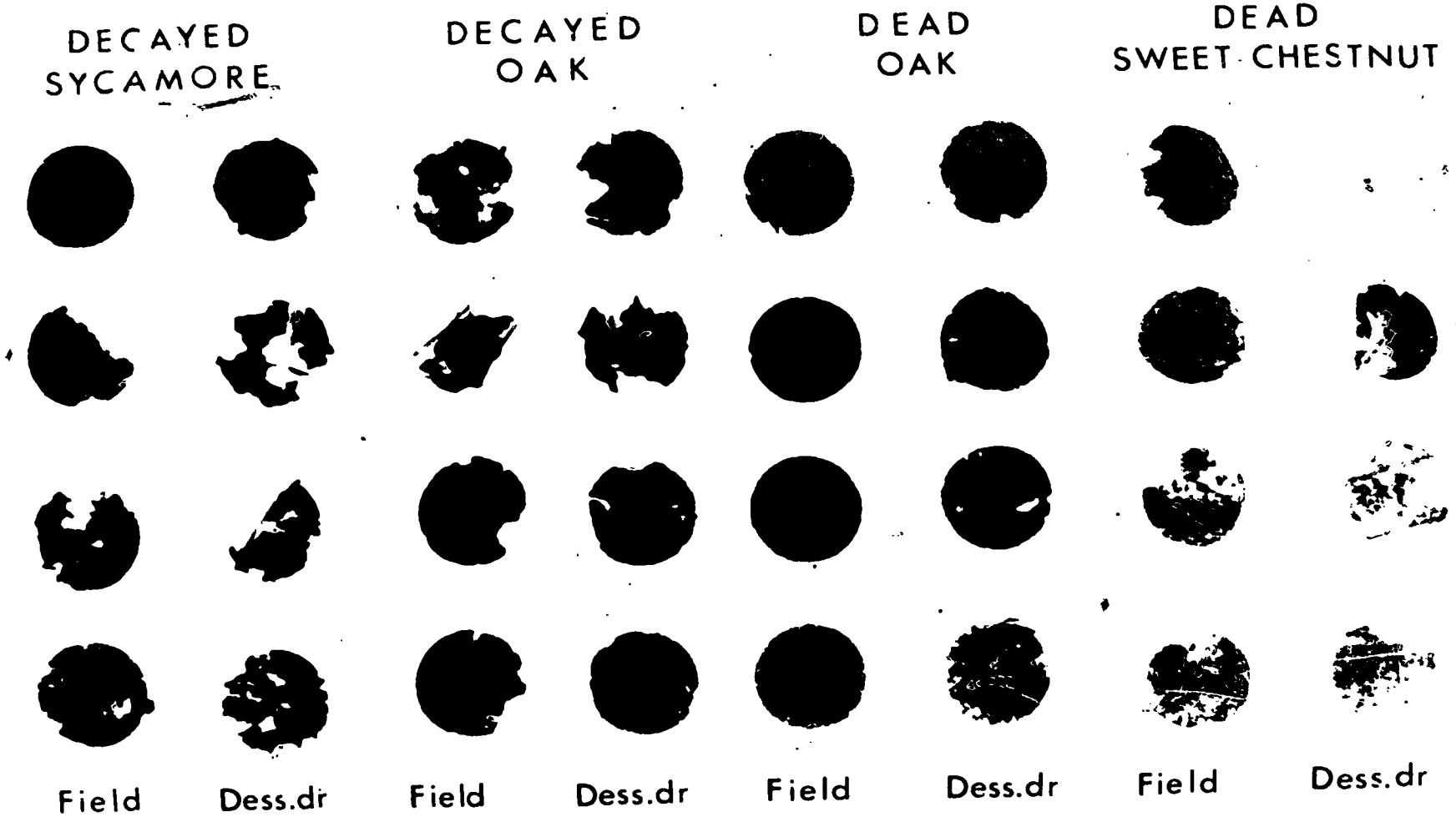
Four foods; decaying Sycamore, decaying Oak, dead Oak, and dead Sweet Chesthut, were collected in the field, cut into 3 cm discs and stored for 7 days over a dessicant. The discs were then placed in feeding chambers alongside foods which had just been collected in the field so that any re-colonisation by bacteria could take place. Four to seven days was assumed to be long enough for thorough re-wetting and re-colonisation. Four discs of each re-wetted food were then placed in separate feeding chambers alongside four 3 cm discs of the same foods, which had been recently collected in the field. Twenty five individuals representing all life stages were introduced into each feeding chamber. After 24h feeding the animals were removed, and the food remains photographed.

Results.

Fig.19 shows the results obtained. It is clear that for all the four foods offered, there was no difference in palatibility between the natural and the re-wetted dessicator dried material.

Fig.19

The amounts of re-wetted dessicator dried food, and food taken directly from the field, which were eaten by P.scaber during a 24h. experimental period.


DECAYED SYCAMORE
DECAYED OAK
DEAD OAK
DEAD SWEET CHESTNUT
Field
Dess.dr
Field
Dess.dr
Field
Dess.dr
Field
Dess.dr

Note that absolute dry weights are necessary for the accurate determination of rates of assimilation, ingestion, and egestion, because the variation in water content of live food material offered may introduce errors into the experiments. Absolute dry weights may only be determined by drying the material in an oven at temperatures above 100°C, or preferably in a vacuum oven at 60°C because volatiles are likely to be evaporated at temperatures above 100°C. A further experiment was therefore designed to determine the percentage water loss from dessicator dried food material after it had been vacuum dried at 60°C. Table 16 shows the results obtained from 10 samples, each of which consisted of one disc each of dead Thistle, decaying Sycamore, and fallen log bark. The mean water loss calculated according to the formula:-

Table 16

Percentage water loss when dessicator dried foods were vacuum dried.

Dessicator dried wt.mg.	Vacuum dried wt.mg.	%water loss
63.1	60.3	4.4
73.6	70.3	4.5
95.5	91.6	4.1
61.0	58.4	4.3
66.2	63.8	3.7
71.9	74.4	4.5
61.2	58.8	4.0
51.1	49.6	3.0
54.3	52.3	3.7
46.2	44.8	3.0

$\bar{X} = 3.9 \pm 0.54\%$

Dessicator dried wt - Vacuum dried wt x 100 was found to be 3.9±0.54% Vacuum dried wt.

2. Ingestion, egestion, and assimilation of food under near natural conditions using re-wetted dessicator dried food material.

Introduction

The experiments with O.asellus showed that there was great variation in assimilation between individuals of the same size group feeding on the separate foods, necessitating the employment of the mean percentage assimilation efficiency for each group. Therefore it was decided to feed P.scaber on a mixture of preferred foods (dead Thistle, leaves, decaying Sycamore leaves, and fallen log bark). to determine the mean assimilation efficiency of all life stages.

Methods

Individuals of all life stages were collected during March 1966 and fed on shredded carrot until orange faecal pellets were produced. Discs of the foods dead Thistle, decaying Sycamore, and fallen log bark, were dessicator dried, weighed, and re-wetted in the manner described previously. 10x1 cm feeding chambers were prepared, and into each was introduced one disc of each food. Knowing the percentage water loss when the dessicator dried foods were

vacuum dried, it was possible to determine the initial absolute dry weight of the food offered. The live weight of each animal was determined before the experiment began. Individuals of the 0-3, and 3-6 mm groups were introduced 20 and 5 per feeding chamber for the reasons given earlier; individuals of the remaining groups were isolated one per chamber. All the feeding chambers were then placed in the field and the animals allowed to feed for 24h; black faecal pellets were collected every 6h. After 24h feeding the food remains were collected, and shredded carrot was introduced; the animals were removed, and the experiment ended when the first orange faecal pellets was produced. Dry weights of the faeces produced and the food remains were determined. The dry weight of food ingested was calculated by the difference in dry weight between the food offered at the beginning of the experiment, and the food remains after 24h feeding. The dry weight of food assimilated was calculated by the difference in dry weight of food ingested and the faeces produced. Assimilation efficiency was calculated as a percentage of the dry weight of food assimilated divided by the dry weight of food ingested.

Results

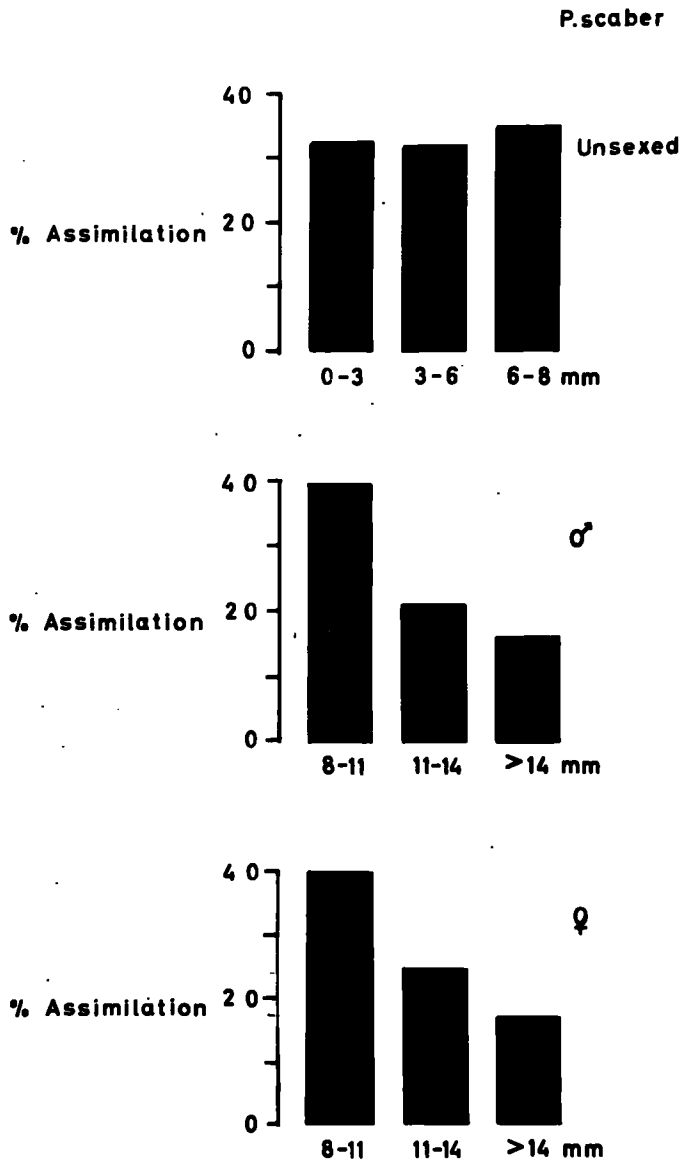
(a) Assimilation

Table 17 and column 5 of Table 18 show the results for all life stages of P.scaber. Fig.20 shows histograms of the data presented

Fig.20.

P. scaber:

Histograms showing the mean % assimilation of all life stages


P.scaber
40
20
0
% Assimilation
Unsexed
0-3
3-6
6-8 mm
40
20
0
% Assimilation
♂
8-11
11-14
>14 mm
40
20
0
% Assimilation
♀
8-11
11-14
>14 mm

in column 3 of Table 17. The ranges indicate that great variation in assimilation efficiency occur within size groups, thus emphasising the need for many replicate experiments, so that a reasonably accurate mean value for this efficiency may be obtained.

Table 17

Significance of the mean % assimilation calculated for all life stages of P.scaber.

Size group	Mean live wt.mg.	Mean % Assim. SD	°of freedom	't'	p=
0-3 mm	2.8	31.81 ± 14.91 (12.5 - 58.1)	14	0.640	NONE
3-6 mm	10.8	31.13 ± 12.43 (14.3 - 66.7)	19	0.856	NONE
6-8 mm	19.8	34.37 ± 15.59 (11.1 - 69.0)	19	1.429	NONE
8-11 mm ♀	43.2	39.58 ± 18.61 (6.9 - 71.4)	9	1.664	NONE
8-11 mm ♂	38.5	39.58 ± 15.78 (20.0 - 70.0)	9	1.962	NONE
11-14 mm ♀	60.7	24.47 ± 13.03 (8.0 - 49.3)	9	1.103	NONE
11-14 mm ♂	61.4	21.06 ± 14.16 (4.8 - 50.0)	9	1.737	NONE
>14 mm ♀	94.8	16.99 ± 14.73 (4.4 - 48.8)	9	2.492	>.05
>14 mm ♂	76.9	16.04 ± 14.65 (4.8 - 50.0)	9	2.707	>.05

Application of the 't' test for small samples gave significant differences in assimilation efficiency between size groups, values of $p = > 0.001$ being obtained in many cases (see Table 17). Assimilation efficiency ranged from 16.04% for the >14mm size group to 39.59% for the 8 - 11 mm group, females generally showing a greater assimilation efficiency than males. It is interesting to note that the 8 - 11 mm female size group of both O.asellus and P.scaber have the highest assimilation efficiency of all the life stages. The overall mean assimilation efficiency calculated from a total of 115 separate experiments for P.scaber was 29.26%.

(b) Rates of Ingestion

Calculation of the rate of ingestion for all size groups of P.scaber was effected by the employment of the two methods used previously for O.asellus. Column 4 of Table 18 shows the results obtained by direct measurement in the present summer study with P.scaber. It is clear that the 8 - 11 mm female groups, as with O.asellus showed the highest rate of ingestion (2.330 mg dry wt/ 24h). Column 4 of Table 19 shows the results obtained by calculation from the winter faeces production data (Table 9), where 70.74% of the food ingested is produced as faeces, and 29.26% is assimilated. A comparison of Table 18 and 19 shows that the rates of ingestion for each size group were similar, with the exception of the high value

obtained for the 8 - 11 mm females in the summer experiment. The data were pooled so that a regression of ingestion rate upon live weight could be calculated. Fig.21 shows the result of a double logarithmic plot of ingestion rate (X) upon live weight (Y). The straight line was calculated by the least squares method; a correlation coefficient of 0.92 was obtained, and the formula Log X = -0.887 + 0.577. Log Y was calculated.

Table 18

Faeces production, food ingested, and food assimilated (mg dry wt/24h) by all life stages of P.scaber during the summer season.

Ranges in brackets

Size group	Mean L.wt.	Faeces prod.	Food ingested	Food assimilated
0 - 3 mm	2.8	0.018 (0.01-0.03)	0.028 (0.01-0.05)	0.010 (0.001-0.003)
3 - 6 mm	10.8	0.373 (0.10-0.75)	0.548 (0.15-1.10)	0.175 (0.05-0.55)
6 - 8 mm	19.8	0.705 (0.40-1.45)	1.130 (0.45-2.30)	0.425 (0.05-1.00)
8 - 11 mm ♀	43.2	1.405 (0.30-2.35)	2.300 (1.05-3.40)	0.925 (0.10-1.40)
8 - 11 mm ♂	38.5	0.665 (0.15 -1.60)	1.260 (0.20-3.10)	0.595 (0.05-1.55)
11 - 14 mm ♀	60.7	1.045 (0.70-1.70)	1.485 (0.85-3.35)	0.440 (0.10-1.65)
11 - 14 mm ♂	61.4	1.120 (0.50-2.30)	1.420 (0.60-2.50)	0.300 (0.05-0.90)
>14 mm ♀	94.8	1.275 (0.90-2.20)	1.560 (1.00-2.30)	0.285 (0.05-1.05)
>14 mm ♂	76.9	0.960 (0.55-1.75)	1.160 (0.60-1.90)	0.200 (0.05-0.75)

P.scaber:

Regression of ingestion rate upon live weight. The line is a least squares estimate of the regression.

* From winter faeces production experiments

● From summer assimilation experiments

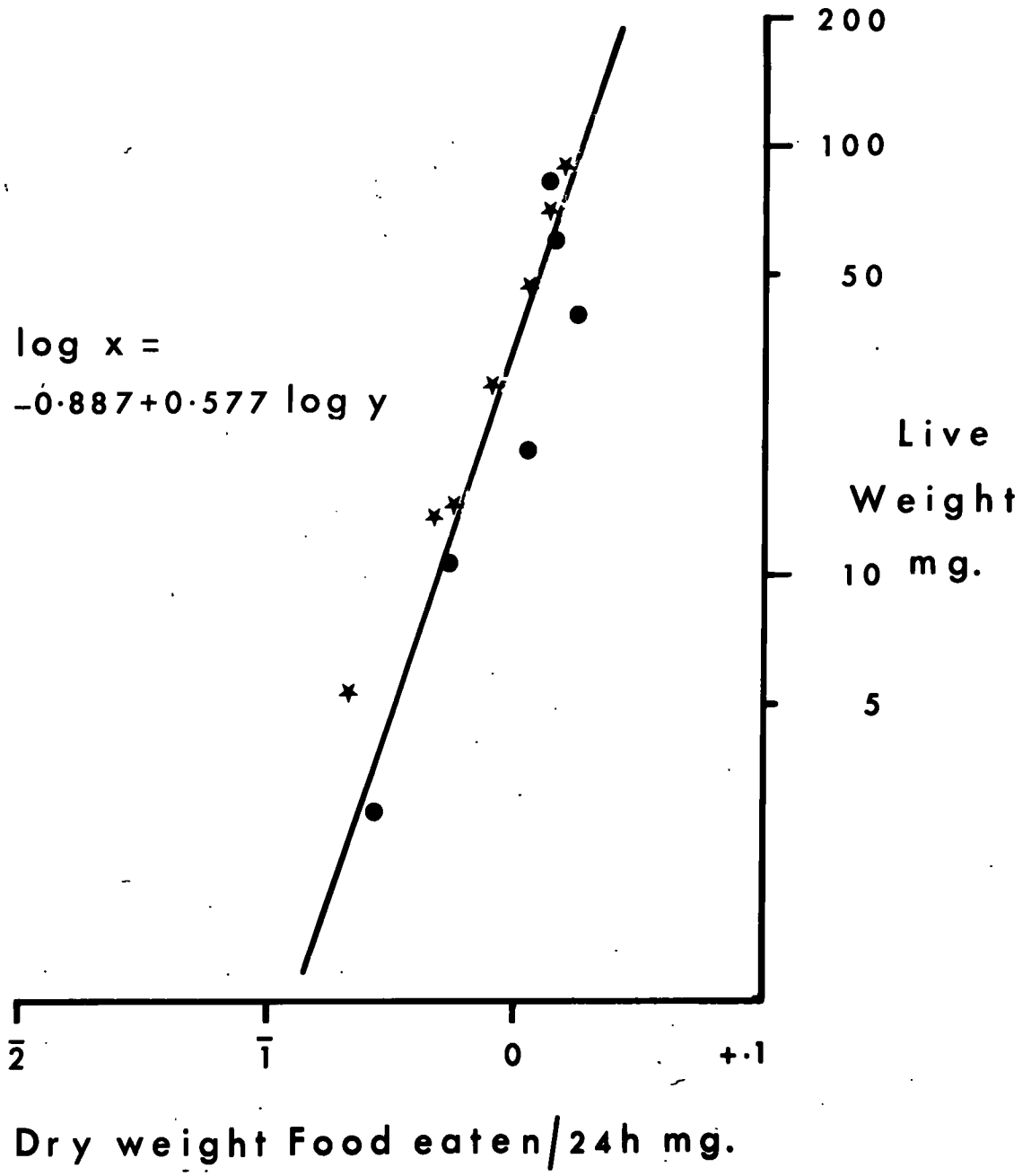

log x =
-0·887+0·577 log y
200
100
50
10
5
Live
Weight
mg.
$\bar{2}$
$\bar{1}$
0
+·1
Dry weight Food eaten/24h mg.

Table 19

Food ingested, and food assimilated as calculated from
(a) the known dry weights of faeces produced/24h obtained in the winter faeces production experiments, and
(b) the assimilation efficiency of 29.26%.

Size group	Mean live wt. mg.	Faeces prod.	Food ingested	Food assim.
0 - 3 mm	5.3	0.151	0.213	0.062
3 - 6 mm	13.4	0.349	0.493	0.144
6 - 8 mm	14.9	0.408	0.577	0.169
6 - 8 mm	27.7	0.586	0.828	0.242
8 - 11 mm	48.0	0.804	1.137	0.333
11 - 14 mm	71.0	0.982	1.386	0.406
>14 mm	91.5	1.113	1.573	0.460

(c) Rates of egestion

Data from two direct measurements shown in Table 18 and 19 were available. Column 3 of Table 18 shows the results obtained from the summer season assimilation experiments, and column 3 of Table 19 shows similar results which were obtained from the winter faeces production experiments. The data from the two experiments were pooled, so that a regression of faeces production upon live weight could be calculated. Fig.22 shows the result of

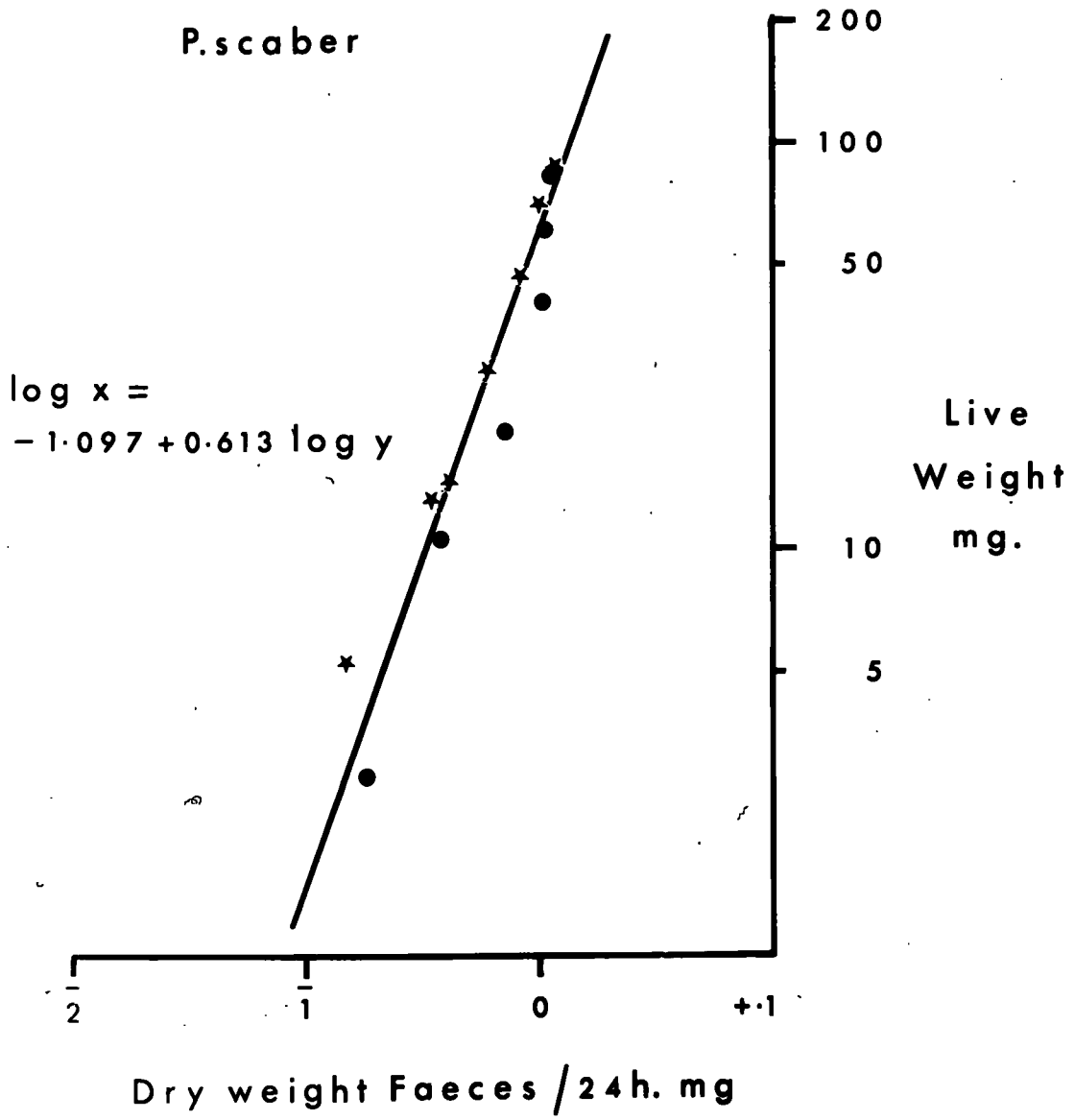
Fig.22

P.scaber:

Regression of egestion rate upon live weight. The line is a least squares estimate of the regression.

