THE BIOENERGETICS OF A POPULATION OF *ASELLUS AQUATICUS* (L.) (CRUSTACEA, ISOPODA)

by

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1. INTRODUCTION

Many of the early studies of ecological energetics dealt with aquatic ecosystems (Odum & Odum 1955; Odum 1957; Teal 1957; Richman 1958;) and Engelmann (1966) suggested that this may be due to the more complex nature of terrestrial communities. However, from about 1960 until the commencement of the International Biological Programme, energy studies have mostly been made at the population rather than ecosystem level, and it is aquatic populations that have been relatively neglected. This is perhaps related to the difficulties encountered in sampling populations in freshwater habitats.

Moreover, the decomposition of organic material in freshwater has been less well studied than in terrestrial habitats (Dickenson & Pugh 1974). As the leaves of trees and similar plant material (allochthonous material) can be the major source of energy to aquatic ecosystems (Nelson & Scott 1962; Hines 1963; Minshall 1967; Otto 1974; Cummins 1973; Iversen 1973) it is important to determine the role which various populations play in converting this energy to a form available to other trophic levels. There have, however, been few quantitative studies on the role of detritivores in streams and lakes. Recent exceptions to this include studies of the stonefly (Pteronarcys scottii Ricker) by McDiffet (1970). Partial budgets have been determined for Potomophylax cingulatus Steph. (Otto 1974), Asellus aquaticus L. (Fitzpatrick 1968), A. aquaticus (Prus 1971, 1972) and for Gammarus pulex L. (Nilsson 1974). Studies concerning the life cycle of A. aquaticus in the River Thames, in southern England, have been made by Steel (1961), and, in two lakes in Sweden, by Andersson (1969).

The aim of the present study was to produce a complete energy budget for a population of Asellus aquaticus by combining field population data with studies of respiratory and feeding activity in the laboratory. The site selected for this study was Wistow Lake, near Leicester, England.

Population density and biomass and its seasonal variations were determined by means of samples taken at four-weekly intervals. At the same time, size class structure and therefore life cycle data were obtained. This enabled the estimation of population production.

Respiration measurements were made in the laboratory. It was hoped that by transferring animals from the lake to the respirometer with as little change in temperature as possible, and by determining respiratory rate at the field temperature, that problems of acclimation and temperature stress would be avoided. Thus it was hoped to measure the respiratory rate of representatives of all size classes at monthly intervals, and so avoid the theoretical objections that can be made against studies which measure the respiration rate at only one season and for few life stages.

Food consumption was also measured in the laboratory. It was hoped to obtain consumption rates for each of the size classes and by also measuring the faeces produced, estimate the assimilation and assimilation efficiency ($\frac{A}{C}$ .100).

Thus each of the parameters in the following equations could be calculated and so a total annual energy budget determined for the population.

C		P		R		F
Energy of food consumed	=	Energy of new tissue produced	+	Energy of respiration	+	Energy of faeces produced

A		P		R
Energy assimilated	=	Energy of new tissue produced	+	Energy of respiration

Symbols used throughout this work are those recommended for the International Biological Programme (Petrusewicz & Macfadyen 1970). Asellus aquaticus (L.). A. aquaticus was chosen for this study as it is widely distributed and often abundant in many freshwater habitats - lakes, rivers, canals, ponds and ditches, in Nottinghamshire and Leicestershire. It therefore appeared to be an important detritivore in many freshwater ecosystems.

There are three indigenous species of Asellus in the British Isles (Moon 1953), and one recently introduced North American species, A. communis Say., which is not widespread (Williams 1972). A. cavaticus Schiödte is a subterranean animal from wells and caves in southern England and S. Wales. It lacks eyes and pigment. A. meridianus Racovitza is, like A. aquaticus, widely distributed in lakes, rivers and ditches in the East Midlands, but is absent from canals, except for parts of the disused Grantham Canal (Moon, pers. comm.). Both species are present throughout most of the British Isles and their geographical distributions overlap. They sometimes occur together (Williams 1962) but in Leicestershire mixed populations are not common (Moon, pers. comm.).

Although occasional individuals may be difficult to identify, most specimens are easily identified by the shape of the pleopods (Fig. 1). In the female Asellus the first pleopods are absent. In A. aquaticus the second pleopods are characteristically rounded compared with the smaller, triangular pleopods of A. meridianus. The male Asellus has two pairs of pleopods and in addition two copulatory styles are apparent. Again, the pleopods in the two species have distinctive shapes (Fig. 1).

Thus when measuring and sexing the sample animals in the present study, their identification could be checked. All the animals collected

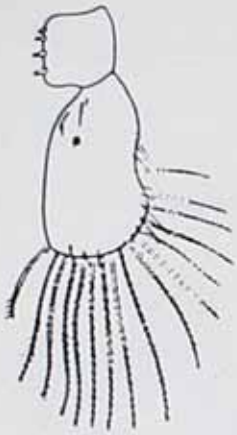
Fig. 1 Left pleopods of *A. aquaticus* and *A. meridianus*.

a) 1st pleopod, male. b) 2nd pleopod, male. c) "first" pleopod, female. Drawings from Hynes, Macan & Williams (1960).

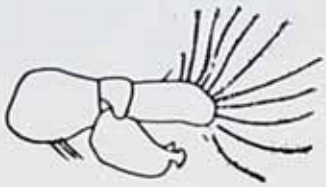
FIGURE 1.

A. aquaticus.

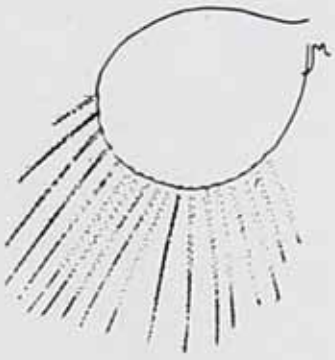
A. meridianus.



a) 1st. pleopods, male.



b) 2nd. pleopods, male.



c) "First" pleopods, female.

Fig. 2 A comparison of the head and abdominal pigmentation patterns of *A. aquaticus* and *A. meridianus*. Abdominal drawings modified from Dupey (1967). In *A. meridianus* the unpigmented areas on the abdomen coincide with the distribution of the anterior and posterior groups of Zenker's organs so that the anterior and posterior unpigmented areas are very prominent.

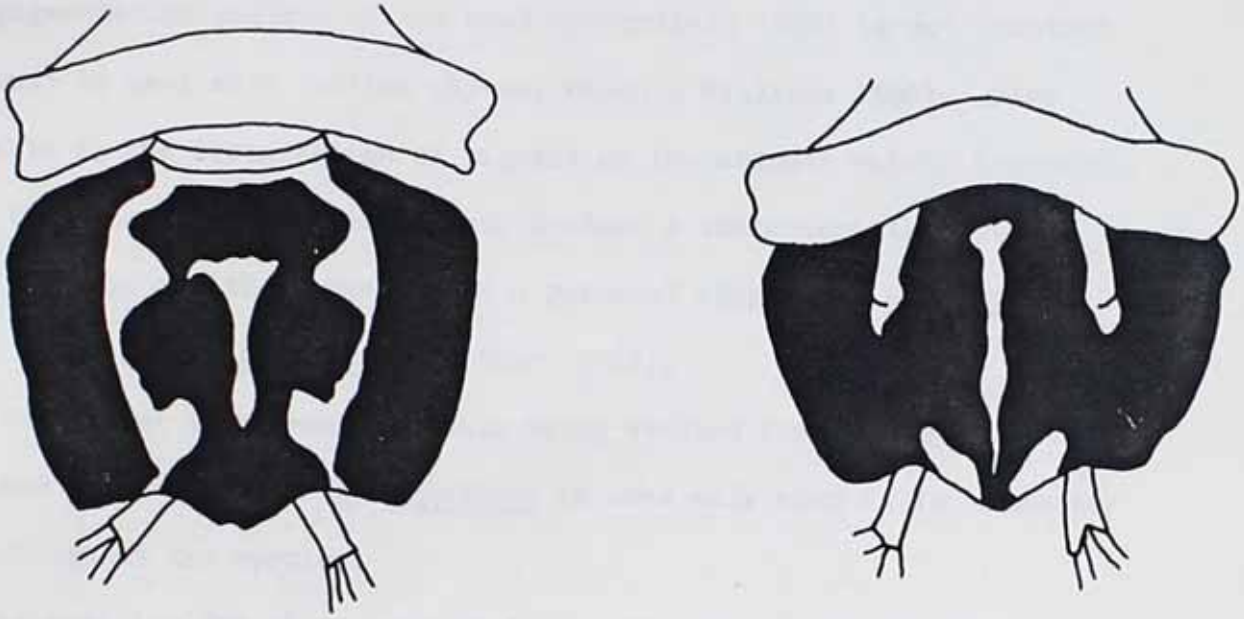
FIG. 2

pigmentation patterns

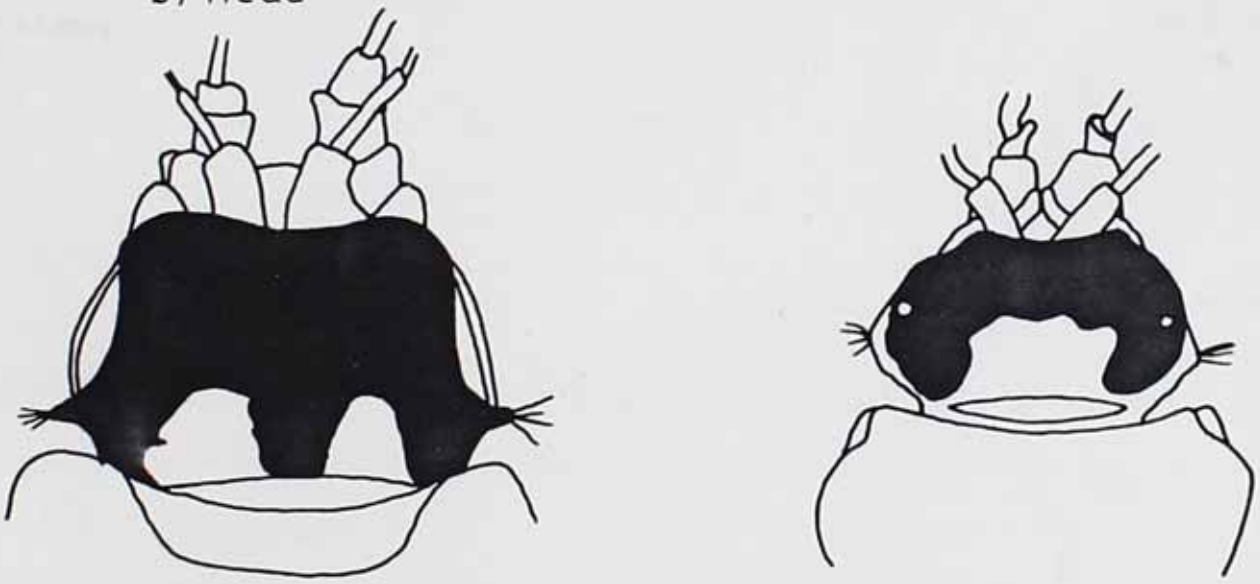
A. aquaticus

A. meridianus

a) Abdomen



b) Head



from Wistow Lake were Asellus aquaticus (L.). Less than 0.5% were found to have aberrant pleopods, making identification less certain. Most of these were checked by Professor H.P. Moon and confirmed as A. aquaticus.

Further diagnostic features of both species are shown in Fig. 2. The pigmentation pattern of the head (Scourfield 1940) is not constant and must be used with caution (Hynes, Macan & Williams 1960). More reliable is the distribution of pigment on the abdomen which, together with the underlying Zenkers organs, produce a characteristic pattern (Fig. 2). In addition, these form a perianal ring in A. meridianus which is absent in A. aquaticus (Dupey 1967).

Throughout this thesis animals being studied from Wistow Lake are referred to as Asellus. A. aquaticus is used only when it is necessary to distinguish the species.

Authorities for plant species follow Clapham, Tutin and Warburg (1952) for angiosperms, Watson (1957) for bryophytes and Bellinger (1974) for algae.

2. POPULATION STUDIES

2.1 Study site

The population studied is found in a small lake (Wistow Lake), situated approximately 6 miles SW of Leicester (SP 643959)($52^{o}33'N, 1^{o}3'W$). The lake covers an area of approximately 9,800 m^2 and was constructed as an ornamental lake when the grounds of Wistow Hall were landscaped between 1810 and 1820 (Brooks, pers. comm.). It is now fished occasionally for sport. The lake is very shallow (maximum depth 1.4m), the bottom is muddy and the water opaque, so that the bottom is generally not visible.

The northern and western margins are fringed with a narrow (1 m) reedswamp of Typha latifolia L. and Epilobium hirsutum L. and a line of alder (Alnus glutinosa L.) trees spaced some 20 m apart. The eastern and southern margins have been artificially cut back and are shaded by a narrow strip of woodland consisting mainly of alder (A. glutinosa), sycamore (Acer pseudoplatanus L.) and hawthorn (Crataegus sp.) and with a ground flora dominated by nettles (Urtica dioica L.). (Fig. 3).

The lake is fed by a small drain, 0.5 m across, at the eastern end, so there is no appreciable water movement. Excess water drains at the western end into the river Sence. Analysis shows that the water is hard and contains substantial amounts of all the major ions. Table 1 gives the water analysis data, together with that of Esthwaite Water (the most eutrophic of the Lake District Lakes), and Burton Well Water (a characteristic hard water) for comparison.

Despite the plentiful supply of nutrient ions, only two species of submerged aquatic plants were recorded in Wistow Lake; Fontinalis antipyretica L. and Potomogeton berchtoldii Fieb., neither being very

Fig. 3 Map of Wistow Lake showing distribution of algal areas, reedswamp, woodland and drainage.

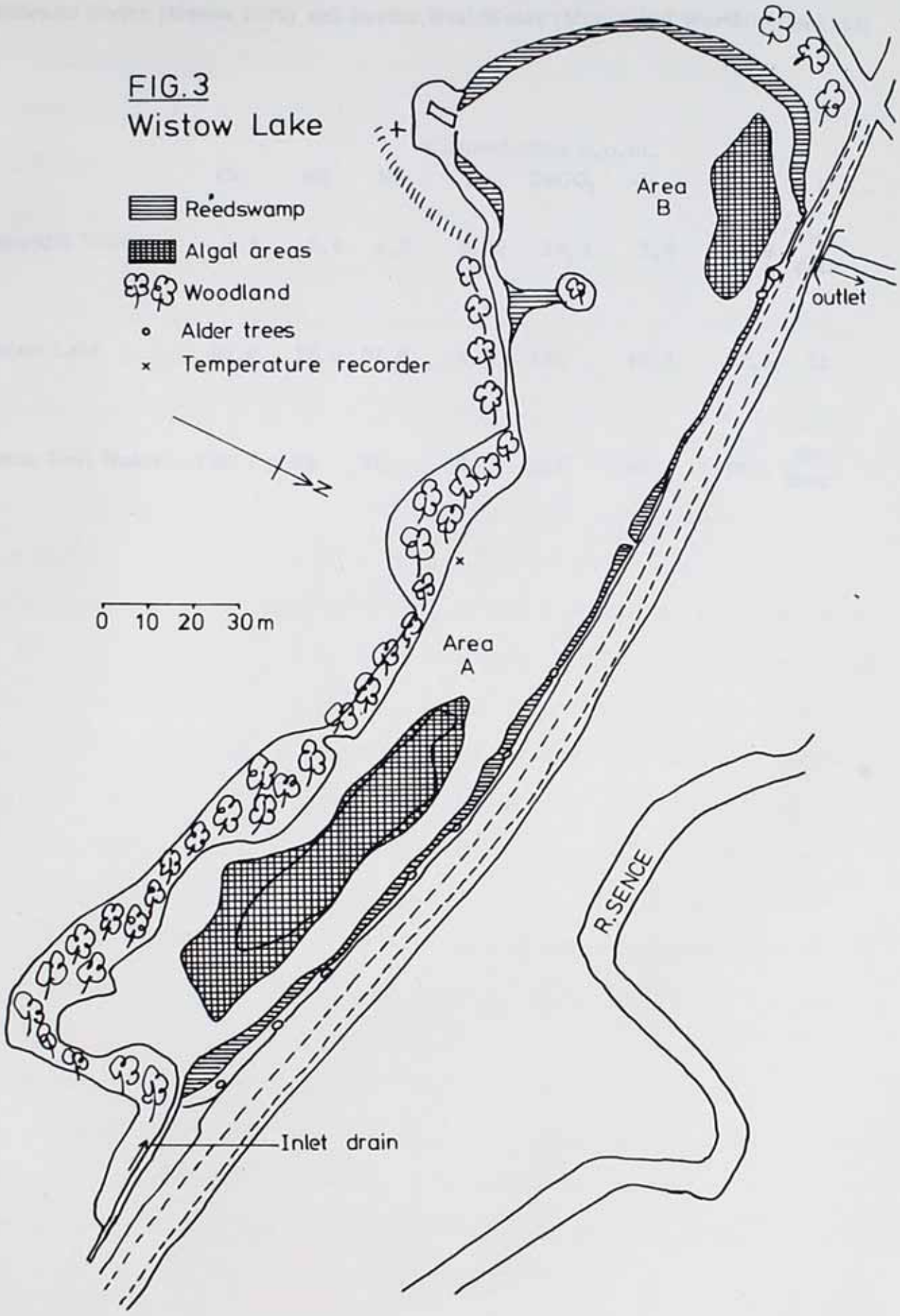


FIG. 3
Wistow Lake
Reedswamp
Algal areas
Woodland
Alder trees
Temperature recorder
N
0 10 20 30 m
Area B
Area A
outlet
R. SENCE
Inlet drain

TABLE 1. Concentration of the major ions in Wistow Lake compared with Esthwaite Water (Macan 1970) and Burton Well Water (Macan and Worthington 1951)

	Concentration p.p.m.							
	Ca	Mg	Na	K	$CaCO_3$	Cl	SO_4	P
Esthwaite Water	8.3	3.5	4.7	0.90	18.3	7.6	9.9	No data
Wistow Lake	98.0	15.0	21.0	4.8	194	40.6	97.5	53
Burton Well Water	159	39	51	57	280	90	378	No data

abundant. Two areas of the lake bottom were covered with a filamentous alga, Cladophora sp. The floating aquatics Lemna minor L. and Lemna trisulca L., were also present.

2.2 Methods

a) Field sampling. Samples for population analysis were collected every four weeks from September 1973 to September 1974 using an Ekman-Birge grab similar to that described by Edmondson & Winberg (1971) and sampling an area of 225 cm^2 (15 x 15 cm). The samples were taken randomly by dividing a map of the lake into 5 m x 5 m squares; the squares were then arbitrarily numbered and samples taken according to a table of random numbers. The grab was operated from a boat and the sample was taken as close as possible to the centre of the square, the position of each being located in the field by using previously selected landmarks around the lake. The grab operated well on algal, muddy and leafy bottoms, but very occasionally failed to close because of Typha rhizomes or twigs. When this occurred, the sample was discarded and the sampling procedure repeated. After collection, the grab contents were transferred to polythene bags and labelled individually.

Preliminary sampling showed that samples containing the filamentous alga , Cladophora, contained much higher numbers of Asellus than the rest of the lake. In order to reduce the variance of the population estimates, the samples were divided into 'algal' and 'non-algal' types on collection and sampling continued until ten samples of each had been collected. Field work was facilitated when it became clear that the alga was limited to two areas (Fig. 3). These two areas were unequal in size, therefore the number of samples taken in each area was apportioned so as to be self weighting. Seven samples were thus removed from the algal area designated 'area A' and three from 'area B'.

After the first 3 collections it became clear that the samples taken adjacent to the reedswamp contained higher numbers of Asellus than the rest of the 'non-algal' area. Consequently an 'edge' area along the northern and western shore was designated and three further random samples taken from this region at each sampling time. Thus a stratified sampling procedure was adopted, with 23 samples collected every four weeks. More samples would have been desirable, but this was the maximum number that could be collected and sorted in one week. I believe that this method effectively sampled the whole open water population of Asellus. Some Asellus, however, live in the marginal reedswamp and it was not possible to sample this area in the time available. Wistow Lake was chosen partly because of the small area occupied by marginal reedswamp and emergent vegetation and the error due to this omission is thought to be small.

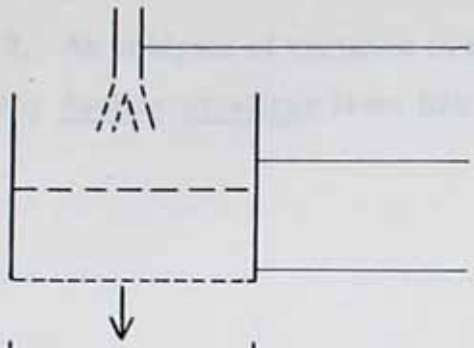
b) Sorting. Samples were transported to the laboratory immediately after collection in polythene bags where they were stored at 10°C (± 2°C) and sorted in the subsequent four days. The Asellus had now to be sorted from the mixture of fine mud and varying quantities of filamentous algae, dead tree leaves, dead Fontinalis stems and other plant remains. This was achieved by washing the material through a coarse sieve (which retained the plant remains) followed by a fine sieve, which retained the animals, but discarded the mud. The procedure is shown in Fig. 4. The fine debris and animals were placed in a petri dish.

One quarter of the contents of the petri dish were sorted at a time by placing the material in an enamel tray with water. To aid searching, the enamel tray was divided into squares and the squares were searched methodically in turn. Searching continued until two complete searches of

Fig. 4 Diagram to show the method used to separate A. aquaticus from detrital material in the field samples.

Fig.4. The method used to sort the field samples for Asellus aquaticus.

(i)

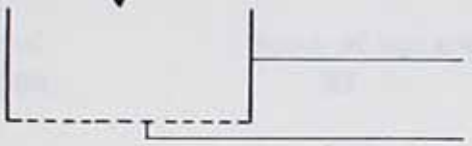


Contents of polythene bag emptied into sieve and washed with a jet of water

Coarse sieve retains algae, twigs, leaves, etc. Mesh size = 5.6 mm

Fine sieve retains animals and fine debris. Mesh size = 0.6 mm

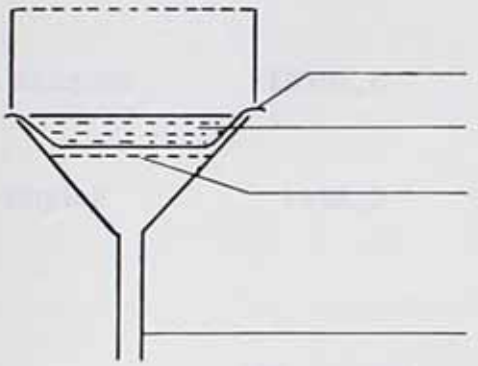
(ii)



Fine sieve only

Mud is washed through

(iii)



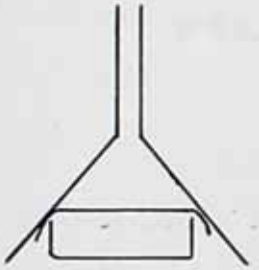
Fine nylon gauze

Animals collected in mass of fine debris

Perforated zinc gauze

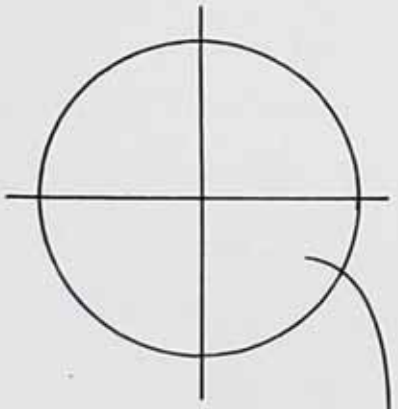
Large glass funnel

(iv)



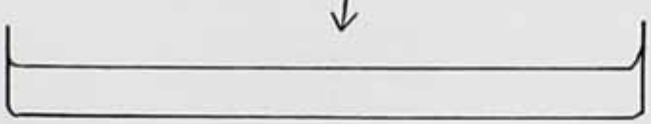
Funnel inverted and debris transferred to a large (15 cm) petri dish

(v)



Petri dish placed on a template and detritus divided into 4 equal portions

(iv)



One quarter at a time suspended in water in a white enamel tray and hand sorted

TABLE 2. An analysis of variance to test the validity of the sub-sampling routine in counting Asellus aquaticus from field samples.

Source of variation	Sums of squares SS	Degrees of freedom	Mean squares
Between samples	19999.6	9	2222.2
Within samples	1492.0	30	49.7

$$F = \frac{MS_b}{MS_w} = \frac{2222.2}{49.7} = 44.71227$$

$P < 0.001$

the tray (taking approximately two minutes) yielded no more animals. If more than 20 animals were found in the first quarter of the sample, the remaining quarters were discarded (these animals were kept in lake water and returned to the lake at the next visit).

c) Validity of sub-sampling. The validity of the above sub-sampling procedure was tested after the first sampling when all four sub-samples from the petri dish were counted so that the variance within samples, s^2_w, was compared with the variance between samples, s^2_b, as shown in Table 2.

From this analysis it can be seen that the variance between samples is much greater than the variance within samples. Thus the error in estimation of the population mean is relatively little affected by within samples variation. The above sub-sampling routine was at first applied to all algal samples, but when sub-sample numbers were less than 20, then all four sub-samples were counted.

d) Other sources of error.

i) Small animals (less than 1.5 mm) are capable of passing the sieve and small Asellus from the time they leave the brood pouch until they reach this size are not estimated. The use of finer sieves made the washing difficult and very time-consuming. If the mud was not efficiently washed away, errors would be introduced in the sorting.

ii) Some animals are retained in the coarse sieve with the coarse debris. Checks on the material left in the coarse sieve during the first sampling indicated that errors up to 3% could be obtained in this way. The largest errors were in the algal samples. During all subsequent sampling, the coarse material was searched for Asellus and if any were found the material was re-washed. Errors from this source are therefore small.

iii) Some animals are not found in the sorting tray. On five occasions the sorting procedure was prolonged for a further two minutes and on only one occasion was a further animal found.

e) Measurements. The animals removed from the tray were anaesthetised using 1% Sandoz MS 222 (Ethyl-m-aminobenzoate methane sulfonic acid) solution and then transferred to 70% alcohol. Subsequently the length of each of the animals was measured by placing it in 0.5 mm size classes. This was done by placing the animals on a 0.5 mm ruled graticule and gently holding the Asellus flat on its dorsal surface with needles while viewing through a stereo-binocular microscope. Measurements were made from the mid-front of the head (as seen from the ventral surface) to the mid-point of the posterior of the abdomen. The sex was determined at the same time by observing the shape of the pleopods (Fig. 1). Animals under 3 mm in length were not sexed as this cannot always be done reliably. A small proportion of some samples showed animals with aberrant pleopods (section 1), which made sexing difficult. The numbers were too small however to significantly affect the results.

f) Analysis. The numbers of male and female animals in each size class was determined and converted to a percentage of the whole set of samples from each area. The numbers of animals measured in the non-algal areas were small, but in those months in which a sufficient number were counted, a chi-squared test showed that the size distribution between algal and non-algal areas and between algal and edge areas, was not significantly different. It was therefore assumed that all areas showed a similar size distribution and the measurements for all the areas were pooled.

Further analytical procedures are described under the appropriate headings.

2.3 Life history

Changes in the numbers in each size class are shown in Fig. 5 (females) and Fig. 6 (males). Animals under 3 mm are equally divided amongst males and females. The number of gravid females is shown in Fig. 5 and the percentage of gravid females is given in Table 3.

The diagrams clearly show that the population had two distinct breeding seasons, as indicated by the presence of gravid females in the population. The first began in February and lasted until June. New juvenile recruits to the population first appeared at sampling time 9, 29th April. The second period lasted from July to September. A further recruitment of juveniles first appeared on 19th August. More frequent sampling would be necessary to determine the precise period during which no gravid females may be found around the end of June. Netted samples taken on 7th July, 1974, contained gravid females, which indicates that the period is quite short.