* From winter faeces production experiments

● From summer assimilation experiments


P.scaber
log x =
−1·097 + 0·613 log y
200
100
50
10
5
Live
Weight
mg.
$\bar{2}$
$\bar{1}$
0
+·1
Dry weight Faeces / 24h. mg

a double logarithmic plot of faeces production (X) upon live weight (Y). The straight line was calculated by the least squares method; a correlation coefficient of 0.97 was obtained, and the formula $\text{Log } X = -1.097 + 0.613_{\log Y}$ was calculated.

With the results outlined in Chapter 2 and the present chapter, it was possible to proceed to the calculation of the 'best estimates' of all the parameters of the equation:-

Assimilation = Ingestion - Egestion

The methods employed and the results obtained form the basis of the following chapter.

Chapter 4

The calculation of the 'best estimate' of I (assimilation) or energy entering the individual.

Because of the lack of knowledge of the life stage composition of natural populations of Oniscus asellus and Porcellio scaber it is not possible to calculate the energy assimilated by the populations per unit area of habitat per annum. Under these circumstances the employment of the 'best estimate' proposed by Phillipson (1962, 1963) is permissable. 'Best estimates' for food assimilated per gram live weight per 24h were calculated from the data on ingestion, egestion and assimilation presented in the previous chapters.

Methods

Calorific values of the foods used and faeces produced were obtained by combusting pelleted samples in a micro-bomb calorimeter (see Chapter 6). Two methods were employed to calculate the 'best estimates' of food assimilated, food ingested and food egested per gram live weight per unit time by both species. The data for method I were obtained from the winter faeces priduction experiments (Table 14 O.asellus; Table 19 P.scaber). For method 2 the data presented in Tables 13 and 15 O.asellus, and Table 18 P.scaber,

which were obtained from the summer assimilation experiments, were used.

Tables 20-23 show the methods employed to calculate the 'best estimates' of I (assimilation) by these two methods.

(1) The totals of the mean weights of each size group were determined and expressed in milligrams.

(2) The total weights of food ingested and egested were converted to calories by means of the measured values for food and faeces (see Chapter 6). The number of calories assimilated were calculated as Ingestion (cal) minus Egestion (cal).

(3) The results were then expressed as the 'best estimate' of calories assimilated per 24h by 1 gram live weight of isopod. Tables 24 and 25 show the summarized results of assimilation, ingestion and egestion for both species. The 'best estimates' by both methods and their means are presented as mg/g.live weight of isppod/24h and cal/g.live weight of isopod/24h.

Table 20

Calculation of the 'best estimate' of I (assimilation) for *O.asellus* using the data obtained in the winter faeces production experiments.

Size group	Mean live wt. mg.	Mean ingestion (mg. dry weight per 24h.)	Mean egestion (mg. dry weight per 24h.)	Mean assimilation (mg. dry weight per 24h.)
0-3 mm	1.7	0.04	0.076	0.028
3-6 mm	8.2	0.229	0.167	0.062
3-6 mm	10.2	0.360	0.262	0.098
6-8 mm	14.5	0.457	0.333	0.124
6-8 mm	16.4	1.230	0.890	0.340
8-11 mm ♀	35.8	1.460	1.060	0.400
8-11 mm ♂	32.0	1.620	1.180	0.440
11-14 mm ♀	63.0	2.100	1.530	0.570
11-14 mm ♂	64.5	2.061	1.500	0.561
>14 mm ♀	11.20	2.570	1.870	0.700
>14 mm ♂	99.0	2.320	1.690	0.630
(1) TOTAL	457.2	14.511	10.558	3.953 mg.

Total mg is multiplied by mean cal val of:- (food = 4.186) (faeces = 4.212) Kcal/g.

to give

(2) TOTAL CALORIES	60.743	44.470	(16.273) Cal.

(3) ∴ 1 g live weight of *O.asellus* assimilates $\frac{16.273 \times 1000}{457.3}$ Cal/24h.

I = 35.585 cal/g live wt/24h.

Table 21

Calculation of the 'best estimate' of I (assimilation) for *O.asellus* using the data obtained in the summer assimilation experiments.

Size group	Mean live wt.mg.	Mean ingestion (mg. dry weight per 24h)	Mean egestion (mg. dry weight per 24h)	Mean assimilation (mg. dry weight per 24h)
0–3 mm	0.69	0.079	0.053	0.026
3–6 mm	7.32	0.256	0.171	0.085
6–8 mm	16.71	1.082	0.820	0.262
8–11 mm ♀	42.74	2.761	1.316	1.445
8–11 mm ♂	39.44	2.047	1.123	0.924
11–14 mm ♀	84.72	2.296	1.855	0.441
11–14 mm ♂	76.95	2.687	2.067	0.620
>14 mm ♀	142.50	2.484	1.776	0.708
>14 mm ♂	117.42	1.906	1.333	0.573
(1) TOTAL	528.49	15.598	10.514	5.084 mg.

Total mg is multiplied by mean cal.val. of:- (food = 4.186) (faeces = 4.212) Kcal/g.

to give

(2) TOTAL CALORIES	65.293	44.285	(21.008) cal.

(3) ∴ 1 g. live weight of *O.asellus* assimilates:- $\frac{21.008 \times 1000}{528.49}$ cal/24h.

I = 39.751 cal/g. live wt./24h.

Table 22

Calculation of the 'best estimate' of I (assimilation) for P.scaber using the data obtained from the winter faeces production experiments.

Size group	Mean live wt. mg.	Mean ingestion (mg. dry weight per 24h)	Mean egestion (mg. dry weight per 24h)	Mean assimilation (mg. dry weight per 24h)
0-3 mm	5.3	0.213	0.151	0.062
3-6 mm	13.4	0.493	0.349	0.144
6-8 mm	14.9	0.577	0.408	0.169
6-8 mm	27.7	0.828	0.586	0.242
8-11 mm	48.0	1.137	0.804	0.383
11-14 mm	71.0	1.388	0.982	0.406
> 14 mm	91.5	1.573	1.113	0.460
(1) TOTAL	271.8	6.209	4.393	1.816 mg.

Total mg is multiplied by mean cal. val of:- (food = 4.186) (faeces = 3.909) Kcal/g.

to give

(2) TOTAL CALORIES	25.991	17.172	(8.819) cal.

(3) ∴ 1 g. live weight of P.scaber assimilates $\frac{8.819 \times 1000}{271.8}$ cal/24h

I = 32.447 cal/g. live wt./24h.

Table 23

Calculation of the 'best estimate' of I (assimilation) for P.scaber using the data obtained from the summer assimilation experiments

Size group	Mean live wt.mg.	Mean ingestion (mg dry weight per 24h)	Mean egestion (mg dry weight per 24h)	Mean assimilation (mg dry weight per 24h)
0-3 mm	2.8	0.028	0.018	0.010
3-6 mm	10.8	0.548	0.373	0.175
6-8 mm	19.8	1.130	0.705	0.425
8-11 mm ♀	43.2	2.330	1.405	0.925
8-11 mm ♂	38.5	1.260	0.665	0.595
11-14 mm ♀	60.7	1.485	1.045	0.440
11-14 mm ♂	61.4	1.420	1.120	0.300
>14 mm ♀	94.8	1.560	1.275	0.285
>14 mm ♂	76.9	1.160	0.966	0.200
(1) TOTAL	408.9	10.921	7.566	3.355 mg.

Total mg is multiplied by mean cal. val. of:- (food = 4.186) (faeces = 3.909) Kcal/g

to give

(2) TOTAL CALORIES	45.715	29.575	(16.140) cal.

(3) ∴ 1 g. live weight of P.scaber assimilates:- $\frac{16.140 \times 1000}{408.9}$ cal/24h

I = 39.472 cal/g. live wt/24h.

Table 24

Summary of the 'best estimates' of assimilation, ingestion and egestion for 1g. live wt. of O.asellus

(a) by weight (mg dry wt/24h) and

(b) by calories (cal/24h.)

Expt.	Food Assimilated	Mean	Food Ingested	Mean	Food Egested	Mean
(a) Winter	8.64	9.13	31.73	30.62	23.09	21.49
Summer	9.62		29.51		19.89	
(b) Winter	35.585	37.668	132.830	128.188	97.245	90.520
Summer	39.751		123.546		85.795	

Table 25

Summary of the 'best estimate' of assimilation, ingestion and egestion for 1 g. live wt. of P.scaber

(a) by weight (mg.dry wt/24h) and
(b) by calories (cal/24h).

Expt.	Food Assimilated	Mean	Food Ingested	Mean	Food Egested	Mean
(a) Winter	6.68	7.56	22.84	25.09	16.16	17.53
Summer	8.43		27.33		18.90	
(b) Winter	32.447	35.960	95.625	103.713	63.178	67.753
Summer	39.472		111.800		72.328	

Knowing the 'best estimates' of assimilation, ingestion and egestion, the equations given by Phillipson (1960b) may now be satisfied in terms of dry weight or calories.

1. Wt of food assimilated = Wt. of food ingested - Wt. of faeces egested

	(mg. dry wt/g.live wt./24h)		(mg. dry wt/g.live wt./24h)		(mg. dry wt/g.live wt./24h.)
(a). *O.asellus*	9.13	=	30.62	-	21.49
(b). *P.scaber*	7.56	=	25.09	-	17.53

2. Energy of food assimilated = Energy of food ingested - Energy of faeces egested

	(cal/g.live wt/24h.)		(cal/g.live wt/24h)		(cal./g.live wt/24h.)
(a). *O.asellus*	37.668	=	128.188	-	90.520
(b). *P.scaber*	35.960	=	103.713	-	67.753

Thus for the equation I = R + Y :-

I = 37.668 cal/or 9.13 mg per g.live wt/24h *O.asellus*

I = 35.960 cal or 7.56 mg per g. live wt/24h. *P.scaber*

SECTION 2

The evaluation of the 'best estimate' of respiratory energy loss (R or T Δ S) by Oniscus asellus and Porcellio scaber.

Chapter 5

Respiratory metabolism of the isopods O.asellus and P.scaber

Introduction

Respiratory metabolism for O.asellus has been published by Phillipson and Watson (1965). The lack of literature concerning respiratory metabolism studies for animals of the type designated by Macfadyen (1963) and others, as 'large decomposers' in all their life stages was reported in that paper. A study of P.scaber supplements the O.asellus study, and is reported here. A 'best estimate' of respiratory energy loss per unit weight per unit time is presented for both O.asellus and P.scaber, which should facilitate the calculation, from biomass data, the annual respiratory energy loss per unit weight, per unit area, by any population of these two species.

1. O.asellus

Abstract of Phillipson and Watson (1965): The complete paper

appears as an appendix, but a summary of the results is given below.

(1) Approximately 700 individuals of O.asellus of all sizes were subjected to oxygen consumption tests between March 1963 and March 1964.

(2) In the relationship live weight to length a change occurs at approximately 20 mg and 7.5 mm, which also coincides with a change in the respiratory rate to live weight relationship. The high oxygen uptake at live weights less than 20 mg is clearly associated with growth.

(3) At weights greater than 20 mg the respiratory rate per unit weight is fairly constant, except during May, June and July when seasonal aberrance, associated with reproductive activities occurred.

(4) A linear relationship exists between the live weight of an individual and the number of embryos and/or young per brood. Weight increase above 100 mg is mainly accounted for by an increase in the number of young per brood.

(5) Seasonal differences in respiratory rates per unit weight occur between March and August, and are more than twice as high as those obtained for the winter months.

(6) Two methods of calculating a 'best estimate' of oxygen consumption per unit weight per unit time are given. These two estimates are close: 4.992 and 5.328 mm $^3O_2$/mg/24h. Using an oxycalorific equivalent of 5 K.cal/litre the 'best estimates' were converted to calories, the two estimates being:- 25.000 and 26.7000 cal/gram live weight/24h.

2. P.scaber

Approximately 800 individuals of all sizes were collected in the field and subjected to oxygen consumption tests between June1964 and June 1965. The respirometer used was the continuously recording one described by Phillipson (1962). Measurements of oxygen consumption were made at 16 ± 0.1°C and the humidity of the metabolism chamber was kept above 90% RH by means of a strip of damp filter paper 3 x 1 cm. The record for each individual was continuous over a period of at least 48h, but the rates of oxygen consumption were calculated from the results obtained for the 24h period between 6 and 30h after the experiment began. Individuals were placed in the respirometer within one hour of collection, and were not fed in the laboratory or in the apparatus. Date of capture, sex, live weight, total body length, total body width, breeding condition, and respiratory rate were recorded for each individual.

Results

Length/weight and length/width relationships.

Graphs showing the relationship of length to live weight, and body width, were constructed for each month of the year, but they were so alike that only those for June and December are given (Figs.23,24 and 25). It is clear that a change in the relationship of live weight to length occurs at approximately 16 mg live weight (equivalent to a length of 7.0 mm). This change coincides with that observed in the respiratory rate to live weight relationship shown in Figs.26-29.

Oxygen consumption

Figs. 26-29 show the respiratory rate per unit weight plotted against live weight for each month of the year. All the graphs show a similar curve with an inflexion within the live weight range of 10-20 mg. Over 20 mg live weight the respiratory rate per unit weight is fairly constant for each month. The marked increase in rate per unit weight shown by O.asellus in the months of May to July was not as apparent in the P.scaber experiments.

Breeding season and respiratory rate

All female P.scaber used for oxygen consumption experiments were dissected. The condition of the ovaries was noted and, when present, the number of embryos and/or young contained in the brood pouch

Fig.23

P.scaber:

The relationships of body length to body width during the months of December 1964 to June 1965. Unsexed individuals *, adults ●.

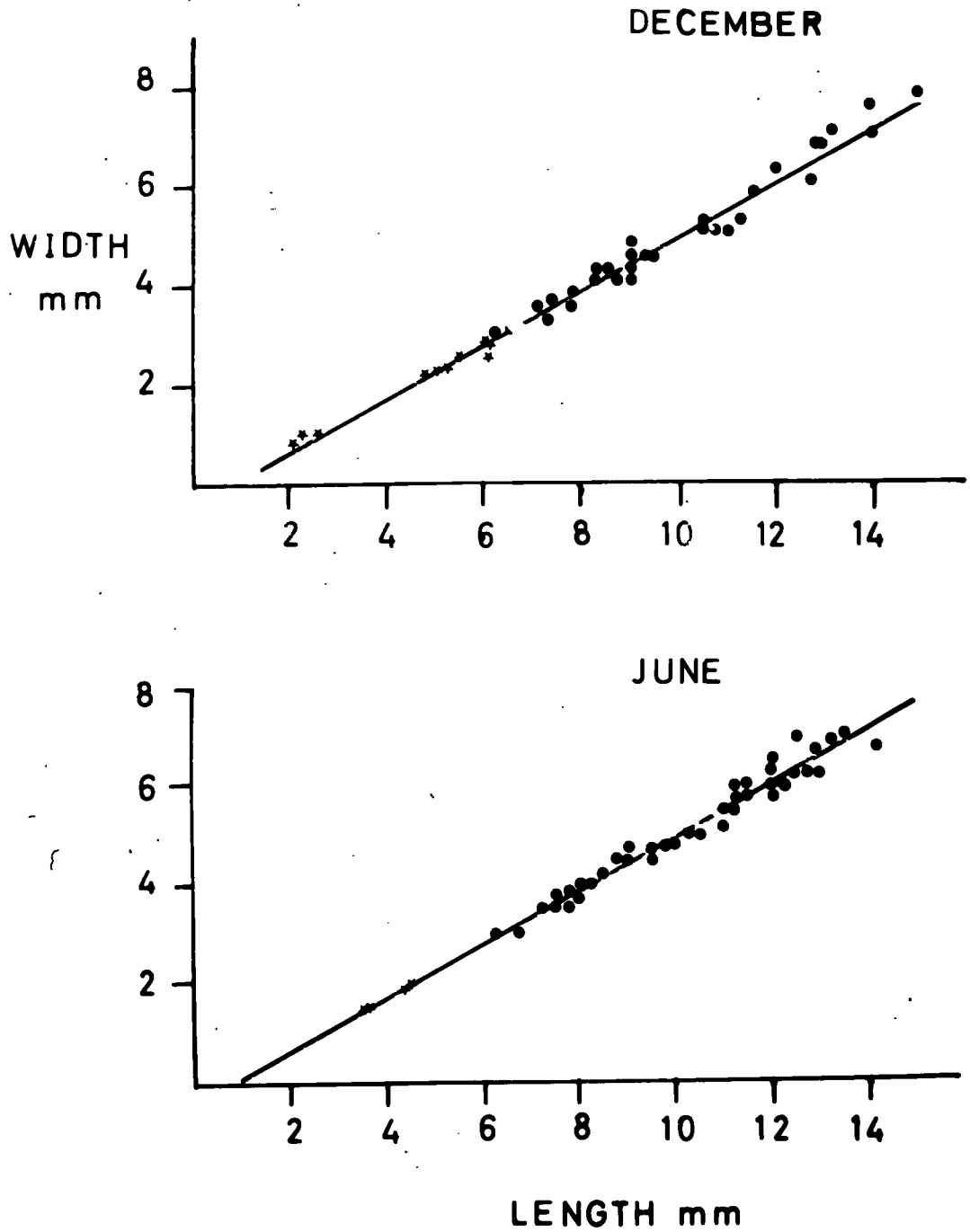

DECEMBER
WIDTH
mm
8
6
4
2
2
4
6
8
10
12
14
JUNE
8
6
4
2
2
4
6
8
10
12
14
LENGTH mm

Fig.24.

P.scaber:

The relationships of length to live weight, June 1964 and 1965.
Unsexed individuals ✱ , males ● , females ✪

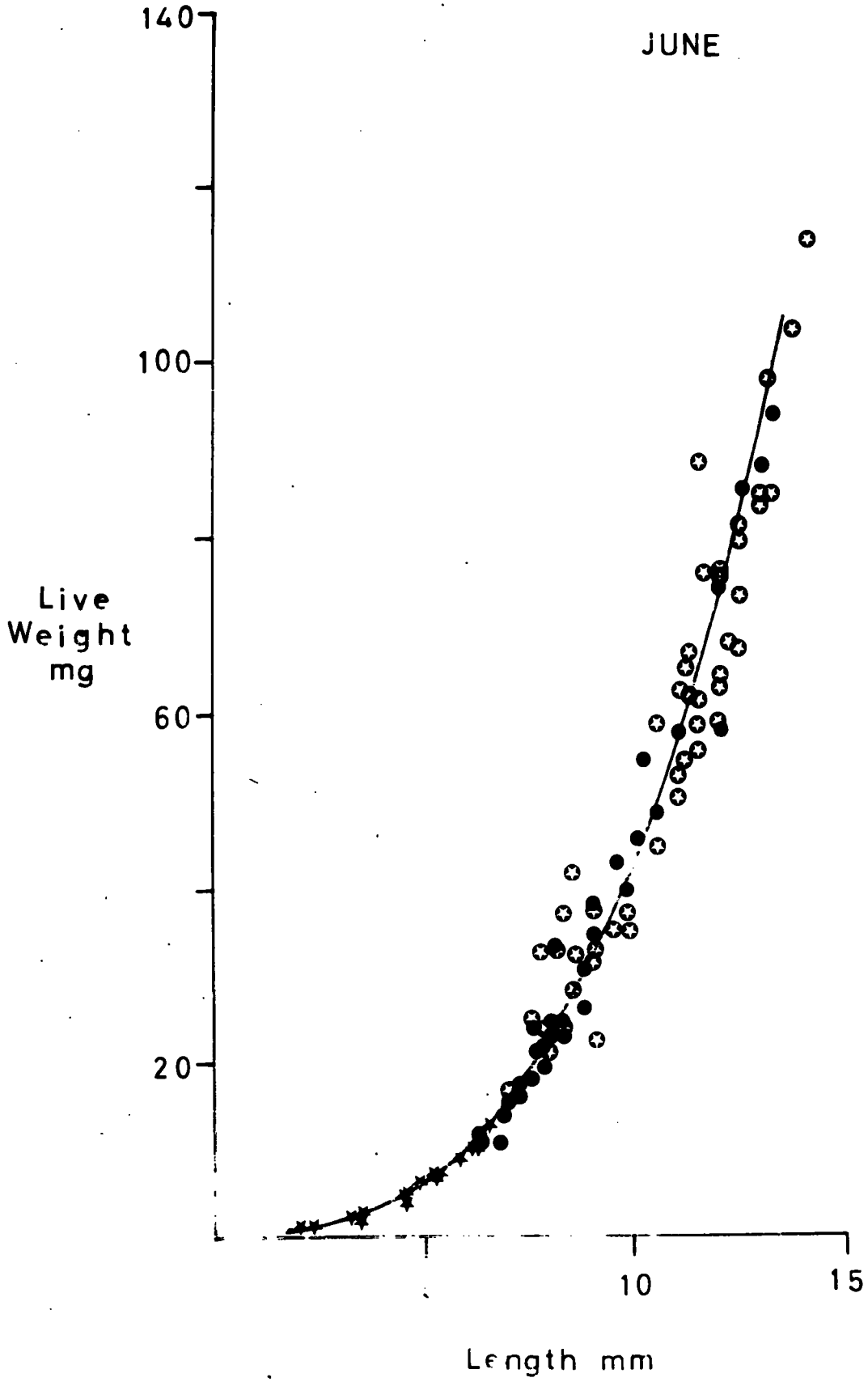
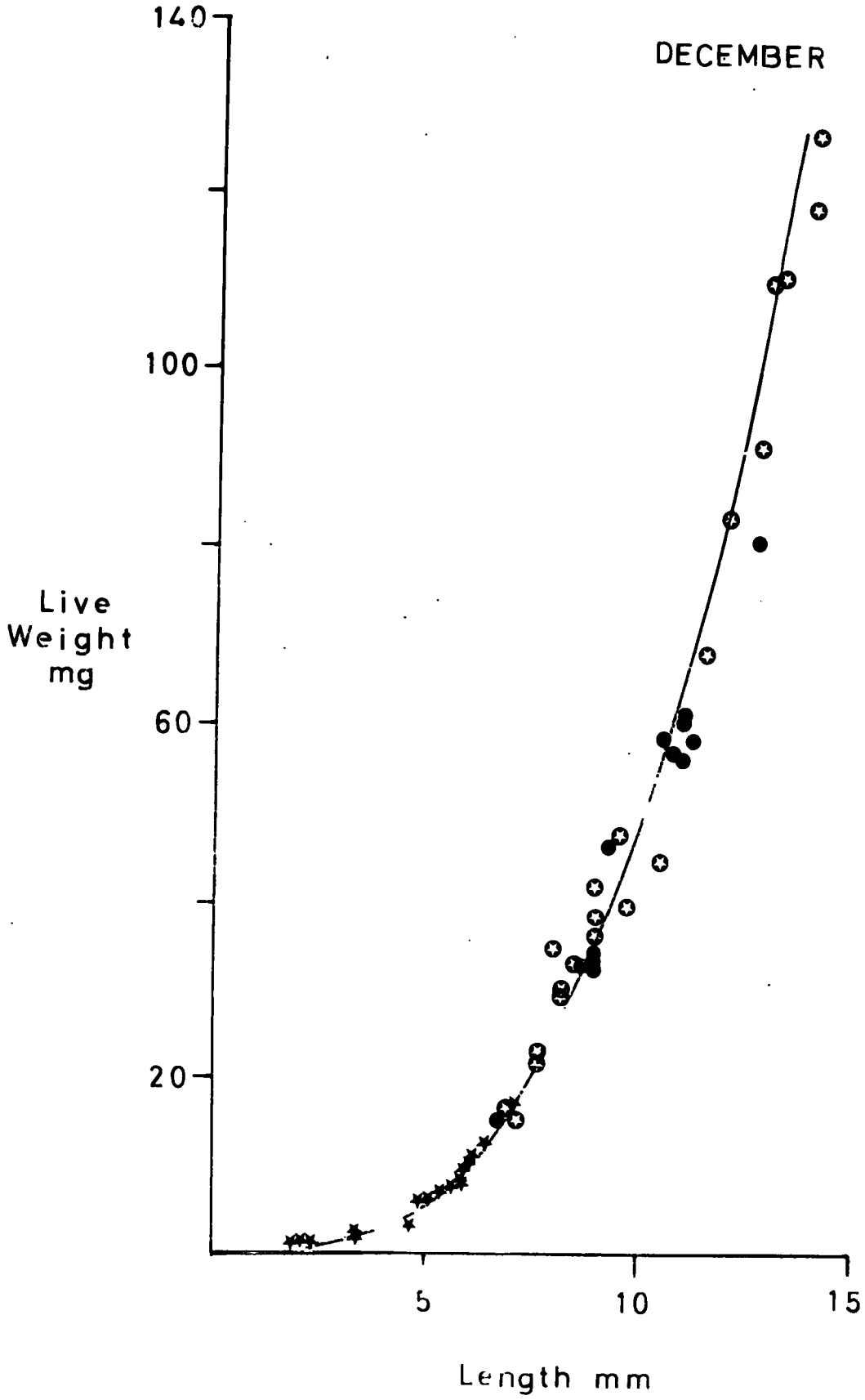

JUNE
140
100
60
20
Live
Weight
mg
10
15
Length mm

Fig.25

P.scaber:

The relationship of length to live weight, December 1964.
Unsexed individuals ✱ , males ● , females ✪


DECEMBER
140
100
60
20
Live
Weight
mg
5
10
15
Length mm

counted. Table 26 shows the ovary condition of all animals dissected for each month of the year.