At Wistow we can therefore distinguish a spring cohort of young appearing between the end of April and mid-June (the result of the first breeding activity) and an autumn cohort of animals liberated between mid-August to late September (the result of the second breeding activity). A more detailed interpretation can then be made as follows.

At Wistow, Asellus was first observed in pre-copula in January and gravid females were present in the February samples. The larger females bred first, the smallest gravid females at this time being 7.00 mm in length (Table 3). Progressively smaller females entered the breeding population and by the beginning of April gravid females in the 5.00 - 5.5 mm

size class were found. The analysis of the population structure (Section 2.4) suggests that the first females to breed in February 1974 were from the 1973 spring cohort, but by the beginning of April the larger females from the cohort liberated in autumn 1973 were beginning to breed. By the end of April most of the spring 1973 cohort females had reproduced and died, but the autumn 1973 animals continued this first breeding activity until the beginning of June.

Thus the February to June breeding period produced the spring 1974 cohort between the end of April and late June.

Gravid females again appeared in the sample taken on 22nd July. This breeding population was composed of the spring 1974 cohort which had grown quickly during May, June and July (Figs. 5 & 6). See also growth curves (Figs. 19 & 21). These gravid females were often smaller than the animals which had bred earlier (down to 4.5 mm in length) (Table 3). The autumn 1974 cohort thus appeared mainly between mid-August and mid-September. Very few gravid females were present in the September sample in either 1973 or 1974. Some of the spring cohort do not breed in the autumn and thus survive the winter. Steel (1961) states that after breeding in the autumn some animals survive the winter and breed again the following spring.

This interpretation of the life history of Asellus at Wistow Lake is essentially similar to that described by Steel (1961) for the River Thames population. It differs in the following respects: -

i) Steel showed two peaks of breeding activity separated by a decline in July, whereas in Wistow Lake there was a complete absence of gravid females for a short period in June (Table 3).

ii) The breeding season extended into October in the River Thames, but at Wistow there were very few gravid females in September (0.4% in 1973, and

3.6% in 1974) and no gravid females in October 1973.

iii) Throughout the year the percentage of gravid females was less at Wistow than in the River Thames (Table 3).

Fitzpatrick (1968) found no gravid females from April to August in a pond near Durham (England).

Andersson (1969) studied the life history of A. aquaticus in two Swedish lakes. The life cycle in each is compared with that in Wistow Lake in Fig. 7.

In Lake Pajeb Måskejaure, situated on the arctic circle at an altitude of 438 m, the young did not appear until the beginning of August. They showed most growth during the following summer, by the end of which they had reached a mean length of 6.1 mm. They did not breed however until June or July of their third summer, by which time they had reached a mean length of 6.7 mm.

Lake Erken is further south (50 km east of Uppsala and at an altitude of 11 m). Reproduction began earlier, in May, and the first young appeared at the end of June. A few animals may reproduce during their first summer (and therefore resemble the Wistow population) but the majority did not breed until the following May.

In Wistow the life cycle was shortened still further. Breeding started earlier and growth was faster, so allowing a distinct brood later in the summer (autumn brood). Growth also continued during the winter, so that the autumn brood reproduced the following spring. These life cycles are summarised in Fig. 7. The shorter spring reproductive period reported by Fitzpatrick may be due to the autumn cohort not reproducing in the May and June period, but requiring a longer growth period until the following autumn. More data is required to support this hypothesis however.

Fig. 5 Length-frequency histograms for female A. aquaticus from Wistow Lake at each sampling date. Size classes less than 3.0 mm divided equally between males and females. The mean number of animals m^{-2} in each size class is shown for each sampling time. The number of gravid females is shown in solid lines.

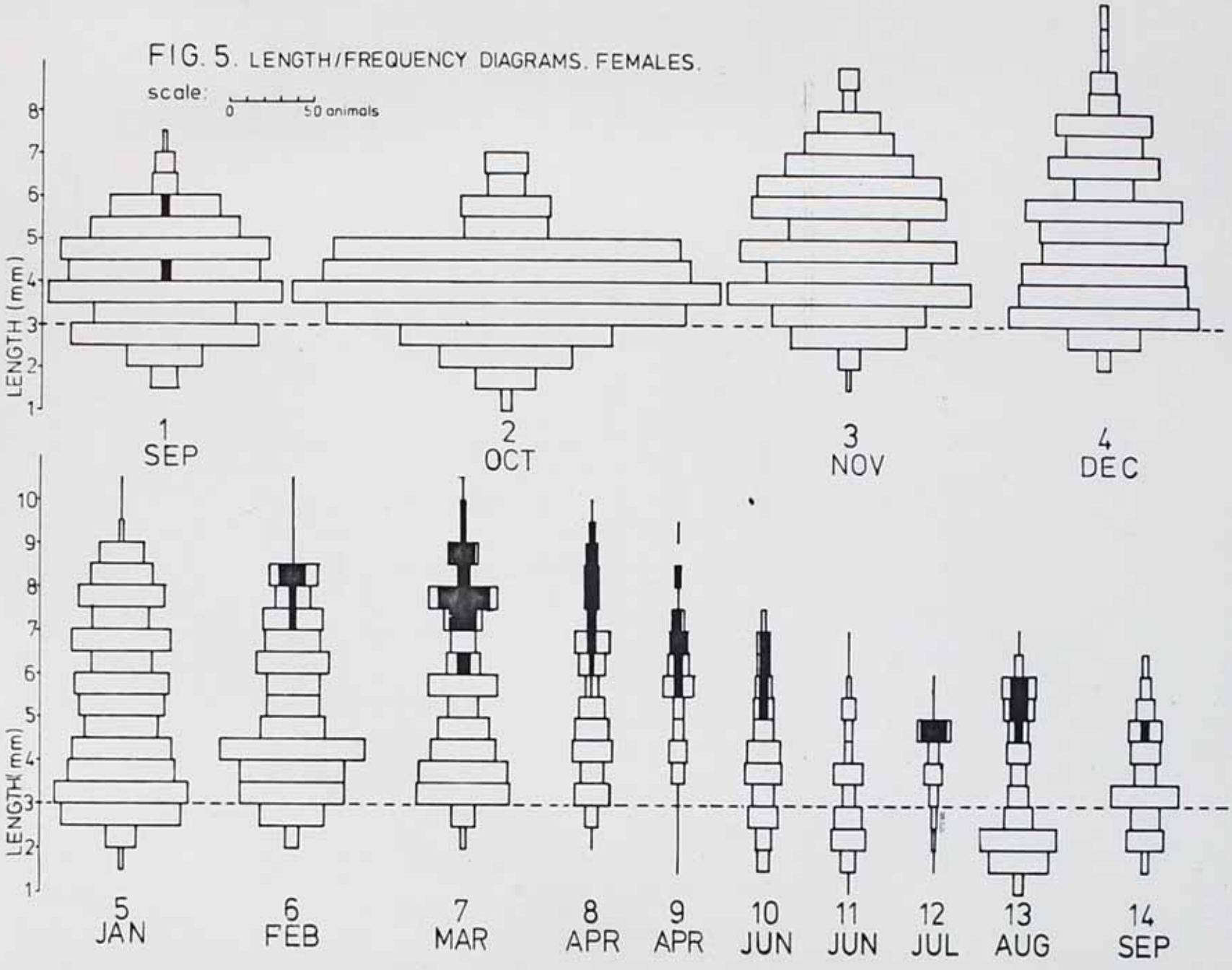


FIG. 5. LENGTH/FREQUENCY DIAGRAMS. FEMALES.
scale: 0 50 animals
LENGTH (mm)
1 SEP
2 OCT
3 NOV
4 DEC
5 JAN
6 FEB
7 MAR
8 APR
9 APR
10 JUN
11 JUN
12 JUL
13 AUG
14 SEP

Fig. 6 Length-frequency histograms for male *A. aquaticus* from Wistow Lake at each sampling date. Size classes less than 3.0 mm divided equally between males and females. Each diagram shows the mean number of animals m^{-2} in each size class.

FIG. 6. LENGTH/FREQUENCY DIAGRAMS. MALES.

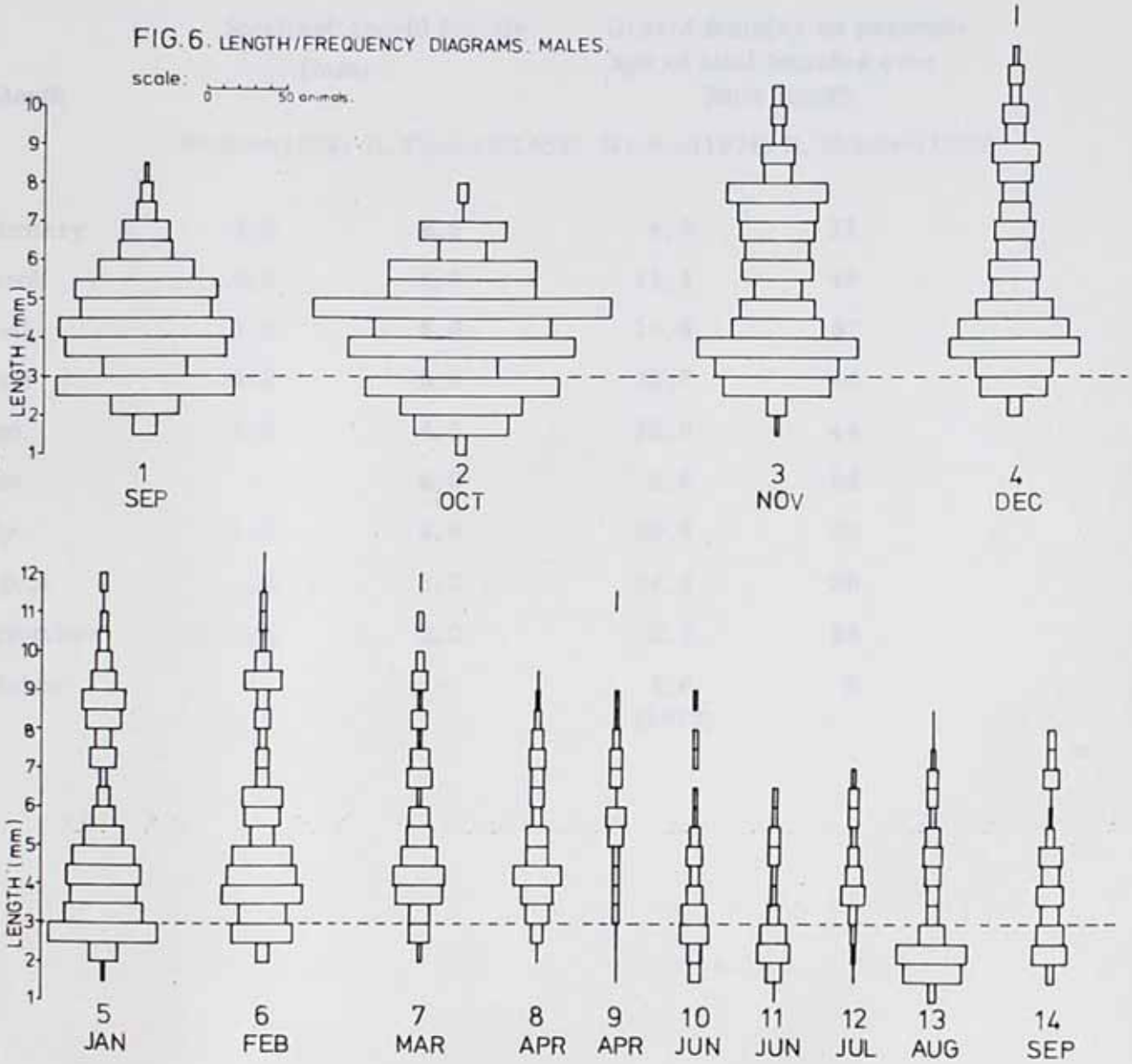
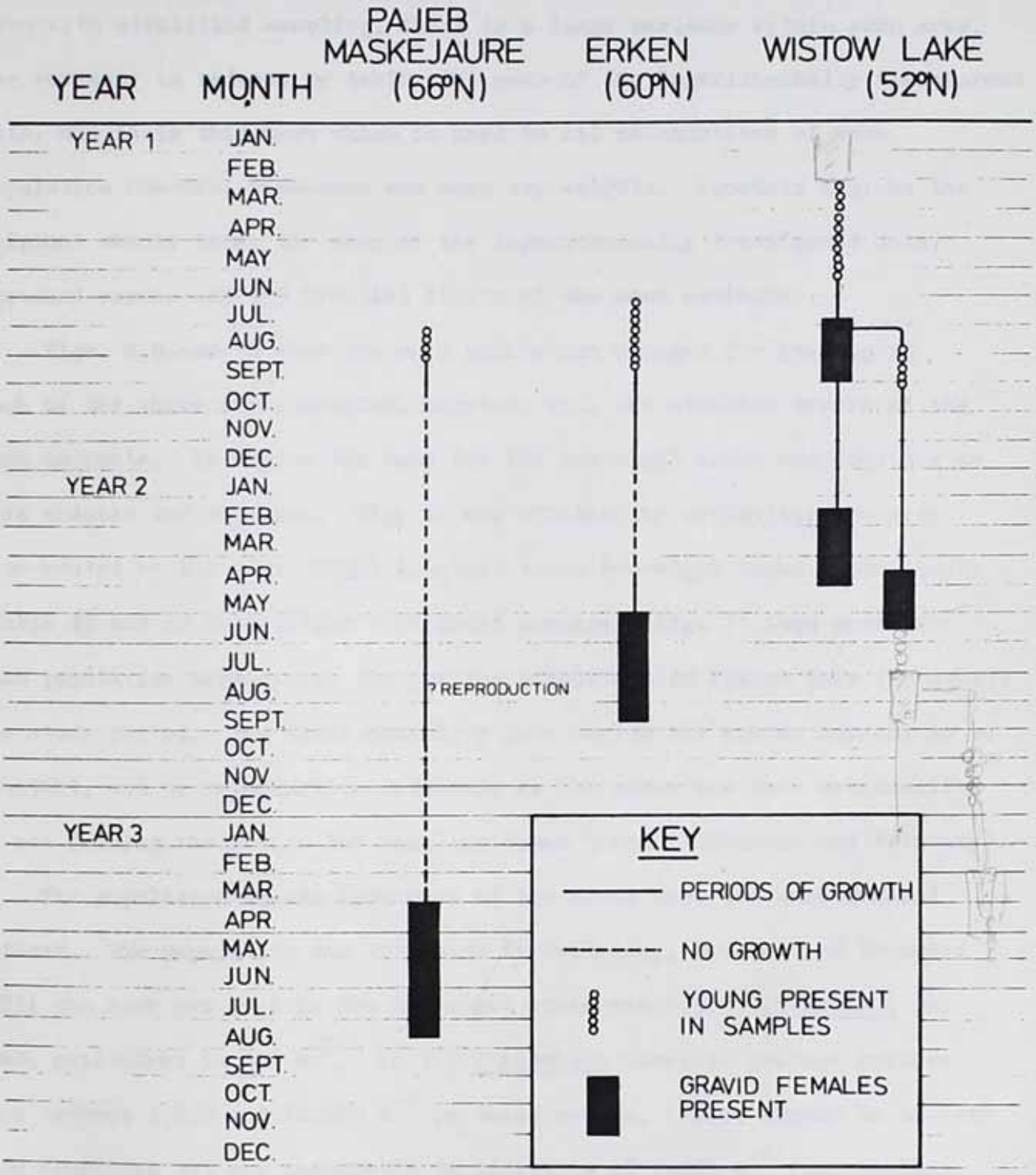


TABLE 3. The length of the smallest gravid female and the percentage of gravid females of A. aquaticus in Wistow Lake during 1974, compared with data for A. aquaticus from the River Thames in 1959 (Steel 1961).

Month	Smallest gravid female (mm)		Gravid females as percentage of total females over 3mm length	
	Wistow(1974)	R. Thames(1959)	Wistow(1974)	R. Thames(1959)
February	7.0	6.0	4.7	11
March	6.0	6.0	21.4	49
April	5.5	5.5	19.9	67
April	5.5	5.0	32.8	44
June	5.0	4.0	15.9	44
June	-	4.0	0.0	54
July	4.5	4.0	32.8	30
August	4.5	3.5	34.2	38
September	4.5	3.0	3.6	58
October	-	-	0.0 (1973)	5

Fig. 7 Diagram to illustrate the life history of A. aquaticus at three different latitudinal sites. Data for Pajeb Maskejaure and Erken from Andersson (1974).

FIG.7. LIFE HISTORY



2.4 Population density

Sampling and sorting methods have been described in section 2.1. Even with stratified sampling, there is a large variance within each area. The variance is reduced by taking the mean of the logarithmically transformed data, and it is this mean which is used in all calculations of mean population numbers, biomasses and mean dry weights. Appendix A gives the original sample data; the mean of the logarithmically transformed data, standard errors and 95% fiducial limits of the mean estimate.

Figs. 8,9 and 10 show the mean population changes for Asellus in each of the three areas sampled, together with the standard errors of the mean estimate. In Fig. 8 the data for the two algal areas are combined as this reduces the variance. Fig. 11 was obtained by estimating the area represented by the edge, algal A, algal B and non-algal areas respectively (Table 4) and so calculating a weighted average. Fig. 11 thus shows the mean population density for the Asellus population in Wistow Lake throughout the study period. The total mortality rate during the winter appears to be constant, and no reproduction occurred, so the curve has been rationalized by not joining the points for sampling times 5 and 6 (January and February).

The population counts from each of the areas show the same general pattern. The population was very high in September, October and November 1973; the mean per grab in the non-algal areas was 8.5 - 9.5 Asellus per grab, equivalent to 400 m^{-2}. In the Cladophora however, average numbers were between 4,000 and 12,000 m^{-2} in these months. These appear to be very high densities but are comparable to densities of 7,000 m^{-2} from similar algal mats in Pajeb Maskejaure and up to 10,700 m^{-2} in Erken, Sweden (Andersson 1974). There are a number of possible explanations for the

Fig. 8 The mean population density, with standard errors of the mean, of *A. aquaticus* in the total algal area of Wistow Lake, September 1973 to September 1974.

Mean and standard errors are detransformed from logarithms.

FIG.8 - Algal areas

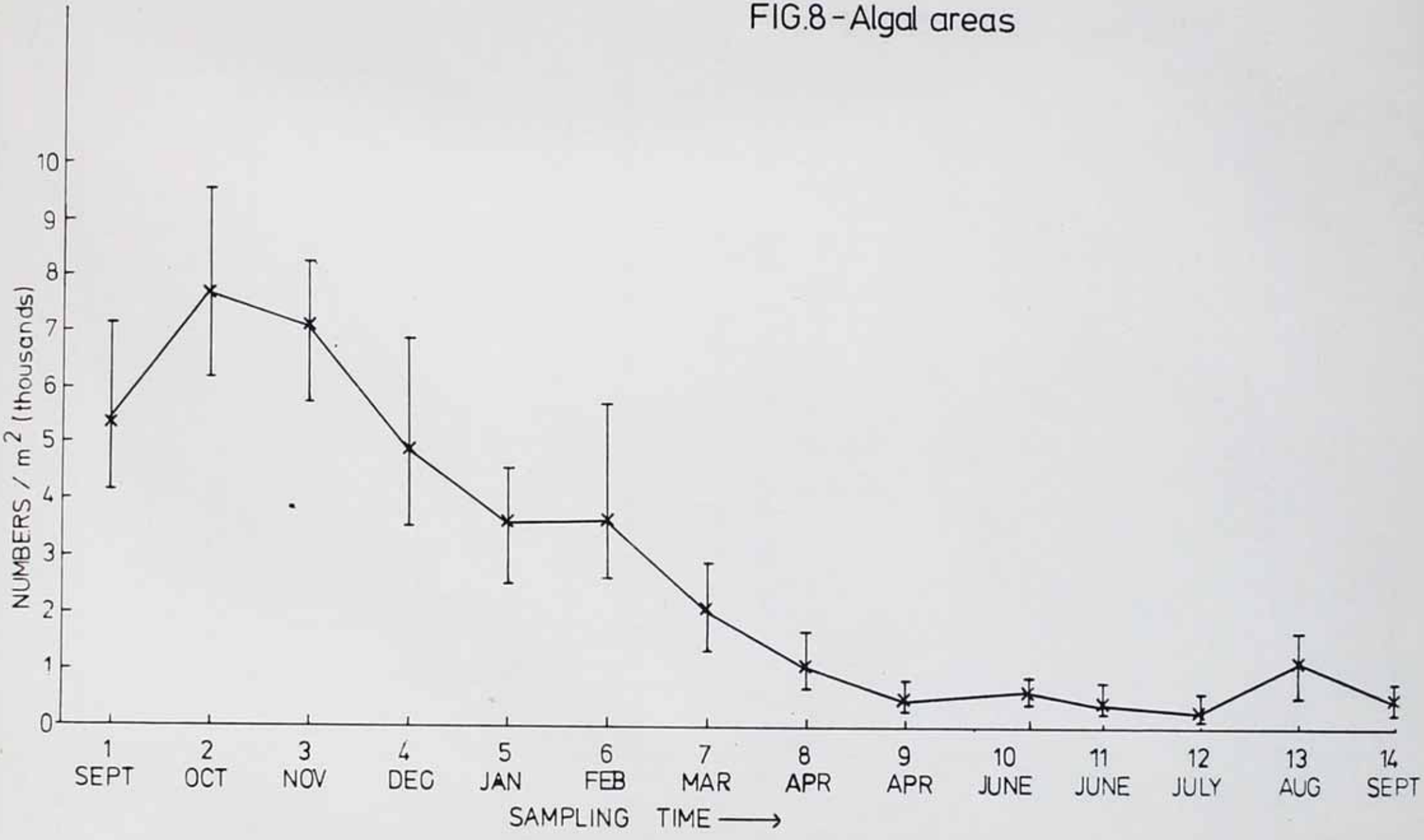


Fig. 9 The mean population density, with standard errors of the mean, of A. aquaticus in the non-algal area of Wistow Lake, September 1973 to September 1974.

Mean and standard errors are detransformed from logarithms.

FIG. 9 - Non-algal areas

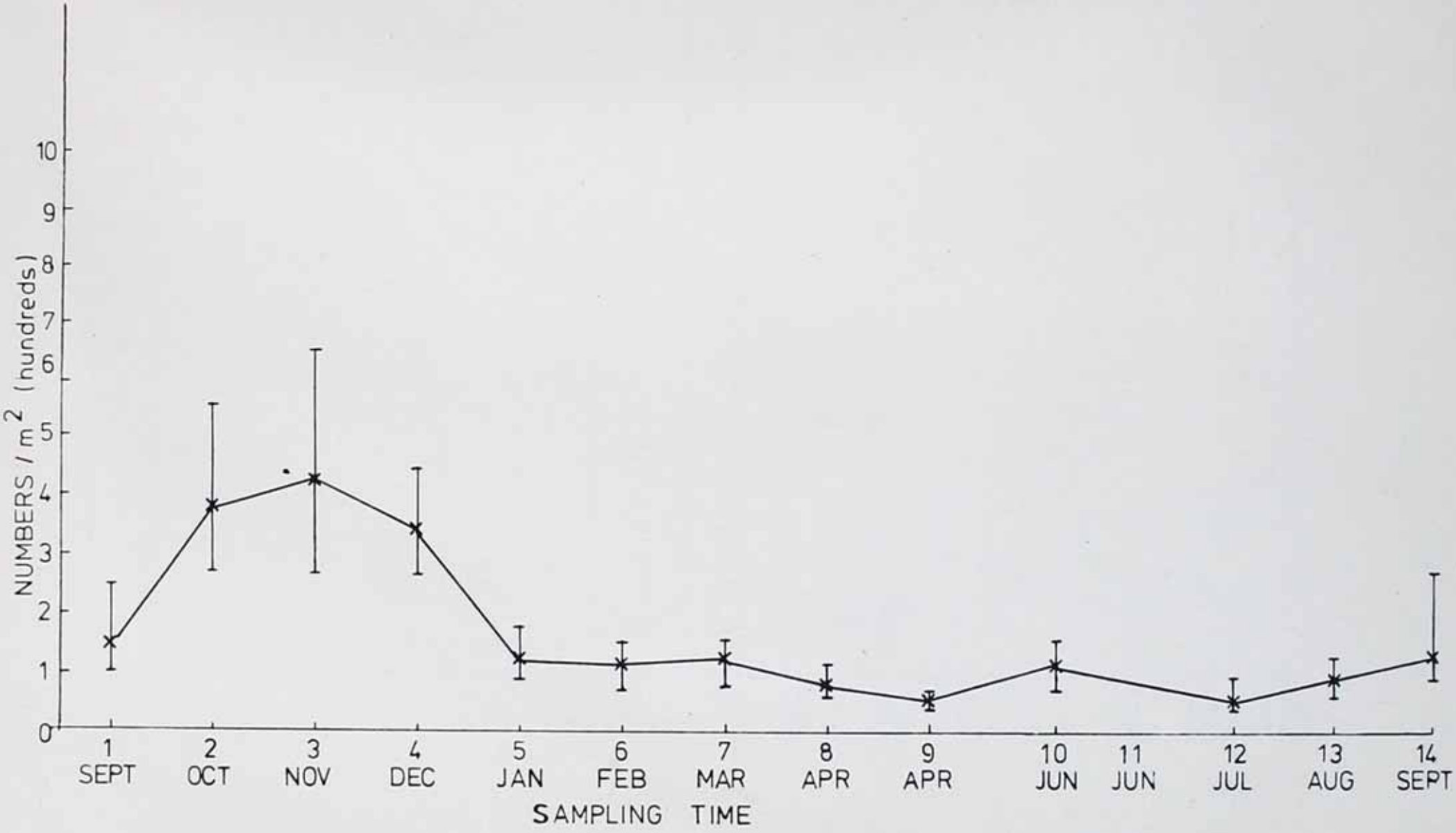


Fig. 10 The mean population density, with standard errors of the mean, of A. aquaticus in the edge area of Wistow Lake, September 1973 to September 1974.

Mean and standard errors are detransformed from logarithms.

FIG. 10 Edge area

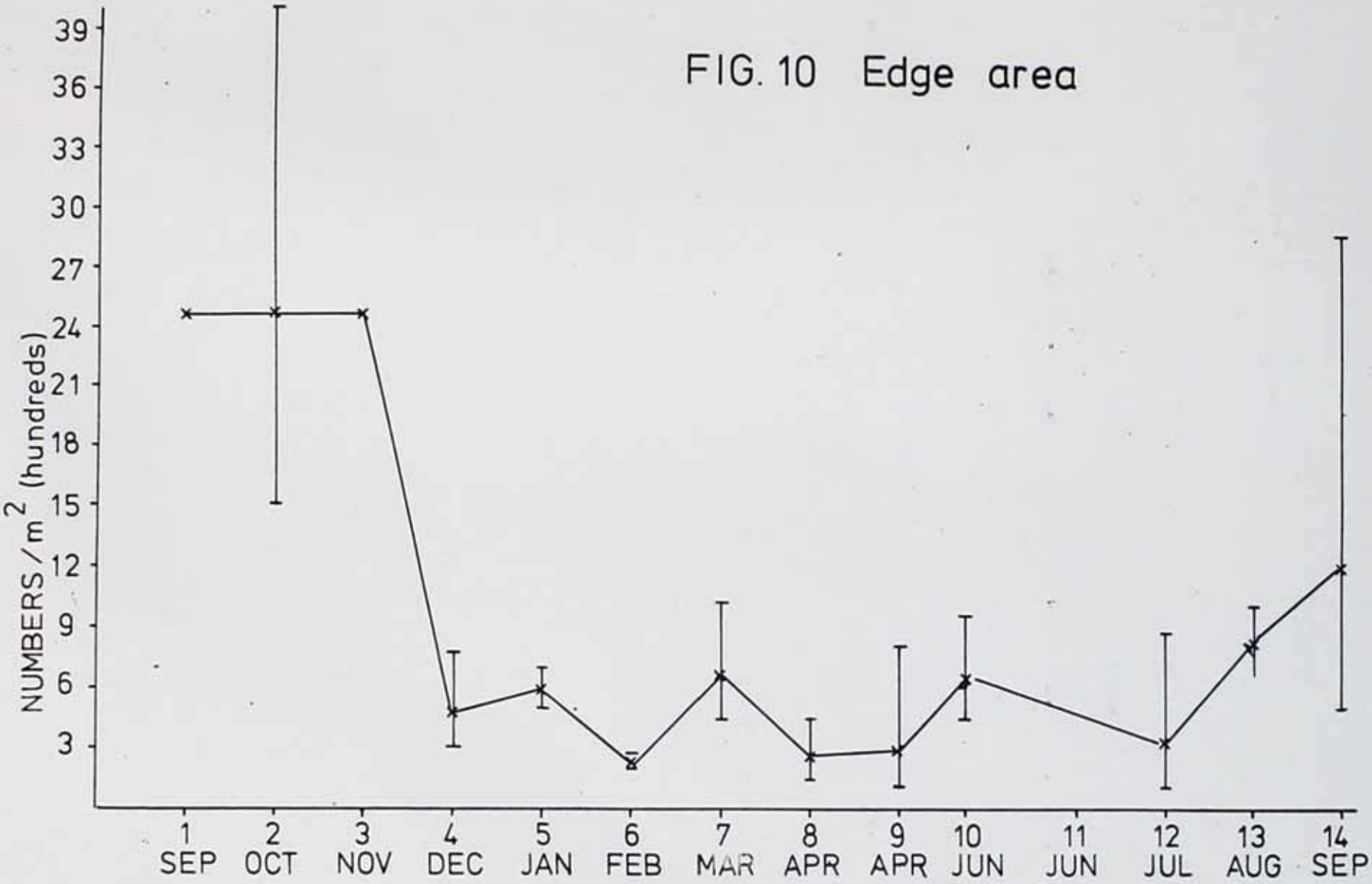


TABLE 4. Area and number of samples for algal A, algal B, non-algal and edge sampling area in Wistow Lake.