Table 26

Gonad condition of adult female P.scaber used for respiratory rate measurements from June to December 1964, and January to June 1965.

	Number of adults with			
1965	Small eggs	developing eggs	early embryos	late embryos/ young
January	31	6	0	0
February	8	24	0	0
March	2	18	0	0
April	0	24	0	0
May	0	28	13	0
1965 June	0	2	46	1
1964 July	11	0	0	17
August	22	0	0	2
September	16	16	0	0
October	14	4	0	0
November	40	0	0	0
December	20	0	0	0

It is clear that ovaries develop at first gradually, and later rapidly to a maximum in May when early embryos begin to appear in the brood pouch. After the first brood is liberated in August, the

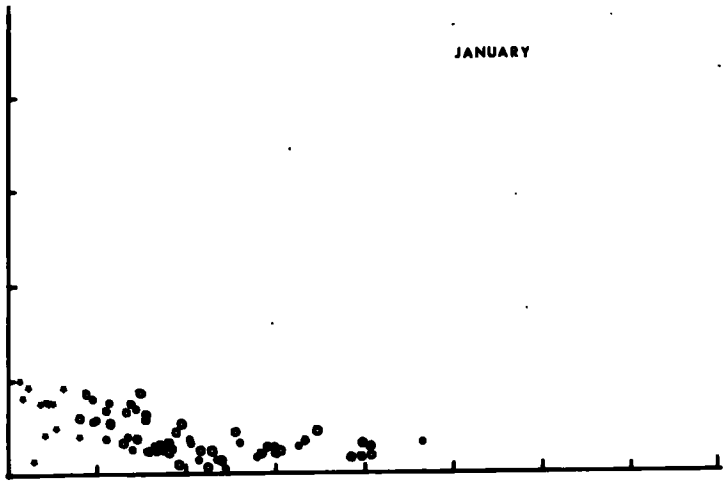
P.scaber:

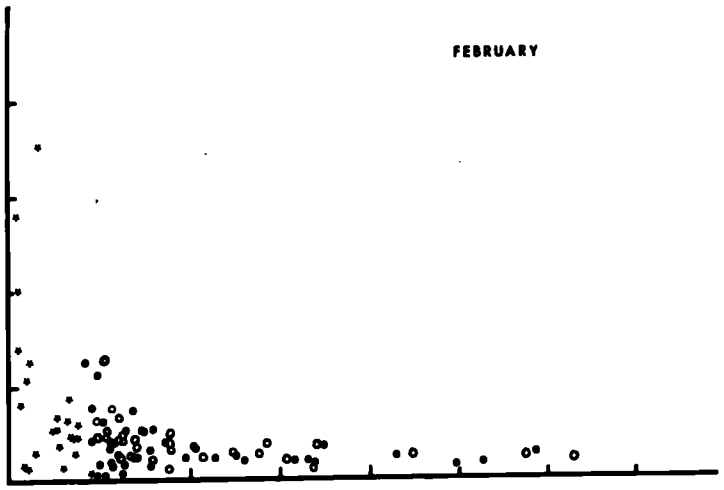
Respiratory rate per unit weight plotted against live weight from June 1964 to June 1965.

- ★ Unsexed individuals
- ● Males
- ○ Females without brood pouch
- ☆ Females + early embryos
- ✪ Females + late embryos

Fig. 2b

January to March


JANUARY


FEBRUARY

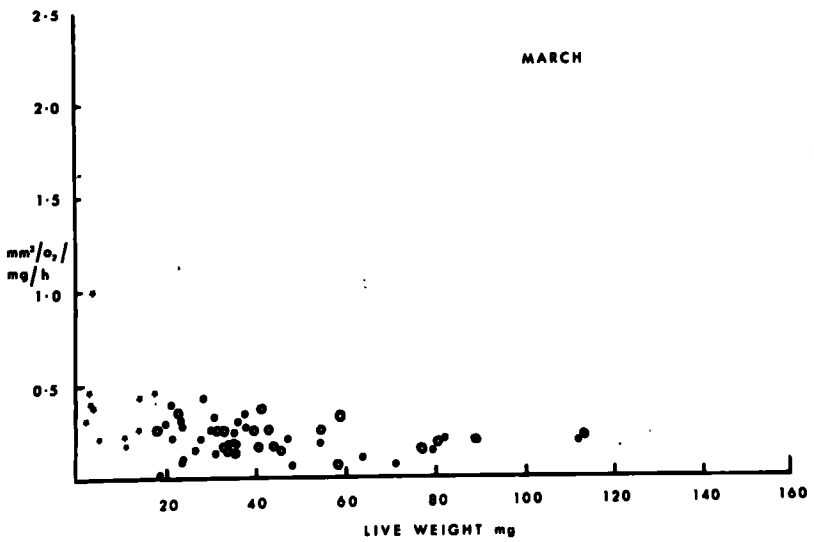
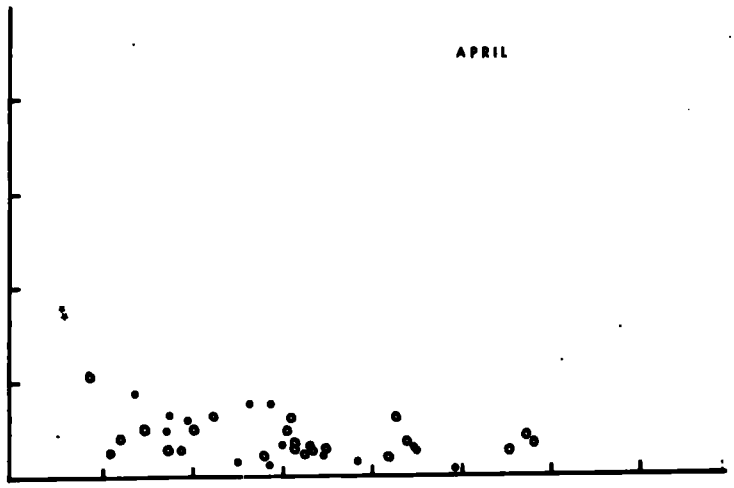
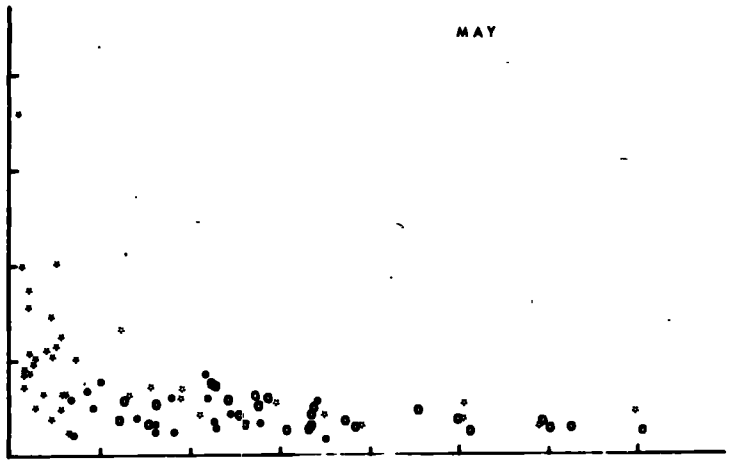

MARCH
2·5
2·0
1·5
mm³/o₂/
mg/h
1·0
0·5
20
40
60
80
100
120
140
160
LIVE WEIGHT mg

Fig. 27

April to June


APRIL


MAY

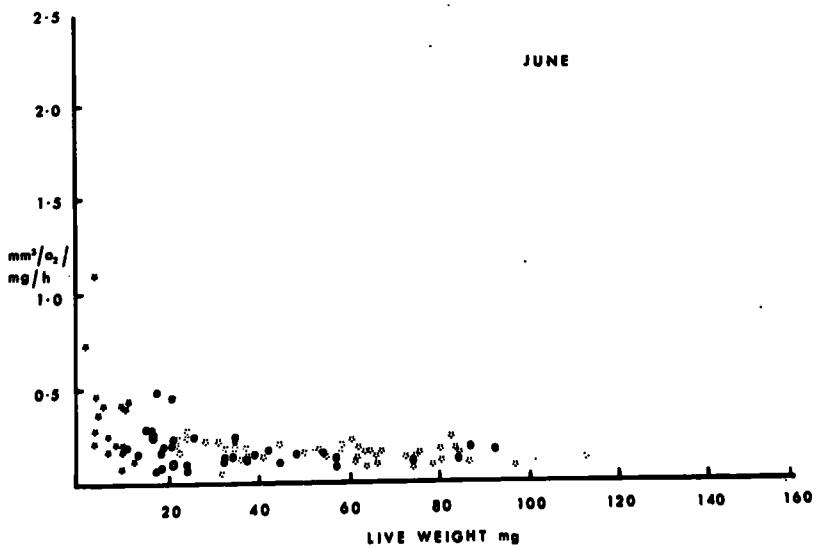

JUNE
2·5
2·0
1·5
mm³/o₂/
mg/h
1·0
0·5
20
40
60
80
100
120
140
160
LIVE WEIGHT mg

Fig.26

July to September

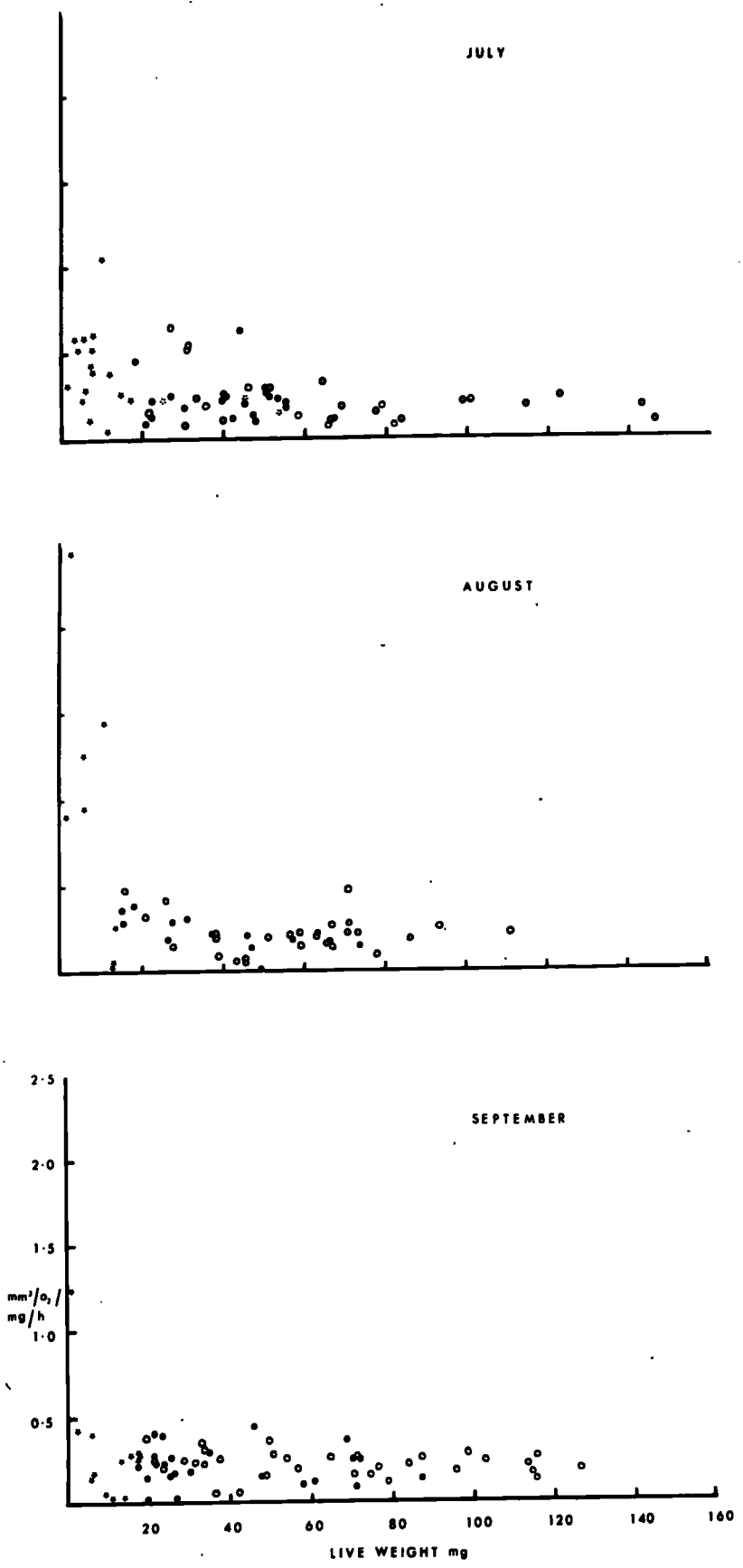
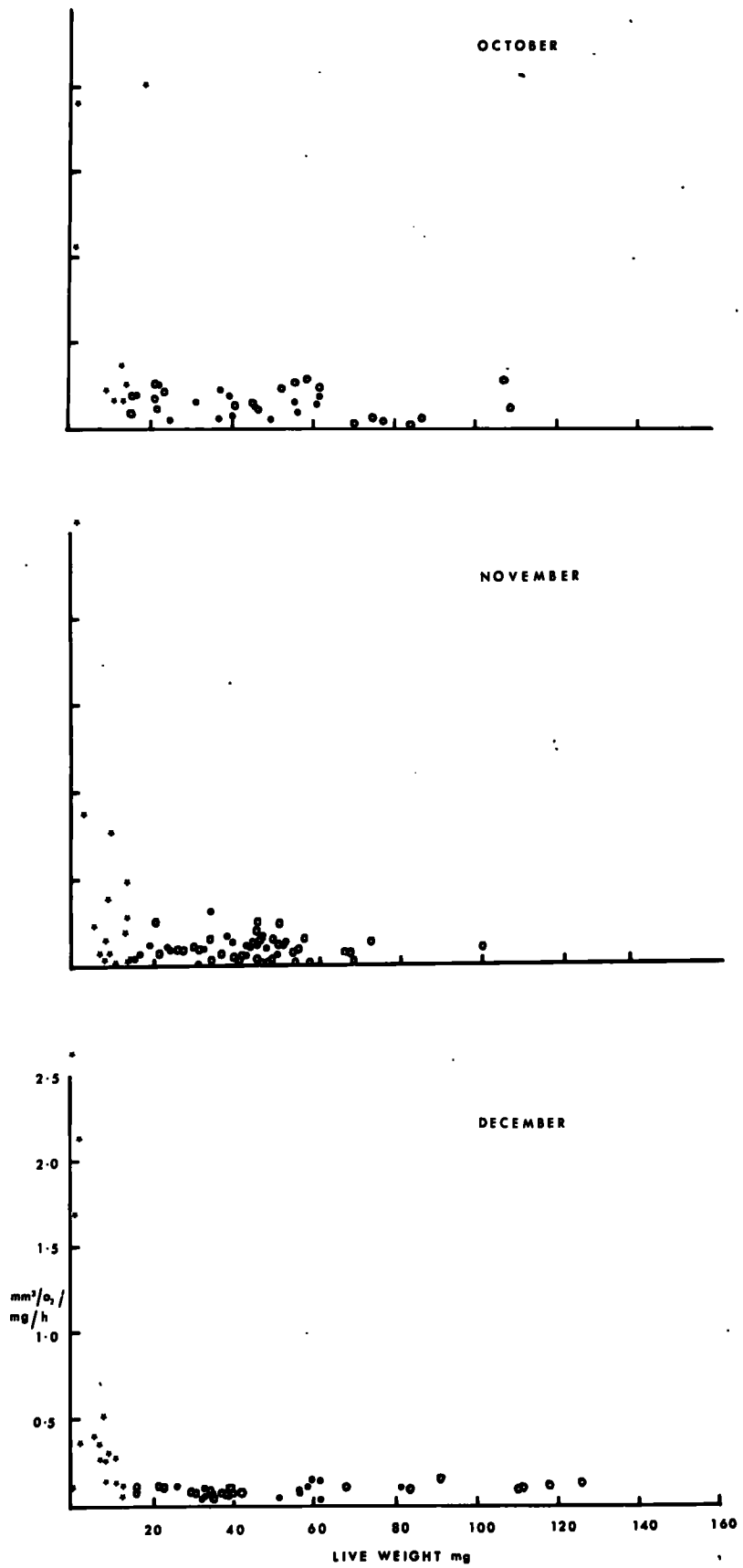

JULY
AUGUST
SEPTEMBER
2·5
2·0
1·5
mm³/o₂/
mg/h
1·0
0·5
20
40
60
80
100
120
140
160
LIVE WEIGHT mg

Fig.29

October to December


OCTOBER
NOVEMBER
DECEMBER
2·5
2·0
1·5
mm³/o₂/
mg/h
1·0
0·5
20
40
60
80
100
120
140
160
LIVE WEIGHT mg

ovaries begin to develop rapidly in order to produce a second brood. In this case a second brood failed to develop.

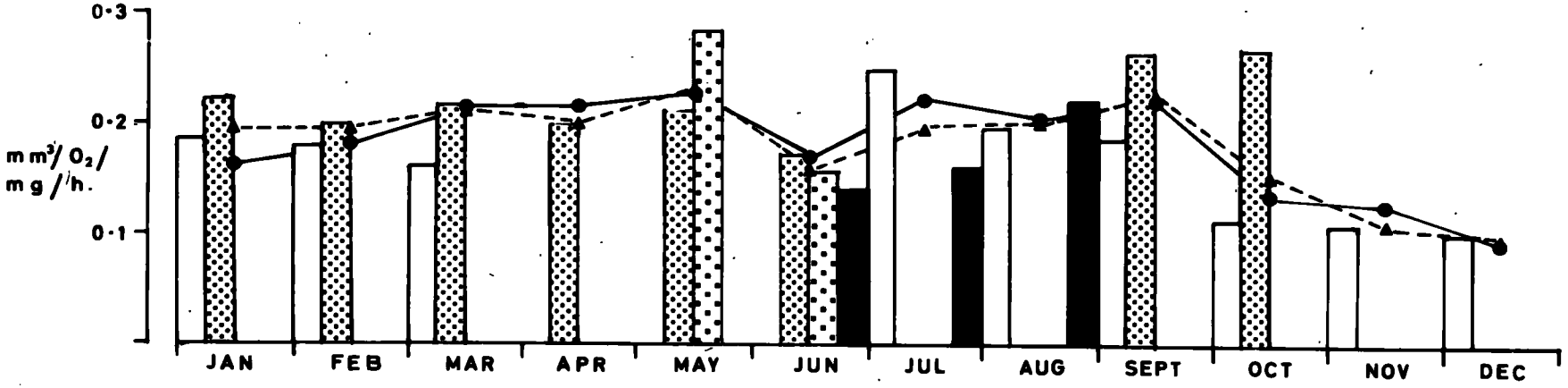
Season and respiratory rate

The ratio of juveniles to adults, or breeding to non-breeding individuals, in the experiments indicated in Figs. 26-29 may not reflect the field situation. However, if it is assumed that the greatest proportion of the biomass throughout the year is composed of individuals exceeding 16 mg live weight, then a comparison of mean monthly respiratory rates will indicate minimum seasonal differences in respiratory energy loss. Fig.30 shows that seasonal differences do occur in both sexes. The mean respiratory rates for the summer months (April to September) 0.211 and 0.199 mm $^3O_2$/mg/h for males and females respectively are considerably higher than the 0.151 and 0.158 mm $^3O_2$/mg/h (males and females) obtained for the winter months (October to March). Consideration of the results in Table 26 and Fig.30 indicates a definite trend for respiratory rates being dependant on ovary development. A steady increase of oxygen consumption from January to May reflects ovary development. In June, a sudden drop in respiratory rate occurred in females after the mature eggs had been deposited in the brood pouch. The rate rose again in July when all the brood pouches contained embryos which were about to be

Fig.30

P.scaber:

Mean monthly respiratory rate per unit weight of individuals which exceed 16 mg.live weight; Males ●, females ▲; also the mean respiratory rate per unit weight of females which contain undeveloped eggs □, developing eggs ⊡, early embryos ⁘, and late embryos/young ■, grouped by month of occurrence.


0·3
0·2
0·1
mm³/O₂/
mg/h.
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC

released. This increase in respiratory rate continued to September when the ovaries were again developing rapidly, only to drop suddenly in October to December when ovaries contained underdeveloped eggs.

Annual respiratory metabolism

Because of the variability of respiratory rate with size, breeding condition, and season, and the lack of knowledge of the life stage composition of a natural population of P.scaber, it was not possible to calculate directly the respiratory energy loss per unit area of habitat per annum. Under these circumstances the employment of the 'best estimate' technique proposed by Phillipson (1961, 1962) was again permissable. Table 27 shows the methods employed in calculating a 'best estimate' of oxygen consumption. In both methods it was assumed that where it was not practical to assess the gonad condition accurately, the weight of the animal would reflect gonad condition. This assumption was made for juveniles (<16 mg live weight), and they were grouped in the four categories shown in Table 27. Individuals greater than 16 mg live weight were sexed.