Area	No. of samples per month	Area (m^2)
Edge	3	1045
Algal A	7	1298
Algal B	3	411
Non algal	10	7035
Total area of Lake	23	9789

Fig. 11 The mean population density of Wistow Lake, calculated as the weighted average of the algal, non-algal and edge areas at each sampling time, from September 1973 to September 1974.

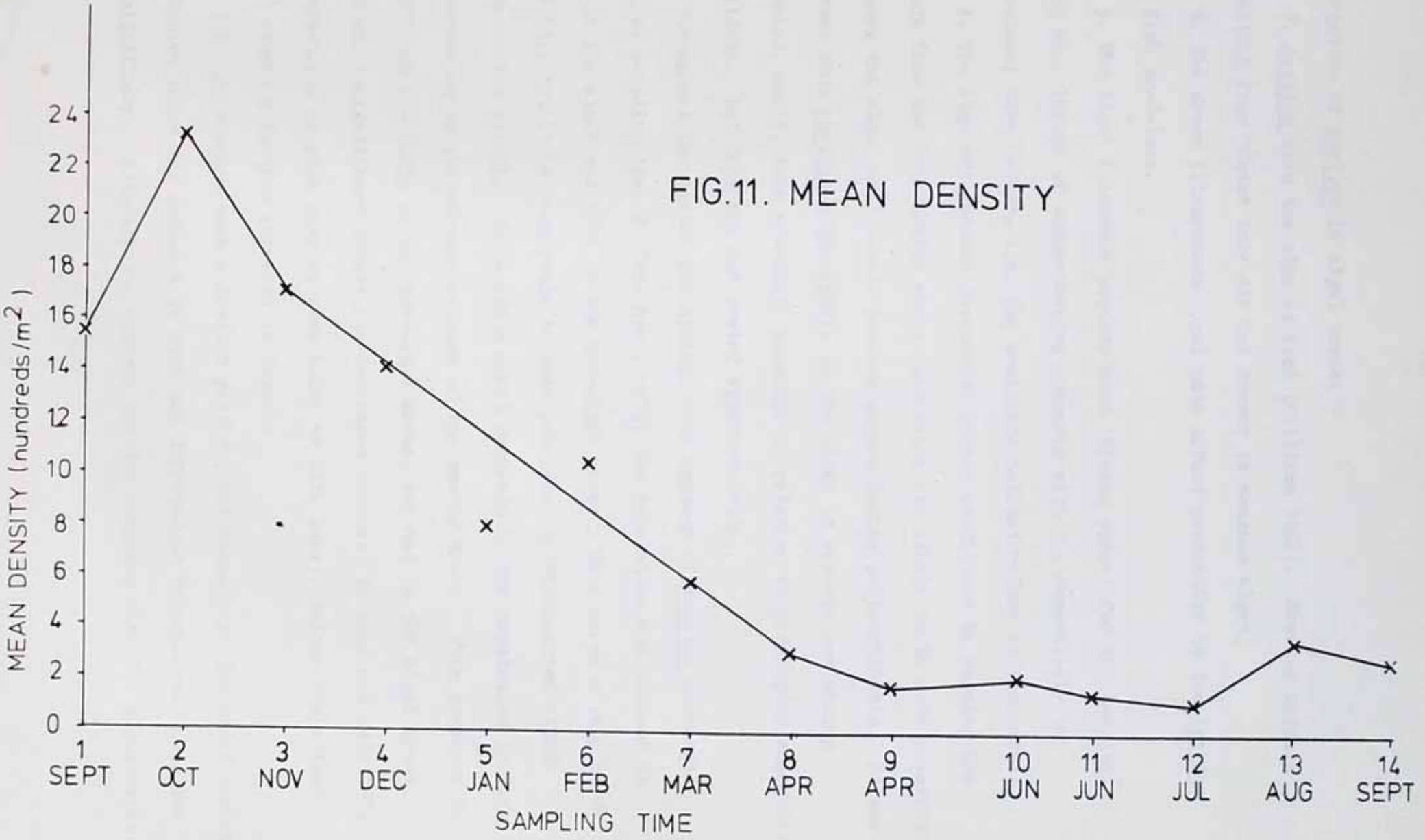


FIG.11. MEAN DENSITY
MEAN DENSITY (nundreds/m2)
0
2
4
6
8
10
12
14
16
18
20
22
24
1 SEPT
2 OCT
3 NOV
4 DEC
5 JAN
6 FEB
7 MAR
8 APR
9 APR
10 JUN
11 JUN
12 JUL
13 AUG
14 SEPT
SAMPLING TIME

aggregation of Asellus in algal areas: -

1. Asellus uses the alga as food (Williams 1962). However animals in culture from Wistow Lake did not appear to consume algae.

2. The dense filamentous algal mats afford protection to the Asellus from fish predators.

3. The algal filaments provide more 'living space' for the Asellus, giving many layers of accommodation compared with the essentially two dimensional lake bottom, i.e. the available habitat volume is increased.

4. The alga may provide favourable living conditions by raising the animals from the lake bottom where conditions are likely to be more anaerobic. Moreover the alga will itself produce oxygen during photosynthesis. It was observed that Asellus often crawls up the sides of vessels containing unaerated, muddy, lake material; possibly in relation to developing anaerobic conditions. But this was not tested experimentally.

Throughout the winter and spring, mean numbers of Asellus decreased until at sampling time 9 (29th April 1974) the population was reduced to 1/15 in the algal and 1/10 in the non-algal areas. This seems a very high mortality, but it is comparable to data published by Fitzpatrick (1968) and Andersson (1969). There was a small increase in the population in June, corresponding to the maximum release of the spring brood. This increase is significant ($P < 0.05$) in the non-algal areas, but not in the algal areas. Small and insignificant population decreases occurred in June and July 1974 (no non-algal or edge samples were taken on 24th June), before the autumn brood caused a further increase in August.

The edge samples show a similar pattern, but because of the small number of samples taken the variance is high and differences between the means are not significant. Although the numbers are low compared with the algal areas,

the high variance, combined with the difficulty of estimating the exact area to which these data apply, makes this one of the main sources of error in the population study. As described in Section 2.1, edge samples were taken close to the emergent vegetation and it is not known to what extent these data apply to the mean within this marginal vegetation. Wistow Lake was partly chosen for the small amount of marginal, emergent vegetation, but in many freshwater studies, particularly of small water bodies, this source of error will be large unless the practical problems of sampling this type of vegetation can be overcome.

The most significant feature of the data however, is that the population density in the autumn of 1974 did not recover to the mean density found at the beginning of the study in 1973. The present investigation was not designed to elucidate the causes of population fluctuations, but as this phenomenon must cast some doubt as to the general applicability of a productivity study on this species in Wistow Lake, it is worth speculating on its possible causes. There are two categories of possible explanations.

1. This was part of a normal fluctuating pattern of abundance in the Asellus population. Such patterns have been studied in a number of insect populations (Varley, Gradwell & Hassell 1973). The key factor causing such fluctuations may be either biotic (e.g. parasite or predator) or climatic (e.g. temperature). Either explanation is possible at Wistow Lake. The fishing tenants at Wistow report fluctuations from year to year in the fish being caught. In 1974 there were more large perch (Perca fluviatilis L.) than usual and tench (Tinca tinca L.) spawned early, in April. Thus changes in predators occur from year to year.

1974 had a colder summer than 1973, with lower water temperatures in August and September (Section 3.2). Steele (1961) reported that A.meridianus

bred more successfully in 1959 in a warm summer than in 1958, which had been cold; but did not comment on whether this applied to A. aquaticus. Some freshwater lakes show unstable population patterns, e.g. Loch Leven (Morgan 1972), but no key factor analysis has been conducted with a freshwater invertebrate population.

2. The second group of hypotheses envisages some catastrophic or interference effect on the population.

a) Alterations were made to the bridge over the outflow stream from Wistow Lake in November 1973 - January 1974. This caused a layer of mud to be deposited over the algal area B and may well be the cause of the greater mortality in this area. However, the level of the lake was not affected and there appeared to be no effects elsewhere.

b) The amount of algae in the areas A and B (Fig. 3) declined during the winter of the study and did not recover in the summer of 1974. The extent of the algal beds were mapped in March 1974 by means of transects across the width of the lake at 5 or 10 m intervals. This map is shown in Fig. 3. It showed that the area occupied by the alga was substantially the same as had been deduced from the earlier sampling data. A second mapping in August 1974 showed that the density of alga was much less and consequently the boundaries were less clear. Also, there were patches within the area that contained virtually no alga. Thus the decline and lack of recovery of the Asellus population is correlated with, and may be causally connected to, the similar change in the alga.

It appears that the primary cause of the failure of population numbers to recover is the apparent failure of the spring reproductive period to produce a significant population increase. The sex ratios are of some significance here. Both Steele (1961) and Fitzpatrick (1968) showed that

as reproduction in A. aquaticus begins in February - March, the percentage of male animals in the population falls from 45 - 50% to 20 - 25%, which can only be explained by the male animals dying before the gravid females after copulation. My data (Fig. 12) show a sudden rise in the proportion of males in early April 1974. This occurred before young animals were recruited into the population and could only be caused by a higher female than male mortality. Thus it may be that at Wistow there was a premature mortality of gravid females in the late March period which led to a low reproductive rate.

Gravid females appear to be more susceptible to adverse environmental conditions (note for instance the greater number of deaths in feeding experiments) than non-gravid animals, and it could be that a change such as an increase in pesticide level in the lake water was responsible for the female deaths and/or a decline of the alga.

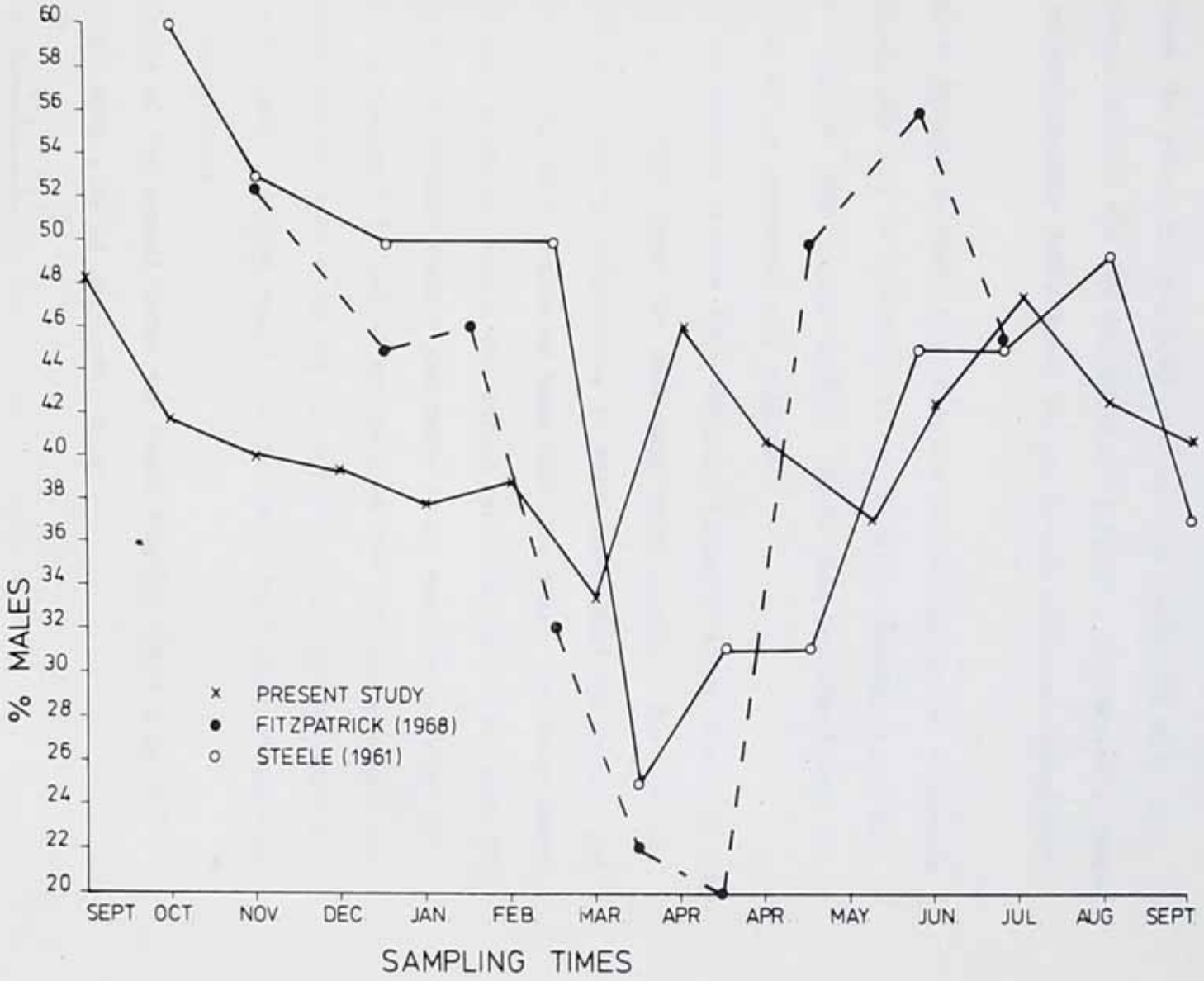
An analysis of the water for pesticide concentration was carried out in September 1974, but it showed only low concentrations of γ- HHC (0.010 - 0.017 $\mu g\ l^{-1}$) and aldrin (0.034 - 0.038 $\mu g\ l^{-1}$). It is possible that any contamination could have been flushed through the lake during the spring reproductive period leaving no trace in the autumn.

Despite therefore the large variances associated with each population density estimation it is possible to follow the changes in the Asellus population with some confidence. There were large and significant differences between areas covered with algae and areas where this was absent. The average weighted population density at the start of the investigation (autumn 1973) was approximately 2,000 m^{-2} but by autumn 1974 the weighted average had fallen to approximately 200 m^{-2}. However increases due to recruitment of juveniles in June and August could be detected.

Fig. 12 Seasonal variation of the sex ratio of A. aquaticus in Wistow Lake compared with a pond near Durham, U.K., (Fitzpatrick 1968) and the River Thames (Steel 1961).

Male animals expressed as a percentage of the total population over 3 mm.

FIG. 12. Percentage males



2.5 Cohort analysis

Introduction. It has been seen that for most of the study year the population consisted of two cohorts, giving a bimodal distribution in the size class/frequency histograms. The two cohorts show a considerable overlap because the young are produced over several weeks and with only a short interval between the two reproductive periods. Furthermore, there appears to be considerable differences in the growth rates of individual animals.

In order to calculate field growth rates and ultimately to calculate population production, it is necessary to separate the length/frequency bimodal curve into its constituent curves. To do this as objectively as possible the following procedure was followed.

Analysis. The assumption is made that the size (length) distribution of the larger cohort is a normal curve for each population sample. The mode of this curve is then found by inspection. In most cases this was clear, but in a few curves there was a choice of more than one peak. In these cases the use of running means to smooth the curves or reference to the data for the preceding and subsequent months indicated which was likely to be the correct mode. In months 7,11 and 12 the peak of the running averages was used as the mode for the male data, as the curve thus calculated gave a better fit to the data. Asellus under 3 mm in length were divided equally between males and females.

The variance of the normal curve was found (Taylor 1965) from the data on the right hand side of the mode, thus: -

$$s^2 = \frac{2\sum_{i=1}^{n}(x_i - m_i)^2}{(2n + n_{mi} - 1)}$$

where n : number of animals to one side of the modal size class

n_{mi} : number of animals within the modal size class

x_i : mid-points of each of the size classes

m_i : modal value, i.e. mid-point of the modal size class

Using the mode and variance, the proportion of the area under the curve within each size class could then be found using tables of areas of the normal curve.

. The left hand (younger cohort) distribution was then obtained by subtracting the right hand curve from the original data. Numbers, biomass and mean dry weight were calculated from these residual proportions, but for clarity, three point running averages were calculated and these are shown in Figs. 13 and 14. It can be seen that the residual proportions also give smooth normal or slightly skewed curves.

Thus the proportion of each monthly census in each size class of each cohort was known and using the weighted mean monthly density (Section 2.3), the numbers in each size class were calculated. In all calculations the density was taken from Fig. 11 where the population changes have been rationalized.

Results. In the following discussion, the cohort born in the spring is designated the S cohort. S_{73} refers to that cohort born in 1973, and S_{74} to the spring cohort of 1974. Similarly, the later cohort is referred to as the A (autumn) cohort and labelled A_{73} and A_{74} according to the year of birth.

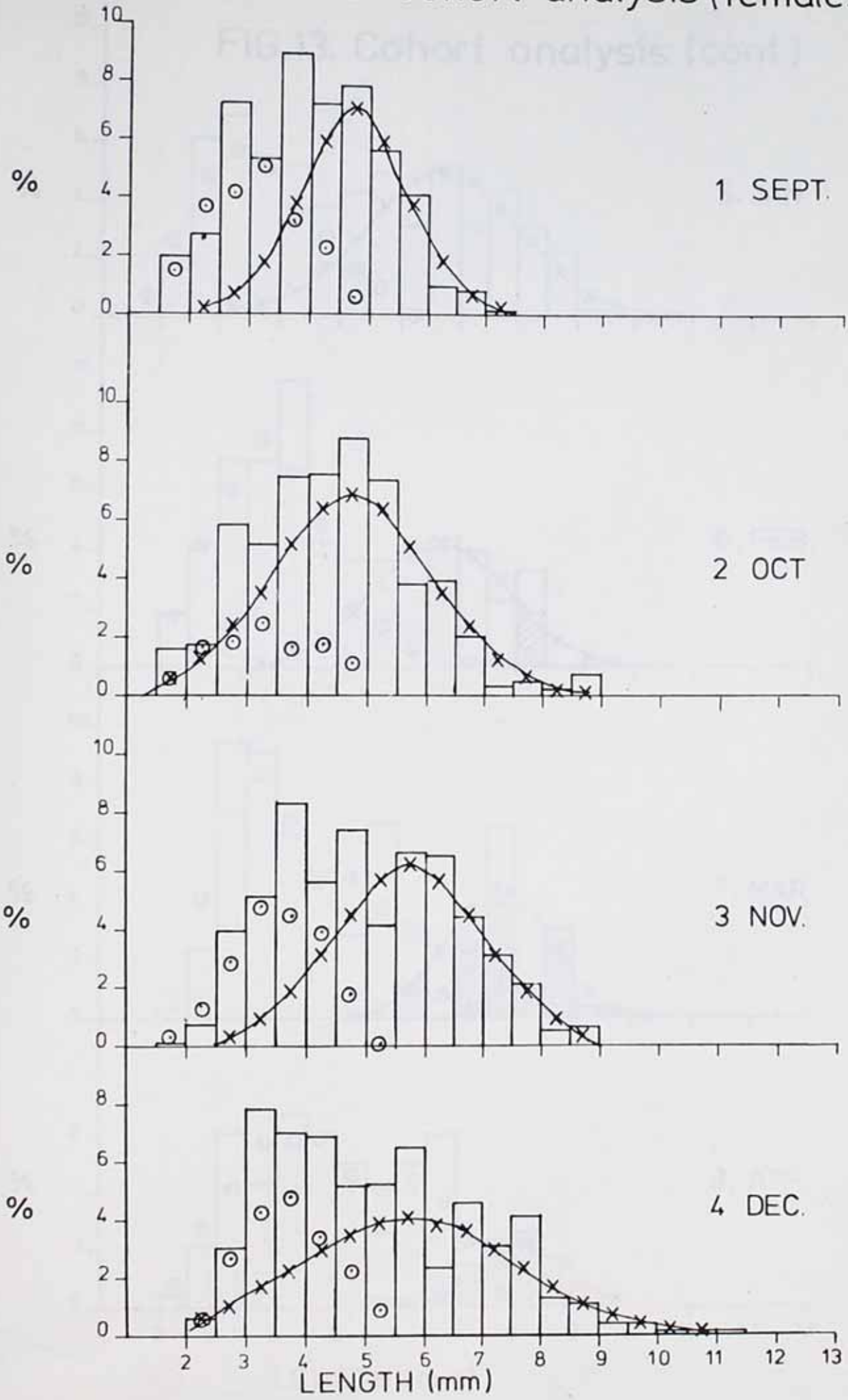
Fig. 14 shows the size-frequency distributions of the male animals at each census as histograms, together with the calculated size/frequency distributions superimposed as smooth curves. The numbers in each size class

Fig. 13 Length-frequency histograms of *A. aquaticus* females from Wistow Lake for each sampling time (September 1973 to September 1974). Each size class expressed as a percentage of the total population.

Normal curves have been fitted, as described in the text, to the right-hand side of the bimodal distribution and a smooth curve drawn for the left-hand side by calculating three-point running averages of the residual percentages.

Symbols as for Fig. 15

FIG.13 Cohort analysis (females)



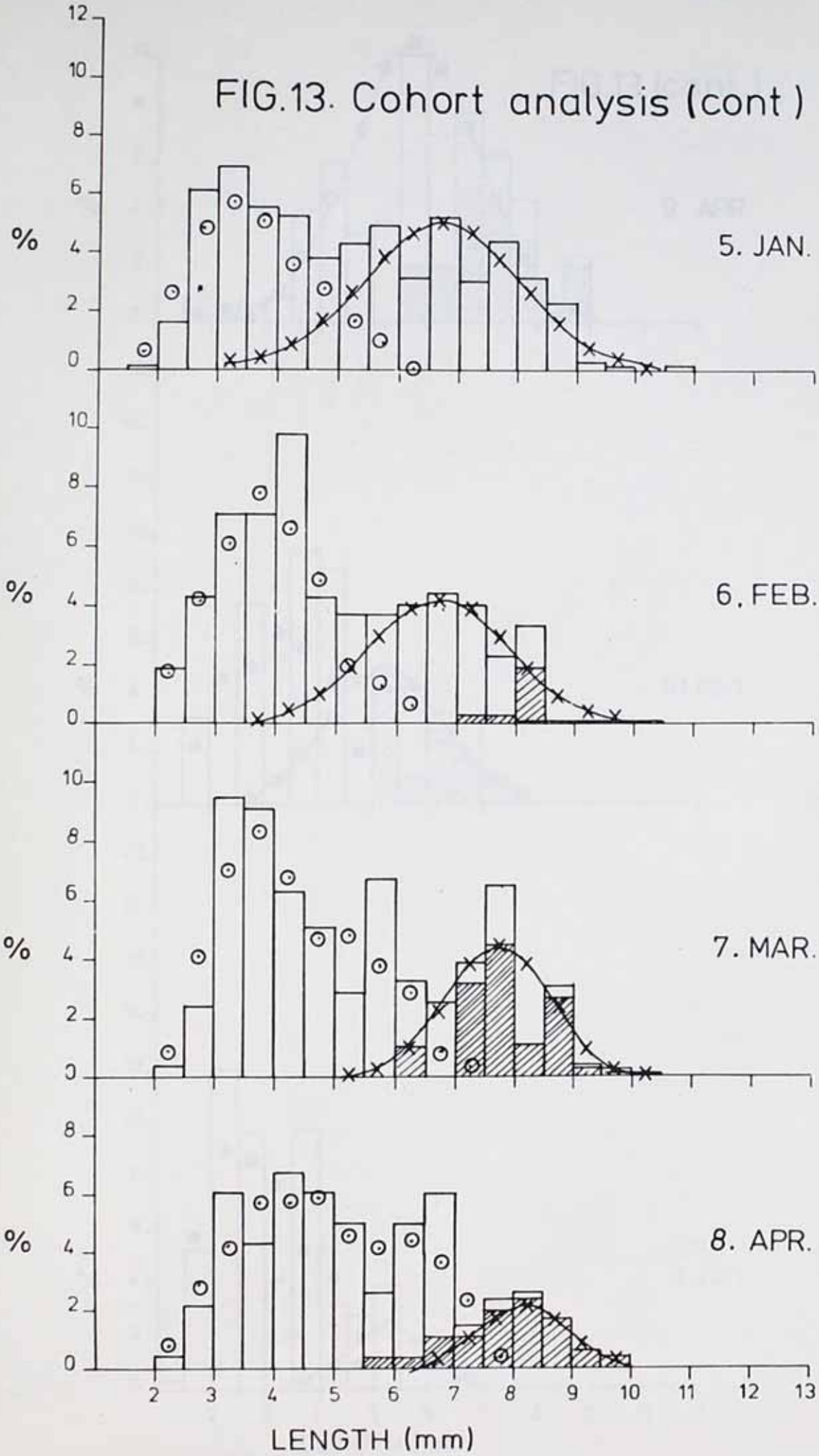


FIG.13. Cohort analysis (cont)
%
5. JAN.
6. FEB.
7. MAR.
8. APR.
LENGTH (mm)

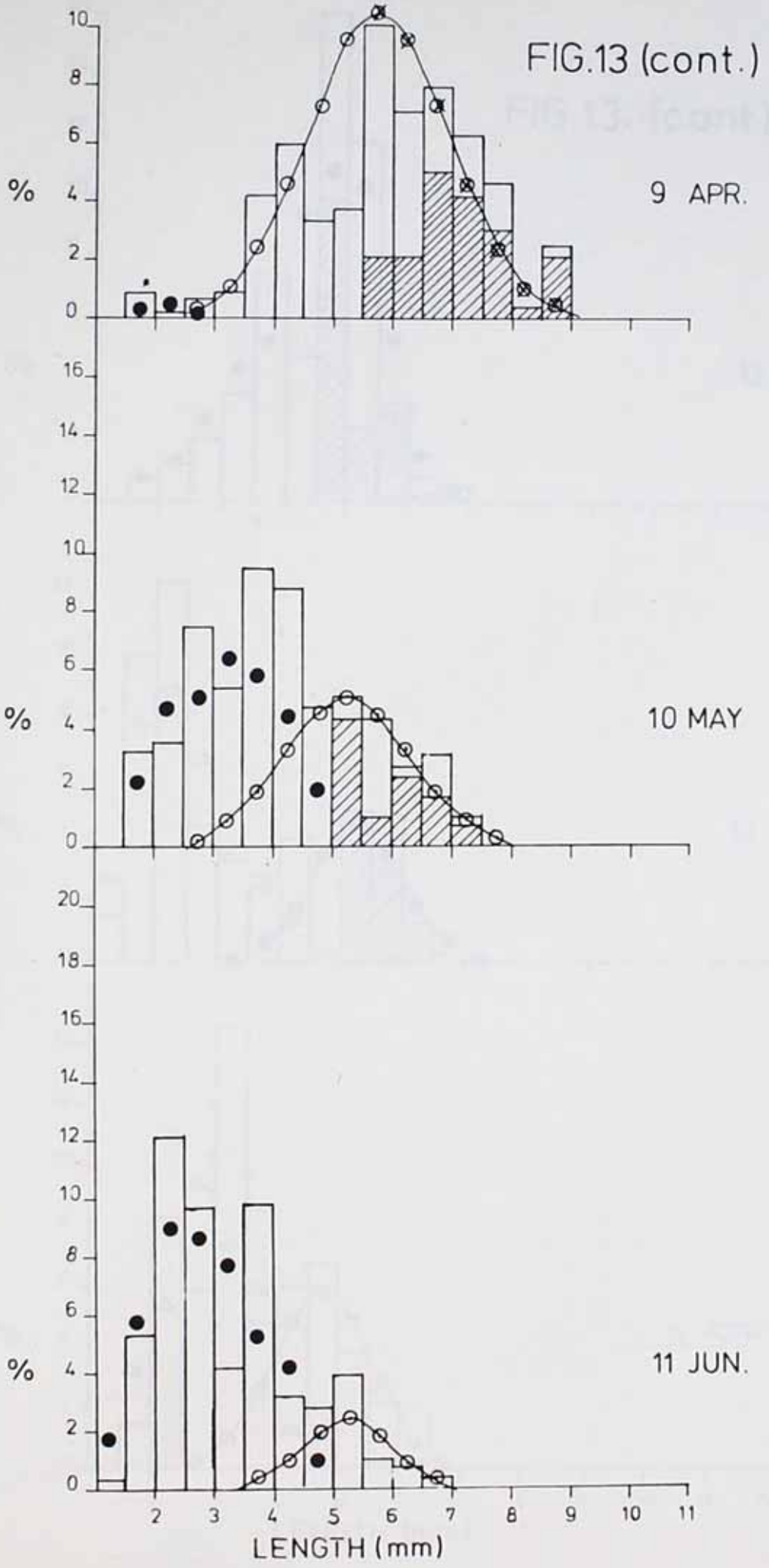


FIG.13 (cont.)
9 APR.
10 MAY
11 JUN.
%
LENGTH (mm)

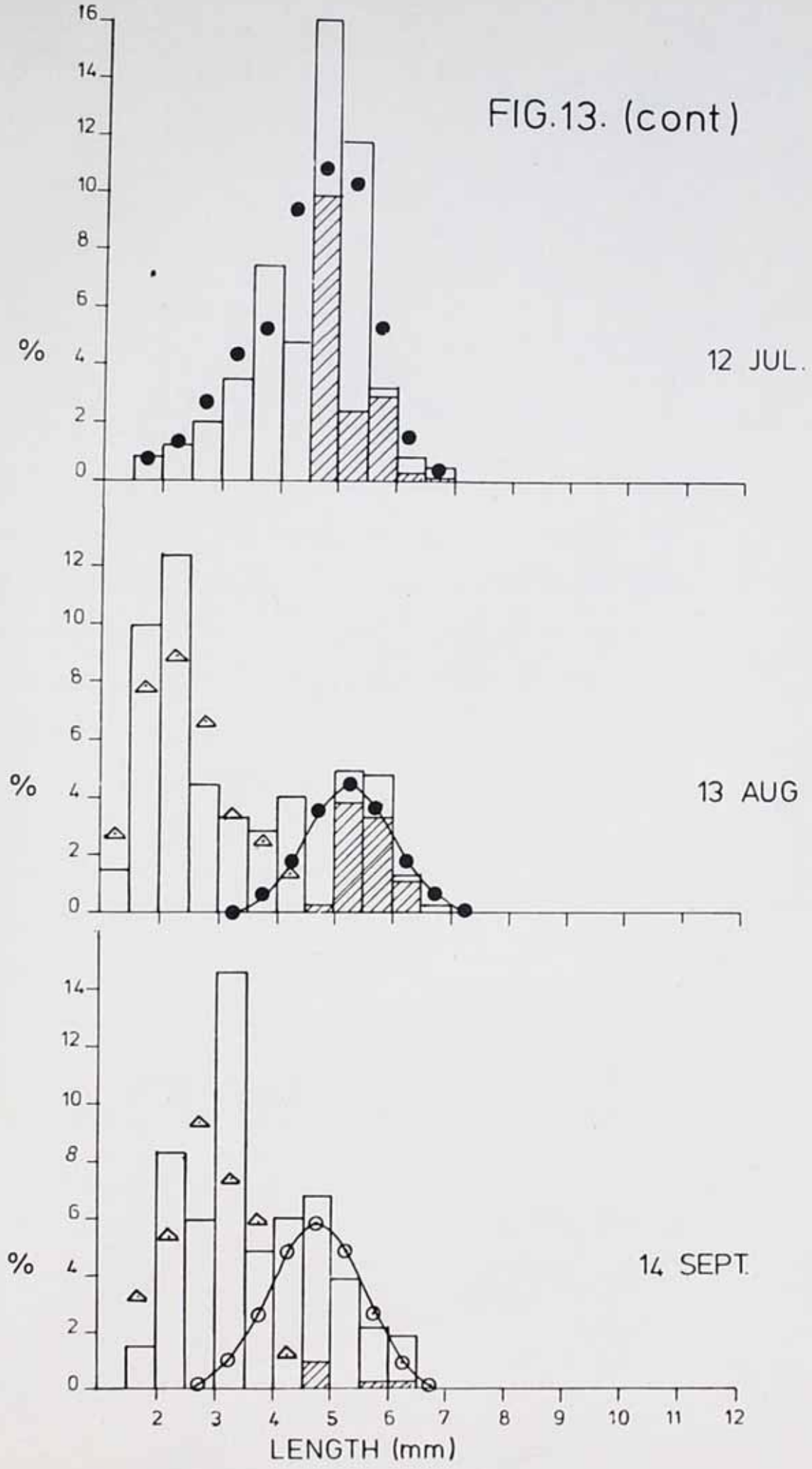


FIG.13. (cont)
%
12 JUL.
13 AUG
14 SEPT.
LENGTH (mm)

Fig. 14 Length-frequency histograms of *A. aquaticus* males from Wistow Lake for each sampling time (September 1973 to September 1974). Each size class expressed as a percentage of the total population. Normal curves have been fitted, as described in the text, to the right-hand side of the bimodal distribution, and a smooth curve drawn for the left-hand side by calculating three point running averages of the residual percentages.

Symbols as for Fig. 15

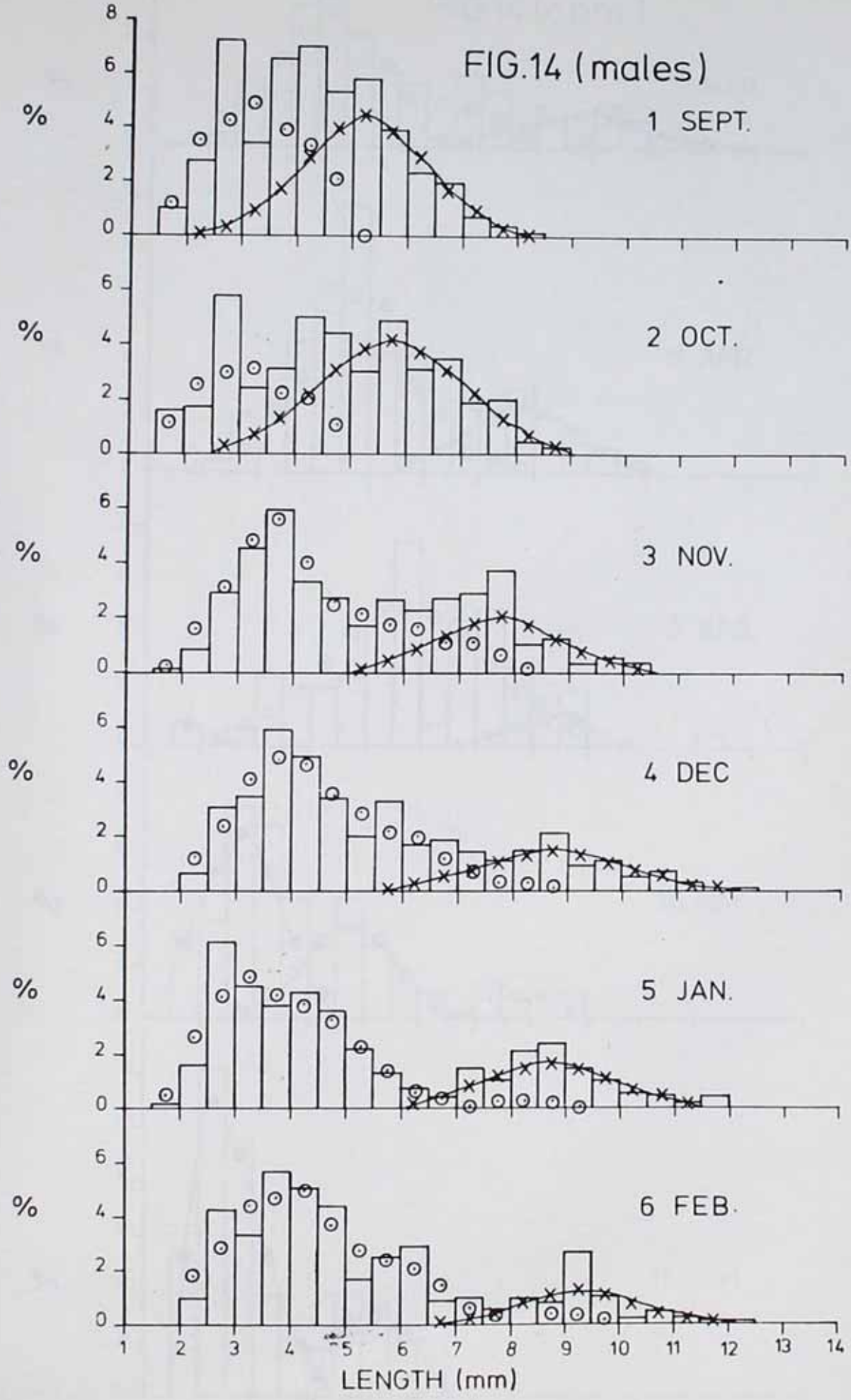


FIG.14 (males)
1 SEPT.
2 OCT.
3 NOV.
4 DEC
5 JAN.
6 FEB.
%
0
2
4
6
8
1
2
3
4
5
6
7
8
9
10
11
12
13
14
LENGTH (mm)

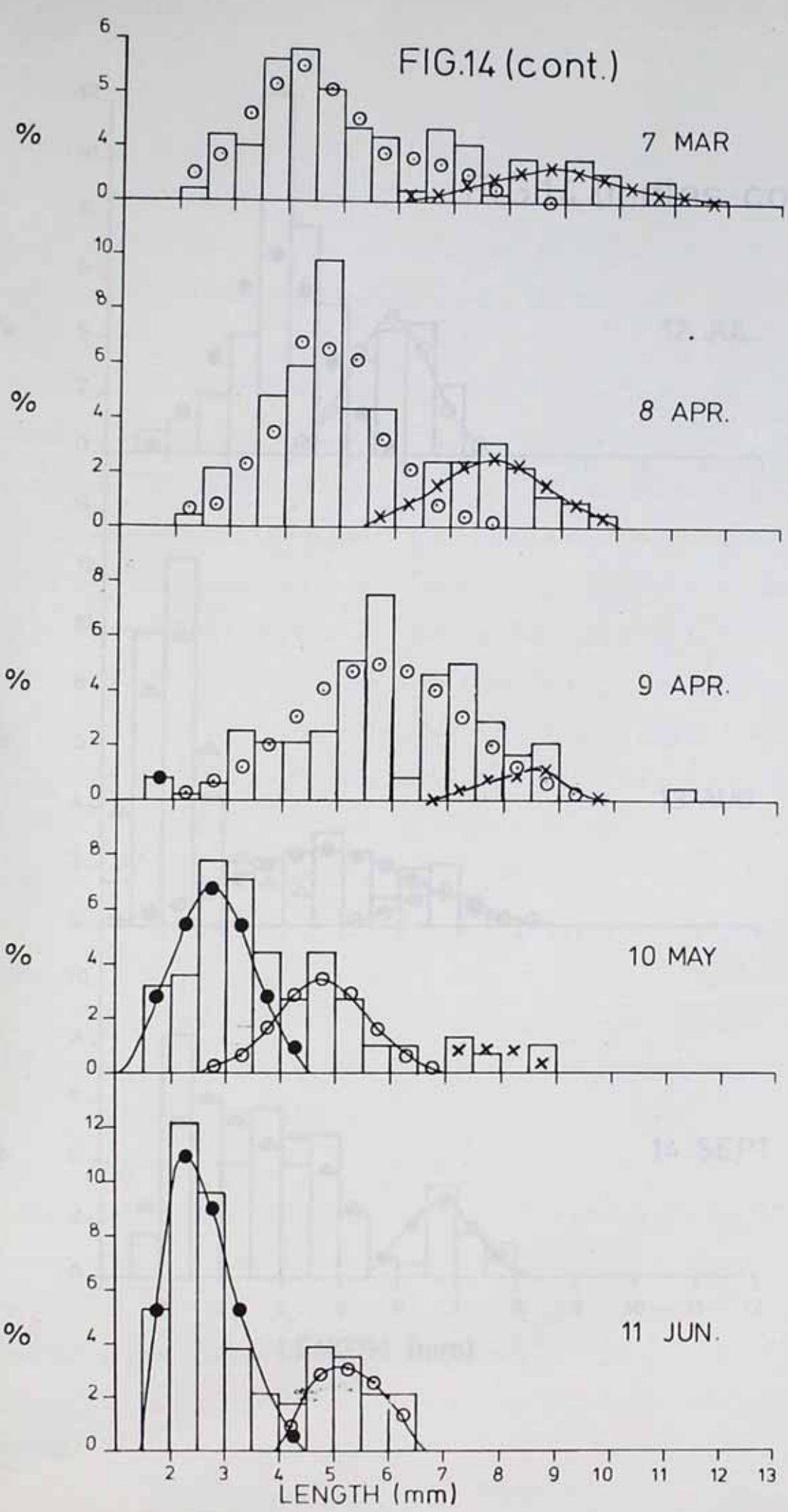


FIG.14 (cont.)
%
7 MAR
8 APR.
9 APR.
10 MAY
11 JUN.
LENGTH (mm)

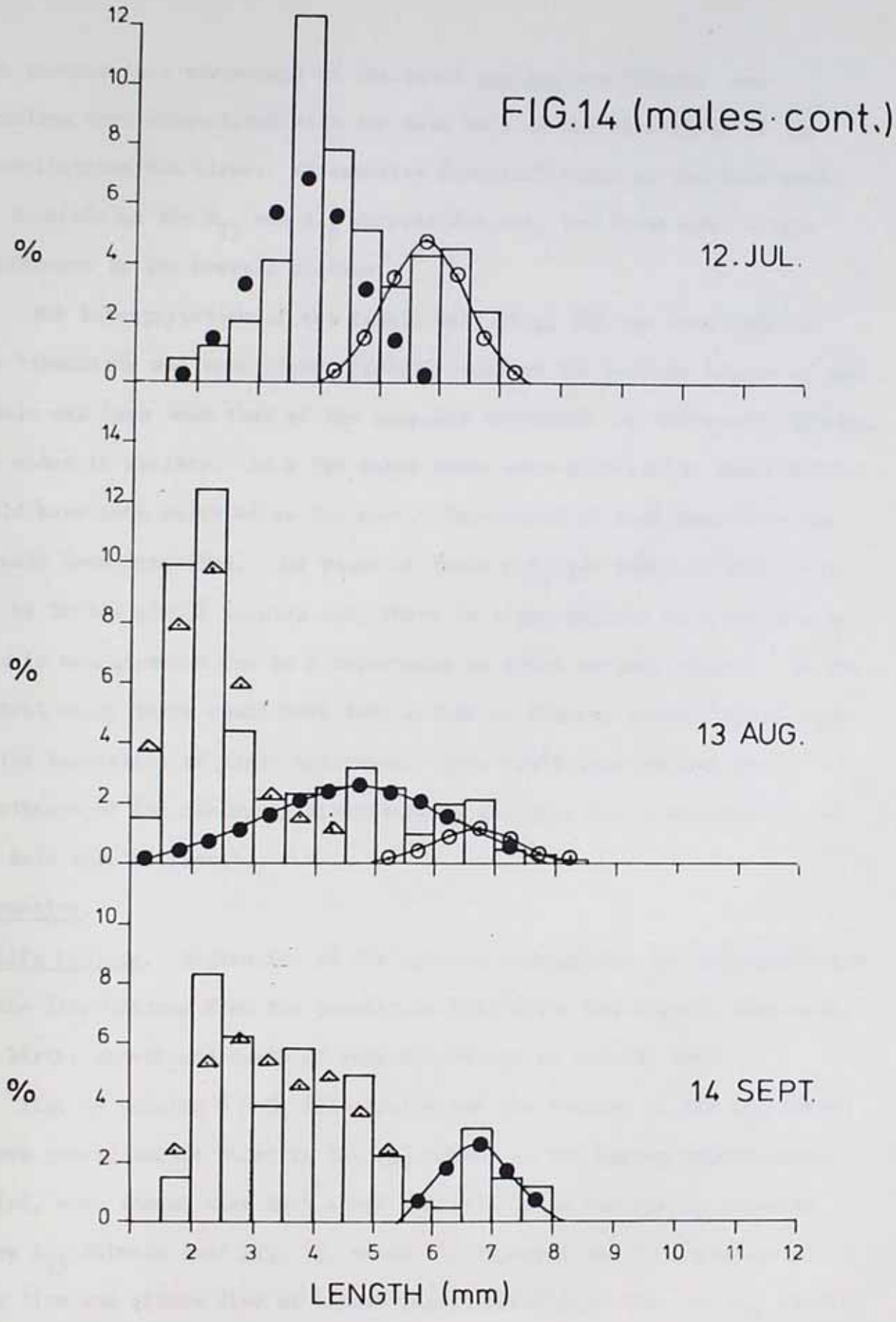


FIG.14 (males · cont.)
%
12. JUL.
%
13 AUG.
%
14 SEPT.
LENGTH (mm)

are plotted as a percentage of the total Asellus population. Few problems were encountered with the male data as the bimodality of the distributions was clear. Alternative interpretations of the data would be possible as the S_{73} and A_{73} cohorts die out, but these make little difference to the overall picture.

The interpretation of the female data (Fig. 13) was less easy as the bimodality was less clear, probably because the average length of the female was less than that of the male, and therefore the difference between the modes is smaller. In a few cases there were alternative peaks which could have been selected as the mode. The method of mode selection has already been described. The cause of these multiple peaks is uncertain, but as Taylor (1965) pointed out, there is a probability of a subjective bias in measurements due to a reluctance to score certain scales. In the present study there could have been a bias in placing animals which were on the borderline of class intervals. This would thus disturb the smoothness of the frequency distributions and make the interpretation of the data more difficult.

Discussion.

i) Life history. Separation of the cohorts strengthens the interpretation of the life history from the population data which has already been made. The birth, growth and death of each cohort can be clearly seen.

Fig. 13 (months 6 - 9) illustrates how the females in the S_{73} cohort become gravid before those in the A_{73} cohort in the spring reproductive period, even though they both added individuals to the new S_{74} cohort. A few A_{73} animals (see Fig. 13, month 11) appeared not to reproduce at this time and either died or became indistinguishable from the S_{74} cohort. The birth of this cohort between April and May 1974 is clearly shown, as is the formation of the A_{74} cohort in August.

ii) Population density. Both the male and female data (Figs. 15 & 16) show that there was a rapid decline in numbers in the S_{73} cohort between October and November 1973. There is some difficulty in interpreting the September and October data (sampling times 1 & 2) as there was a marked increase in numbers in October. Whilst it is possible that the A_{73} cohort was still increasing in size, it is clearly impossible for the S_{73} cohort to increase at this time. The difference can be accounted for by sampling error. Virtually all the females of this cohort died by the end of April and the males by the end of May 1974.

The A_{73} cohort showed an increase in the autumn, possibly as new individuals reached a sufficient size to be included in the samples. They then showed a lower mortality rate than the S_{73} cohort, thus they became the major component of the overwintering population. The males showed an almost linear mortality until May, and then a few individuals persisted in the population until August, whereas all the females died by June 1974. The S_{74} brood was small, only about 120 new individuals m^{-2} being produced. If it is assumed that every gravid female in the S_{73} cohort in March, and in the A_{73} cohort in late April, produced a brood, then 106 females m^{-2} produced broods. Thus the mean number of young surviving to 1.5 mm in length was only 1.1 $female^{-1}$.

The A_{74} brood reached a total of 240 m^{-2}, this being produced from a gravid female population of about 31 m^{-2}. Thus each female produced approximately 8.0 individuals which reached 1.5 mm in length. Had this rate of increase been achieved in the spring, then the population would have returned to its autumn 1973 density.

iii) Sex ratio. The sex ratio for each cohort at each census was calculated assuming a 1:1 ratio in the animals below 3.00 mm in length. Steel (1961) claimed that A. aquaticus from the 3.0 - 3.5 mm size class from the River

Thames showed no significant difference in the numbers of males and females in any month, and therefore assumed animals below 3.0 mm were also in a 1:1 sex ratio, However, the males in Wistow Lake and the River Thames showed a faster growth rate than the females. Thus in any cohort there is at first an approximate 1:1 ratio in the 3.0 - 3.5 size class, but the proportion of males falls as the male mode passes this point. Eventually there are more females than males in this size class (Table 5). If sex ratios are calculated on animals above 3.0 mm in length, the ratio will be affected by this differential recruitment. Thus the precise sex ratio at any one time will depend upon growth rates and the 1:1 ratio assumed here for animals below 3.0 mm only applies immediately after brood production. This assumption will not hold if monogenic brood production occurs as reported by Seitz (1954).

Nevertheless, it can be seen (Fig. 17) that there is a decrease in the proportion of males throughout the non-reproductive period, which must have been due to a higher male than female mortality, followed by an increase after the onset of reproduction due to the greater mortality of gravid females. In the S_{74} cohort, a similar rise in the percentage of males occurred, but as a larger number of the population survived to reproduce the following spring, this was soon followed by the same downward trend. The A_{74} ratio in September 1974 is similar to the A_{73} ratio found in September 1973; but there is considerable difference in the S_{74} and S_{73} ratio. This however could be due to differences in the timing of reproduction in the two years. There is a similar discrepancy in the mean weight of male animals in the S_{74} and S_{73} cohorts.

The method used to separate the size/frequency distribution into its component cohorts is open to a number of criticisms, as follows:

Fig. 15 Number of male A. aquaticus m^{-2} in Wistow Lake in each cohort at each sampling time from September 1973 to September 1974.

FIG.15. Male density.

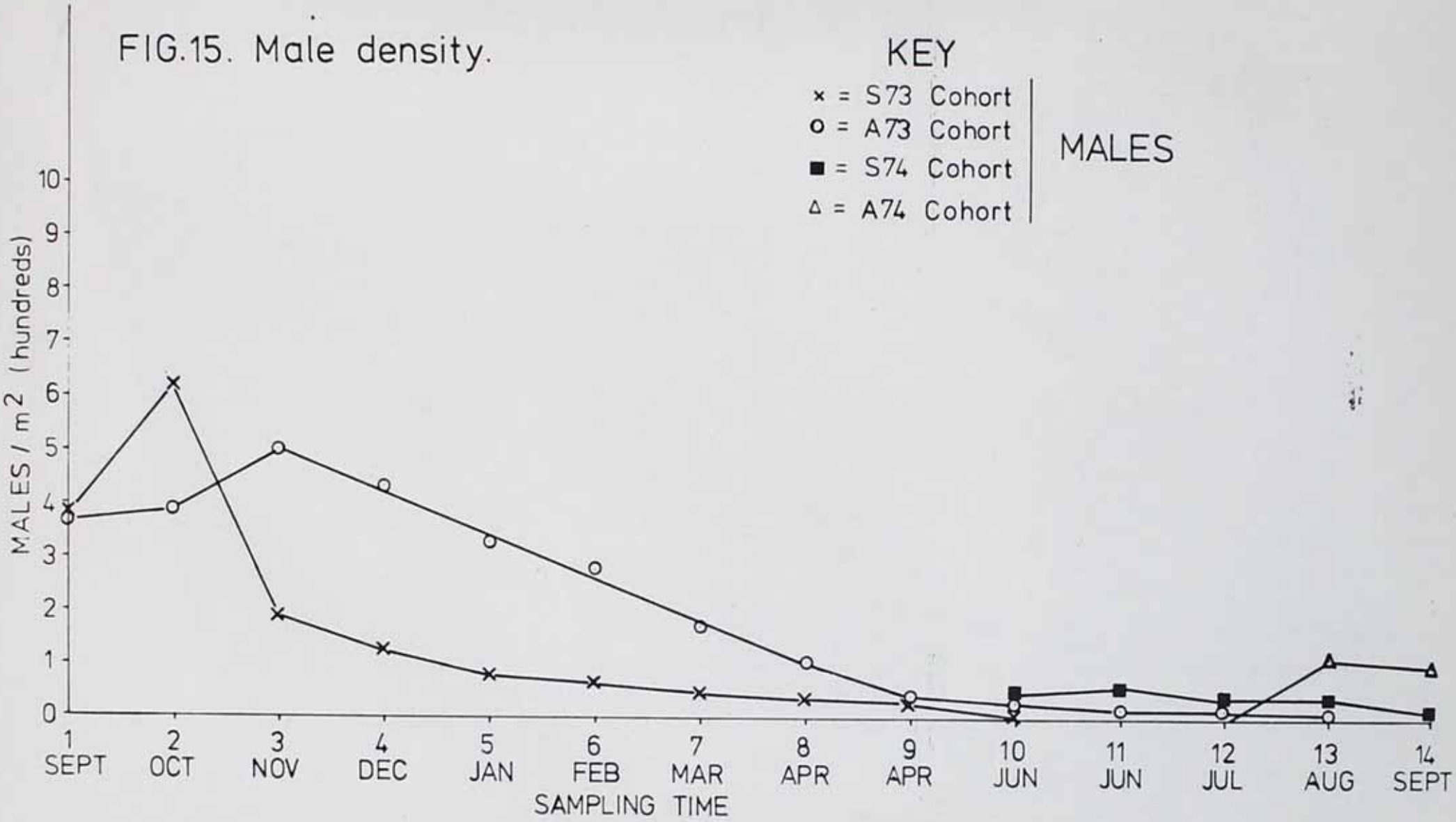


Fig. 16 Number of female *A. aquaticus* m^{-2} in Wistow Lake in each cohort at each sampling time from September 1973 to September 1974.