It was also assumed that the time of occurrence of males would reflect gonad condition, consequently the males were grouped according to month of occurreence in the two methods of calculating a 'best estimate'. The gonad condition of females could be assessed, and in method 1 the females were grouped into those with small eggs, those

with developing eggs, those with early embryos, and those with late embryos/young. In method 2 the females, like the males, were grouped according to month of occurrence.

Calculation of a 'best estimate' of oxygen consumption by method 1 gave a result of 4.249 mm $^3O_2$/mg/24h, and by method 2, 4.122 mm $^3O_2$/mg/24h. To convert the oxygen consumption figures to calories an oxycalorific equivalent of 6 K.cal/litre was used. The 'best estimate' thus obtained of respiratory energy loss (R or $T\Delta S$) for P.scaber was, by method 1 21.245 cal/g.live wt/24h, and by method 2 20.610 cal/g.live wt/24h.

Table 27

The two methods employed in calculating a 'best estimate' of oxygen consumption for P.scaber

	JUVENILES				ADULT MALES											
Category	4.0 mg	4.1-8.0	8.1-12.0	12.1-16.0	January	February	March	April	May	June	July	August	September	October	November	December
Mean L.wt.(mg)	2.22	5.94	10.13	14.25	40.24	40.15	49.66	58.06	40.45	37.52	39.49	44.97	39.64	41.11	36.09	50.38
mm^3O_2/individ/h	2.214	2.659	3.506	4.159	5.744	5.971	10.938	10.523	8.610	5.943	8.900	8.364	8.398	5.390	4.767	4.585

	ADULT FEMALES				
Category	small eggs	devel.eggs	early embryos	late embryos/ young	TOTAL ADULT FEMALES
Mean L.wt.(mg)	51.65	58.28	59.58	76.48	245.99 (B_1)
mm^3O_2/individ/h	7.452	11.670	10.028	12.060	41.210 (B_2)

ADULT FEMALES											
January	February	March	April	May	June	July	August	September	October	November	December
44.34	40.73	49.66	63.43	67.24	59.02	66.98	60.04	65.04	58.69	45.32	63.83
6.481	6.652	7.965	11.231	13.720	8.525	11.599	12.332	13.913	8.303	4.751	6.783

TOTAL Juveniles and Adult Males
550.30 (A_1)
99.771 (A_2)

TOTAL Adult Females
684.32 (C_1)
112.255 (C_2)

Calculation of 'best estimate'

Method 1 $$\frac{A_2 + B_2}{A_1 + B_1} = \frac{140.981}{796.290} = 0.177 \text{ mm}^3O_2\text{/mg/h or } 4.249 \text{ mm}^3O_2\text{/mg/24h}$$

Method 2 $$\frac{A_2 + C_2}{A_1 + C_1} = \frac{212.026}{1234.620} = 0.172 \text{ mm}^3O_2\text{/mg/h or } 4.122 \text{ mm}^3O_2\text{/mg/24h.}$$

SECTION 3

The measurement of growth ($Y_1 + Y_2 + Y_3$) of the isopods Oniscus asellus and Porcellio scaber.

General Introduction

$Y_1 + Y_2 + Y_3$ remain to be measured to satisfy the equation $I = R + Y_1 + Y_2 + Y_3$ for O.asellus and P.scaber. Little attention has been given to the measurement of the parameters $Y_1 + Y_2 + Y_3$ for all life stages of terrestrial invertebrates. Calculations of growth from population data were made by Odum and Smalley (1959) for the grasshopper Orchelimum fidicinium; Engelmann (1961) various soil Arthropods, mainly Oribatei; Odum et al (1962) the grasshopper Melanopus femur - rubrum, M. biliteratus, and the tree cricket Oecanthus nigricornis; Golley and Gentry (1964) the southern harvester ant Pogonomyrmex badius; Wiegert (1964) the spittle bug Philaenus spumarius; and (1965) various Orthoptera; and Saito (1965) the isopod Ligidium japonicum. Studies on the growth by length of isopods have been made by Heeley (1941); Hatchett (1947); Matsakis (1955); Bakker (1956) Brereton (1956); Paris and Pitelka (1963) and Wieser (1965).

Only Saito (1965) has attempted to calculate growth or production of all life stages of a species designated by Macfadyen (1963)

and others as a 'large decomposer'. The present study gives such data for the two isopods O.asellus and P.scaber. Growth may be measured in two ways:-

(1) Detailed population studies enable population growth, production of young and growth by moult to be measured directly and accurately providing an efficient sampling programme is carried out.

(2) When biomass data and the life stage composition of a population is unknown, the growth per unit time of individuals representing all life stages may be measured. Such information permits the construction of a growth curve over the whole life span, and the weight increase per unit time for each life stage can thus be estimated. This latter method was used to calculate growth of O.asellus and P.scaber. The lack of knowledge of the life stage composition of natural populations of the two species of isopods being studied made it impossible to calculate directly the energy used for body growth, growth of reproductive tissue and growth by moult per unit area of habitat per annum, therefore the employment of the 'best estimate' technique proposed by Phillipson (1962, 1963) was necessary. To calculate the best estimate of growth the following data were considered necessary for all the life stages of the two isopod species:-

1. The rates of growth (mg live weight) of individual isopods per unit time
2. The dry weights of non reproductive and reproductive tissue comprising the above live weight increases per unit time
3. The energy in calories equivalent to the abovementioned dry weights.

A 'best estimate' of growth ($Y_1 + Y_2 + Y_3$) could therefore be calculated, thus facilitating the calculation, from biomass data, of the annual energy of growth per unit area of habitat by any population of O.asellus or P.scaber. Chapters 6,7 and 8 show how this information was obtained.

Chapter 6

Calorific values of isopod material.

Introduction

Information concerning the calorific values of animal material is sparse. Calorific values have been given by Gere (1956) for the caterpillar Hyphantria cunea; Odum and Smalley (1959) for the grasshopper Orchelimum fidicinium; Golley (1961) for unspecified insects; Slobodkin and Richman (1961) for unspecified mites and beetles; Golley and Gentry (1964) for the ant Pogonomyrmex badius; Wiegert (1964) for the spittle bug Philaenus spumarius and (1965) for various Orthoptera; and Saito (1965) for the isopod Ligidium japonicum.

The methods used in determining the calorific values of biological materials have been described by Phillipson (1964) who also reported the availability of a micro bomb calorimeter which was capable of combusting samples of 5-100 mg dry weight. This last mentioned apparatus was used in the present studies.

Methods

For each species samples were obtained of male and female bodies of all life stages at different seasons, reproductive tissue in all

developmental stages, moulted exoskeletons, preferred foods and the faeces produced from these foods. Samples were vacuum dried at 60°C, finely ground with an agate pestle and mortar, pelleted, and stored over a dessicant. Calorific values were obtained by combusting pellets of approximately 10 mg dry weight in a slightly modified model of the Phillipson (1964) micro bomb calorimeter, which had previously been calibrated with benzoic acid. Operation of the bomb was described by Phillipson (1964). At least three determinations were made on each sample.

Results

Calibration of the bomb:

The values of ten consecutive combustions of benzoic acid were determined. A mean value of 0.7573 ± 0.005 mV/100 cal (S.E. 0.002, c.v. 0.064) was obtained. The calibration was periodically checked and was found not to vary. The mean calibration figure was used for calculation of the calorific value of all materials subsequently burned (see Appendix for sample data sheet).

Calorific values of exuviae:

Attempts to determine the calorific value of moulted exoskeletons were discontinued after repeated failure of combustion for these samples indicated that they contained a high percentage of mineral, thus having no significant calorific value.

Calorific values of isopod bodies, reproductive tissue, foods and faeces:

Tables 28.29 and 30 a.b. show the results obtained for 140 separate determinations.

Body tissues

(a) O.asellus 20 combustions for juveniles and male bodies, and 40 for juvenile and female bodies gave mean calorific values for all life stages of 3.622 and 3.567 K.cal/g.dry wt respectively. (See Table 28)

(b) P.scaber 13 and 20 determinations gave mean values for all life stages of 3.488 (males) and 3.475 (females) K.cal/g.dry wt. respectively. (See Table 28).

Reproductive tissue

Because of the proportionately small size of underdeveloped ovaries it was assumed that they did not make a significant contribution to the mean calorific value of whole animals, therefore separate measurements were not made for this material. Determinations were made for ripe or developing ovaries, and early and late embryos. The following mean values (k.cal/g.dry wt.) were obtained:-

Ripe or developing ovaries : O.asellus 5.328; P.scaber 5.431

Early embryos : O.asellus 6.507; P.scaber 6.528

Late embryos : O.asellus 5.587; P.scaber 5.633

(See Table 28)

Calorific values of preferred foods:

Table 29 shows the results obtained. The mean calorific value of all foods previously used in the determination of I (assimilation) was 4.186 K.cal/g. dry wt.

Calorific values of faeces:

(a) O.asellus: Clearly there was a possibility that the calorific value of faeces produced would vary with the type of food eaten and the life stage of the animal eating it. Therefore an attempt was made to see if the calorific value of faeces varied with the type of food and the life stage of the animal. The 6-8 mm and 11 - 14 mm size groups of O.asellus were fed separately with discs of each of the four foods, Dead Sweet Chestnut leaves, Dead Oak leaves, Decaying Oak leaves and Decaying Sycamore leaves. The faeces produced by each life stage from each food were pelleted and combusted. Table 30 shows that significant differences did occur, but not knowing the life stage composition and the amounts of each food actually consumed by each life stage of a field population, the mean value for all faeces of 4.212 K.cal/g.dry wt was determined, and assumed to represent the calorific value of faeces being produced by all individuals in the field.

(b) P.scaber: Individuals of all life stages were allowed to defecate in feeding chambers which were placed in the field. No food was offered, therefore the faeces collected were produced from foods

Table 28

Mean calorific values obtained for body and reproductive tissue for all life stages of O.asellus and P.scaber.

Material	n	O.asellus Cal Val (k.cal/g dry wt.)	S.E.	% ash	C.V.
Devel.ovaries	3	5.338 ± 0.090	0.052	2.92	1.69
Early embryos	3	6.507 ± 0.025	0.015	3.37	0.39
Late embryos	3	5.587 ± 0.025	0.014	15.07	0.45
0-3 mm bodies	4	3.944 ± 0.092	0.046	27.53	2.33
3-6 mm bodies	3	2.920 ± 0.229	0.132	29.88	7.83
6-8 mm bodies	3	2.906 ± 0.017	0.010	31.87	0.60
8-11mm ♂ bodies	3	4.187 ± 0.070	0.040	30.68	1.66
8-11mm ♀ bods. + NR	5	4.154 ± 0.119	0.053	29.23	2.86
8-11mm ♀ bods. - R	3	3.720 ± 0.071	0.041	27.91	1.90
8-11mm ♀ bods. - BP	3	3.950 ± 0.088	0.051	33.64	2.24
11-14mm ♂ bods.	38	4.153 ± 0.148	0.085	30.42	3.56
11-14mm ♀ bods. +NR	3	3.913 ± 0.054	0.031	29.60	1.39
11-14mm ♀ bods. - R	3	3.380 ± 0.022	0.013	30.97	0.64
11-14mm ♀ bods. - BP	3	3.170 ± 0.030	0.017	31.66	0.95
> 14mm ♂ bodies	4	2.925 ± 0.047	0.024	34.94	1.61
> 14mm ♀ bods. +NR	4	3.445 ± 0.087	0.043	34.85	2.52
> 14mm ♀ bods. - R	3	3.557 ± 0.040	0.023	28.22	1.13
> 14mm ♀ bods. -BP	3	3.723 ± 0.080	0.046	32.57	2.14

contd....

Table 28 (contd...)

P. scaber

Material	n =	Cal val (k.cal/g dry wt)	S.E.	% ash	C.V.
Devel. ovaries	4	5.431 ± 0.113	0.056	2.47	2.08
Early embryos	3	6.528 ± 0.029	0.016	1.05	0.44
Late embryos	3	5.633 ± 0.028	0.015	13.66	0.46
0-3mm bodies	NO	DATA AVAILABLE			
3-6mm bodies	3	3.367 ± 0.135	0.078	25.37	4.01
6-8mm bodies	4	3.908 ± 0.049	0.025	24.39	1.26
8-11mm ♂ bods.	3	3.523 ± 0.040	0.023	26.26	1.14
8-11mm ♀ bods.+ NR	NO	DATA AVAILABLE			
8-11mm ♀ bods.- R	3	3.347 ± 0.074	0.043	31.81	2.22
8-11mm ♀ bods -BP	3	3.151 ± 0.024	0.014	27.01	0.75
11-14mm ♂ bodies	3	3.523 ± 0.025	0.014	26.61	0.71
11-14mm ♀ bods. + NR	NO	DATA AVAILABLE			
11-14mm ♀ bods - R	3	3.860 ± 0.051	0.029	27.25	1.32
11-14mm ♀ bods - BP	3	3.162 ± 0.087	0.050	30.80	2.75
> 14mm ♂ bods	NO	DATA AVAILABLE			
> 14mm ♀ bods. + NR	NO	DATA AVAILABLE			
> 14mm ♀ bods. - R	3	3.533 ± 0.057	0.033	29.34	1.62
> 14mm ♀ bods. - BP	NO	DATA AVAILABLE			

NR = Undeveloped ovaries

R = Developing ovaries

BP = Brood pouch

eaten in the field. A mean calorific value of 3.909 K.cal/g.dry wt. was obtained.

All the mean values thus obtained for body tissue, reproductive tissue, foods, and faeces were later used to convert the 'best estimates' obtained for I (Chapter 4) and $Y_1 + Y_2$ (Chapter 8) into calories per gram live weight per unit time.

Table 29

The mean calorific values of foods

Food material	n	Cal value K.cal/g.dry wt.	S.E.	% ash	c.v.
Dead S.Chestnut leaves	3	4.313±0.017	0.010	3.90	0.34
Dead Oak leaves	3	4.030±0.057	0.033	3.46	1.40
Dec.Oak leaves	3	4.623±0.040	0.023	3.53	0.87
Dec.Sycamore leaves	4	4.220±0.049	0.025	9.64	1.17
Dead Thistle leaves	3	3.733±0.072	0.042	7.74	1.94
Mean all foods	16	4.186±0.290	0.073	5.91	6.94

Table 30

(a) The Mean calorific values obtained from faeces produced when different life stages of O.asellus were fed on four separate food items.

(b) The mean calorific value of faeces produced by individuals of P.scaber which had been feeding in the field.

Faeces materials		n =	Cal value K.cal/g.dry wt.	S.E.	% ash	c.v.
(a)Dead S. Chestnut faeces	6-8mm	3	4.147±0.021	0.012	3.20	0.50
	11-14mm	3	3.783±0.013	0.007	3.32	0.33
Dead Oak faeces	6-8mm	3	4.257±0.043	0.025	4.43	1.00
	11-14mm	3	4.097±0.060	0.035	6.29	1.47
Decaying Oak faeces	6-8mm	3	4.323±0.010	0.006	17.83	0.22
	11-14mm	3	4.360±0.099	0.057	9.89	2.28
Decaying Sycamore faeces	6-8mm	3	4.327±0.005	0.003	12.10	0.12
	11-14mm	3	4.403±0.017	0.010	12.99	0.39
Mean all faeces		24	4.212±0.197	0.040	8.89	4.68
(b))P.scaber faeces		3	3.909±0.045	0.026	13.91	1.15

Chapter 7

Wet weight/dry weight relationships of body and reproductive tissue

Introduction

Because of the variation of live weight due to varying water content, Engelmann (1966) emphasised the need for weight determinations in energetics studies to be in terms of dry weight. Live weight/dry weight relationships of whole animals have been given by Hubbell, Sikora and Paris (1965) for the isopod Armadillidium vulgare; and Saito (1965) for the isopod Ligidium japonicum. The present study presents data for wet weight/dry weight relationships of all life stages and breeding conditions of the species O.asellus and P.scaber, thus facilitating the conversion to dry weights of the live weight data from growth experiments (Chapter 8).

Methods

Experiments were performed to obtain wet weight/dry weight data for individuals of all life stages during both the non breeding and breeding seasons.

(a) Males and non breeding females.

Individuals of both species representing all life stages were collected in the field. Males were collected at all seasons, but females were only collected when they contained undeveloped ovaries.

Each individual was weighed live, vacuum dried at 60°C, and the dry weight determined.

(b) Breeding females

Breeding females (>16 mg live weight or 7 mm length) of both species were collected in the field during the first week of March 1966. The animals thus collected were transferred to unglazed plant pots which had been prepared in the following manner. Pots were sunk into the ground in the field, the tops being allowed to project 15 cms above soil level. A mixture of soil and gravel was introduced until it filled the pot to soil level. A litter layer was placed on top of the soil to simulate natural conditions. A weatherproof board kept in place by heavy stones sealed each pot. Every three days samples of isopods were dissected to determine the presence of rapidly developing ovaries, early or late embryos, the description of which has already been given by Phillipson and Watson (1965). Several authors have reported the mean duration of embryo development in the brood pouch of isopods:- Pierce (1907); Verhoeff (1939); Howard (1940); Heeley (1941); Hatchett (1947); and Bakker (1956). Knowing the time of formation of a brood pouch for a certain individual, it was therefore possible to estimate when early or late embryos were likely to be present. Early and late embryos were assumed to be present 7 days and 28 days respectively after the formation of a brood pouch. When a brood pouch formed,

the date was noted, and the animal isolated to be later inspected for either early or late embryo determination.

At least 30 individuals of each species representing all life stages were collected for each reproductive stage (developing or ripe ovaries, early embryos, and late embryos), each individual being analysed in the following manner:- The head and hepatopancreas were withdrawn cephalically, and the gut and abdominal segments withdrawn caudally. The legs were cut off with fine scissors. The body remaining was placed ventral surface uppermost in a petri dish containing semi molten wax. When the wax hardened, the ventral surface was removed by means of fine dissecting needles under a binocular microscope. The reproductive material was carefully removed and the number of eggs or embryos counted. Adherant wax was removed from the body remains, and the latter plus the parts previously removed were placed in a 2 x $\frac{1}{2}$" tube. The reproductive material was placed on a small cover slip. Both body remains and reproductive material were vacuum dried at 60°C and separately weighed.

Results

(a) Live weight/dry weight relationships of male and non breeding female bodies.

The percentage water content of each individual was calculated according to the formula $\frac{\text{Live wt} - \text{Dry wt} \times 100}{\text{Live wt.}}$. Mean water contents of 68.99 ± 3.46 and 67.85 ± 2.45 were determined for *O.asellus* and *P.scaber* respectively. Figs. 31 a.b. show that live weight is linearly related to dry weight. The regression was calculated by the least squares method, and the following formulae were calculated:-

$$X = 2.916Y + 5.469 (r = 0.99) \text{ O.asellus}$$

$$X = 2.880Y + 2.220 (r = 0.99) \text{ P.scaber}$$

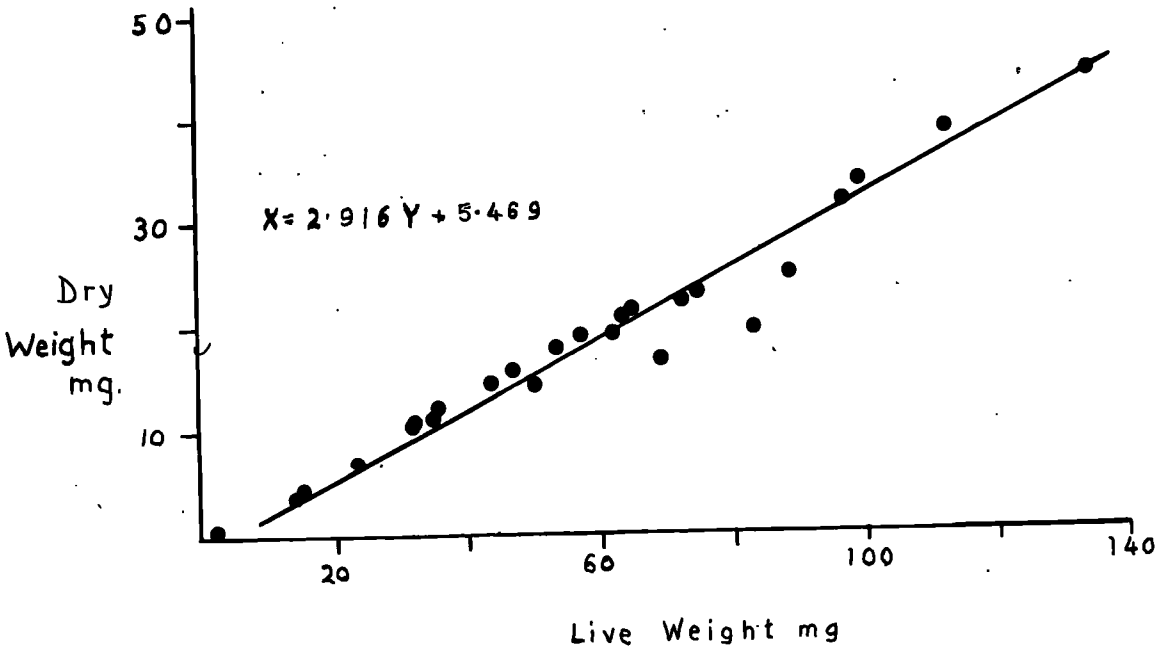
where Y is the dry weight, and X the live weight.

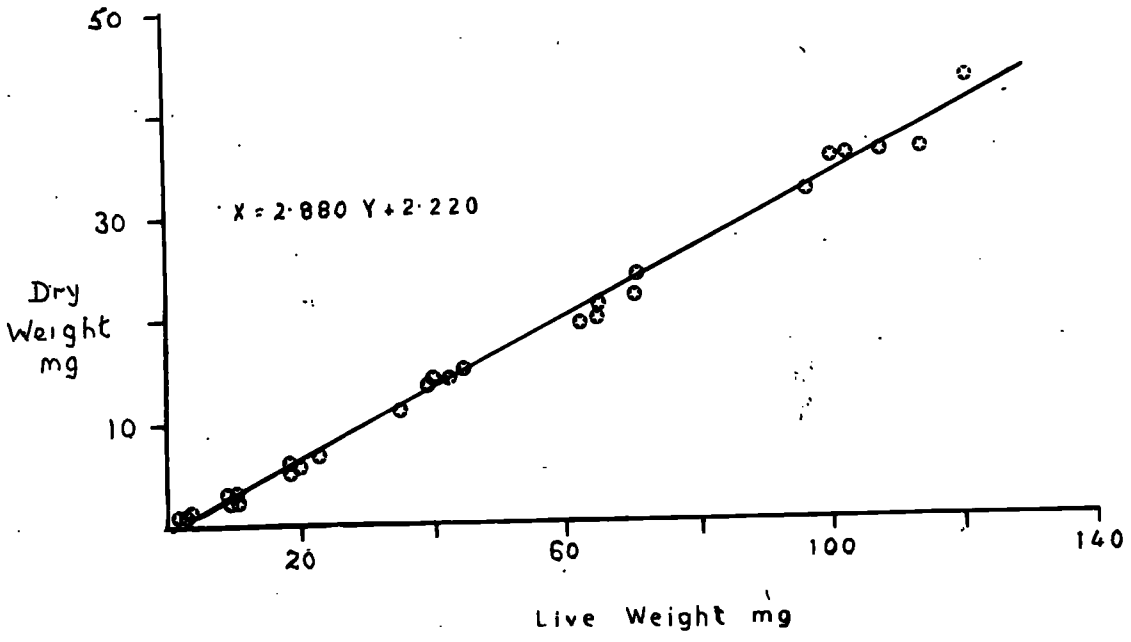
(b) Live weight/dry weight relationships of body tissue to reproductive tissue.

Figs. 32 to 37 illustrate the linear relationships obtained from the analysis of the data collected from the breeding females. Each regression was calculated by the least squares method.

(a) O.asellus:
Regression of live weight upon dry weight. The line is a least squares estimate of the regression.

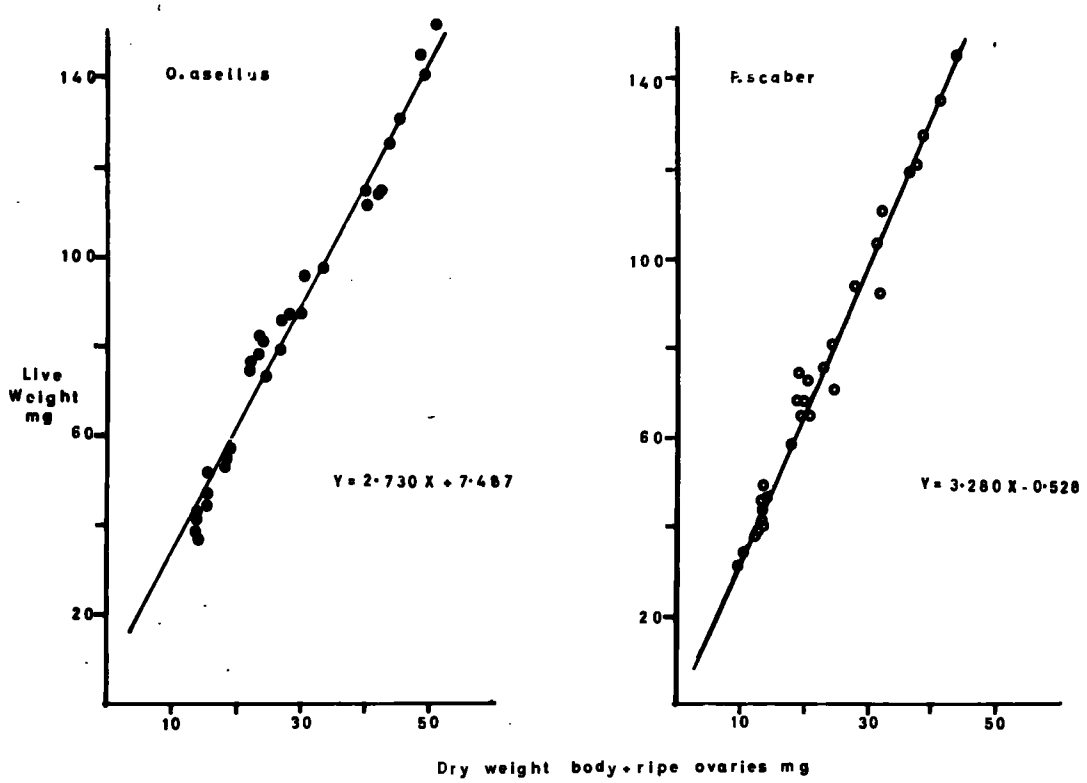
(b) P.scaber:
Regression of live weight upon dry weight. The line is a least squares estimate of the regression

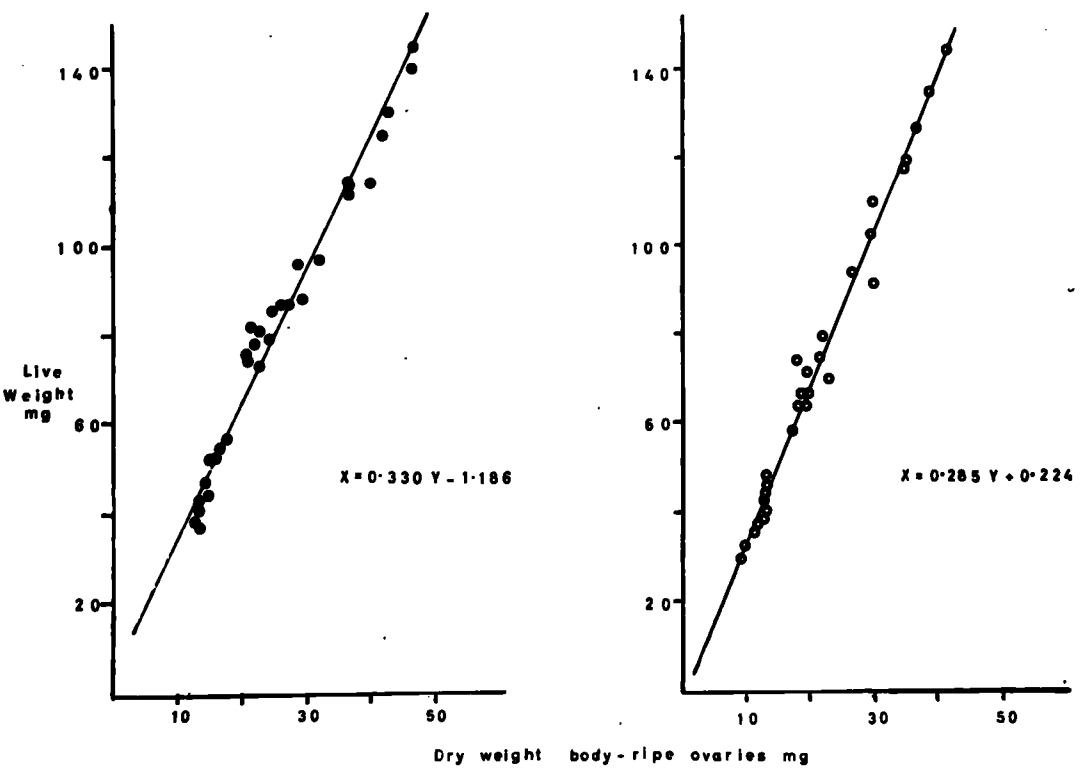

50
30
10
Dry
Weight
mg.
X= 2·916 Y + 5·469
20
60
100
140
Live Weight mg


50
30
10
Dry
Weight
mg
X = 2·880 Y + 2·220
20
60
100
140
Live Weight mg

(a) Regression of total live weight of female upon dry weight of female body + ripe ovaries (developing eggs).

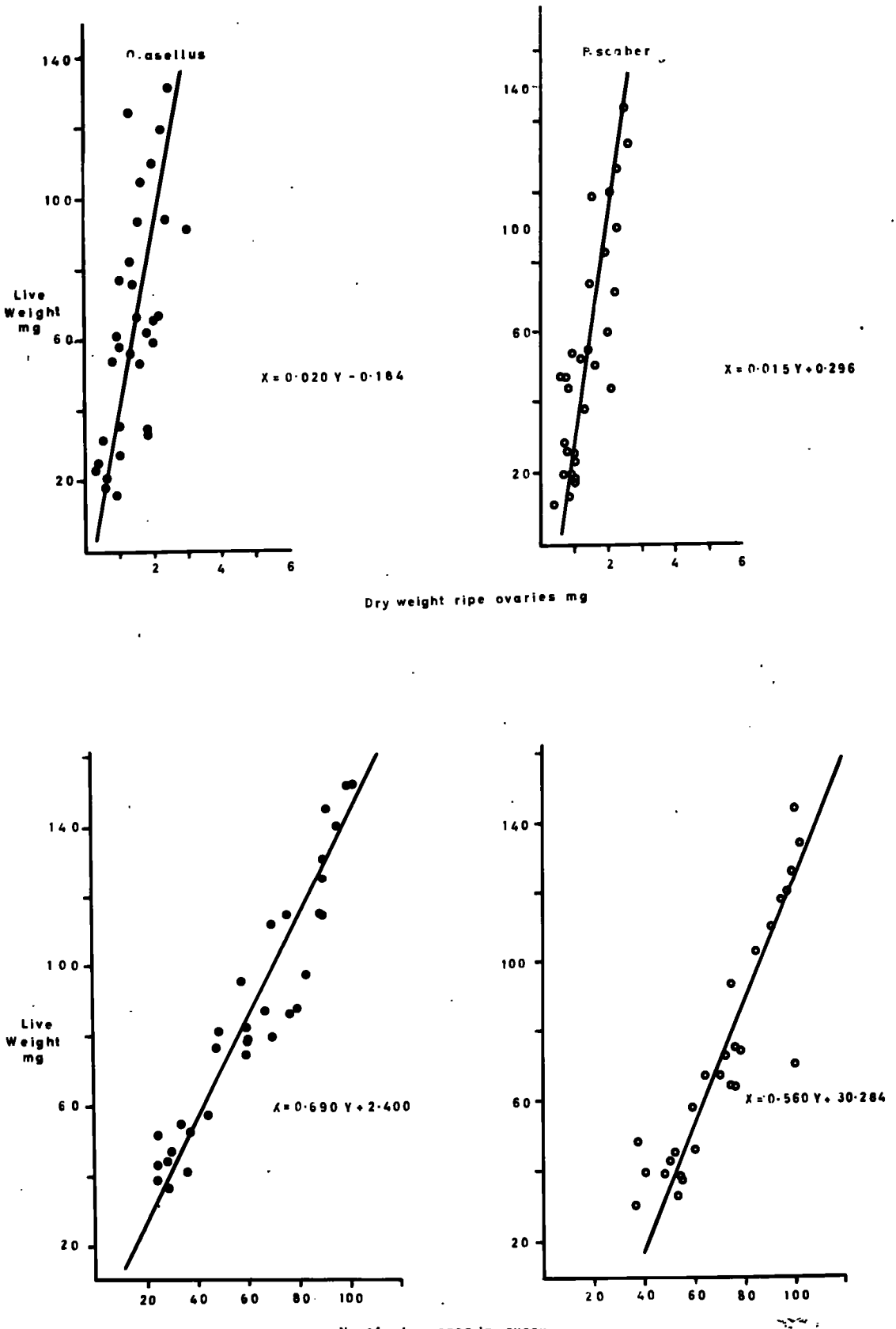
(b) Regression of dry weight of female body - ripe ovaries (developing eggs) upon total live weight of female


O. asellus
F. scaber
Live Weight mg
140
100
60
20
10
30
50
Y = 2·730 X + 7·487
Y = 3·280 X - 0·528
Dry weight body + ripe ovaries mg


Live Weight mg
140
100
60
20
10
30
50
X = 0·330 Y - 1·186
X = 0·285 Y + 0·224
Dry weight body - ripe ovaries mg

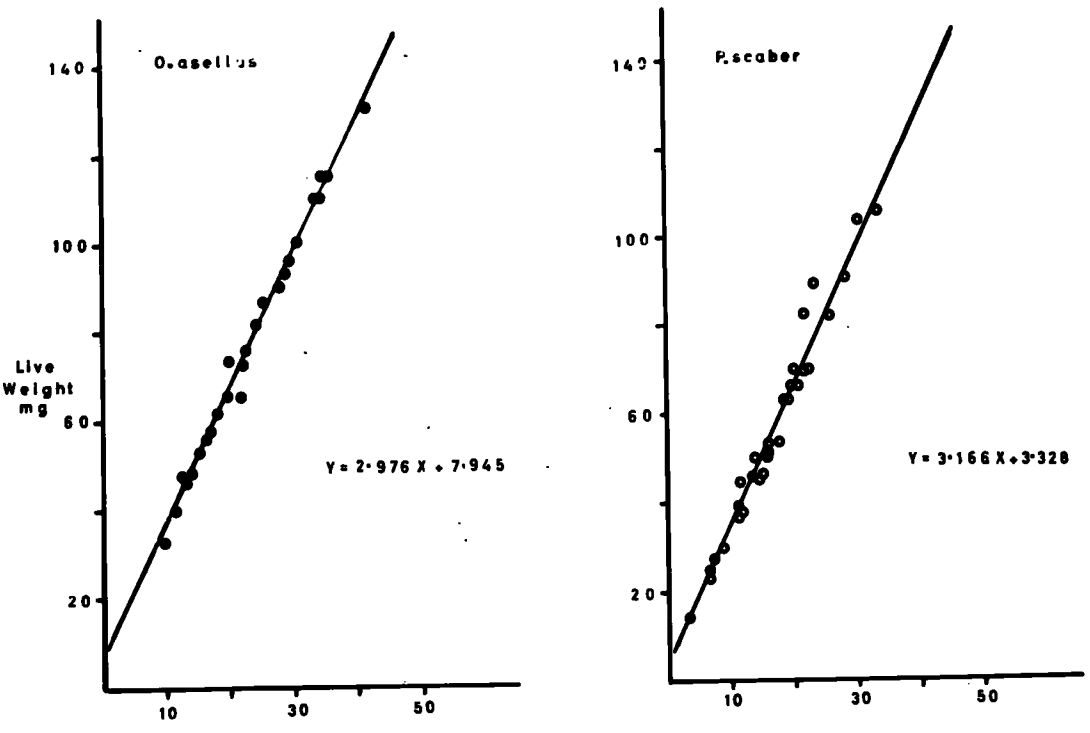
(a) Regression of dry weight of ripe ovaries (developing eggs) upon total live weight of female

(b) Regression of the number of ripe or developing eggs in the ovary upon total live weight of female


O. asellus
P. scaber
Live Weight mg
140
100
60
20
2
4
6
X = 0·020 Y - 0·184
X = 0·015 Y + 0·296
Dry weight ripe ovaries mg
X = 0·690 Y + 2·400
X = 0·560 Y + 30·284
20
40
60
80
100
No. of ripe eggs in ovary

(a) Regression of total live weight of female upon dry weight of female body + early embryos

(b) Regression of dry weight of female body - early embryos upon total live weight of female


O.asellus
P.scaber
Live Weight mg
140
100
60
20
10
30
50
Y = 2·976 X + 7·945
Y = 3·166 X + 3·328
Dry weight body + early embryos mg

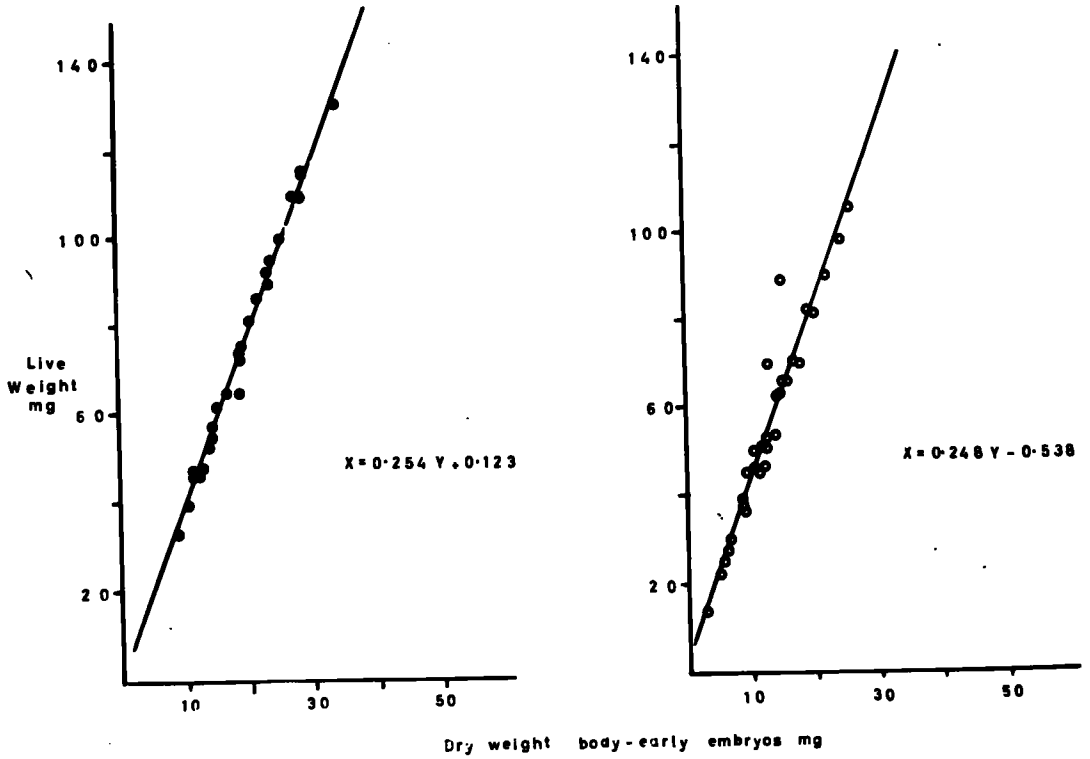
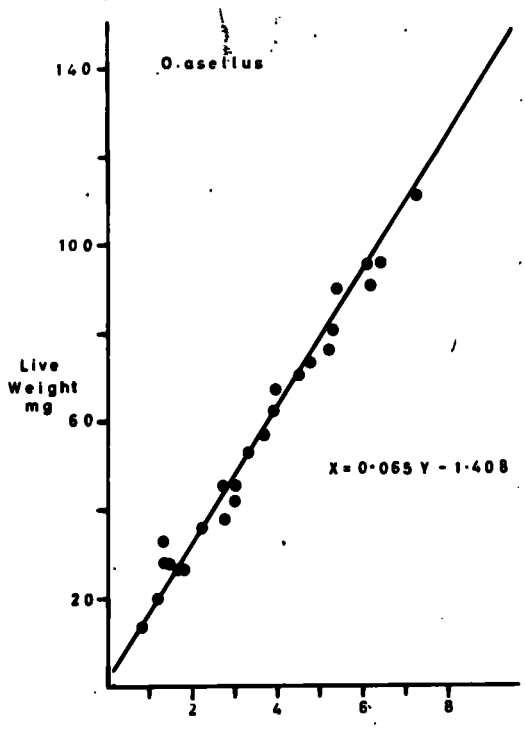
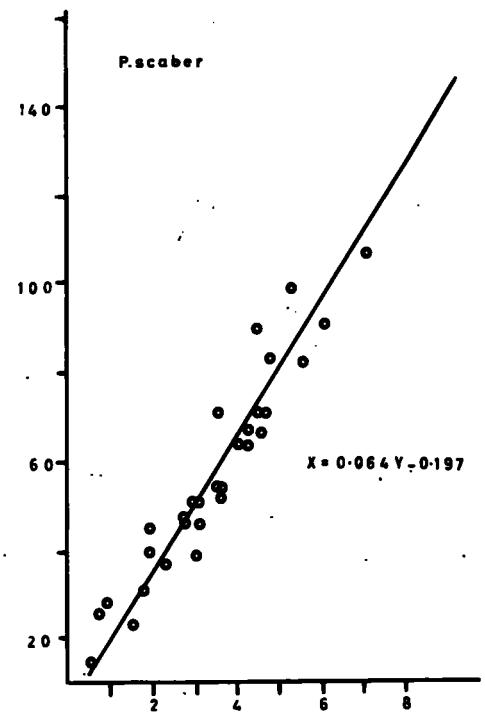

Live Weight mg
140
100
60
20
10
30
50
X = 0·254 Y + 0·123
X = 0·248 Y - 0·538
Dry weight body - early embryos mg

Fig.35.

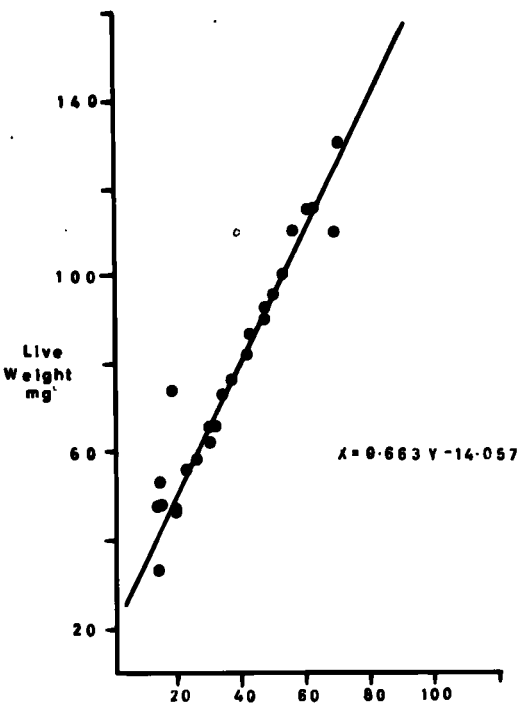
(a) Regression of dry weight of early embryos upon total live weight of female

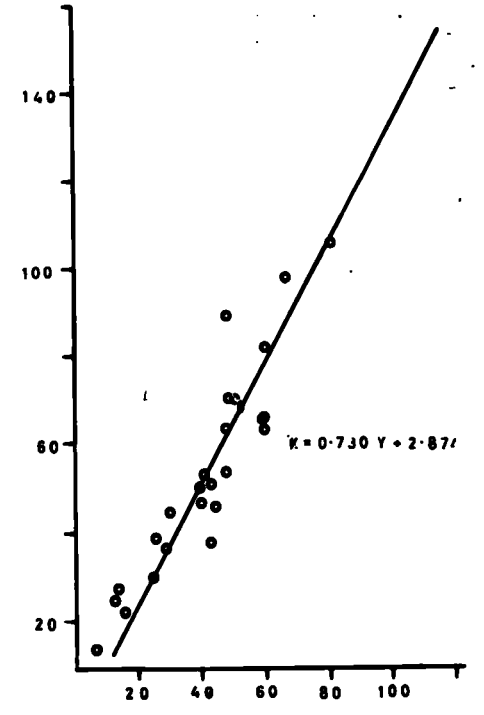
(b) Regression of number of early embryos upon total live weight of female





Dry weight early embryos mg

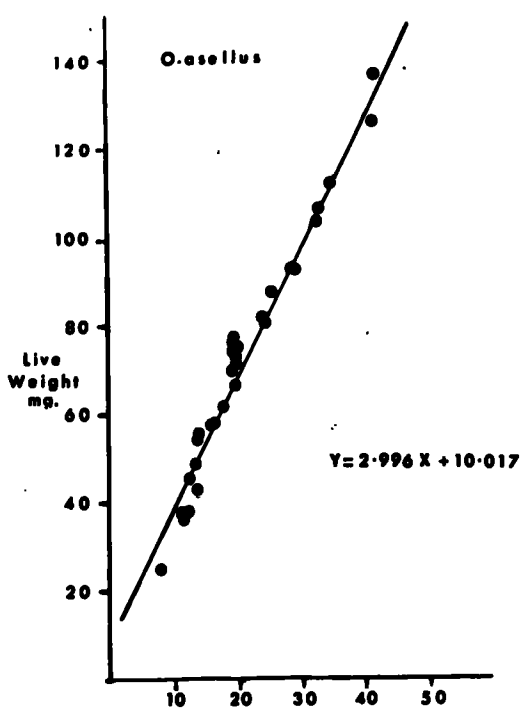


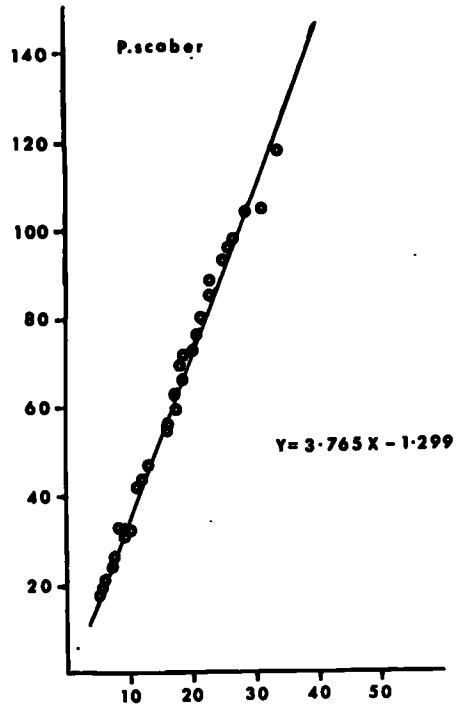


No. of early embryos in brood pouch

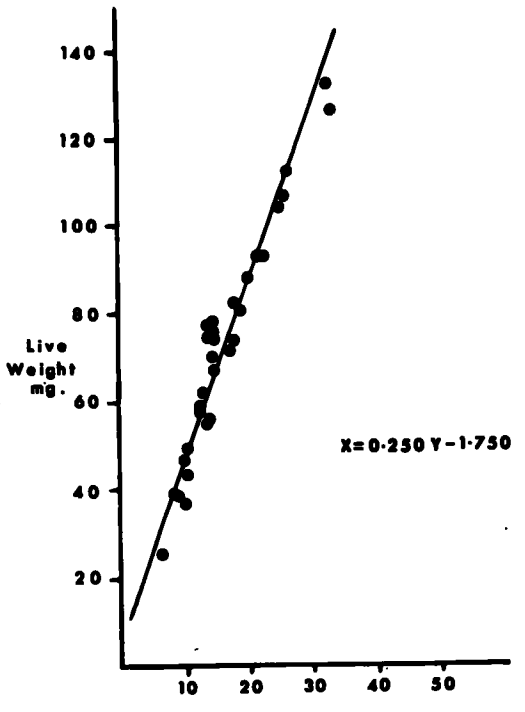
(a) Regression of total live weight of female upon dry weight of female body + late embryos

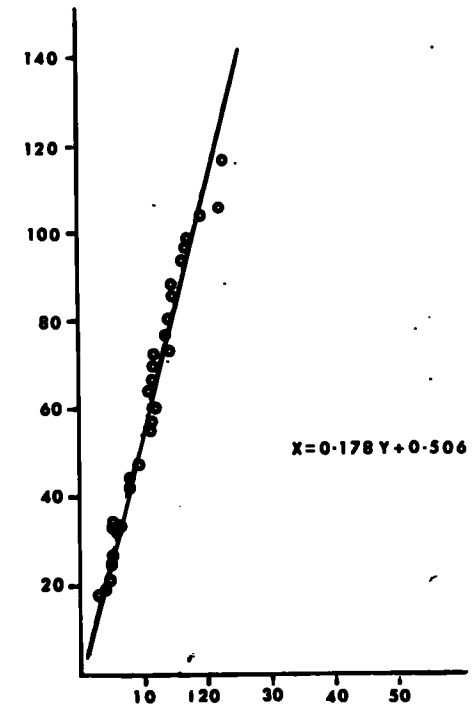
(b) Regression of dry weight of female body - late embryos upon total live weight of female





Dry weight body+late embryos mg.