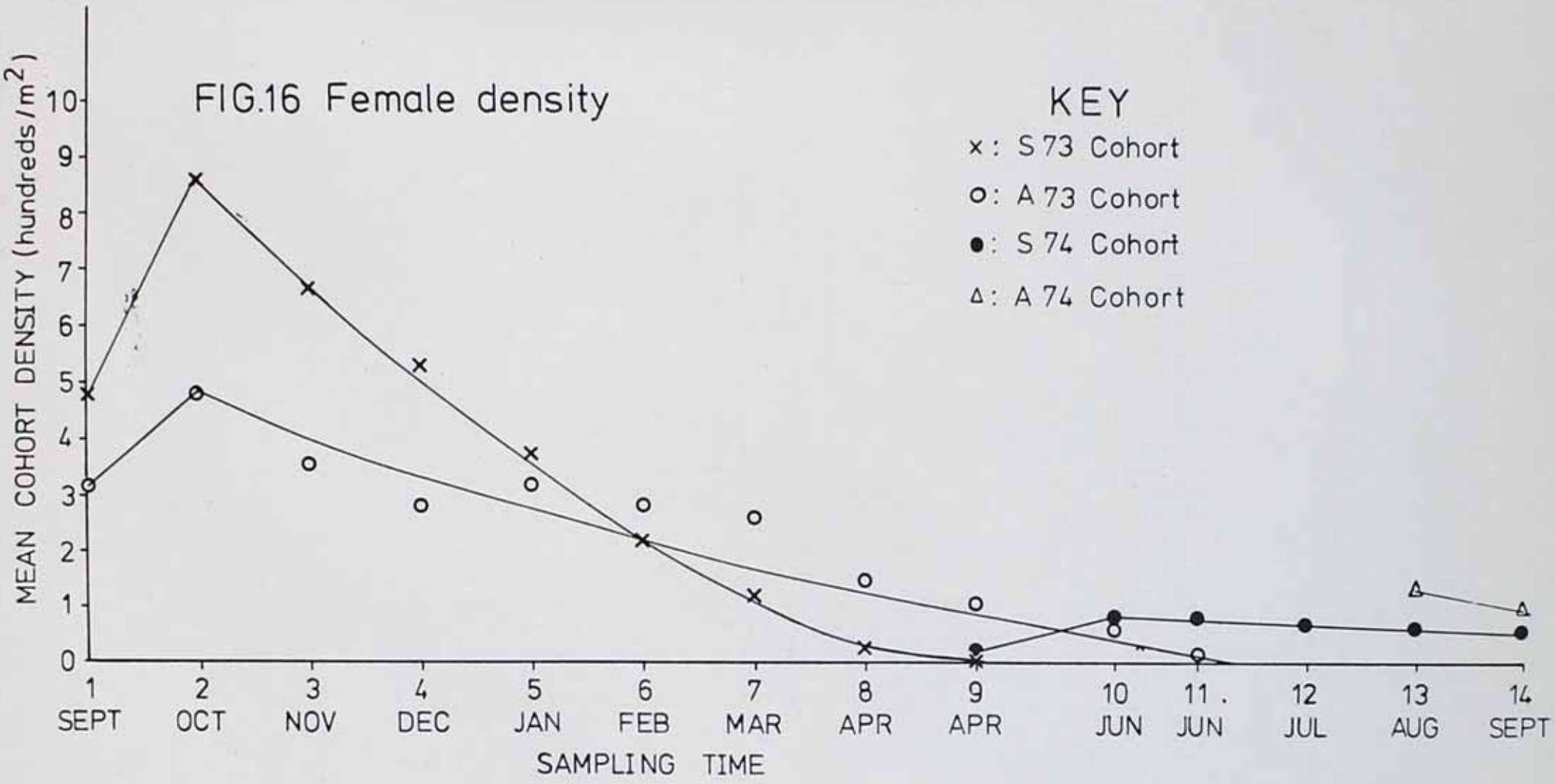


FIG.16 Female density
KEY
x : S 73 Cohort
o : A 73 Cohort
● : S 74 Cohort
Δ : A 74 Cohort
MEAN COHORT DENSITY (hundreds/m²)
0
1
2
3
4
5
6
7
8
9
10
1 SEPT
2 OCT
3 NOV
4 DEC
5 JAN
6 FEB
7 MAR
8 APR
9 APR
10 JUN
11 JUN
12 JUL
13 AUG
14 SEPT
SAMPLING TIME

Fig. 17 Number of male A. aquaticus in Wistow Lake as a percentage of the total population over 3.0 mm in each cohort at each sampling time from September 1973 to September 1974.

FIG 17 Percentage males

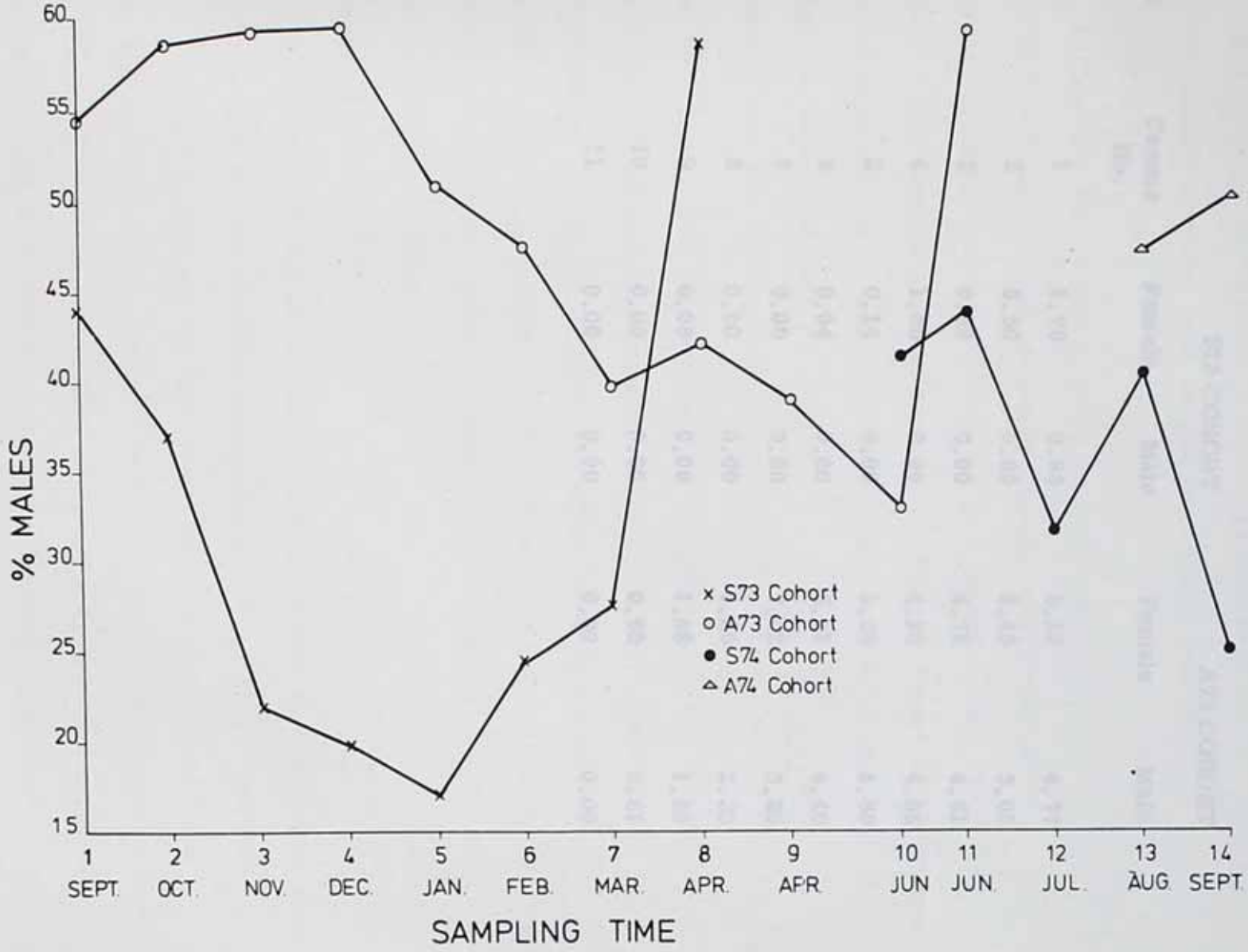


TABLE 5. The number of males and females of Asellus aquaticus in the 3.0 - 3.5 mm size class expressed as a percentage of the whole population at each sampling date.

Month	Census No.	S73 COHORT		A73 COHORT	
		Female	Male	Female	Male
Sept.	1	1.70	0.85	5.12	4.77
Oct.	2	5.50	0.69	2.45	3.05
Nov.	3	0.88	0.00	4.78	4.81
Dec.	4	1.65	0.00	4.26	4.05
Jan.	5	0.14	0.00	5.66	4.80
Feb.	6	0.04	0.00	6.12	4.40
Mar.	7	0.00	0.00	7.02	3.20
Apr.	8	0.00	0.00	4.20	2.30
Apr.	9	0.00	0.00	1.08	1.20
June	10	0.00	0.00	0.89	0.61
July	11	0.00	0.00	0.00	0.00

1) The bimodality is not always clear. This is probably due to:-

a) The difficulty of measuring the length of animals which are slightly elastic and have to be held flat with needles.

b) Unconscious operator bias in placing animals into size classes (Taylor 1965)

c) Differences in the growth rates of individual animals.

d) Cohorts being produced over a relatively long period of time.

2) The size frequency distribution may not be a normal curve. There is probably a higher mortality of larger animals giving a skewed distribution.

3) There is some measure of subjectivity in the selection of the mode where more than one peak is present.

4) The method may only distinguish fast growing from slow growing individuals.

The efficiency of the method can only be tested in terms of the reasonableness of the results obtained. With minor exceptions, which will be discussed later, the analysis has given coherent results which suggest the method is reasonable. If this is so, the method will be useful in energetics studies of populations where a major problem is the identification of individual cohorts.

2.6 Biomass and growth rates

The proportion of each size class belonging to each of the cohorts is known (Figs. 13 & 14) and the mean population m^{-2} (Fig. 11). Thus the number m^{-2} in each size class of each cohort could be determined. The data for the mean population density were taken from the rationalised curve of Fig. 11, which in practice involved using the original data except for sampling times 5 and 6. The biomass and mean dry weight individual^{-1} were then computed for each cohort at each sampling time from the length/dry

weight regression (Fig. 18). There was no significant difference between mean dry weight of male and non-gravid females, but a separate regression was calculated for gravid females (Fig. 18). The regression equations were: -

Males and non-gravid females:

$$\text{Log } y = -2.05261 + 2.77115 \log x$$

$$(s.e._b = \pm 0.06752;\ r = 0.98012;\ P < 0.001)$$

Gravid females:

$$\text{Log } y = -1.03894 + 1.85357 \log x$$

$$(s.e._b = \pm 0.06752;\ r = 0.88184;\ P < 0.001)$$

where y = individual dry wt (mg) and x = length (mm)

Dry weights were determined by vacuum drying at 60°C for 16h before weighing.

i) Males (Fig. 19). At the beginning of the investigation in September 1973, the two cohorts A_{73} and S_{73} were present, the former having a mean dry weight of 0.3 mg and the latter a mean dry weight of 0.95 mg. The spring cohort grew rapidly during the winter, reaching a peak of 4.25 mg individual^{-1} in early February 1974. This represents an average growth rate of 0.27 mg individual week^{-1} despite the low temperatures at this time (see section 3.2). By this time many of the males were in copula and the decline in mean dry weight is presumably caused by the death of the larger animals following copulation. After April the numbers were too small to give reliable mean individual dry weights.

The A_{73} males, however, showed only a slow growth rate throughout the winter, approximately 0.016 mg individual^{-1} week^{-1}, reaching a mean dry weight of 0.80 mg in April. It may be that the actual growth rate was higher than this, as the larger individuals may have copulated and died. This is shown by the May 1974 census, when the mean dry weight decreased

but following this the smaller individuals continued to grow (0.06 mg individual^{-1} week^{-1}) throughout May, June, July until August, when they presumably took part in the autumn reproduction (Fig. 19). Nevertheless, there is a marked difference in the two cohorts and the S_{73} cohort, which in the autumn 1973 was three times the dry weight of the A_{73} males were able to grow rapidly despite the cold conditions during the winter, whereas the smaller A_{73} cohort showed a much smaller growth rate at this time. It is interesting to note that the mortality of the males more than compensates for their increase in size, so the total male biomass of the A_{73} and S_{73} cohort falls (Fig. 20) throughout the winter period.

The S_{74} cohort was first identifiable at the end of April 1974. The mean individual dry weight increased slowly at first (this may be due to a slow growth rate, but also results from new recruits to the population depressing the mean) but by July the exponential growth phase had started. The mean individual dry weight in September 1974 was higher than that found in September 1973. This could have been due to a faster growth rate in 1974, or there could have been a fall in the mean dry weight between September and October as a result of post copulatory mortality.

The A_{74} cohort had established itself at approximately the same mean dry weight as in September 1973, when sampling finished. However, the biomass was much smaller, due to a much smaller population density (Fig. 20).

ii) Females. (Fig. 21). The pattern for female growth was similar to that of the male. The S_{73} cohort grew less quickly than the males throughout the winter (0.075 mg ind^{-1} week^{-1}) until they became gravid, when their mean weight increased more rapidly.

The A_{73} cohort females, like the males, grew only slowly during the winter, indeed, by May, the males averaged 0.7 mg individual^{-1} and the females 0.6 mg

Fig. 18 Relationship between dry weight and length of non-gravid (female and male) and gravid *A. aquaticus* from Wistow Lake.

Regression equations are: -

Gravids $\log y = -1.03894 + 1.85357 \log x$ ($r = 0.98012$; $n = 71$; $P < 0.001$)

Non-gravids $\log y = -2.05261 + 2.77115 \log x$ ($r = 0.88184$; $n = 21$; $P < 0.001$)

where y = dry weight (mg); x = length (mm)

FIG.18

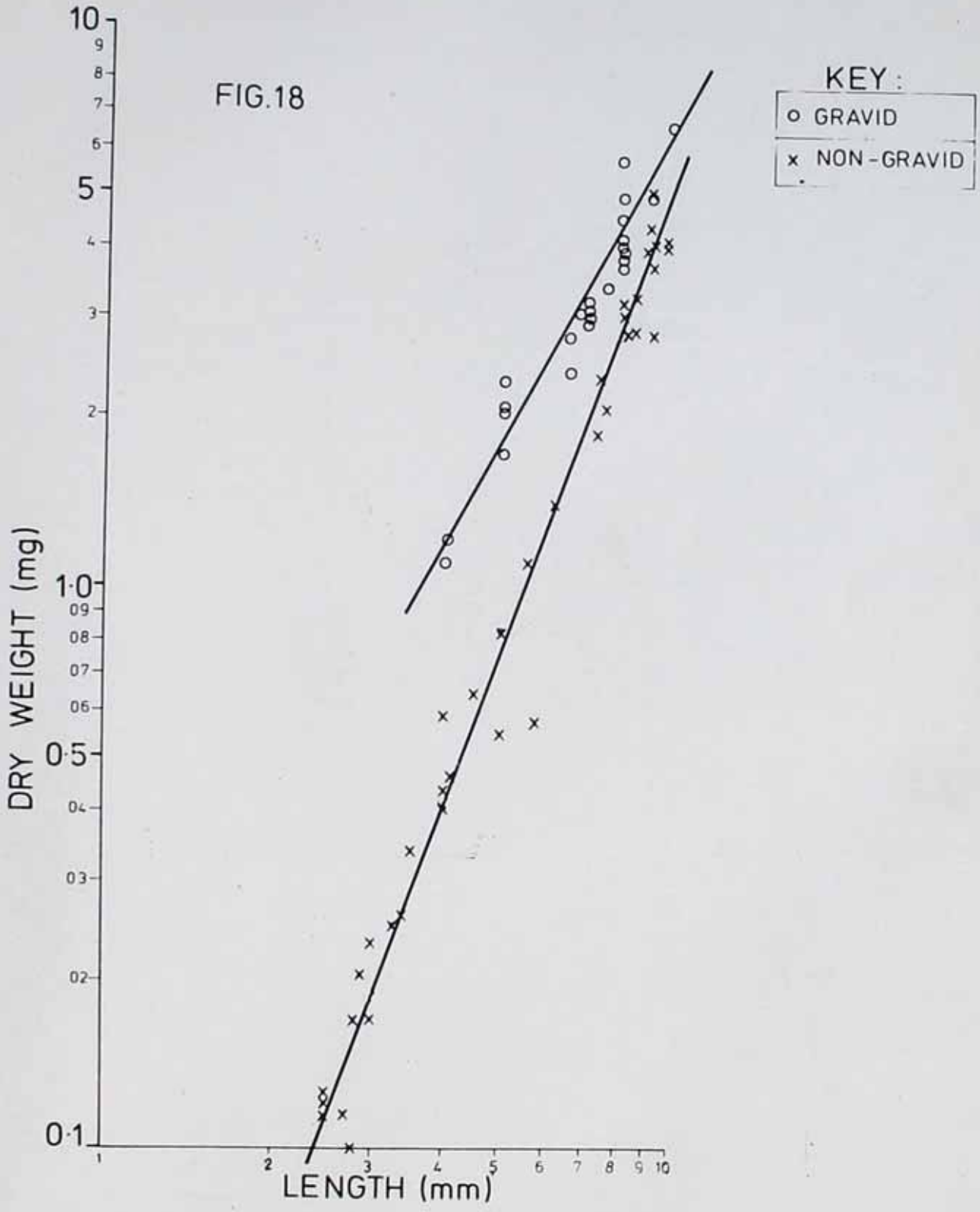

KEY :
o GRAVID
x NON-GRAVID
DRY WEIGHT (mg)
10
9
8
7
6
5
4
3
2
1·0
09
08
07
06
0·5
04
03
02
0·1
1
2
3
4
5
6
7
8
9
10
LENGTH (mm)

Fig. 19 Mean dry weight indiv^{-1} of *A. aquaticus* males in each cohort at each sampling time. Wistow Lake, September 1973 to September 1974

FIG.19 Mean dry weight-males.

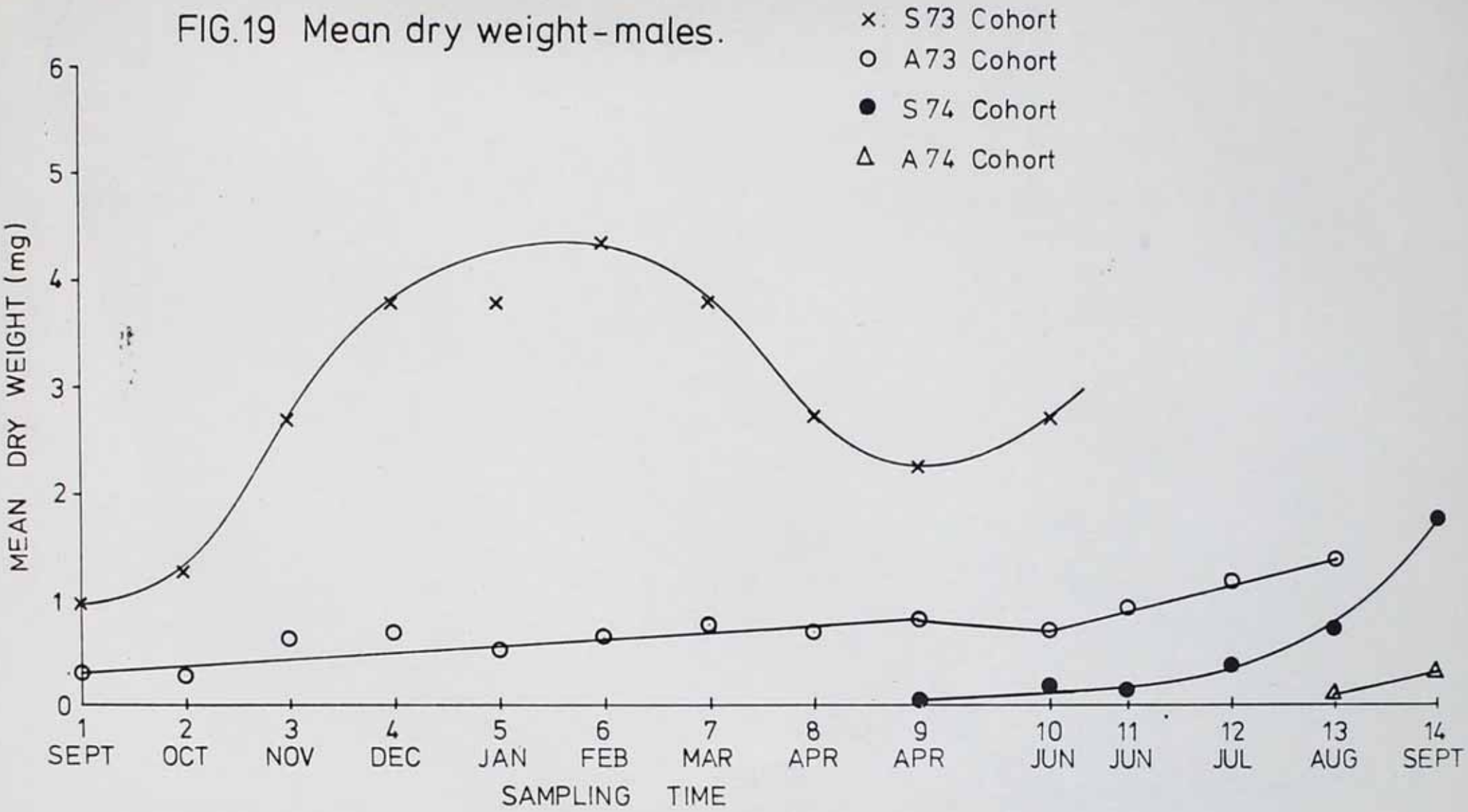


Fig. 20 Biomass (mg D.W. m^{-2}) of A. aquaticus males of each cohort, calculated as described in the text. Wistow Lake, September 1973 to September 1974.

FIG. 20 Male biomass

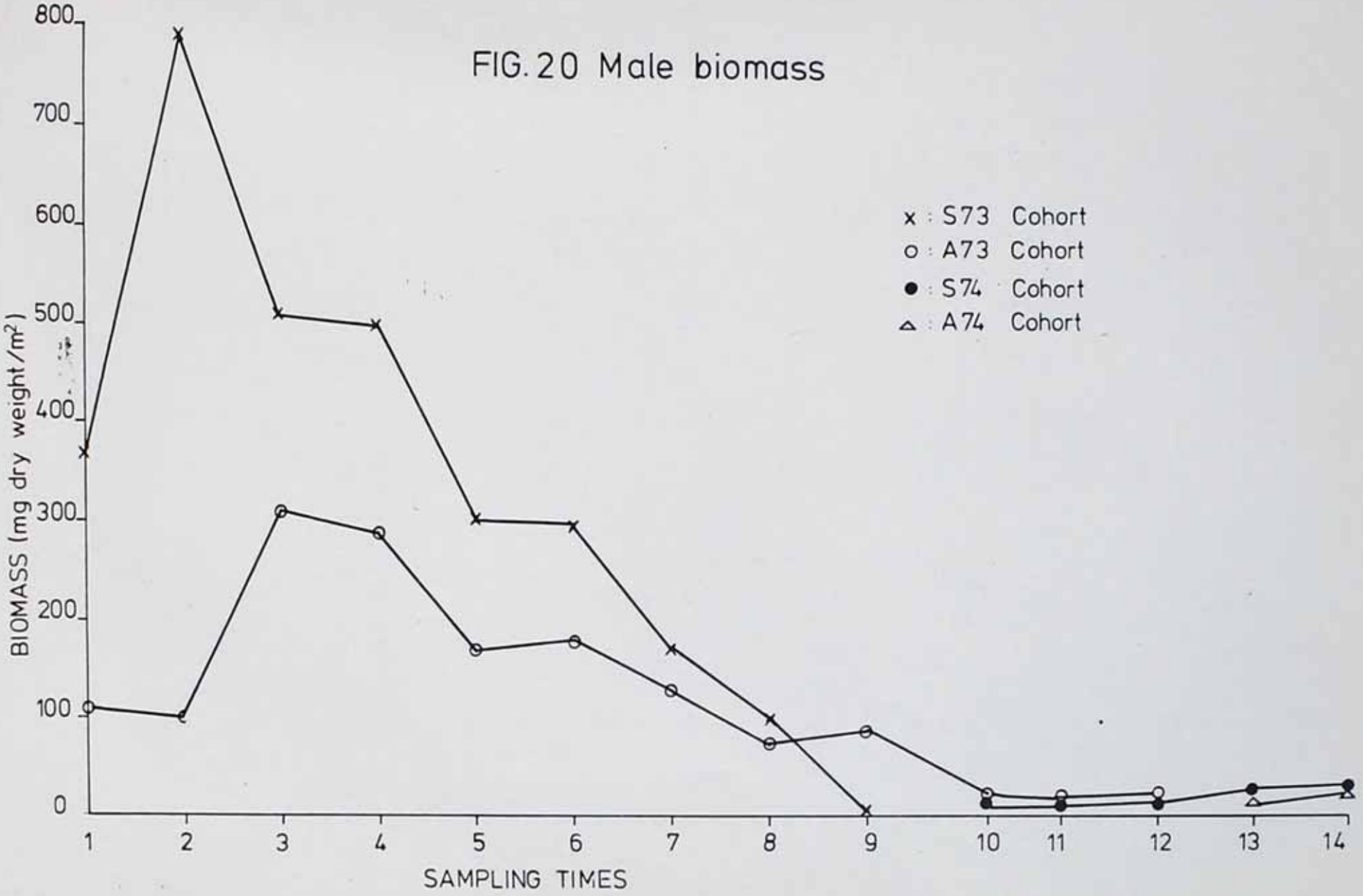


Fig. 21 Mean dry weight indiv^{-1} of A. aquaticus females in each cohort at each sampling time. Wistow Lake, September 1973 to September 1974.