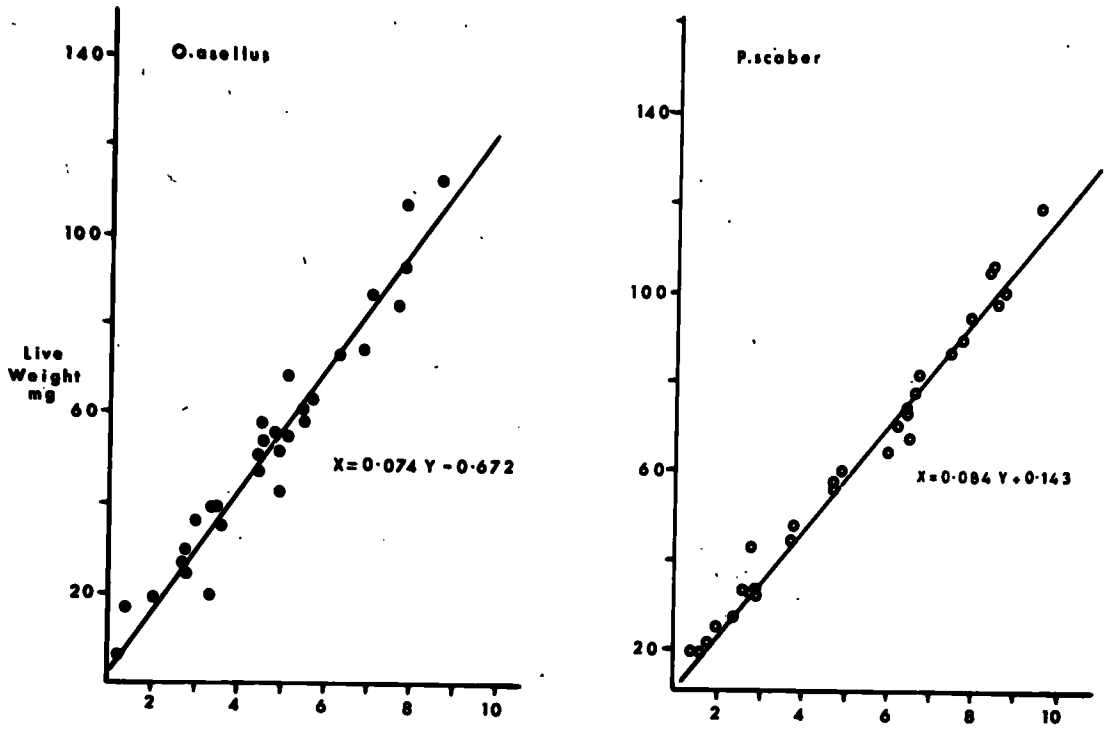


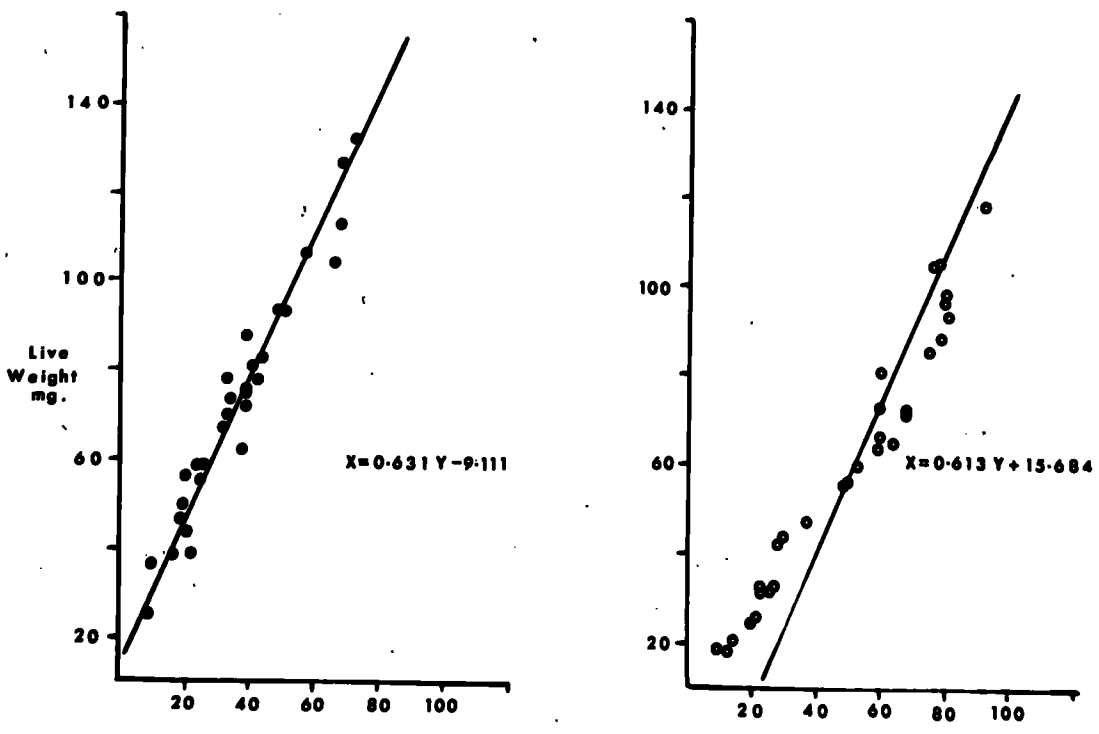


Dry weight body-late embryos mg.

(a) Regression of dry weight of late embryos upon total live weight of female

(b) Regression of number of late embryos upon total live weight of female


O.asellus
P.scaber
Live Weight mg
140
100
60
20
2
4
6
8
10
X=0·074 Y - 0·672
X=0·084 Y + 0·143
Dry weight late embryos mg.


Live Weight mg.
140
100
60
20
20
40
60
80
100
X=0·631 Y - 9·111
X=0·613 Y + 15·684
No. of late embryos in brood pouch

Chapter 8

Measurements of the rates of growth ($Y_1 + Y_2 + Y_3$) of the two isopod species Oniscus asellus and Porcellio scaber.

Introduction

Initially data on growth rates in both O.asellus and P.scaber were hoped for but, owing to an accident in which the P.scaber individuals under observation died, it proved necessary to make use of the data given by Wieser (1965) for this species.

1. Growth of body tissue (Y_1)

(a) O.asellus

Methods

Thirty individuals were collected in August 1965 immediately after liberation from the brood pouch. Each was weighed, measured for length and width, and placed in a 2 x 1" corked tube containing a strip of damp filter paper 4 x 2 cm, which maintained a RH $>$ 95%. A small quantity of litter and log bark was also placed in each tube to provide both food and crevices, in which the animal would shelter. Each tube was numbered with a diamond pencil and left in a safe place in the field. Larger individuals were collected in September 1965. Beyer (1957/58) and Phillipson and Watson (1965) gave evidence to show that one year old O.asellus are approximately 8.0 mm in length or 20 - 25 mg live weight, therefore individuals of this length and live weight were collected and assumed to represent

one year olds. The two other most commonly occurring size groups in the field at the time of collection were (a) 10.5 to 11.5 mm (approximately 60 mg live weight) and (b) 13.0 to 14.0 mm (approximately 90 mg live weight). These two groups were assumed to represent (a) two year olds and (b) three year olds. Twenty five animals of each sex were taken for each age class, and their live weights determined. An identification mark was made on the dorsal surface of each individual by applying a dot of cellulose dope of known colour and position onto the dorsal surface. Males and females from each age class were placed fifteen to a feeding chamber which had been prepared in the usual manner (Chapter 1), but supplied with a liberal quantity of litter, log bark, and flat stones, thereby simulating field conditions. Each feeding chamber was sealed, numbered, and placed in the field along with the tubes containing the 0 year age class (young) individuals. When the young were large enough to be marked without causing them damage, they were introduced into the feeding chambers. Monthly observations over a period of nine months to May 1966 gave details of live weight, length, and width increase. Moulting frequency was difficult to determine as isopods frequently eat their exuviae. Measurement of the 0 year class was effected by placing them under a binocular microscope containing a micrometer eye piece. The 1 to 3 year classes were measured with sliding

calipers which were graduated in 0.1 mm units. The length was taken to be the distance from the anterior extremity of the cephalon to the tip of the telson. An error up to ± 1.0 mm could be expected due to the contraction or expansion of the thoracic segments.

Results

As the experiments were discontinued at the end of May, certain assumptions had to be made in order to estimate annual growth.

(a) 0 year age class: There is evidence from the literature Heeley (1941); Matsakis (1955); Beyer (1957/58); Brereton (1956); Paris and Pitelka (1962); Phillipson and Watson (1965); and Wieser (1965) that isopods grow rapidly from birth to a length of approximately 7 to 8 mm (20-25 mg) at one year old. The mean percentage increase in weight from birth to May was 40% per month (0.55 mg to 9.12 mg); it was calculated that a mean percentage increase from June to August of 30% per month would enable to weight of 20 - 25 mg to be reached.

(b) 1 and 2 year age classes: It was assumed that these age classes would continue to grow from June to September at least as rapidly as the mean rate of growth per month from October to May. The mean percentage weight increase per month during this period October to May was 10% (1 year age class) and 4% (2 year age class), therefore

these two figures were used to estimate growth for the two age classes from June to September.

(c) Female bodily growth: It was impossible to estimate separately the body (i.e. non reproductive) growth of females from April by the method described under (b), because of factors associated with the development of reproductive tissue from the month of April. However, evidence was available to make the assumption that the growth of female body tissue approximated to that of male bodily growth, in that non breeding female body growth up to March followed closely that shown by males. Further, males and females at the end of the breeding season of the same length and width have similar live weights. Section 1 showed that females tend to ingest and assimilate more than males during the breeding season, which suggests that the energy and materials required for the production of reproductive tissue may come from such a source without affecting the rate of bodily growth. Therefore the data obtained for male growth was used to calculate the rate of growth of body tissue (Y_1).

(d) The energy of growth by moult: Wieser (1965) calculated that in three years an isopod moults approximately twenty four times, producing approximately 740 mg dry weight of exuviae. However, evidence from the literature Verhoeff (1919); Hatchett (1947); Patanè (1949); Bakker (1956); and the author's own observations, indicate that

most exuviae are eaten. This evidence, and the repeated failure of combustion of exuviae in the microbomb calorimeter (Chapter 6) suggest that available energy originally in the exuviae is reabsorbed. Energy loss by moult was therefore assumed to be negligible.

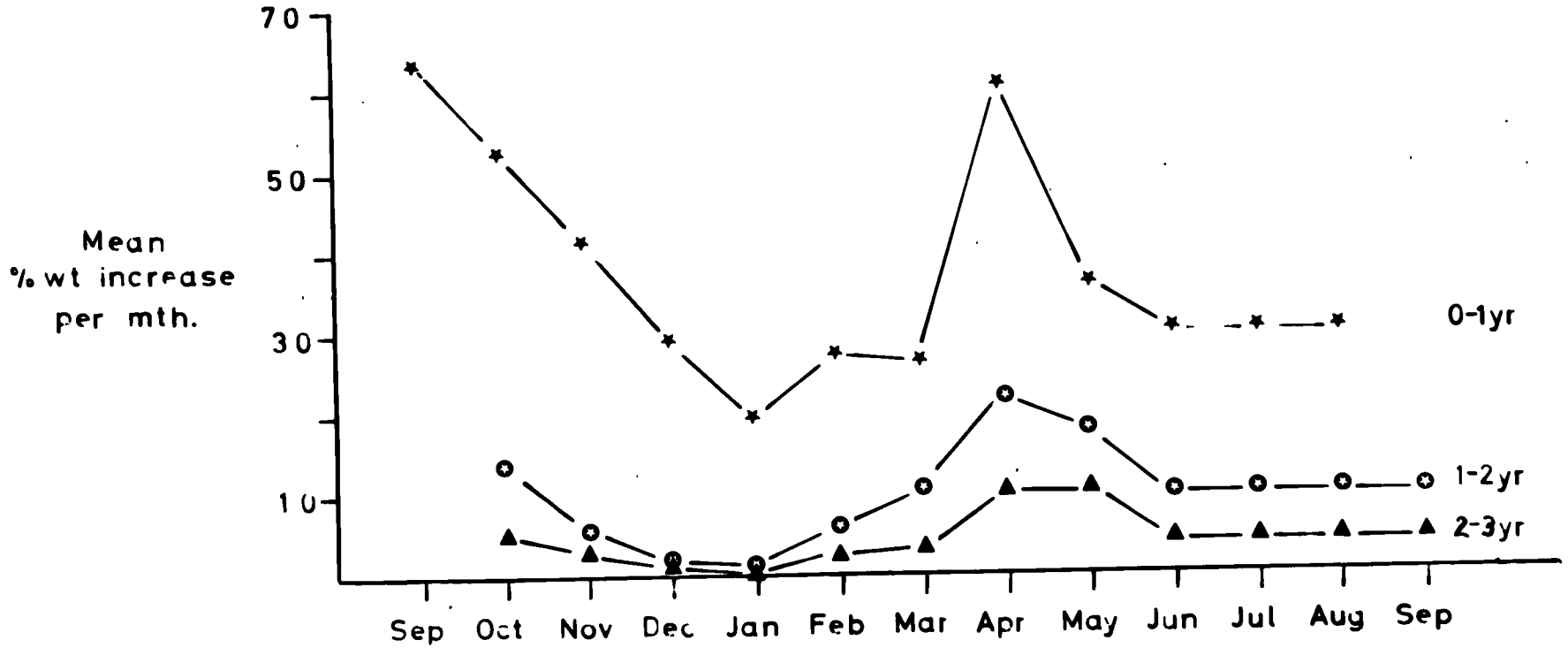
Making the assumptions mentioned it was possible to calculate the rate of growth per month for all age classes. Table 31 shows a summary of the results obtained.

It can be seen that O.asellus grows from a live weight at birth of 0.55 mg (1.7mm) to 19.9mg (7.3mm) during its first year. A live weight of 64.7 mg (11.0mm) is reached at two years old, and a live weight of 93.9 mg (13.1mm) at three years old. No data was obtained for the three year age class owing to the early death of all the animals, a feature assumed to hold for natural conditions. The mean rate of growth per month expressed as the percentage live weight increase per month, and the live weight increase per month (mg) was calculated; Figs.38 and 39 show the results obtained. It is clear that growth is not constant throughout the year, but is affected by season. Fig.40 shows a single logarithmic plot of the mean live weights obtained for each age class for each monthly observation. The growth curve thus obtained for the whole life span is sigmoidal for each age class, illustrating

Fig.36

O.asellus:

% live weight increase per month of all age classes


Mean
% wt increase
per mth.
70
50
30
10
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
0-1yr
1-2yr
2-3yr

O.asellus: Mean live weight increase (mg) per month of all age classes.

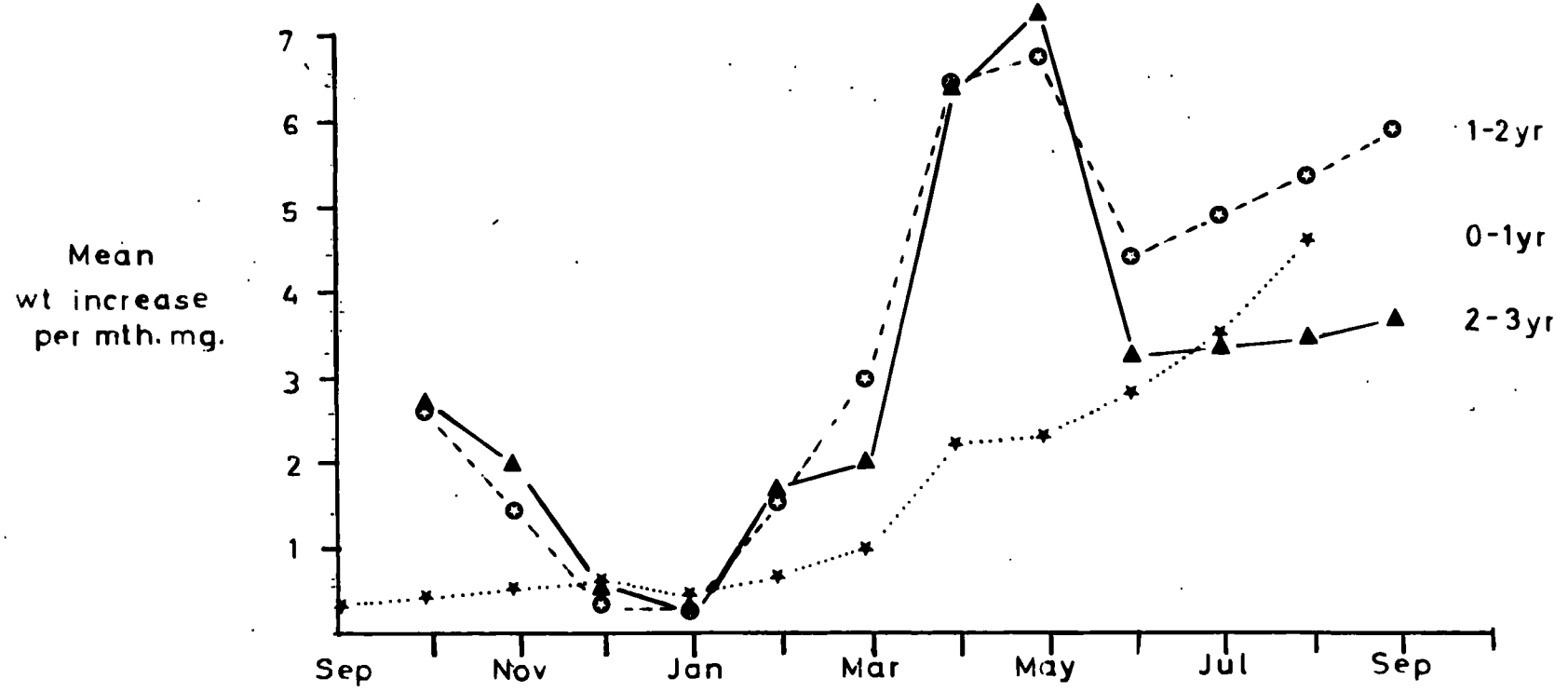

Mean
wt increase
per mth. mg.
7
6
5
4
3
2
1
Sep
Nov
Jan
Mar
May
Jul
Sep
1-2yr
0-1yr
2-3yr

Fig.46

Growth curve of *O.asellus*

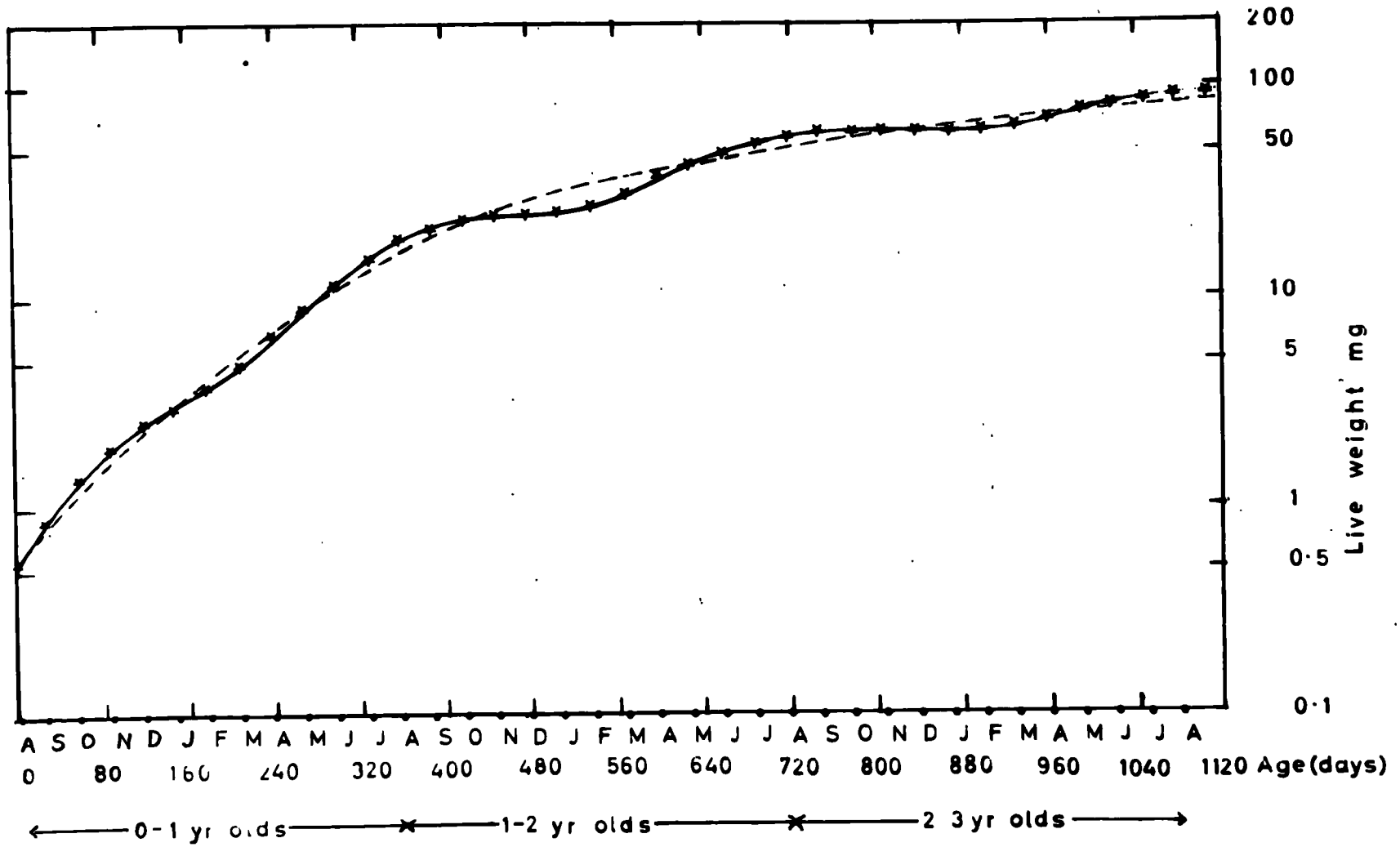

200
100
50
10
5
1
0·5
0·1
Live weight mg
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
0 80 160 240 320 400 480 560 640 720 800 880 960 1040 1120 Age(days)
0-1 yr olds
1-2 yr olds
2 3 yr olds

Table 31

The mean rates of bodily (non reproductive) growth of three age classes of O.asellus

Period of growth	Age class	Initial L.wt (mg)	Initial length (mm)	Final L.wt. (mg)	Final length (mm)	Growth/ mth (mg)	Growth/ mth (mm)
12 mths	0	0.55	1.7	19.9	7.3	1.61	0.47
9 mths (May)				9.12	4.0	0.95	0.44
12 mths	1	2.2	8.0	64.7	11.0	3.63	0.25
8 mths (May)				44.2	10.3	2.81	0.28
12 mths	2	56.9	10.8	93.9	13.1	3.10	0.19
8 mths (May)				80.2	12.2	2.90	0.18

the seasonal effect upon growth. A 'best fit' hyperbolic curve was drawn by eye.

(b) P.scaber

The most comprehensive information in the literature concerning growth of P.scaber was considered to be that presented by Wieser (1965). Wieser's data was drawn from previous data given in the literature, which was given in terms of growth by length per month. Wieser converted these growth rates into terms of mg. live weight according to a previously

determined live weight/length ratio. The data were presented as a single logarithmic plot of live weight against time of release from the brood pouch, the calculations being made according to Bertalanffy's (1951) exponential equation.

Fig.41 shows Wieser's graph in a somewhat modified form. The X coordinate was divided into months as well as days, and the age classes (0,1 and 2) inserted. August was assumed to be time t_o, that is, the month of liberation from the brood pouch. It was possible to read off the mean live weights at birth, one, two, and three years old. P.scaber was estimated to grow from 0.2 mg (1.5 mm approx) to 23.0 mg (7.4 mm approx) in its first year, and reach 61.0 mg (10.5 mm approx) and 90.0 mg (13.0 mm approx) in its second and third years respectively. It would seem that P.scaber grows at the following rates:-

0 year class 1.90 mg/Live wt/mth : 0.50 mm/mth

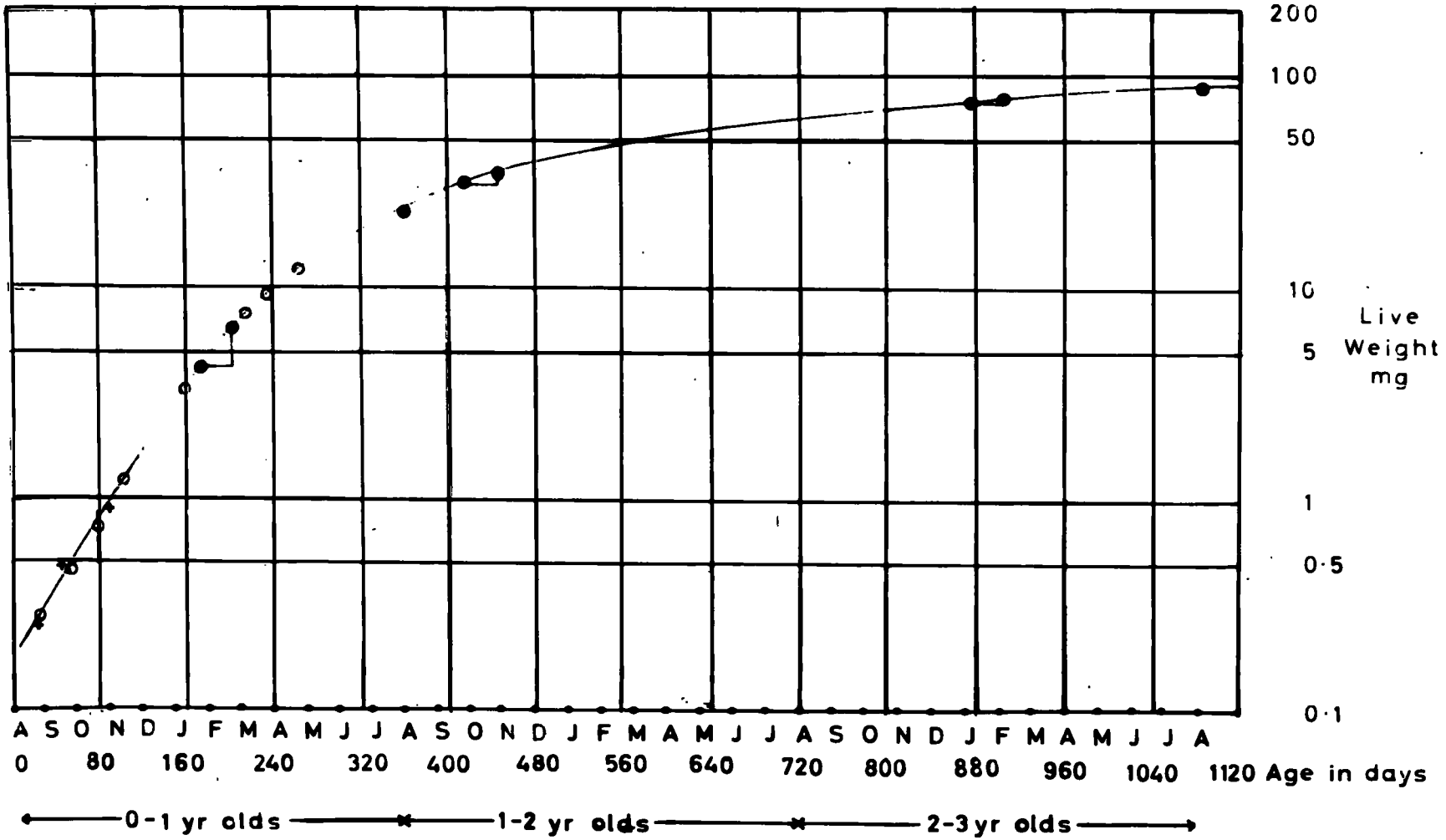
1 year class 3.17mg/Live wt/mth : 0.25 mm/mth

2 year class 2.41 mg/Live wt/mth : 0.21 mm/mth

A comparison of Figs.40 and 41 shows that the O.asellus growth curve approximates to Wieser's estimated growth curve for P.scaber. It is evident that both species have a rapid rate of growth in the first year of life, which becomes less with age. Presumably, after three years body growth is slight.

Fig.41

Growth curve of P.scaber, according to Wieser (1965)


200
100
50
10
5
1
0·5
0·1
Live Weight mg
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
0 80 160 240 320 400 480 560 640 720 800 880 960 1040 1120 Age in days
0-1 yr olds
1-2 yr olds
2-3 yr olds

2. Growth of reproductive tissue (Y_2) of O.asellus and P.scaber.

Respirometry studies (Chapter 5) and the literature indicate that the maximum breeding season months are April to July. In an average year it can be assumed that ovaries develop rapidly during April and May the eggs being deposited in the brood pouch during June, early embryos develop to become late embryos in July and are liberated as young during late July and early August. Knowing this, and assuming that male and female body growth is similar, the mean live weights of mature females (i.e. 1 and 2 year class) as shown by the growth curves during these months, were assumed to be equivalent to the live weights of female body (non reproductive) tissue. Knowing the percentage water content of body tissue, (Chapter 7) 68.99 $\pm$ 3.46% O.asellus and 67.85 $\pm$ 2.45% P.scaber, it was possible to determine the mean dry weights of female body tissue represented by the mean live weights of males. These dry weights may therefore be expressed as the total dry weight of female minus the reproductive tissue. The formulae calculated by the least squares method in the live weight/dry weight experiments (Chapter 7) for live weight of breeding females (Y) on Dry weight females minus reproductive tissue (X) were:-

O.asellus

$Y = 2.995\ X + 4.533$ ($r = 0.99$) Ripe ovaries

$Y = 3.857\ X + 1.060$ ($r = 0.99$) Early embryos

$Y = 3.759\ X + 10.952$ ($r = 0.99$) Late embryos

P.scaber:

$Y = 3.440 X + 0.672$ ($r = 0.99$) Ripe ovaries

$Y = 3.960 X + 3.136$ ($r = 0.99$) Early embryos

$Y = 5.502 X - 1.523$ ($r = 0.99$) Late embryos

The live weight of breeding females was thus calculated. From this live weight it was possible to estimate the dry weight of reproductive tissue present using the formulae presented in Figs.33a (Ripe ovaries), 35a (Early embryos), and 37a (Late embryos), which are:-

O.asellus:

$X = 0.020 Y - 0.184$ ($r = 0.91$) Ripe ovaries

$X = 0.065 Y - 1.408$ ($r = 0.96$) Early embryos

$X = 0.074 Y - 0.672$ ($r = 0.97$) Late embryos

P.scaber:

$X = 0.015 Y + 0.296$ ($r = 0.81$) Ripe ovaries

$X = 0.064 Y - 0.197$ ($r = 0.95$) Early embryos

$X = 0.084 Y + 0.143$ ($r = 0.99$) Late embryos

Table 32 shows the results obtained for both species.

3. Energy of growth

Growth is seen to vary according to season, and the size and breeding condition of isopods. The lack of knowledge of the life stage composition of populations of O.asellus and

Table 32

The dry wts (mg) of reproductive tissues produced by female O.asellus and P.scaber over a life span.

Age Class	April		May		June		July	
	Mean L. Wt.	Mean dry wt. reprod.	Mean L. wt.	Mean dry wt. reprod.	Mean L.wt.	Mean dry wt. reprod.	MeanL. wt.	Mean dry wt.reprod.
O.asellus								
1-2yr	38.5	0.6	44.4	0.7	58.1	2.4	72.8	4.7
2-3yr	74.1	1.3	81.1	1.4	96.7	4.9	115.4	7.9
P.scaber								
1-2yr	57.7	1.2	61.2	1.2	71.9	4.7	104.7	8.9
2-3yr	95.1	1.7	97.5	1.8	117.3	7.3	138.9	11.8

Table 33

P.scaber.Calculation of the 'best estimate' of body growth (Y_1)

0-1 yr old	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Total
Mean wt. increase (mg)	0.13	0.24	0.44	0.70	1.20	1.70	2.60	2.40	3.10	3.30	4.00	3.00	22.81 A
Mean live wt.(mg)	0.32	0.56	1.00	1.70	2.90	4.60	7.20	9.60	12.70	16.00	20.00	23.00	99.58 a

1-2 yr old	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Total
Mean wt. increase (mg)	4.2	4.2	4.5	3.5	3.0	3.5	2.2	2.8	3.0	3.0	2.0	3.0	39.0 B
Mean live wt.(mg)	27.2	31.5	35.0	38.5	41.5	45.0	47.2	50.0	53.0	56.0	58.0	61.0	543.9 b

2-3 yr old	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Total
Mean wt. increase (mg)	0.5	3.5	2.0	3.0	2.0	3.0	3.0	4.0	2.0	2.0	1.5	2.5	29.0 C
Mean live wt.(mg)	61.5	65.0	67.0	70.0	72.0	75.0	78.0	82.0	84.0	86.0	87.5	90.0	918.0 c

$$\text{Mean L.wt.} = \frac{a + b + c}{36} = 43.37 \text{ mg}$$

$$\text{Mean wt. increase/mth} = \frac{A + B + C}{36} = 2.523 \text{ mg}$$

Cal. val ♂ bodies = 3.488; ♀ bodies = 3.475 k.cal/g.dry wt.

'Best estimate' ♂ body growth = 2.082 cal/g. live wt/24h.

'Best estimate' ♀ body growth = 2.075 cal/g. live wt/24h.

∴'Best estimate' body growth = $\frac{♂ + ♀}{2}$ = 2.079 cal/g. live wt/24h.

∴A 43.37 mg animal increases wt. by 2.523 mg live wt/mth.

A 1000 mg animal increases wt. by 58.17 mg live wt/mth

= 0.597 mg dry wt/24h.

Table 34

O.asellus. Calculation of the 'best estimate' of body growth (Y_1)

0-1 yr old	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Total
Mean weight increase (mg)	0.345	0.465	0.564	0.639	0.484	0.676	1.091	2.238	2.315	2.838	3.523	4.592	19.770 A
Total live wt. (mg)	23.270	36.500	46.069	47.556	46.890	72.808	78.768	91.793	109.476	155.493	201.292	258.700	1168.615 a n=207

1-2 yr old	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Total
Mean weight increase (mg)	2.633	1.438	0.367	0.338	1.558	3.030	6.464	6.750	4.415	4.875	5.350	5.880	43.098 B
Total live wt. (mg)	593.7	605.4	613.6	624.0	715.9	734.2	844.8	929.1	923.4	1016.5	1119.1	1229.3	9951.0 b n=264

2-3 yr old													
Mean weight increse (mg)	2.739	2.011	0.528	0.288	1.720	2.080	6.433	7.273	3.227	3.340	3.460	3.607	36.706 C
Total live wt. (mg)	1072.8	1108.8	1117.8	1060.8	969.0	999.0	1101.0	1203.0	1252.5	1302.0	1356.6	1408.7	13952.0 c n=191

Mean L.wt. $= \frac{a + b + c}{3} = 38.8$ mg

Mean wt. increase/mth $= \frac{A + B + C}{36} = 2.766$ mg

∴ A 38.8 mg animal increases wt by 2.766 mg live wt/mth.

A 1000 mg " " " "71.29 " " "

$= 0.756$ mg dry wt/24h.

Cal. val. ♂ bodies = 3.622; ♀ bodies 3.567 k.cal/g.dry wt.

'Best estimate' ♂ body growth = 2.738 cal/g.live wt/24h.

'best estimate ♀ body growth = 2.697 cal/g.live wt/24h.

∴ 'Best estimate' body growth $= \frac{♂ + ♀}{2} = 2.718$ cal/g.live wt/24h.

Table 35

O.asellus. The calculation of the 'best estimate' of growth of reproductive tissue (Y_2) over a life span. All weights are means (mg).

Age class

0 -1yr. No reproduction

1 -2yr 53.47 mg live wt of ♀ produces 4.7 mg dry wt of late embryos

2 -3yr 91.84 mg live wt of ♀ produces 7.9 mg dry wt of late embryos

(a)

1 -2yr: $\frac{53.47}{12} = 4.456$ mg l.wt; $\frac{4.7}{12}$ = 0.392 mg dry wt.

4.456 mg live wt produces 0.392 mg dry wt late embryos/mth.

1 gram live wt " 87.971 mg " " " " "

= 2.903 mg " " " " /24h.

= 16.219 cal/24h

(b)

2 - 3yr: 7.653 mg live wt of ♀ produces 0.658 mg d.wt late embryos/mth.

1 gram live wt of ♀ " 85.979 mg " " " " "

= 2.838 mg " " " " /24h.

= 15.856 cal/24h

Thus 3g ♀ gives 32.075 cal/24h

1g ♀ gives 10.692 cal/24h.

Assuming a 1:1 sex ratio, 1g live wt of animal gives:-

$\frac{10.692}{2} = 5.347$ cal/24h.

∴ 'Best estimate' Y_2 = 5.347 cal/g live wt of O.asellus/24h.

Table 36

P.scaber. The calculation of the 'best estimate' of growth of reproductive tissue (Y_2) over a life span. All weights are means (mg).

Age class

0 - 1 yr No reproduction

1 - 2 yr 75.12 mg live wt of ♀ produces 8.9 mg dry wt of late embryos

2 - 3 yr 112.2 mg live wt of ♀ produces 11.8 mg dry wt.of late embryos

(a)

1 - 2 yr: $\frac{75.12}{12}$ = 6.26 mg live wt; $\frac{8.9}{12}$ = 0.742 mg. dry wt.

∴ 6.26 mg live wt produces 0.742 mg dry wt. late embryos/mth.

1 gram live wt. " 118.530 mg dry " " " "

= 3.912 mg " " " " /24h.

= 22.036 cal/24h.

(b)

2 - 3 yr: 9.350 mg live wt. produces 0.983 mg dry wt.late embryos/mth.

1 gram live wt. " 105.134 mg " " " " "

= 3.470 mg " " " " /24h.

= 21.067 cal/24h.

Thus 3g live weight ♀ gives 41.103 cal/24h

1g " " ♀ " 14.368 cal/24h

Assuming a 1:1 sex ratio, 1g live wt. of animal gives:

$$\frac{14.368}{2} = 7.184 \text{ cal/24h}$$

∴ 'Best estimate' of Y_2 = 7.184 cal/G.live wt P.scaber/24h.

P.scaber makes it impossible to calculate directly the amount of the energy assimilated which is used for growth ($Y_1 + Y_2 + Y_3$) per unit area of habitat per unit time. Therefore the 'best estimate' technique is again permissable. Tables 33 and 34 show the method employed in calculating a 'best estimate' of body growth (Y_1) over the life span of P.scaber and O.asellus. Assuming a 1:1 sex ratio the 'best estimate' was calculated as $\frac{\text{Male + Female body growth}}{2}$ giving a result of 2.178 cal /g. live wt of O.asellus/24h and 2.079 cal/g. live wt of P.scaber/24h. Tables 35 and 36 show the methods employed in calculating the 'best estimate' of growth of reproductive tissue 'Y_2) over the life span of each of the two species, using the data given in Table 32. Assuming a 1:1 sex ratio the 'best estimate' of reproductive growth (Y_2) was 5.431 cal/g.live wt of O.asellus/24h, and 7.184 cal/g.live wt. of P.scaber/24h.

The 'best estimate' of $Y_1 + Y_2$ (energy of growth) was therefore 8.149 cal/g.live wt of O.asellus/24h, and 9.263 cal/g.live wt of P.scaber/24h.

SECTION 4

The evaluation of the energy flow equation $I = R + Y_1 + Y_2 + Y_3$ for O.asellus and P.scaber.

Introduction

The 'best estimates' given for each of the parameters $I = R + Y_1 + Y_2$ in the previous sections made possible the calculation of the energy budgets of O.asellus and P.scaber, and should facilitate the calculation, from biomass data, of the annual amount of litter breakdown and energy flow per unit area of habitat per unit time by any population of O.asellus ar P.scaber. The data for individual age classes given by Saito (1965) for Ligidium japonicum were used to compare the 'best estimate' technique as applied to O.asellus and P.scaber.

Energy budgets of O.asellus and P.scaber.

The 'best estimates' (cal/g.live wt/24h) given in the previous sections were multiplied by 365 thus enabling the data to be presented in terms of k.cal/g.live wt/annum. In addition the 'best estimates' of ingestion, egestion and assimilation were expressed as g.dry wt/g. live wt/annum, thus enabling the calculation of litter breakdown in terms of dry weight. Tables 37 and 38 show the energy budgets of O.asellus and P.scaber respectively.

The 'best estimates' of litter breakdown.

(a) O.asellus

Table 37 shows that 1g live weight of O.asellus ingests 11.18 g.

dry weight (46.789 k.cal) of litter per annum, of which 3.33 g.dry weight (13.749 k.cal) are assimilated, and 7.85 g. dry weight (33.040 k.cal) are made available as faeces for other heterotrophs in the ecosystem.

(b) P.scaber

Table 38 shows that 1g live weight of P.scaber ingests 9.04 g. dry weight (37.855 k.cal) of litter per annum, of which 2.72 g. dry weight (13.125 k.cal) are assimilated and 6.32 g. dry weight (24.730 k.cal) are made available as faeces to heterotrophs.

The 'best estimates' of energy flow

Tables 37 and 38 provide data which enable the evaluation of the equation:-

$$I = R + Y_1 + Y_2 + Y_3 \text{ (not measured)}$$

Thus for 1g live wt. of O.asellus:-

$$13.749 = 9.253 + 0.992 + 1.952 \quad \text{k.cal/annum}$$

and for 1g live wt. of P.scaber:-

$$13.125 = 7.639 + 0.759 + 2.622 \quad \text{k.cal/annum}$$

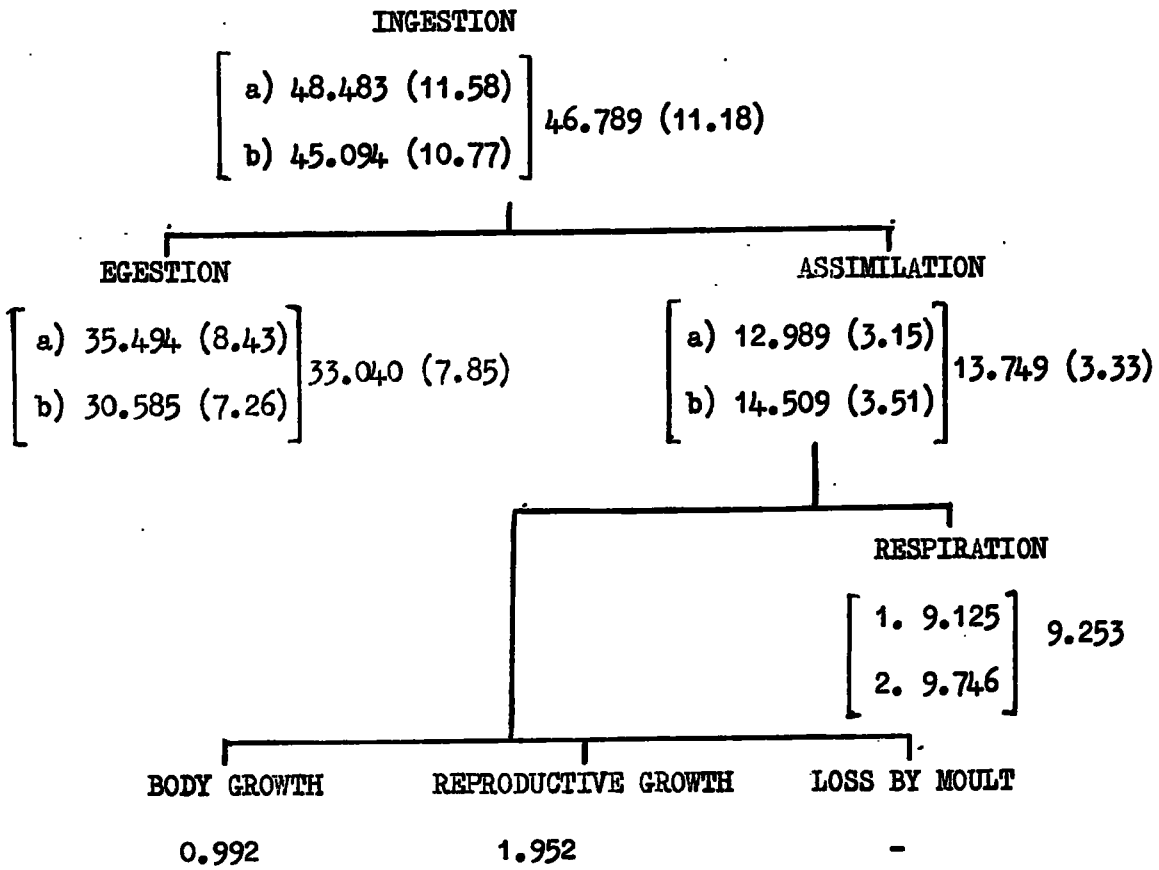
For the parameters actually measured ($R + Y_1 + Y_2$) the energy flow equation shows an error of 11.1% O.asellus and 16.0% P.scaber. Thus the 'best estimates' measured for the contribution of these isopods to total energy flow in a woodland ecosystem are:-

O.asellus: 13.749 or 12.228 k.cal/g. live wt/annum

P.scaber: 14.125 or 11.020 k.cal/g. live wt/annum.