FIG. 21. Mean dry weight - female

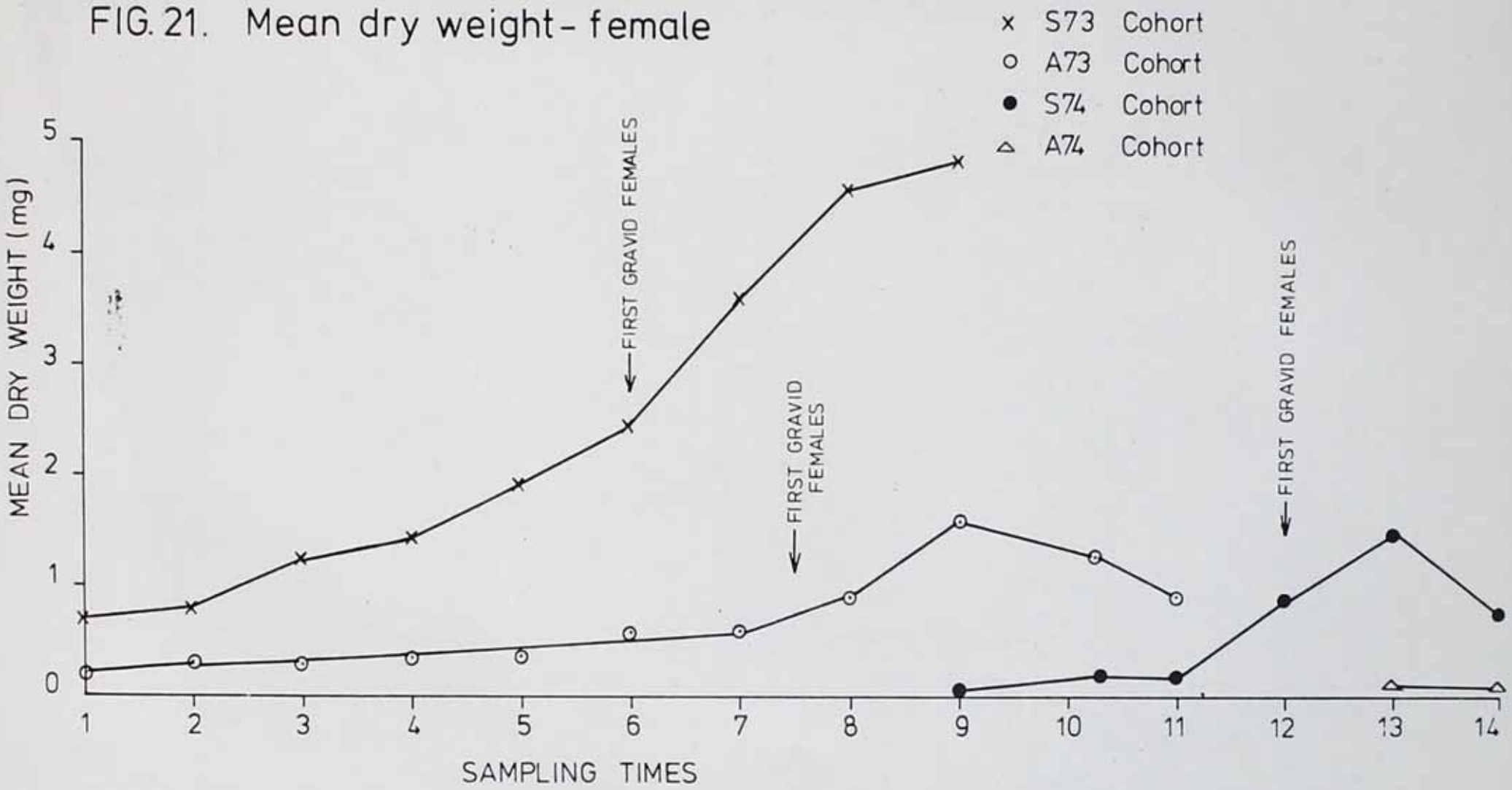
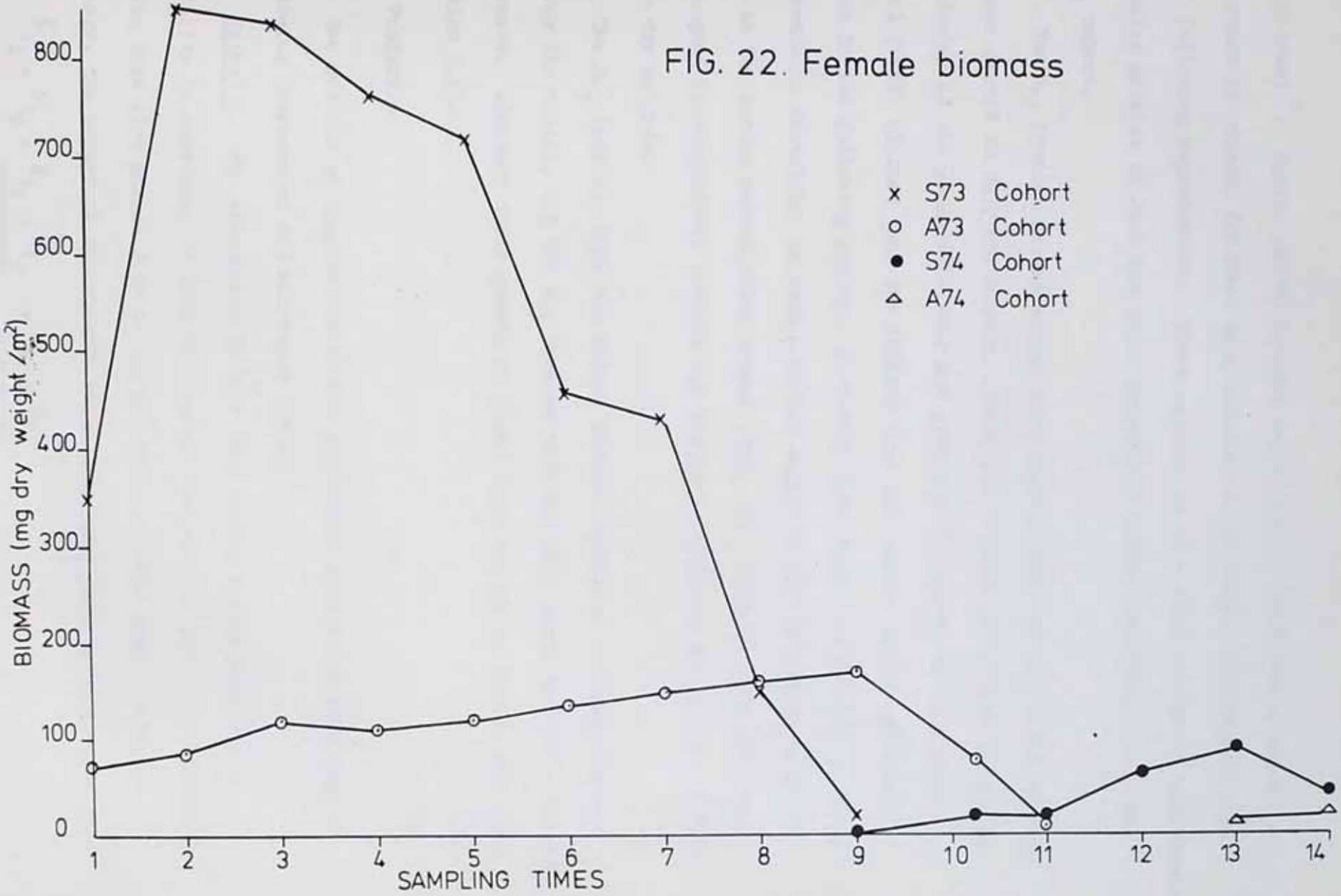


Fig. 22 Biomass (mg D.W. m^{-2}) of *A. aquaticus* females of each cohort calculated from mean densities. Wistow Lake, September 1973 to September 1974.

FIG. 22. Female biomass



individual^{-1}. Again, as the females became gravid there was a rapid increase in growth, followed by a decline as the larger individuals died off following reproduction. There appears to be a small number of non-gravid females present in June and these presumably became amalgamated with the S_{74} cohort.

The S_{74} females gained weight more rapidly than the S_{74} males as they became gravid in July and August. There was a decrease in mean weight in September as the young were shed and possibly the larger females died. Steel (1961) claimed that the females from the spring cohort can breed again in the following spring. In Wistow Lake there was not such a large increase in mortality, or such a marked change in the sex ratio as there was in the spring reproductive period (Fig. 17). With the females there is a good correspondence between the September 1973 and the September 1974 mean dry weights.

The S_{73} females, like the males, showed a decrease in total biomass during the winter, but the A_{73} females were the only group to show a biomass increase. Although their growth is slow, their mortality is low (see also section 2.4).

2.7 Production

Two methods of computation of the population production were used following Petrusewicz and Macfadyen (1970).

Method 1. The assumption is made that during a time interval T, mortality is constant, so that on average, individuals that are eliminated during this time period live to the mid-point of this time. Thus, on average, the number of individuals which will take part in production is:-

$$\bar{N}_{t_1} = N_{t_2} + \frac{N_{t_1} - N_{t_2}}{2} = \frac{N_{t_1} + N_{t_2}}{2}$$

where N_{t_1} and N_{t_2} are numbers taken at two successive sampling times.

Every individual will, on average, produce:-

$$\Delta W_{t_I} = W_{t_2} - W_{t_1}$$

where W_{t_1} and W_{t_2} are the mean dry weights of an individual animal at the same two sampling times.

Thus, production, P, is calculated as: -

$$P = \frac{N_{t_1} + N_{t_2}}{2} (W_{t_2} - W_{t_1}) = \bar{N}_{t_I} . \Delta W_{t_I}$$

In the calculation of Asellus production, numbers, N, for each sex and cohort were read from the rationalised cohort density curves (Figs. 15 & 16) and mean dry weights were taken from the mean dry weight per individual curves (Figs. 19 & 21).

Method 2. This is Allen's graphical method (Allen 1951), also used by Neess and Dugdale (1959). The number of individuals of each sex and cohort (taken from Figs. 15 & 16) were plotted against the mean dry weight (from Figs. 19 & 21) at each sampling time. The area under the curve represents the production of the cohort.

Annual production for males and females in each cohort was thus calculated for the period September 1973 to September 1974.

Two problems were encountered when applying these methods to A. aquaticus data. Firstly, an estimate has to be made of the production of the young Asellus of the S_{74} and A_{74} cohorts between their time of liberation from the brood pouch (up to this time, their growth is included in the female production) and their appearance in the sample when they reach 1·5 - 20 mm in length.

It is necessary therefore to know two parameters: numbers of young released from the brood pouch, and their mean dry weight at the time of release. The first of these is the more difficult to determine as it is difficult to estimate both the total number of females which liberate young and the average number of young produced. The first cannot be obtained by summing the number of gravid females at each sampling time, as eggs may be carried for more than four weeks (Steel 1961). For this reason the maximum number of gravid females recorded in any cohort was taken as the estimate of the egg producing population.

Steel (1961) gave data for the number of eggs produced per female. He found that the number of eggs carried varied with the female's size and that an average of 29.9% of the eggs were lost during incubation. These data were therefore applied to the present study, to estimate the likely number of young released in each cohort (Table 6) from the number of gravid females found in the population estimates.

The young, when released, are between 0.5 - 1.0 mm in length. This was observed on one brood only when 11 individuals were measured from a single female, but it confirms Steel's (1961) observation. Assuming that the length dry weight regression applied to animals of this size, an estimate was made of the dry weights of the released young, and so the production of these animals was calculated from the time of release until their appearance in the samples. The assumption made in both methods for estimating production is that the mortality rate is constant between the two census times. This may not be so with the very young animals. It seems possible that, with such a large mortality occurring at this time, a greater mortality occurs immediately after release from the brood pouch. Thus the above methods probably estimate the maximum production. A further

TABLE 6. Estimate of the number of young m^{-2} released by each cohort* of Asellus aquaticus in Wistow Lake in 1973-74.

S73 Cohort - March (Sampling date 7)

Size class	No. of gravid females	Estimated no.of eggs per brood*	Estimated no. of embryos released per brood*	Estimated total embryos released	Total Dry Weight (mg)
6.0 - 6.5	6.3	43	30	189	
6.5 - 7.0	0.0	53	37	0	
7.0 - 7.5	18.8	100	70	1315	
7.5 - 8.0	26.7	80	56	1492	
8.0 - 8.5	6.3	98	69	435	
8.5 - 9.0	15.7	98	69	1081	
9.0 - 9.5	1.6	106	74	118	
9.5 - 10.0	0.8	116	81	65	
TOTALS	76.2	-	-	4695	18.74

A73 Cohort - Late April (Sampling date 9)

5.5 - 6.0	1.1	40	28	31	
6.0 - 6.5	3.6	43	30	108	
6.5 - 7.0	3.6	53	37	133	
7.0 - 7.5	8.6	100	70	600	
7.5 - 8.0	7.2	80	56	404	
8.0 - 8.5	5.0	98	69	345	
8.5 - 9.0	0.7	98	69	48	
TOTALS	29.8	-	-	1669	6.66

S74 Cohort - August (Sampling date 13)

4.5 - 5.0	1.1	25	17	19	
5.0 - 5.5	13.7	30	21	288	
5.5 - 6.0	11.9	40	28	334	
6.0 - 6.5	4.2	43	30	126	
TOTALS	30.9	-	-	767	3.06

* Data from Steele (1961)

estimate was therefore made on the assumption that all mortality occurred immediately after release - this therefore gives the minimum production of this stage.

The second problem concerns the decrease in mean dry weight that occurs towards the end of the life span in male S_{73}, male and female A_{73} and female S_{74} (Figs. 23 & 24) animals. There are three possible causes of this decrease: -

a) The decrease could be due to a real loss in dry weight of the animals, i.e. "Weight loss (L): Biomass used for metabolic needs within a time period when R > A" (Petrusewicz & Macfadyen 1970). Such losses represent a negative production and should be deducted from production that has accrued to that data. There is some evidence from animals kept in culture that this situation can occur in post-reproductive individuals of Asellus. However, in the present study, dry weight estimations were made from length measurements. It is unlikely that any reduction in dry weight would be accompanied by a significant reduction in length, so this cannot account for the reduction in mean dry weight that can be seen in some of the Allen curves.

b) The decrease could also be due to the shedding of eggs and embryos. Loss due to this cause should not be considered as negative production but as production of the parent cohort which is subsequently passed on to the progeny as their initial biomass. It is thus P_r or production due to reproduction in the sense of Macfadyen & Petrusewicz (1970) and should therefore not be deducted from the total production.

c) The reduction in mean dry weight may also be due to selective mortality of the larger animals. Apparent negative production due to this cause should also not be deducted. Organic material that has been synthesised

and then lost due to death or predation is included in production estimates.

Thus it is concluded that the apparent negative production periods in the present study are due to the shedding of eggs and embryos and to selective predation or other mortality of the larger animals. Thus production has been calculated up to the point of the largest mean dry weight estimate. This is likely to be an underestimate of production as the smaller, non-reproductive, animals in the cohort are almost certainly growing at this time and thus adding to the cohort production. However, this growth is masked by the above causes. This is seen particularly in the A_{73} males, where the smaller animals go on growing after the death of the larger, and thus add to the cohort production. (Fig. 23 aefd).

Results. Estimates of cohort production by Allen curves are shown in 23 (male) and 24 (female) and estimates by the formula.

$$P = \frac{N_{t_2} + N_{t_1}}{2} (W_2 - W_1)$$

in Tables 7 - 10. A summary of these estimates is given in Table 11.

It can be seen that the two methods give very similar results. The two methods are basically the same, and slight errors must arise through error in estimating the area under the curves. The graphical method has the advantage of clearly showing the problems involved in the analysis.

The males of the S_{73} cohort, despite a lower density than the A_{73} males for most of the winter (Fig. 15), showed a faster growth rate (Fig.19) and therefore contributed five times as much to the total production. The ratio of S_{73} and A_{73} female production is almost exactly the same as the male (4.85:1). Another factor contributing to the smaller A_{73} production is that these animals reproduce and die at a smaller size, and although a few

A_{73} males survived to reproduce in the autumn, their numbers were too small to contribute much to the production.

Despite the small numbers of the S_{74} cohort (male and female), they contributed more to the total production than the A_{73} animals. During the summer of 1974 they showed a $\frac{P}{B}$ ratio of 8.4 (males) and 5.5 (females) (Table 11). The difference again reflects the higher growth rates of the male Asellus. If the numbers of Asellus had increased sufficiently to return the population to the 1973 level, then this cohort would have made a considerable contribution to the total production.

The A 74 cohort was present in the samples for only the last two sampling times, and therefore its contribution was small. It can be seen therefore that the autumn cohort in any Asellus population is likely to play a small role in the total production as it survives for a shorter period than the spring cohort; most of this period is during the winter and growth rates are smaller than the spring cohorts even under the same temperature conditions.

The assumptions that have to be made in estimating the production of S_{74} and A_{74} young (before they enter the samples) introduces a considerable source of error into the estimates of these cohorts, but this is not great in relation to the total production estimate. The error from this source would have been proportionately smaller had numbers not decreased during the study period.

The total production of Asellus in Wistow Lake is therefore estimated as 2.725 $g\ m^{-2}\ y^{-1}$ from an average biomass of 0.734 $g\ m^{-2}$. The females contribute approximately 50% more to these totals than the males.(Table 11).

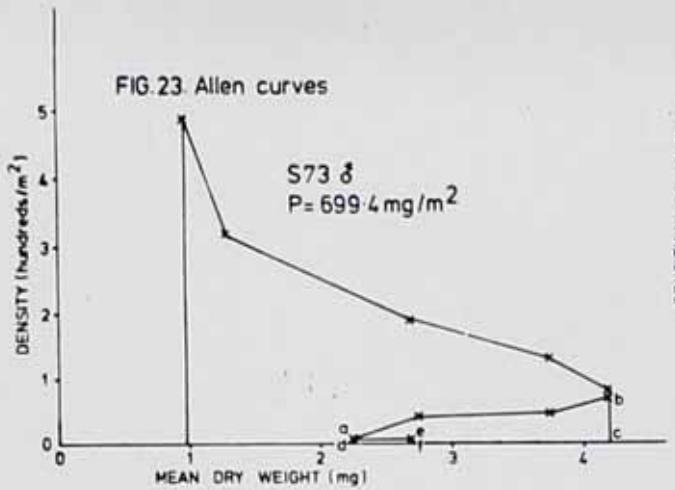
The only previous data concerning Asellus aquaticus production is that of Fitzpatrick (1968) and Andersson (1969). Fitzpatrick gave data from a pond in northern England and calculated a total dry weight production of

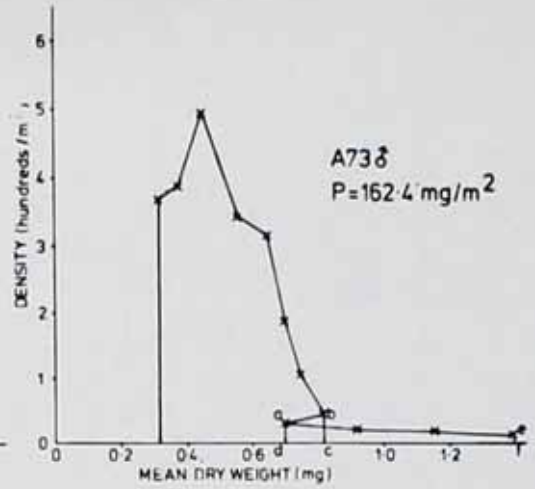
Fig. 23 Allen curves for the estimation of production of males in each cohort of A. aquaticus at Wistow Lake, September 1973 to September 1974. Curves are not drawn to the same scale. Production (P) is given as mg m^{-2} for the period the cohort was present during the study period.

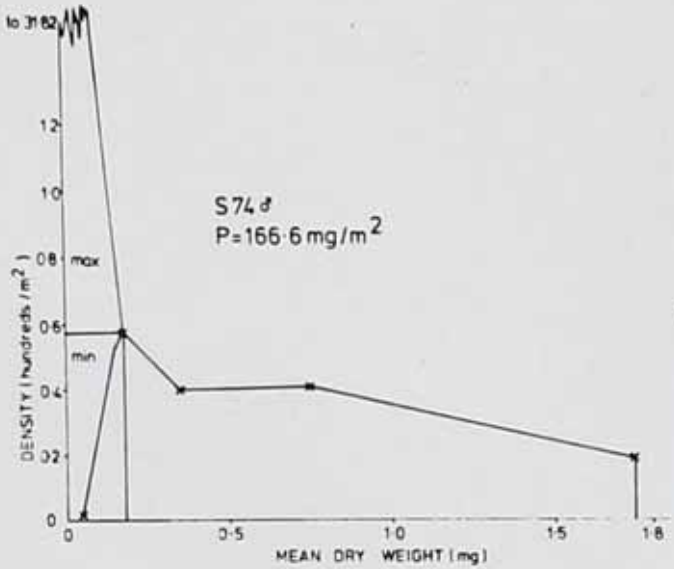
abcd = periods of apparent negative production (see text).

adef = continued production of surviving animals.

FIG. 23 Allen curves







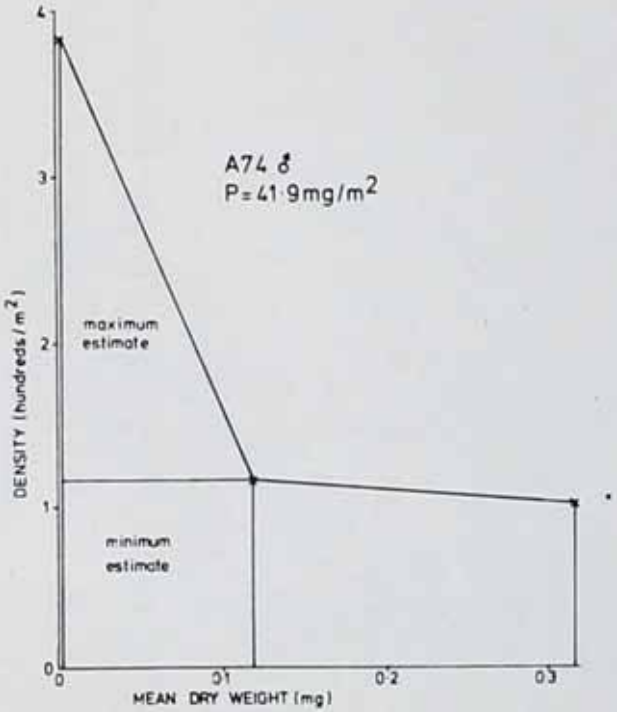
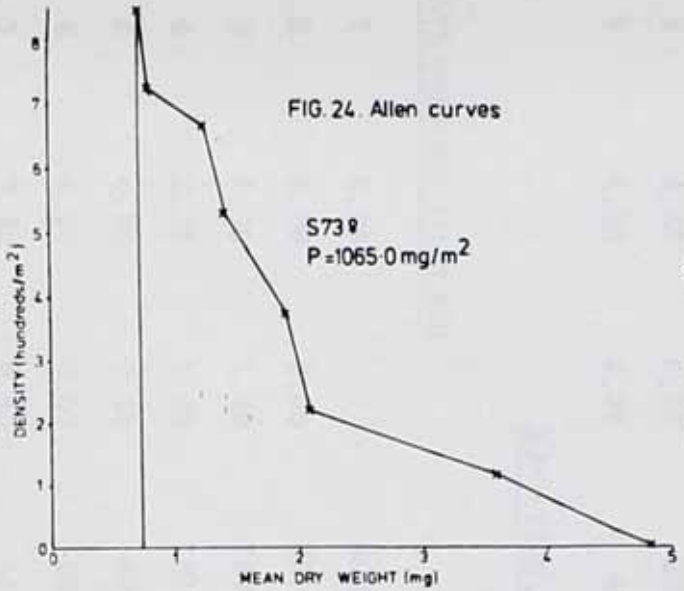
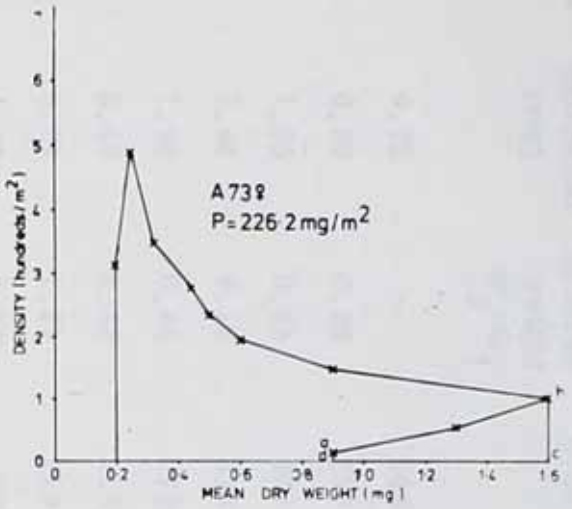


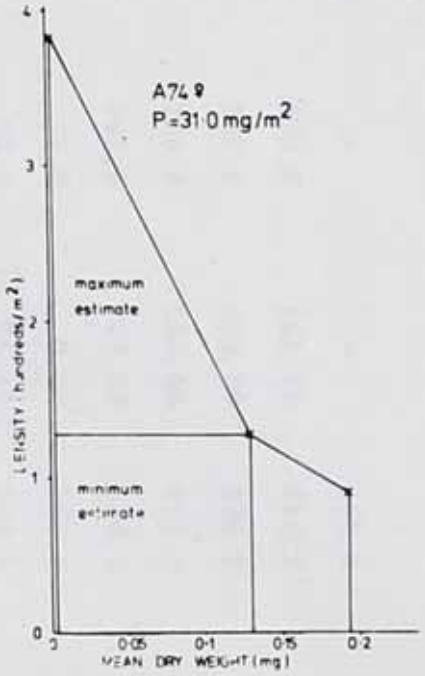
Fig. 24 Allen curves for the estimation of production of females of each cohort of *A. aquaticus* in Wistow Lake, September 1973 to September 1974. Each curve is not drawn to the same scale. Production (P) is given as mg m^{-2} for the period the cohort was present during the study period.

abcd = periods of apparent negative production (see text).

FIG. 24. Allen curves







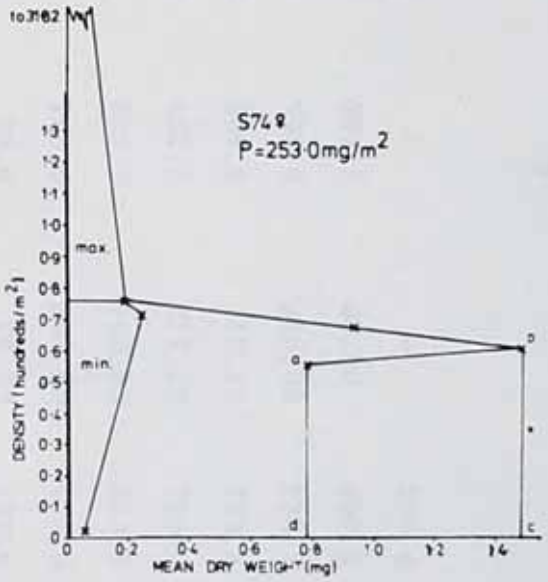


TABLE 7. Estimation of the production of males and females of the S73 cohort of A. aquaticus at Wistow Lake using the formula $P = \frac{1}{2}(N_{t_2} - N_{t_1})(W_{t_2} - W_{t_1})$.

Negative production for any time interval not included in the total (see text).

A) S73 COHORT (FEMALES)

Census No.	Mean wt. individual (mg)	Increase in mean weight $W_2 - W_1$	N/m^2	$\frac{N_{t_2} + N_{t_1}}{2}$	P (mg m^{-2})	B (mg)
1	0.72	-	845	-	-	608.4
2	0.80	0.08	750	797.5	63.80	600.0
3	1.25	0.45	667	708.5	318.82	833.7
4	1.44	0.19	530	598.5	113.72	763.2
5	1.92	0.48	375	452.5	217.20	720.0
6	2.40	0.48	218	297.5	142.80	523.2
7	3.61	1.21	119	168.5	203.89	429.6
8	4.57	0.96	27	73.0	70.08	123.4
9	4.85	0.28	4	15.5	4.34	19.4

$\Sigma P = 1134.65$ ΣB 4620.9 $\bar{B} = 513.44$

B) S73 COHORT (MALES)

1	0.95	-	490	-	-	465.5
2	1.30	0.35	320	405.0	141.75	416.0
3	2.70	1.40	187	253.5	354.90	504.9
4	3.75	1.05	131	159.0	166.95	491.3
5	4.20	0.45	80	105.5	47.47	336.0
6	4.20	0.00	68	74.0	0.00	285.6
7	3.75	- 0.45	45	56.5	[- 25.42]	168.8
8	2.75	- 1.00	38	41.5	[- 41.50]	104.5
9	2.25	- 0.50	7	22.5	[- 11.25]	15.8
10	2.70	0.55	7	7.0	3.85	18.9

$\Sigma P = 714.92$ $\Sigma B = 2807.15$ $\bar{B} = 311.91$

TABLE 8. Estimation of the production of males and females of the S73 cohort of A. aquaticus at Wistow Lake using the formula $P = \frac{1}{2}(N_{t_2} - N_{t_1})(W_{t_2} - W_{t_1})$.

Negative production for any time interval not included in the total (see text).

A) A73 COHORT (FEMALES)

Census No.	Mean wt. individual (mg)	Increase in mean weight $W_2 - W_1$	N/m^2	$\frac{N_{t_2} + N_{t_1}}{2}$	P (mg m^{-2})	B (mg)
1	0.20	-	312	-	-	62.4
2	0.26	0.06	490	401.0	24.06	127.4
3	0.34	0.08	400	445.0	35.60	136.0
4	0.38	0.04	325	362.5	14.50	123.5
5	0.44	0.06	278	301.5	18.09	122.3
6	0.50	0.06	234	256.0	15.36	117.0
7	0.57	0.07	190	212.0	14.84	108.3
8	0.92	0.35	148	169.0	59.15	136.2
9	1.61	0.69	105	76.5	52.79	169.1
10	1.30	- 0.31	60	82.5	[- 25.57]	78.0
11	0.91	- 0.39	15	37.5	[- 14.62]	13.7

$\Sigma P = 234.39$ $\Sigma B = 1193.8$ $\bar{B} = 108.53$

B) A73 COHORT (MALES)

1	0.32	-	376	-	-	120.3
2	0.38	0.06	388	382.0	22.92	147.4
3	0.45	0.07	425	406.5	28.46	191.3
4	0.50	0.05	345	385.0	19.25	172.5
5	0.56	0.06	265	305.0	18.30	148.4
6	0.65	0.09	182	223.5	20.12	118.3
7	0.70	0.05	172	177.0	8.85	120.4
8	0.75	0.05	109	140.5	7.03	81.8
9	0.82	0.07	69	89.0	6.23	56.6
10	0.70	- 0.12	31	50.0	[- 6.00]	21.7
11	0.92	0.10	21	26.0	2.60	19.3
12	1.16	0.24	21	21.0	5.04	24.4
13	1.40	0.24	16	18.5	4.44	22.4

$\Sigma P = 143.24$ $\Sigma B = 1244.7$ $\bar{B} = 95.75$

TABLE 9. Estimation of the production of males and females of the S74 cohort of A. aquaticus at Wistow Lake using the formula $P = \frac{1}{2} (N_{t_2} - N_{t_1}) (W_{t_2} - W_{t_1})$.

Negative production for any time interval not included in the total (see text).

Census No.	Date	Mean wt. individual (mg)	Increase in mean weight $W_2 - W_1$	N/m^2	$\frac{N_{t_2} + N_{t_1}}{2}$	P ($mg\ m^{-2}$)	B (mg)
	Birth	0.00399	-	3182	-	-	12.70
11		0.196	0.192	76	1629.0	14.58 (min) 312.50 (max)	14.88
12		0.945	0.749	68	72.0	53.95	64.27
13		0.497	0.552	62	65.0	35.85	92.80
14		0.790	- 0.706	57	59.5	[- 42.02]	45.05

$\Sigma P = 402.30$ (max) $\Sigma B = 229.70$ $\bar{B} = 45.94$
104.38 (min)

B) S74: MALES

	Birth	0.00399	-	3182	-	-	12.70
11		0.138	0.134	59	1620.5	7.89 (min) 216.73 (max)	8.13
12		0.370	0.232	41	50.0	11.60	15.16
13		0.731	0.362	42	41.5	15.01	30.72
14		1.797	1.065	19	30.5	32.49	34.14

$\Sigma P = 275.83$ (max) $\Sigma B = 100.84$ $\bar{B} = 20.17$
66.99 (min)

TABLE 10. Estimation of the production of males and females of the A74 cohort of A. aquaticus at Wistow Lake using the formula $P = \frac{1}{2}(N_{t_2} - N_{t_1})(W_{t_2} - W_{t_1})$. Negative production for any time interval not included in the total (see text)

A) A74 COHORT: FEMALES

Census No.	Date	Mean wt. individual (mg)	Increase in mean weight W_2-W_1	N/m^2	$\frac{N_{t_2}+N_{t_1}}{2}$	P ($mg\ m^{-2}$)	B ($mg\ m^{-2}$)
	Birth	0.00399	-	383	-	-	1.53
13		0.130	0.126	128	255.5	16.13 (min) 32.20 (max)	16.64
14		0.188	0.058	91	109.5	5.26	17.09

$\Sigma P = 37.46$ (max) $\Sigma B = 35.26$ $\bar{B} = 11.75$

21.39 (min)

B) A74 COHORT : MALES

	Birth	0.00399	-	383	-	-	1.53
13		0.119	0.115	117	250.0	13.98 (min) 29.87 (max)	13.98
14		0.318	0.198	102	109.5	21.72	32.42

$\Sigma P = 35.70$ (min) $\Sigma B = 47.93$ $\bar{B} = 15.98$

51.59 (max)

TABLE 11. Production (mg $m^{-2} y^{-1}$) and mean biomass (mg m^{-2}) estimates for each cohort of A. aquaticus in Wistow Lake for the year September 1973 - September 1974.

	MALES			FEMALES			TOTAL		
Cohort	P	B	P/B	P	B	P/B	P	B	P/B
S73	714.92	311.91	2.29	1134.65	513.44	2.21	1849.57	825.35	2.24
A73	143.24	95.75	1.45	234.39	108.53	2.15	377.63	204.28	1.85
S74	171.41	20.17	8.40	253.34	45.94	5.51	424.75	66.11	6.42
A74	43.64	15.98	2.73	29.43	11.75	2.50	73.07	27.73	2.64
Total for year *	1073.21	300.04	3.58	1651.81	434.26	3.80	2725.02	734.31	3.71

*Mean biomass for year calculated from total biomass at each census divided by the total number of census times (14).

4.86 $g\ m^{-2}$ with Asellus population densities somewhat higher than the present study. Unfortunately, the average biomass is not clear from the pond study. In Fitzpatrick's study the males gave a higher production than the females, but he found no gravid females between April and August (section 2.2), and his study period did not include the months August to November. He may thus have underestimated reproductive production.

If Andersson's data is recalculated as dry weights (assuming a dry weight: fresh weight ratio the same as at Wistow Lake), he found an annual production of 3.37 $g\ m^{-2}$ in Pajeb Maskejaure and 6.33 $g\ m^{-2}$ in Lake Erken. Again, this with higher Asellus population densities than at Wistow Lake.

The most useful method of comparing production at different sites is to relate production to mean biomass. The $\frac{P}{B}$ ratio is a measure of how much new material is synthesised per annum by a given unit of animal material. It is thus a measure of the efficiency of biomass production (Petrusewicz & Macfadyen 1970).

Andersson found a $\frac{P}{B}$ ratio of 1.96 in Pajeb Maskejaure and 2.03 in Lake Erken (males and females were not separated). This is low compared with an overall ratio of 3.71 in Wistow Lake. The smaller ratio in Sweden may reflect differences in growth rates due to colder conditions in winter. Pajeb Maskejaure is covered with ice from December to April and Asellus growth ceased from the end of October until the end of April. In Lake Erken, growth ceased for a shorter period. There was no cessation of growth of A. aquaticus in winter in Wistow Lake; indeed, the S_{73} cohort showed their fastest growth rates ($mg\ ind^{-1}$) in winter (November - December).

It should also be noted that had the population biomass not shown a marked decline during the study period, the S_{74} cohort would have played a much bigger role in determining total production. During the summer its

$\frac{P}{B}$ ratio was much higher (Table 11). Therefore the ratio given here may be an underestimate.

Saito (1969) gives data which allows the calculation of $\frac{P}{B}$ ratios for 1 year old Armadillidium vulgare (Latreille) in a Japanese temperate forest. The index of 2.93 is lower than that obtained in the present study and again there appeared to be no growth of Armadillidium between November and April of the study year.

No estimate has been made in the present study of the production which is lost through the shedding of exuviae in A. aquaticus. Fitzpatrick (1968) calculated that this was 6 - 7% of the total production. Very few complete exuviae were found in cultured animals, which suggests they are often eaten, but clearly this could be a source of error and requires further investigation.

3. RESPIRATION STUDIES

3.1 Introduction

Ecologists have used respiration studies for two primary purposes. Firstly, respiration is measured in order to assess one of the parameters in the formulation of an energy budget. Secondly, it has been used as a convenient measure of metabolic activity in order to assess or compare the role of populations in ecosystem processes (Petrusewicz & Macfadyen 1970). The measurement of respiratory activity however, raises a number of practical problems.

In order to estimate the respiratory activity of the field population, it is necessary to know the respiratory rate of all the life stages or size classes in the population, and its relation to temperature (and perhaps other environmental parameters). In addition, detailed information of population density and size class structures is required. This clearly involves either

a large number of determinations of respiratory activity or the acceptance of an overall population estimate in which a number of assumptions are made concerning the relationship between respiration rate and weight, and respiration rate and temperature (Phillipson, 1963). Whilst it is profitable to explore the latter approach, there are too few data at the present time on which to base an objective estimate of their reliability, and it is necessary to obtain more detailed estimates in order to make this assessment.

If the more detailed computation of population respiration is to be pursued, the invertebrate ecologist requires efficient and reliable methods by which the respiration of single or small groups of animals can be measured. It is for this reason that attempts have been made to develop a continuous recording respirometer (e.g. Macfadyen 1961) and why the more convenient respirometers such as the Gilson differential respirometer (Gilson 1963) have recently been favoured. However, no critical evaluation of the reliability of the Gilson instrument has been made. Lawton and Richards (1970) have shown that the Gilson apparatus gives comparable results to the Cartesian Diver, Warburg and Winkler methods of measuring respiratory rates of aquatic invertebrates. They do not, however, mention the use of control (thermoblank) flasks and few papers give detailed methodology, despite the possibility of large errors arising from such sources as fluctuating room temperature (Carver and Gloyn 1971).

Another problem is to relate respiratory measurements to field conditions. There is no immediate answer to the problem of whether an animal respires in an enclosed vessel at the same rate as it does in the field. Problems concerned with the effect of change in temperatures on the rate of respiration can be overcome however. These short-term changes or acclimation problems have largely arisen in ecological production studies because of the

practice of carrying out respiratory measurements within a restricted time period, so that inevitably the animal is subjected to a substantial temperature change when transferred from field to experimental conditions. Further problems arise with terrestrial animals when they are transferred from fluctuating to constant conditions. It was hoped to overcome both the latter problems by working with an aquatic organism, which is not subjected to large temperature fluctuations (section 3.2), and by carrying out respiratory measurements at intervals throughout the year at the temperature at which the animals were collected in the field. Such a study would also enable an appraisal of the accuracy and sensitivity of the Gilson respirometer at low rates of oxygen uptake. It would also enable the 'best estimate' method of population respiration (Phillipson 1963, 1970) to be compared with more detailed computations. Thus it would provide a measure of one parameter in calculating the energy budget and also give an assessment of the role of the organism in the ecosystem.

3.2 Field temperatures

Method. A Cambridge continuous temperature recorder (The Cambridge Instrument Company) was placed on the southern shore of Wistow Lake for the duration of the study. Here the water was shaded from direct sunlight for most of the day by the fringe of trees (Fig. 3). This position was chosen in order to minimise the possibility of interference. The temperature sensitive mercury filled steel bulb of the recorder was situated on the lake bottom in about 30 cm of water, about 2 m from the shore; this position was dictated by the length of the steel capillary tube which connects the steel bulb to the pen recorder.

Results. Only eleven days data was lost during the year because of interference, and a further twelve days data (in blocks of 2 - 3 days) was

lost because of failure of the pen recorder (See Appendix B). Weekly mean temperatures could therefore be calculated for all but one week of the study period (Fig. 25). Maximum and minimum temperatures for each day were read from the charts and daily and weekly means were calculated as the mean of the maximum and minimum temperatures. Fig. 25 shows the weekly means together with the weekly maximum and minimum temperatures.

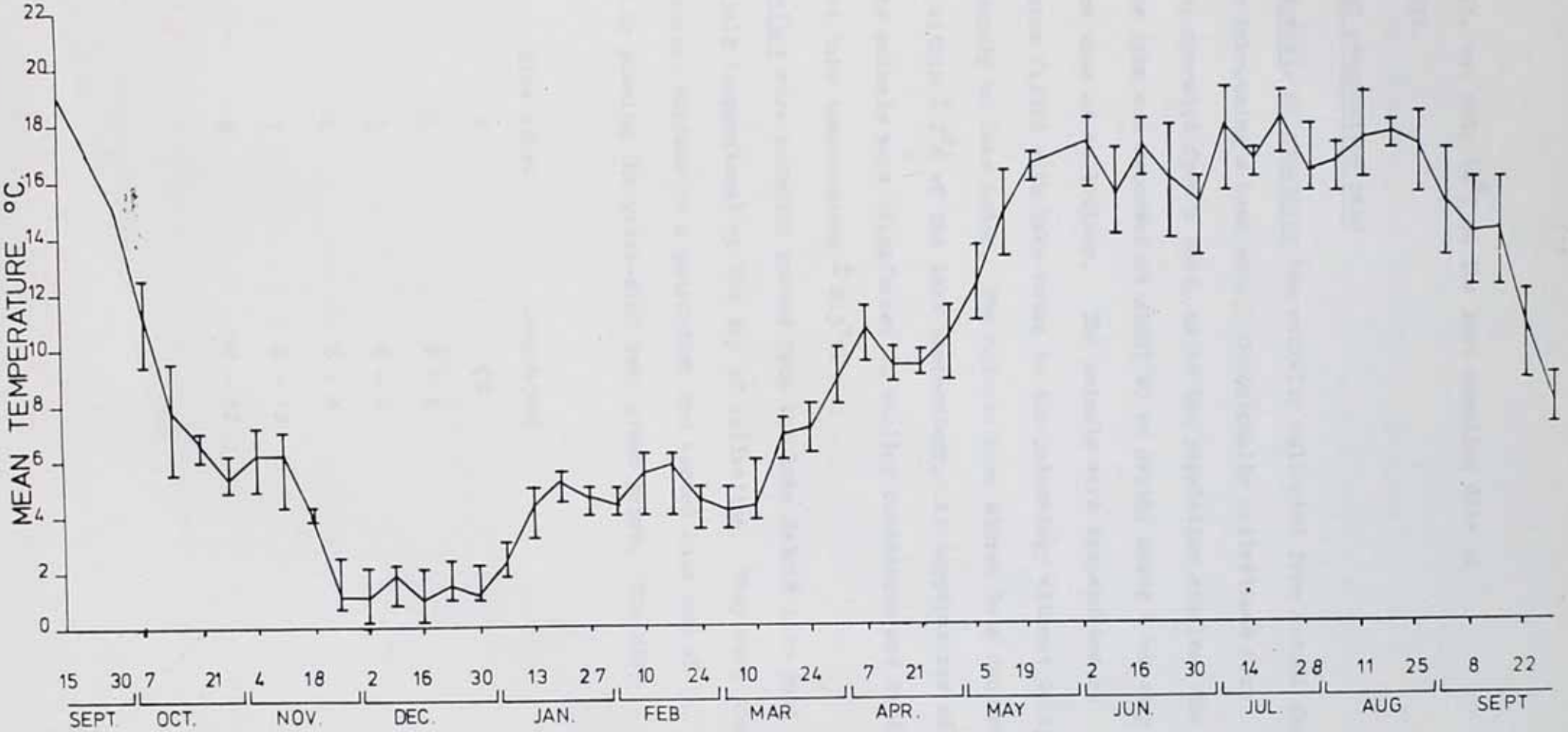
The diurnal temperature variation was very small throughout the year. It reached 2°C on only two days of the year and was between 1 and 2°C on a further 58 days. The remaining days showed a temperature variation of less than 1°C. It was noticeable that the highest temperature recorded in any 24h period often occurred at night. It is thought that the open areas of the lake warmed first during the day and that the shaded southern side (where the temperature recorder was situated) became warmer later in the day due to mixing.

The weekly variation in water temperature never exceeded 4°C; and exceeded 3°C in only 10 weeks of the year. In 28 weeks, more than half the year, it was less than 2°C. Thus Asellus experiences a rather constant temperature regime at the bottom of Wistow Lake.

The field study began in 1973 towards the end of a period of fine weather during which a water temperature of 21°C had been recorded. Temperatures fell rapidly in the autumn and late November/early December was exceptionally cold for Leicestershire. Sampling was delayed for three days in early December because of ice on the lake surface. In contrast, there were no periods of sustained fine weather during the summer, and mean water temperatures fluctuated between 16 and 18°C for most of the mid-May to mid-August period. Temperatures again fell rapidly in the autumn, but much earlier in 1974 than in 1973. Thus the water temperature was 19°C on the first sampling date in

Fig. 25 Weekly maximum, minimum and mean water temperatures from September 1973 to September 1974 in Wistow Lake. Mean temperature was calculated as the mean of the daily maximum and minimum temperatures. Data for September 1973 are based on thermometer readings taken on visits before continuous recording commenced.

FIG. 25.


MEAN TEMPERATURE °C.
22
20
18
16
14
12
10
8
6
4
2
0
15 30 7 21 4 18 2 16 30 13 27 10 24 10 24 7 21 5 19 2 16 30 14 28 11 25 8 22
SEPT. OCT. NOV. DEC. JAN. FEB MAR APR. MAY JUN. JUL. AUG SEPT

mid-September 1973, but only 14°C on the last sampling date on 18th September 1974.

3.3 Measurement of respiration rate

Collection of material. A. aquaticus was normally collected from around the margins of Wistow Lake, using a hand net. Occasionally collections were made using a grab, operated from a boat, as in the population studies. The temperature of the lake was recorded at about 20 cm depth, using a mercury thermometer at the time of collection. The animals were transported in polythene containers filled with lake water to the laboratory without delay, together with a supply of lake water. The animals were stored in a constant temperature room within ± 2°C of the lake temperature. At temperatures of 5°C and below, the animals were transferred to smaller containers and kept in a water bath at lake temperatures ± 0.5°C.

Sorting. The Asellus were normally sorted from the lake debris into pond water (also at field temperature) on the day of collection. They were then placed on their dorsal surface in a petri-dish and sorted into one of 6 length classes by placing the petri-dish over graph paper. The size classes were: -

Size class	Length(mm)
1	<2
2	2 - 4
3	4 - 6
4	6 - 8
5	8 - 10
6	10 - 12

In most experiments, no attempt was made to separate the sexes, as this was time-consuming and would have subjected the animals to undue temperature fluctuations. In later experiments, when working at higher temperatures, the larger animals were sexed (Figs. 27 - 30) and in all cases gravid females were kept separate from non-gravid animals.

The animals were counted into groups in preparation for respirometry: size classes 1 - 3 contained 10 animals per group, class 4 contained 5 animals per group, and size classes 5 and 6 contained 3 - 5 animals per group. No attempt was made to make an equal number of determinations on each size class. The number of determinations depended upon the proportion of each size class in the population sample. In some months, certain size classes were not available (Figs. 5 & 6).

After sorting, the groups were placed in small beakers or specimen tubes and suspended in a water bath maintained at field temperature $\pm$ 0.5°C until required for respirometry.

Respirometry. Determinations of oxygen uptake were made in the three days following the collection of the animals. The Asellus were transferred to 7.5 cm^3 Gilson flasks, each containing 1.0 ml lake water at the field temperature. Fourteen reaction flasks were available on the apparatus (see section 3.4), thus a total of 28 to 42 measurements were normally made at each temperature.

A 1.5 x 1.0 cm piece of filter paper was placed in the centre well of each flask, which was then half-filled with 5% potassium hydroxide solution to absorb carbon dioxide. Each flask was then immediately placed on the Gilson apparatus, the water bath temperature having previously been adjusted and equilibrated to field temperature. The flasks were allowed to equilibrate for one hour before readings commenced.

The detailed procedure for use of the Gilson apparatus is decribed in the next section.

Readings were taken at 30 minute intervals for three to four hours between 11.30h and 15.00h. At the end of this period, the flasks were removed and the animals anaesthetised in 1% Sandoz (Ethyl-m-amino-benzoate methane sulphonic acid) solution. They were then washed in distilled water, blotted dry on tissue paper, transferred to numbered foil pans and weighed (live weight). They were then dried in a vacuum oven at 60°C for 16 - 20h and subsequently weighed to obtain the dry weight to within 0.01 mg.

3.4 The Gilson Differential Respirometer

Introduction. Initial attempts to measure the respiration rate of single individuals and of small groups of Asellus showed that the smaller animals, even in groups of ten, would respire at rates of less than 5.0 $\mu l\ h^{-1}$ at 12°C. Accurate and reliable measurements of these rates were not possible because thermo blanks (control flasks), run at the same time, showed an apparent gas output varying between 0.4 - 3.2 $\mu l\ h^{-1}$ and averaging 1.8 $\mu l\ h^{-1}$ (14 flasks). Carver and Gloyn (1971) had shown that variations in ambient room temperature could cause considerable errors in Gilson respirometer readings, due to the temperature variation in those parts of the respirometer not immersed in the water bath. The results reported above were obtained with the Gilson respirometer situated in a constant temperature room at 15°C $\pm$ 1.5°C. Therefore to measure the respiratory rates of the small size classes of Asellus, it was necessary to reduce the control flask variation, and three further sources of error were identified and investigated.

(i) Heating effects of the refrigeration unit. The initial experiments were conducted in a constant temperature room at 15°C $\pm$ 1.5°C, but it was

found that heat from the refrigeration unit caused the temperature at the rear of the apparatus (in the region of the connecting Tygon tubing) to rise to 19°C. This effect was reduced by fitting an aluminium foil baffle over the tubing, thus deflecting the hot air, and also placing the apparatus in a more efficiently cooled room, with a powerful circulating fan. This reduced the readings of the control flasks to an average of 0.6 μl h^{-1} (20 flasks) with a variation between flasks from 0.0 μl h^{-1} - 1.8 μl h^{-1}. The latter rate is still sufficiently high to cause concern if oxygen uptakes in the region of 5 μl h^{-1} are being measured.

ii) Time taken for equilibration. Despite the above precautions, unacceptable variations were again recorded in the control flasks when making measurements at low temperatures (e.g. 4°C), but with an ambient temperature of 12°C. The normal experimental procedure was to fit the reference flask to the apparatus when the respirometer was switched on about one hour before the experimental flasks were connected. The reference flask was partially filled with a volume of distilled water at the ambient temperature, so that the remaining volume of air in the reference flask was equal to the total volume of air in the reaction and control flasks. Thus 120 cm^3 water were added to a 270 cm^3 flask when using 20 x 7.5 cm^3 flasks, each containing 1 cm^3 water.

The desired bath temperature was then reached within 45 minutes, and the reaction flasks could be connected after one hour and a further hour allowed for equilibrium before readings were begun, i.e. two hours after the reference flask had been fitted.

The variation in the thermo blanks took the form of a steady apparent gas output over the next three hours, e.g. over the period of the oxygen uptake measurements. It was found, however, that if the measurements were

continued for a longer period then the thermo blanks ceased to drift in this manner.

As can be seen from Fig. 26 , when the reference flask contained 120 cm^3 of distilled water, it took 4.5h for the apparent output in the control flasks to cease. With 31 cm^3 the apparent output was less, but equilibration equally long. Only with 10 and 6 cm^3 (which gave very similar results) was equilibration achieved within the 2 hour period normally allowed - and none of the thermo blanks then showed movement greater than 0.5 $\mu l\ h^{-1}$.

These results show that if a large amount of water is used with bath temperatures which are lower than the ambient temperature, then it may take several hours for the reference flask to reach thermal equilibrium. The Gilson instruction manual suggests that sufficient water should be added to the reference flask to give a gas volume exactly equal to that in the reaction vessels. This would normally mean adding about 120 cm^3 of water to the standard 250 cm^3 flask when using 20 x 7.5 cm^3 reaction flasks each containing about 1 cm^3 of liquid, and this could take 4.5h to equilibrate with a temperature differential of 8°C between room and bath temperatures.

The data presented in Fig. 26 (a) suggest that smaller amounts of water, giving a reference flask: active flasks ratio of up to 2:1 will give good results. Umbreit, Burris & Stauffer (1957) suggest that such a ratio will give more stable readings, and this method was used throughout the present study. When working at low temperatures, pre-cooled water was added to the reference flask and/or equilibration of the bath temperature and reference flask was allowed to proceed overnight.

iii) Heating effects of the stirring motor. Some anomalous results in flasks numbered 18,19 and 20 appeared to be due to heat from the stirring motor, which was located on the right hand side at the rear of the water bath. To test this, a baffle was constructed of aluminium foil and fitted to the shaking arm between flask 20 and the motor. Fig. 26 (b) shows the effect of removing this baffle on the air temperature as measured by a thermometer placed close to the tubing leading to the flasks; and on the apparent gas uptake in flask 19. Similar, but smaller outputs were detected in all the reaction flasks in the half of the bath in which the motor was situated (flasks 11 - 20), but flasks 15, 17 and 19 always showed the greatest response.

Clearly, once thermal equilibrium had been reached, the effect on respiratory measurements would be less than the 2 μl suggested in Fig. 26(b), but fitting the heat baffle gave better agreement between control flasks at either end of the bath.

iv) Residual variation. Using the precautions described above, changes in control flasks were normally kept low (about 0.5 μl h^{-1}) but could vary from 0.0 - 4.0 μl over a three hour period. Some of this variation was explicable in terms of variation in ambient temperature, but flasks in the same run could show considerable variation. However, it was noticed that flasks numbered 1 - 10 tended to behave similarly, as did flasks numbered 11 - 20. Thus it became normal practice to run six control (thermo blank) flasks with each batch of 14 reaction flasks. Two control flasks were situated at either end of the water bath and the remaining two in the central positions.

v) Summary of normal procedure.

1. 10 cm^3 of distilled water was added to the reference flask and the Gilson water bath allowed to equilibrate overnight if experimental temperature was different from ambient.

Fig. 26A Time for temperature equilibration of Gilson respirometer with various volumes of water in 250 ml reference flask with bath temperature at 4°C and ambient temperature of 12°C.

Fig. 26B Temperature recorded by thermometers placed on the support arm of the Gilson respirometer adjacent to flasks numbered 10, 15, 20, compared with the ambient temperature and the apparent gas output during the same period in flask 19.

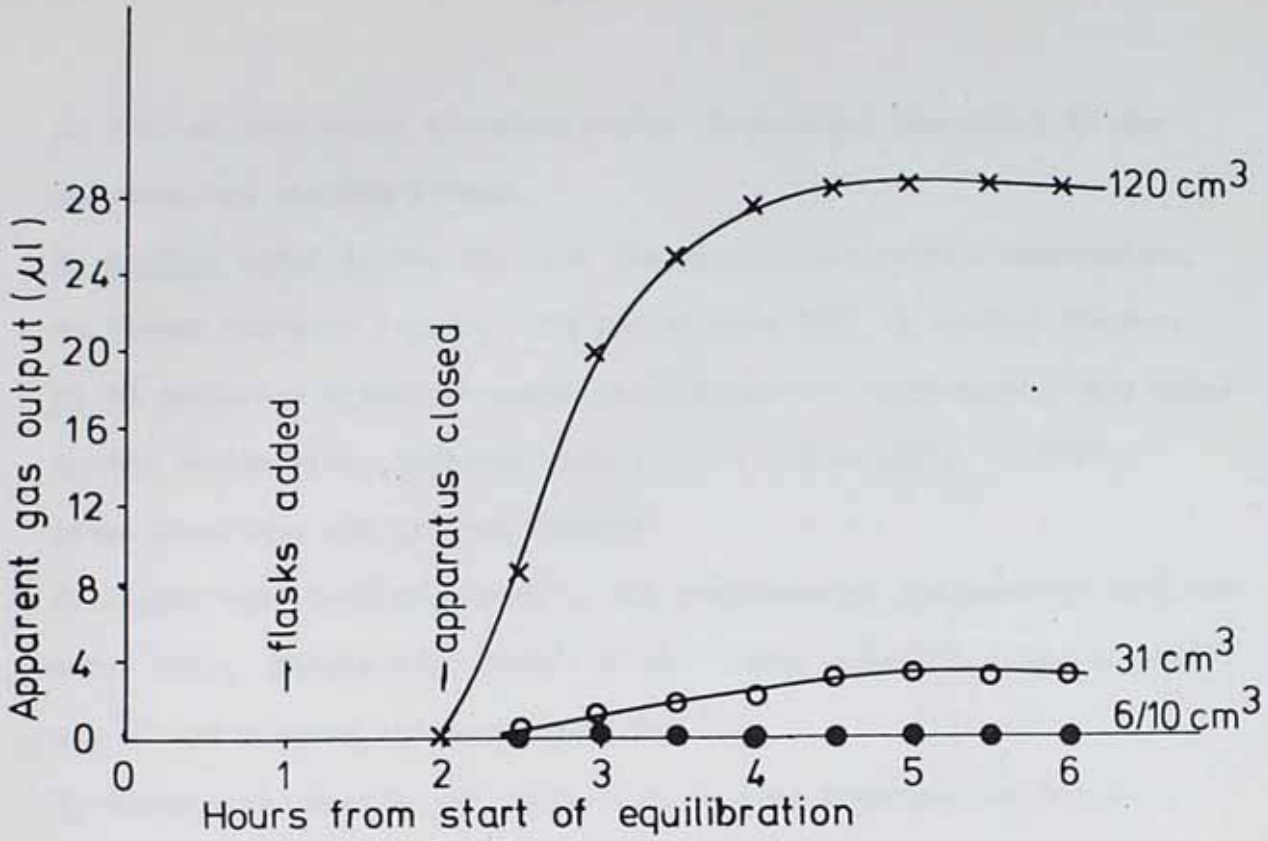


FIG. 26A

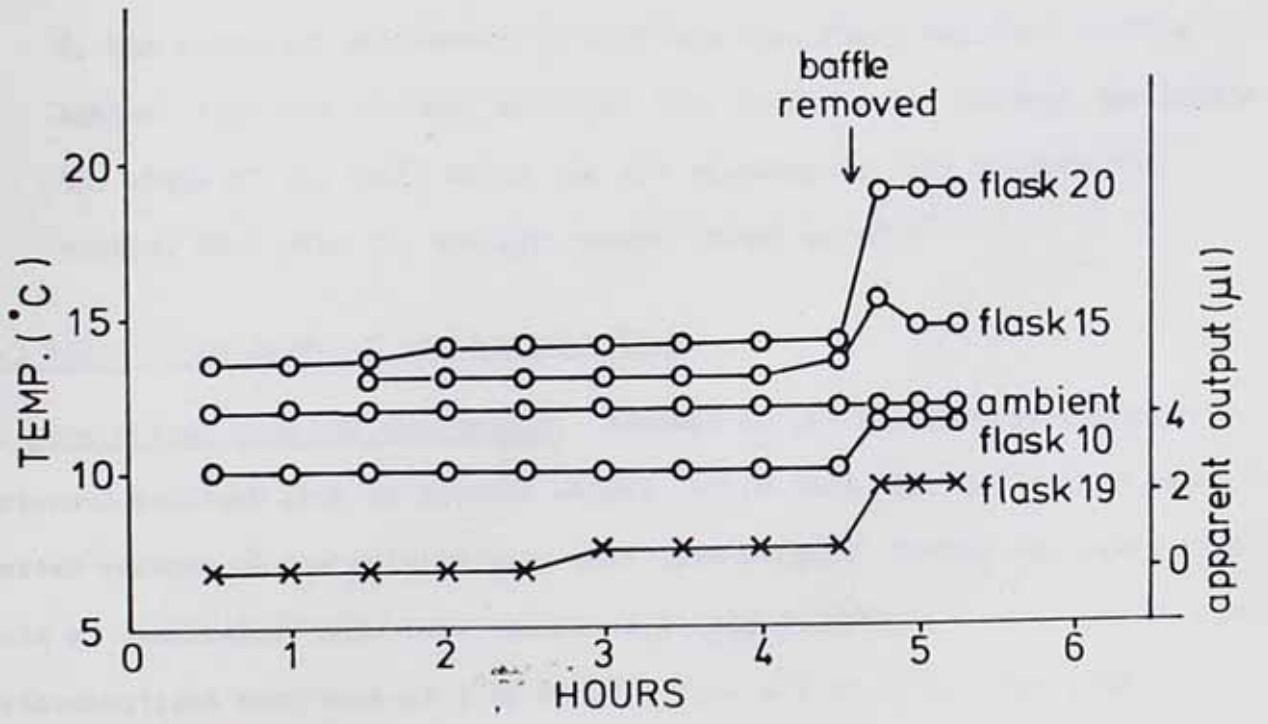


FIG. 26B

2. 1 ml of pond water at experimental temperature was added to the reaction and control flasks.