Table 37

The energy budget ('best estimates') of 1g. live weight of *O.asellus*. k.cal/annum, non bracketed; g.dry wt/annum, bracketed.



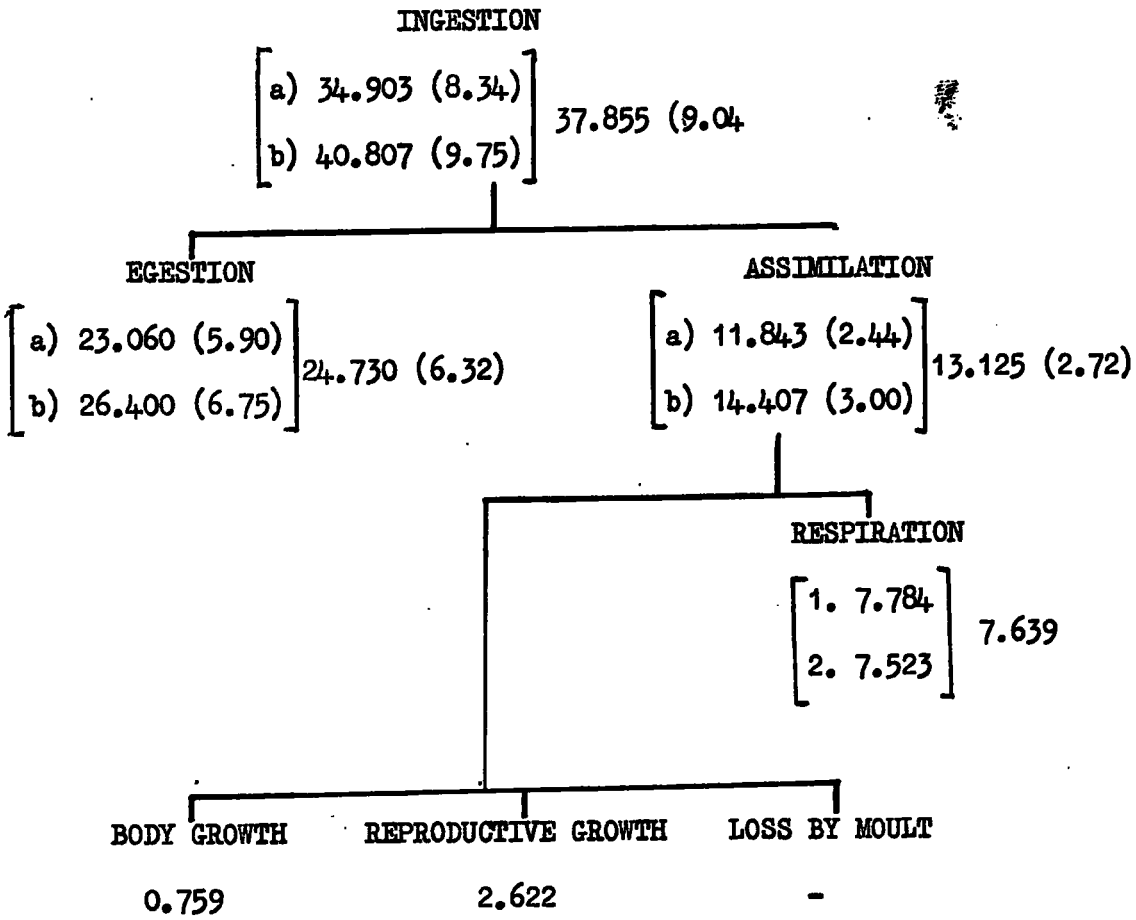
a) = Data from winter faeces production experiments

b) = Data from summer assimilation experiments

1 & 2 = Data from the two methods given

Table 38

The energy budget ('best estimates') of 1g. live weight of P.scaber. k.cal/annum, non bracketed; g. dry wt/annum, bracketed.



a) = Data from winter faeces production experiments

b) = Data from summer assimilation experiments

1 & 2= Data from the two methods given

Consideration of the results obtained for litter breakdown and energy flow indicates that of the food ingested 6.3% (O.asellus) 8.9% (P.scaber) is used for body and reproductive growth, 27.2% (O.asellus) 29.3% (P.scaber) is assimilated, and 72.8% (O.asellus) 70.7% (P.scaber) is returned to the ecosystem as faeces. Of the food assimilated, 67.3% (O.asellus) 58.2% (P.scaber) is respired, and 21.4% (O.asellus) 25.8% (P.scaber) is used for growth and reproduction.

A comparison of two methods of studying energy flow.

(a) Application of energy flow data obtained for individual size classes to populations where the size class composition is known.
(b) Employment of the 'best estimate' technique to populations where only biomass data is available.

Method (a) was pursued by Saito (1965), who studied the energy flow of the isopod Ligidium japonicum in a warm temperate woodland ecosystem. Saito was able to distinguish age classes, and the number of eggs produced by the population. A survival curve for the natural population, derived from the number of eggs produced, was drawn on the basis of population density and monthly age structure; this survival curve coincided with the Type II curve of Deevey (1947). Thus the mortality from one breeding season to the next was assumed to be constant. The mean growth rate of an individual per unit time was calculated as the difference between consecutive mean weights

for the year group in each sample. The decrease in numbers per unit time was calculated from the survival curve. Thus Saito was able to measure population growth and estimate changes in population size. Measurement of respiration rate at field temperatures, and the determination of calorific values of L.japonicum material made possible the calculation of energy flow through the population in terms of k.cal/m^2/annum.

Method (b) was, as already shown, pursued in the present study.

Using the data presented in Saito's paper, the 'best estimates' of L.japonicum were calculated, and compared with those obtained for O.asellus and P.scaber.

	I	= R	+ Y_1	+ Y_2	
O.asellus	13.749	= 9.253	+ 0.992	+ 1.952	k.cal/g.live wt/ann.
P.scaber	13.125	= 7.639	+ 0.759	+ 2.622	" " "
L.japonicum	(11.144)	= 9.400	+ 0.744	+ 0.970	" " "

Saito did not measure I therefore this 'best estimate' was calculated as the sum of R + Y_1 + Y_2. If the 'best estimate' technique is accurate, it should be possible to calculate the energy flow of L.japonicum in k.cal/m^2/annum by multiplying R + Y_1 + Y_2 by Saito's mean biomass figure of 1.444 g. live weight/m^2/annum, and arrive at the figure of 19.9 k.cal/m^2/annum calculated by Saito for L.japonicum.

Multiplication of the 'best estimates' given above for L. japonicum by 1.444 gives:-

I	=	R	+	Y_1	+	Y_2
(16.092)	=	13.574	+	1.118	+	1.40 k.cal/m^2/annum

It is apparent that the 'best estimate' technique underestimates in this case by 17.5%.

Discussion

Engelmann (1966) has given a comprehensive list of the parameters that should be studied for a complete synthesis of energy flow both through and within communities. The two major areas of investigation are population censusing and bioenergetic studies. It is difficult for one worker to measure accurately all of the required parameters, as lack of time is frequently the major difficulty facing any single worker. In the present study a decision had to be made as to whether population censusing or bioenergetic studies should receive the greater emphasis, for it was evident from the literature that a compromise between these two major areas of investigation led to various parameters being either neglected or assumed. Time was limited in the present study and the decision was taken to obtain bioenergetic data in the most accurate manner possible during the time available.

Of the terrestrial invertebrates already studied from a bioenergetic standpoint most showed a relatively simple life history. In the present study, animals with more complex life histories, the isppods O.asellus and P.scaber were chosen. These animals reproduce more than once in a lifetime, and show an overlap of generations, thereby providing an excellent opportunity for the evaluation of methodological procedures, proven for animals with annual life cycles, when applied to animals with a more complex life history.

The quantification of the equations:- Energy of ingestion = Energy of assimilation + Energy of egestion, and Energy of assimilation = Respiratory energy loss + Energy of bodily growth and reproduction, provided a considerable body of information suitable for use with detailed population analyses, or by employment of the 'best estimates' with simple biomass data.

Macfadyen (1961, 1963); Phillipson (1962,1963); and Phillipson and Watson (1965), amongst others have emphasised that biological processes vary with age, physiological condition, and season. Clearly, if one is to approach a reasonably accurate measurement of the metabolic parameters involved in a bioenergetic study, then measurements should be made as far as is possible for all life stages at all seasons, and under as near natural conditions as possible. The separate measurements of the parameters (a) ingestion, egestion, and assimilation to determine I; (b) respiratory energy loss, R; and (c) bodily growth and reproduction, $Y_1 + Y_2$, in this study served to emphasise these points, as variations with life stage, season and physiological condition of the animals were shown in all the measurements.

The food preference experiments proved useful in that they made possible the proffering of foods most likely to be eaten in the field, to animals subjected to assimilation experiments. The preliminary experiments indicated that both species would attempt fresh plant

material, as does A.vulgare Paris and Sikora (1965). Paris and Sikora (1965) suggested A.vulgare may function to a significant extent as a grazing herbivore as well as a scavenger in grassland. The present study showed that O.asellus and P.scaber did not prefer fresh plant material, thus it seems that such foods constitute only an insignificant part of the diet of these two species. Macfadyen (1961) emphasised the need for more food preference studies on soil invertebrates so that 'bottle-necks' in the energy flow picture might be recognised. The present study presents such data for the isopods O.asellus and P.scaber, and it is evident that preference does not change with season, as most of the preferred foods are available all the year round. The large variations in ingestion, egestion and assimilation, shown both within and between different size groups, not only re-emphasise the necessity to study individuals of all life stages, but also indicates the necessity for a large number of replicate experiments for each size group, in order that reasonably accurate estimations of these parameters may be obtained. Earlier work suggested that animals feeding on decaying litter have low assimilation efficiencies: Van der Drift (1951); Gere (1956); and Dunger (1958), among others. Most of these authors did not determine the assimilation efficiency of all life stages, in the main adults were studied. Relatively few animals were used, and no

'marker food' or similar technique was employed. The present study shows that if few animals are used in assimilation experiments, and if these are mainly adult forms, it is possible that low assimilation efficiencies will result. For example Phillipson (1960b) and the present study of P.scaber (Table 17) show that assimilation efficiency tends to decrease with size. Recently Wieser (1965) has reported the assimilation efficiency of P.scaber over all life stages, and quotes an average assimilation efficiency of 25%. This figure is in close agreement with that of 27.2% O.asellus, and 29.3% P.scaber, given in Chapter 3. The present study suggests that the technique whereby re-wetted dessicator dried preferred materials are offered as food under near natural conditions, along with a marker food, is highly suitable for the estimation of the assimilation efficiency of herbivores. However, Hubbell, Sikora and Paris (1965) working with Armadilliduim vulgare demonstrated the feasibility of using radioactive tracers to measure assimilation efficiency under field conditions, but indicated that experimental analysis of the parameters involved in determining radionuclide turnover may be essential in such studies.

The high assimilation and ingestion rates encountered during the summer experiments for the 8 - 11 mm female size group of both O.asellus and P.scaber is interesting in that it coincides with the change in

respiratory rate at this size (7 to 8 mm). The high rates obtained for ingestion and assimilation in this size group, as with respiration, can be attributed to the attainment of sexual maturity.

The peak breeding periods of O.asellus and P.scaber determined in the respirometry experiments agree with those given by Heeley (1941) and Wieser (1963), but in neither species was a second brood produced, as suggested by Heeley (1941). However, P.scaber ovaries were developing rapidly in September, therefore this species was possibly attempting to produce a second brood, but was probably prevented from doing so by the adverse climatic conditions in October, as Beyer (1957/58) has suggested that low temperature in particular suppresses brood pouch formation. The variation of respiratory rate with size, physiological condition, and season, as shown by O.asellus and P.scaber, strengthens the arguments raised by Macfadyen (1961), Phillipson (1962,1963) and others against short term determinations of respiratory rate, and leaves no doubt as to the necessity for all the year round respirometric studies, and at all times of the diel to be made if one is to approach an accurate estimate of the annual respiratory energy loss of a species population.

Earlier studies utilized length measurements rather than live weight in the estimation of growth. Paris and Pitelka (1963) pointed

out that there is great variation between the results of different authors for the same species, and concluded that further information was needed for the growth rates of land isopods. The growth curves presented in this study for O.asellus and P. scaber are considered the best available at present. In P.scaber a length of 13.0 mm (approximately 90.0 mg) is reached at the end of 3 years, and not 3.8 years as postulated by Brereton (1956). The growth curve of O.asellus clearly demonstrates that growth was not constant during the year, but varied with size, season, and breeding condition. A pattern of rapid growth in the first year was indicated, and growth became less marked with age. The effect of season on growth was well illustrated by the sigmoidal curve obtained for each age class. Paris and Pitelka (1963) showed that A.vulgare, like O.asellus and P.scaber had a rapid rate of growth to maturity; Saito (1965) also demonstrated that the rates of growth of the two age classes of L.japonicum followed the same pattern, the 0 year class producing 1.85 K.cal/m^2/yr and the 1 year class producing the considerably lower amount of 0.28 K.cal/m^2/yr. It seems probable that the pattern of growth illustrated by O.asellus and P.scaber will hold for all species of isopod, and one would suggest that isopod species of similar

size ranges e.g. O.asellus, Porcellio spp, and A.vulgare will have similar growth curves.

The growth rates calculated for O.asellus could be criticised, as certain months (June to August) were estimated. However, as the estimated rate was based on the mean rate of each age class during the previous nine months, which included the winter months when only nominal growth took place, this estimated rate will, if anything, be an underestimate because conditions are particularly favourable for growth during the summer months. This being the case, the errors of 11% O.asellus, and 16% P.scaber, shown for the complete energy flow equations would in fact be reduced, which in turn would serve to add further weight to the justification of the methodology used, and the accuracy of the experiments performed.

The comprehensive data on the live weight/dry weight relationships presented in Chapter 7 should enable later workers on population studies of these two species to convert live weights to dry weights, and vice versa, thus eliminating a considerable amount of time and labour in the weighing and analysis of non reproductive, and reproductive material.

The stringent requirements governing the accurate estimation

of energy flow necessitate numerous experiments both by day and by night, at all seasons. Thus automatic recording devices such as the automatic camera, and the continuously recording respirometers, whereby many animals may be studied during each experiment, eliminate the need for continued observation, and considerably reduce the number of experiments to be performed. Such automatic devices hold great promise in bioenergetic studies. The automatic camera is particularly suitable as it allows experiments to be conducted under near natural conditions, and gives a permanent photographic record which may be processed at a later date.

In view of the fact that much criticism has been levelled at respirometric studies at constant temperatures, it is of interest to note that the respiration results obtained at 16 $\pm$ 0.1 ^{o}C (the mean temperature of the habitat) fit well into the energy flow equation, alongside those parameters which were measured separately under near natural conditions. Wieser (1965) has shown that P.scaber does not change its feeding regime until it has been subjected to laboratory conditions for a period of 3 days. One wonders whether metabolic measurements made on such animals, immediately after capture, at the annual mean environmental temperature, would reduce the need for microclimatic measurements and temperature corrections in bioenergetic studies? Indeed, the 'best estimates' calculated for the respiratory energy loss of O.asellus, P.scaber,

and L.japonicum are very similar, the figure for the latter species having been calculated from respirometric measurements at field temperatures, and lead one to believe that measurements conducted at the mean annual temperature of the habitat are justifiable.

As stated in the introduction, no single species of a 'large decomposer' had been studied in all its life stages to investigate energy flow, before the present study commenced. Saito's (1965) comprehensive energy flow study of the isopod L.japonicum, where changes in the population size were estimated, and the fate of the energy entering the population was measured, served to compare the two different methodological approaches to energy flow studies as shown in Section 4. Calculation of the 'best estimates' of $R + Y_1 + Y_2$ (respiratory energy loss + growth + reproduction) for L.japonicum from Saito's data, by the same methods employed for O.asellus and P.scaber made possible a comparison of the three species, and the efficacy of the 'best estimate' technique.

Comparison of the 'best estimates' of each of these three species showed that the figures for R and Y_1 were very similar, but the figure for Y_2 for O.asellus was approximately twice as great, and that for P.scaber approximately three times as great as that for

L.japonicum. Consideration of the results for number of late embryos/young upon live weight in Chapter 7 of O.asellus and P.scaber and Saito's data for young upon length of L.japonicum, showed that an overall mean live weight of O.asellus and P.scaber produce approximately two to two and a half times as many young than an overall mean live weight of L.japonicum. Consideration of the above facts, and knowing that L.japonicum, P.scaber and A.vulgare are present in Saito's study area, and O.asellus, P.scaber and A.vulgare occupy the present study area, it seems probable that L.japonicum and O.asellus occupy similar niches in a woodland ecosystem.

Saito (1965) comparing his results of total energy flow through a L.japonicum population (19.5 k.cal/m^2/yr) with total energy flow through other invertebrate populations as estimated by other workers (Odum & Smalley 1959; Smalley 1960; Kuenzler 1961; and Odum, Connell, and Davenport 1962), showed that the value for L.japonicum was much smaller than the values given for other invertebrates by these authors. It is possible that the low values for L. japonicum will be reflected by populations of O.asellus and P.scaber when the bioenergetic information is applied to population data. The actual role of these isopods in the breakdown of woodland litter, and their contribution to the total energy flow through the ecosystem will become apparent when the results become available from studies currently being conducted as part of a

wider woodland ecosystem study in Durham. For instance, measurements of litter fall, population, analyses, and bioenergetics of other key large decomposers e.g. Diplopoda and Lumbricidae, will make possible the calculation of the percentage of annual litter production broken down by the Isopoda and other 'large decomposers' and a comparison of their importance in promoting energy flow through the woodland ecosystem.

The efficacy of the 'best estimate' technique was tested by multiplication of the 'best estimates' calculated for L.japonicum by Saito's mean biomass figure. The 'best estimate' technique was found to be an underestimate of the order of approximately 17%. Clearly, it is preferable to apply bioenergetic data to detailed population analyses, but as mentioned earlier the time factor often precludes the study in depth of both population and bioenergetic parameters. Two methods have been presented for the calculation of energy flow through populations of O.asellus and P.scaber. Application of the individual life stage data to detailed population analyses will given an accurate estimation of energy flow. However, employment of the 'best estimate' technique with simple biomass data, and the use of a 17% correction factor should enable the energy flow through populations within the geographical range of the two species O.asellus and P.scaber to be rapidly compared. Herein lies the value of the 'best estimate' technique.

Summary

1. Bioenergetics studies on the isopods O.asellus and P.scaber were made to investigate all the parameters of the equations:-

(a) Food ingested = Food assimilated + Food egested

(b) Energy assimilated = Respiratory energy loss + Energy of body growth + Energy of reproduction + Energy loss by moult

$$I = R + Y_1 + Y_2 + Y_3$$

2. Preliminary food preference experiments showed that both species attempted fresh plant material, but these foods were not preferred. Food preference did not differ markedly with season as the preferred foods, dead and decaying leaves, were present at all times of the year.

3. The feeding activity was shown to be limited to the period $1\frac{1}{2}$ hours after sunset and $2\frac{1}{2}$ hours before sunrise. The daytime hours were spent under shelters.

4. A regression of ingestion rate upon live weight was calculated according to the formula $\text{Log } x = -1.555 + 0.807 \text{ Log } Y$ and $\text{Log } x = -0.997 + 0.577 \text{ Log } Y$ for O.asellus and P.scaber respectively.

5. Assimilation efficiency varied with size, but an overall mean figure of 27.2% and 29.3% was calculated for the assimilation efficiency of O.asellus and P.scaber respectively.

6. The high rates of ingestion and assimilation calculated for the 8 - 11 mm female size group of both species may be related to the attainment of sexual maturity.

7. Of the food ingested, 72.8% O.asellus and 70.7% P.scaber was returned to the ecosystem as faeces. A regression of rate of faeces production upon live weight, was calculated according to the formula Log x = - 1.308 + 0.807 Log Y and Log x = - 1.097 + 0.613 Log Y for O.asellus and P.scaber respectively,

8. Oxygen consumption tests were made on O.asellus between March 1963 and March 1964; and on P.scaber between June 1964 and June 1965.

9. In the relationship live weight to length a change occurs at approximately 20 mg or 7.5 mm O.asellus and 16 mg or 7.0 mm P.scaber, which also coincides with a change in the respiratory rate to live weight relationships. The high O_2 uptake at live weights less than 20 mg O.asellus and 16 mg P.scaber is clearly associated with growth.

10. At weights greater than 20 mg O.asellus and 16 mg P.scaber the respiratory rate per unit weight is fairly constant; aberrance during the breeding season was associated with reproductive activities.

11. Calorific values of isopod material were determined with the aid of a microbomb calorimeter suitable for small biological samples.

12. Live weight/dry weight relationships were obtained for body (non reproductive) and reproductive materials of O.asellus and P.scaber.

13. Growth of all life stages of O.asellus was studied between August 1965 and May 1966. The growth curve thus obtained was similar

to that constructed by Wieser (1965) for P.scaber.

14. Growth was shown to vary with season, as illustrated by the sigmoidal curve obtained for all age classes of O.asellus.

15. Animals grew rapidly during their first year, but the rate of growth decreased with age. Both O.asellus and P.scaber grew to a live weight of approximately 90 mg (13.0mm) in three years. Relatively few animals were thought to survive beyond three years old.

16. Methods of calculating the 'best estimates' of the rates of ingestion, egestion, assimilation, respiratory energy loss, bodily growth and reproductive growth are given. The rate of energy loss by moult was not calculated as isopods eat their exuviae, and no calorific value was obtained due to repeated failure of combustion of this material in the microbomb calorimeter.

17. Energy budgets are given for both species, in terms of 'best eatimates' expressed as either g.dry wt/g.live wt of isopod/annum, or K.cal/g.live wt of isopod/annum. Thus it was calculated that 1 gram live wt of O.asellus ingested 11.18 g.dry wt (46.789 k.cal) per annum, of which 3.33 g dry wt (13.749 k.cal) were assimilated, and 7.85 g.dry wt (33.040 k.cal) were returned to the ecosystem as faeces; 1 gram live wt of P.scaber ingested 9.04 g. dry wt (37.855 k.cal) per annum, of which 2.72 g.dry wt (13.125 k.cal) were assimilated, and 6.32 g.dry wt (24.730 k.cal) were returned to the ecosystem as faeces. Respiratory energy loss was 9.253 k.cal and

7.639 k.cal; bodily growth 0.992 and 0.759; and reproductive growth 1.952 and 2.622 k.cal/g.live wt/annum for O.asellus and P.scaber respectively.

18. A discrepancy of 11% and 16% for O.asellus and P.scaber respectively was calculated from the 'best estimates' of the energy flow $I = R + Y_1 + Y_2 + Y_3$ equation.

19. Comparison of the 'best estimates' obtained in the present study with those calculated for L.japonicum from Saito's (1965) data indicated that O.asellus and L.japonicum occupy similar niches in woodland ecosystems. The 'best estimate' was shown to be an underestimate by approximately 17%.

20. It was concluded that the 'best estimate' technique was valuable in that it made possible the rapid comparison of energy flow through populations in different areas of the geographical range of the species being studied.

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