3. Asellus added to the reaction flasks at experimental temperature.

4. Flasks numbered 1,3,10,11,19 and 20 were left as control flasks.

5. 5% potassium hydroxide (also at experimental temperature) was added to the centre well, together with a 1.5 x 1.0 cm piece of filter paper (reaction and control flasks).

6. Flasks were then connected to the respirometer and lowered into the water bath. Flasks were shaken at the lowest possible rate (50 shakes min^{-1}) and allowed to equilibrate for 1h.

7. Micrometer readings of oxygen uptake then recorded for 3 - 4h.

vi) Analysis of results.

1. The average readings of control flasks 1,3 and 10 were used to correct readings of reaction flasks 2 and 4 - 9; and the average readings of control flasks 11, 19 and 20 were used to correct reaction flasks 12 - 18.

2. The corrected gas uptake of each reaction flask was then plotted against time and the best straight line drawn by eye through the points. The slope of the line, which did not necessarily pass through the origin, thus gave the average oxygen uptake in $\mu l\ h^{-1}$.

3.5 Respiration rates of Asellus aquaticus.

1. Respiration rate and dry weight. Because of the problems of removing external moisture from an aquatic animal, it is felt that dry weight is a better measure of the animals size than live weight. During the year, nine sets of respiratory data were collected at eight different temperatures (two determinations were made at 4°C) ranging from 2°C to 18°C. For each

temperature oxygen uptake ($\mu l\ O_2\ ind^{-1}\ h^{-1}$) was plotted against the mean dry weight (mg) of the individual in the group (Figs. 27 - 31). It was found that a double logarithmic plot gave a good linear relationship and linear regressions have been calculated and fitted for temperature. The regression equations, correlation coefficients and standard errors are shown in Table 12 and summarized in Fig.31 (b).

The validity of plotting separate regression lines for each of the temperatures was tested by the method of Ostle (1963). A summary of these tests is given in Table 13.

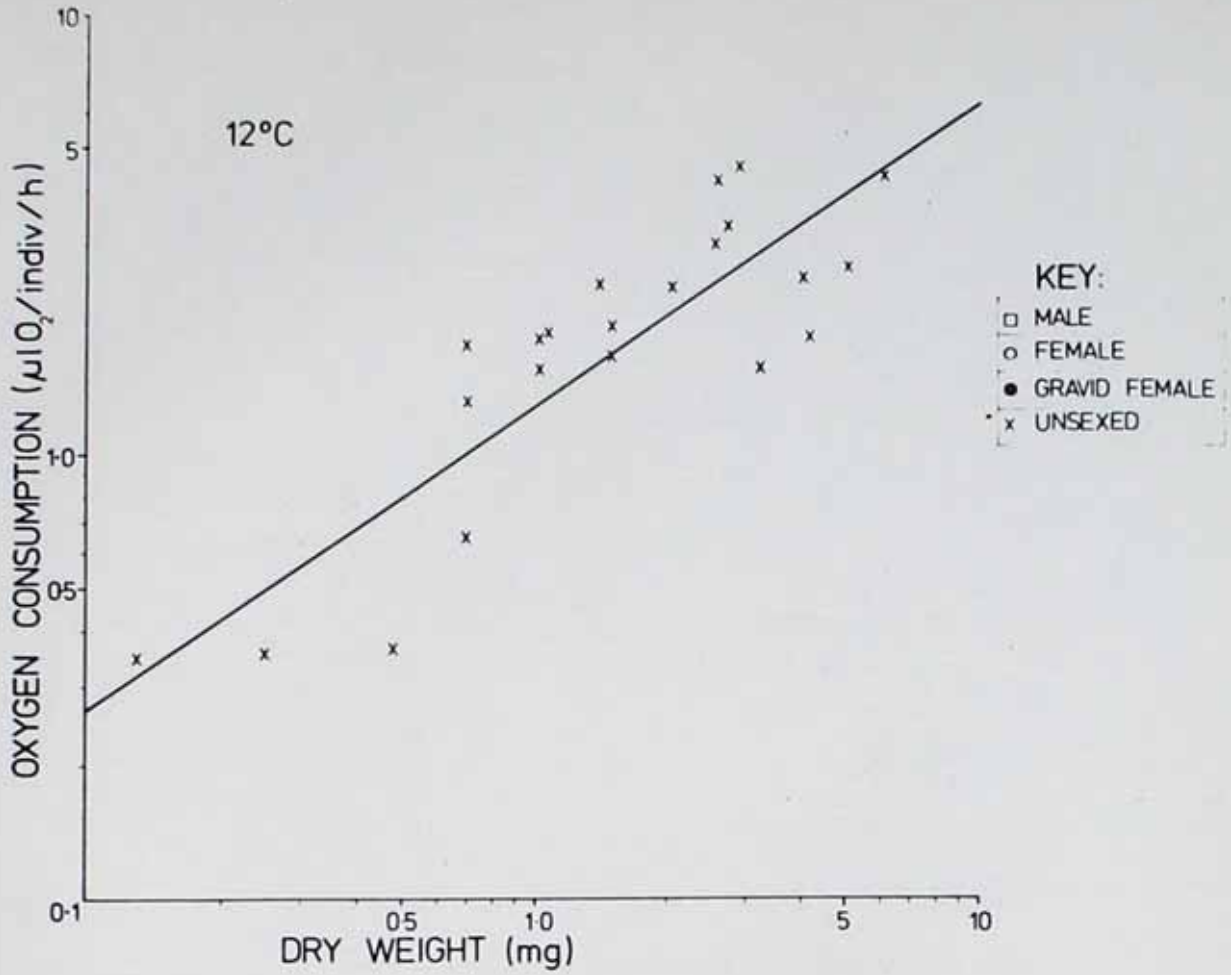
i) Test for homogeneity: this tests the hypothesis that all the data can be described by a single regression line. The analysis shows that the nine regression lines are not homogeneous but are highly significantly different ($P<0.001$).

ii) Test for identity of slopes: this tests the hypothesis that the slopes of the regression lines are not significantly different and the analysis supports this hypothesis.

iii) Test for linearity of temperature means: since the slopes of the regression lines are not significantly different, the lack of homogeneity must result from a difference in the mean rates of respiration at the various temperatures. The residual mean square (S_3) is significantly greater than that within groups ($S_1 + S_2$) ($P<0.001$), thus this hypothesis is confirmed.

Similarly, linear regressions have been fitted to the weight specific respiration rate ($\mu l\ O_2\ mg^{-1}\ h^{-1}$) on dry weight (mg) at each temperature (Fig. 32) and these show a negative relationship. The equations, correlation coefficients and standard errors are given in Table 14.

Fig. 27 Oxygen consumption (μl O_2 ind^{-1} h^{-1}) against dry weight (mg) for A. aquaticus from Wistow Lake at 12°C (October) and 4°C (November). Data are plotted on a double log scale, and individual measurements with the fitted linear regression line are shown for each temperature. Linear regressions for each temperature are given in Table 12.


12°C
KEY:
MALE
FEMALE
GRAVID FEMALE
UNSEXED
OXYGEN CONSUMPTION (µlO2/indiv/h)
10
5
1·0
0·5
0·1
0·5
1·0
5
10
DRY WEIGHT (mg)

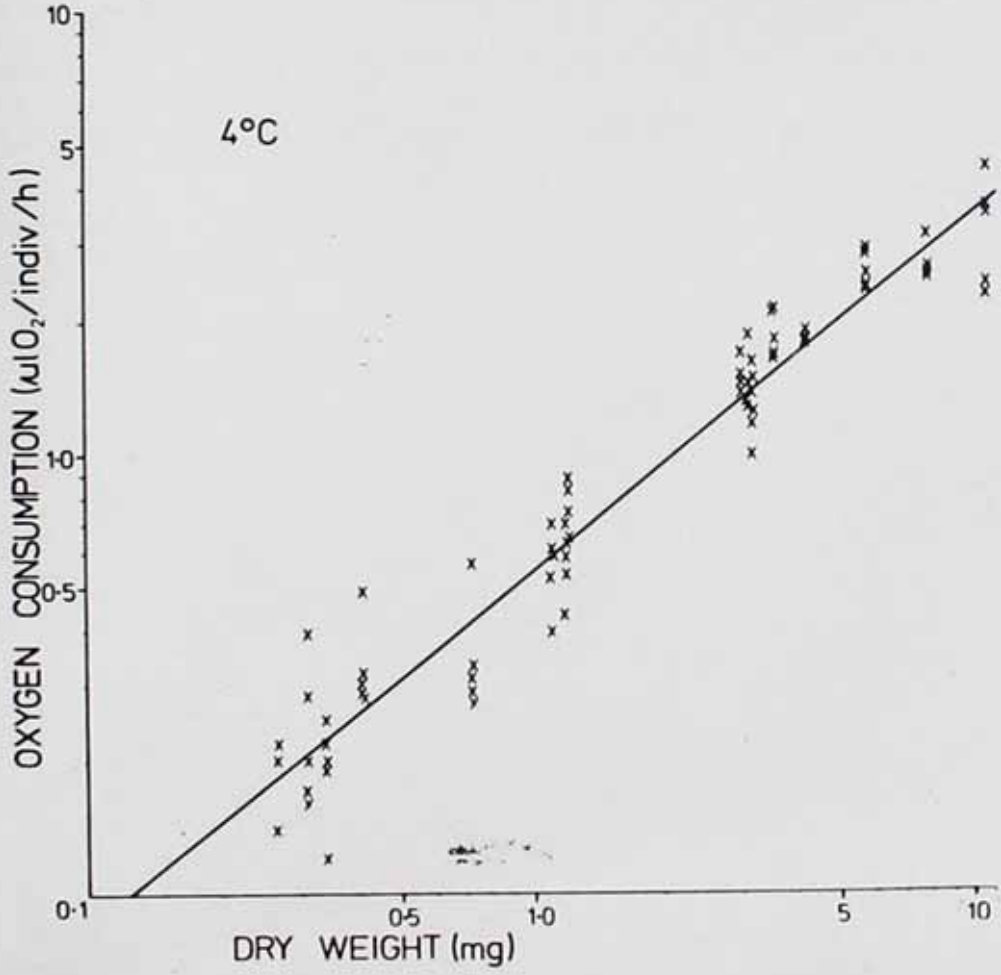
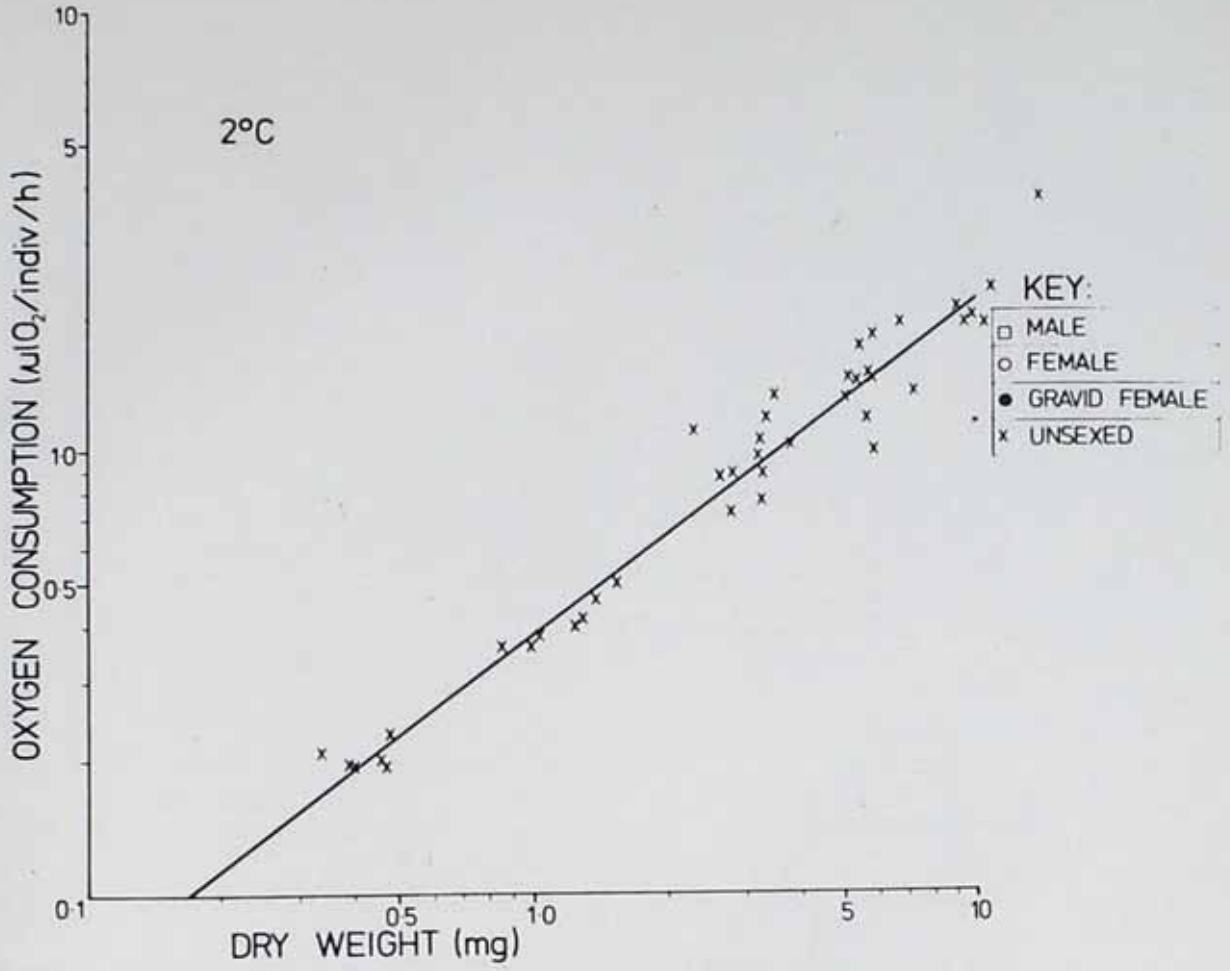

4°C
OXYGEN CONSUMPTION (µlO2/indiv/h)
10
5
1·0
0·5
0·1
0·5
1·0
5
10
DRY WEIGHT (mg)

Fig. 28 Oxygen consumption ($\mu l\ O_2\ ind^{-1}\ h^{-1}$) against dry weight (mg) for A. aquaticus from Wistow Lake at 2°C (December) and 4°C (January). Data are plotted on a double log scale, and individual measurements with the fitted linear regression line are shown for each temperature. Linear regressions for each temperature are given in Table 12.


2°C
KEY:
MALE
FEMALE
GRAVID FEMALE
UNSEXED
OXYGEN CONSUMPTION (μlO2/indiv/h)
DRY WEIGHT (mg)
10
5
10
0·5
0·1
05
10
5
10

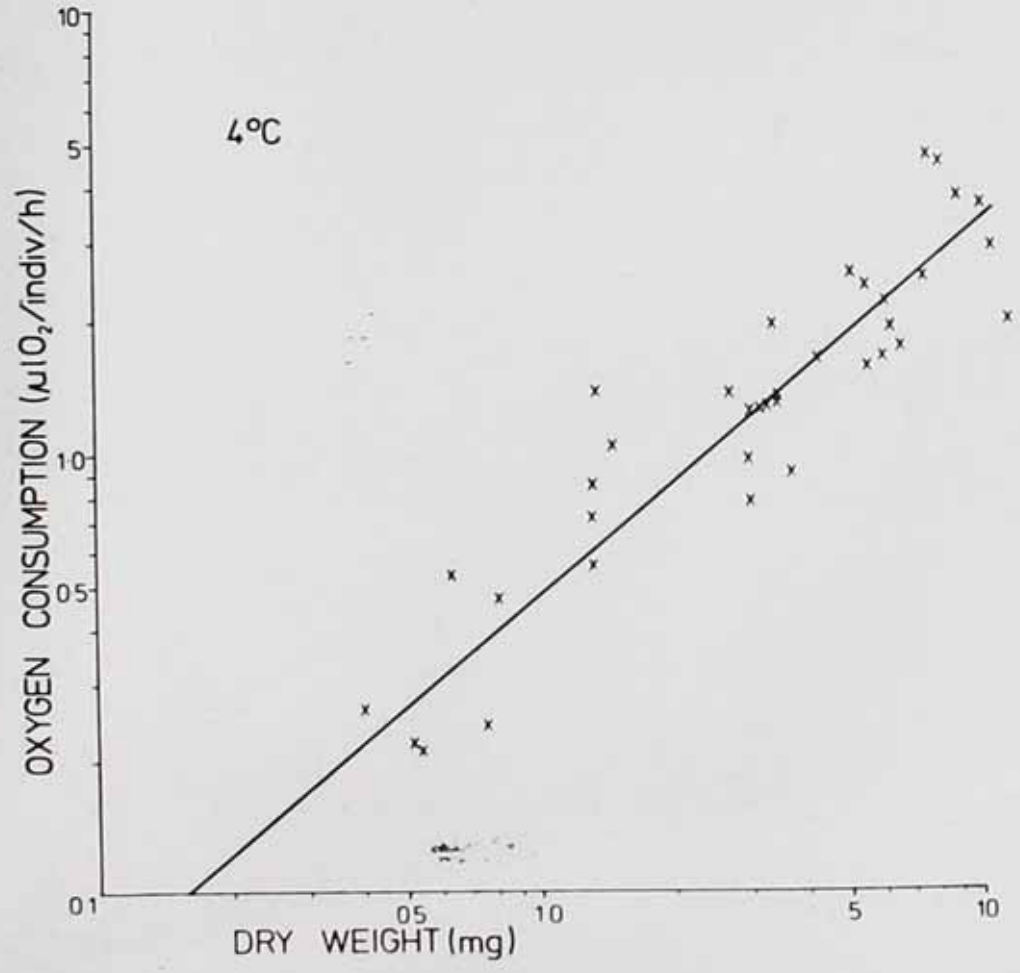
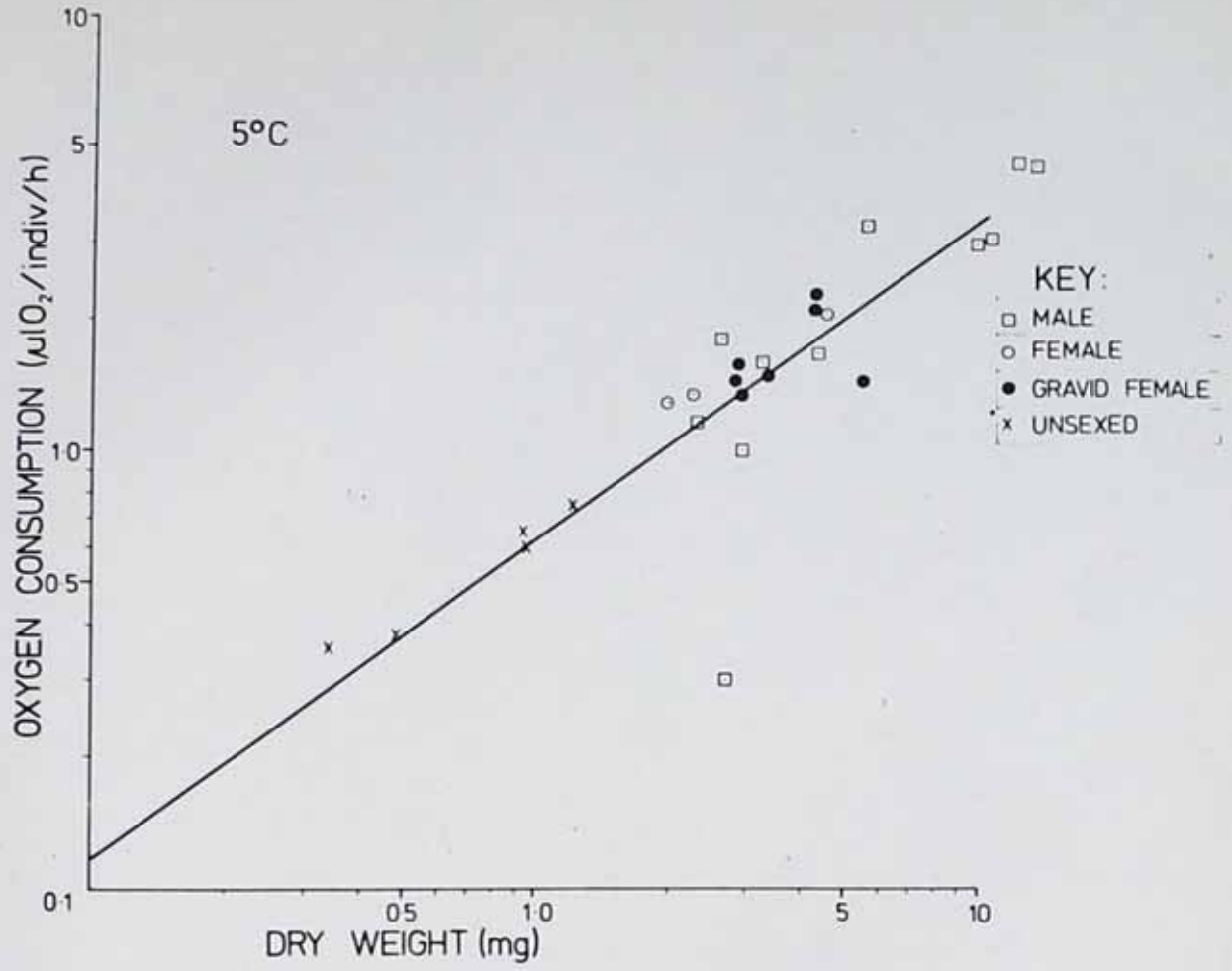

4°C
OXYGEN CONSUMPTION (μlO2/indiv/h)
DRY WEIGHT (mg)
10
5
10
0·5
0·1
05
10
5
10

Fig. 29 Oxygen consumption (μl O_2 ind^{-1} h^{-1}) against dry weight (mg) for *A. aquaticus* from Wistow Lake at 5°C (March) and 7°C (March). Data are plotted on a double log scale, and individual measurements with the fitted linear regression line are shown for each temperature. Linear regressions for each temperature are given in Table 12.


5°C
OXYGEN CONSUMPTION (μlO2/indiv/h)
DRY WEIGHT (mg)
10
5
1·0
0·5
0·1
0·5
1·0
5
10
KEY:
MALE
FEMALE
GRAVID FEMALE
UNSEXED

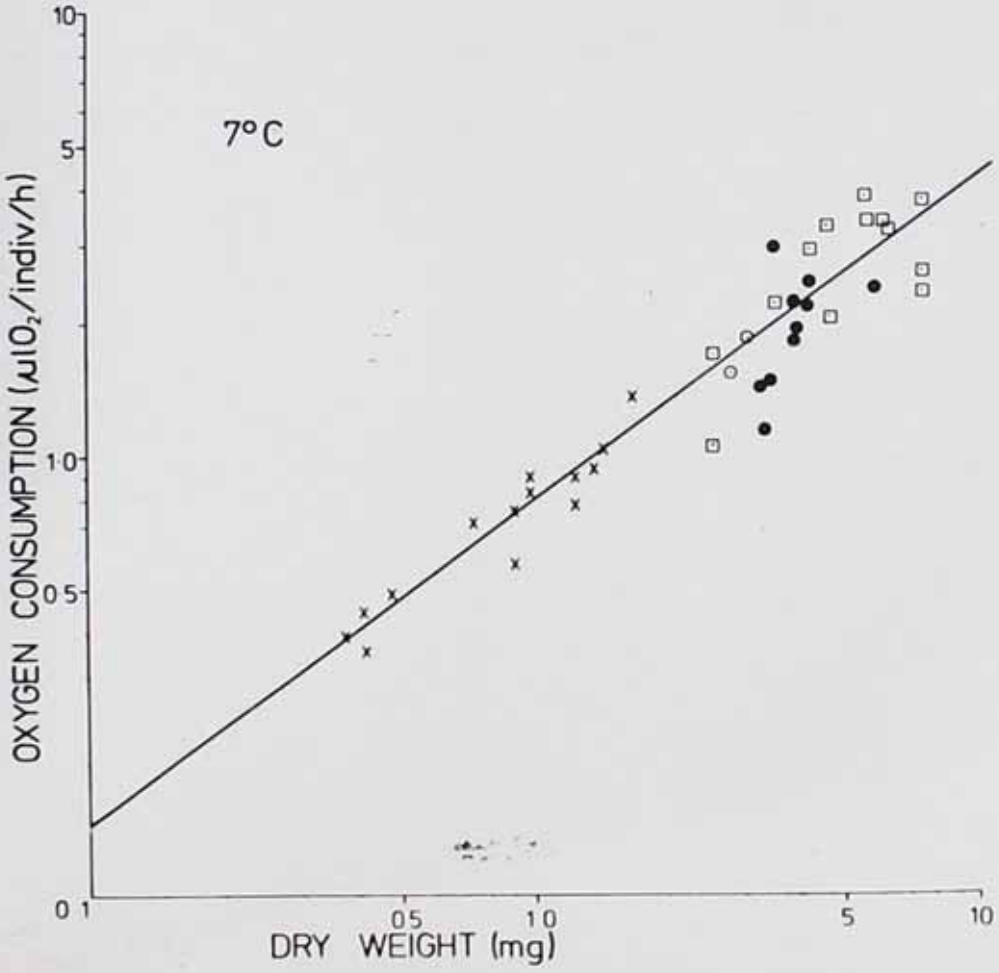
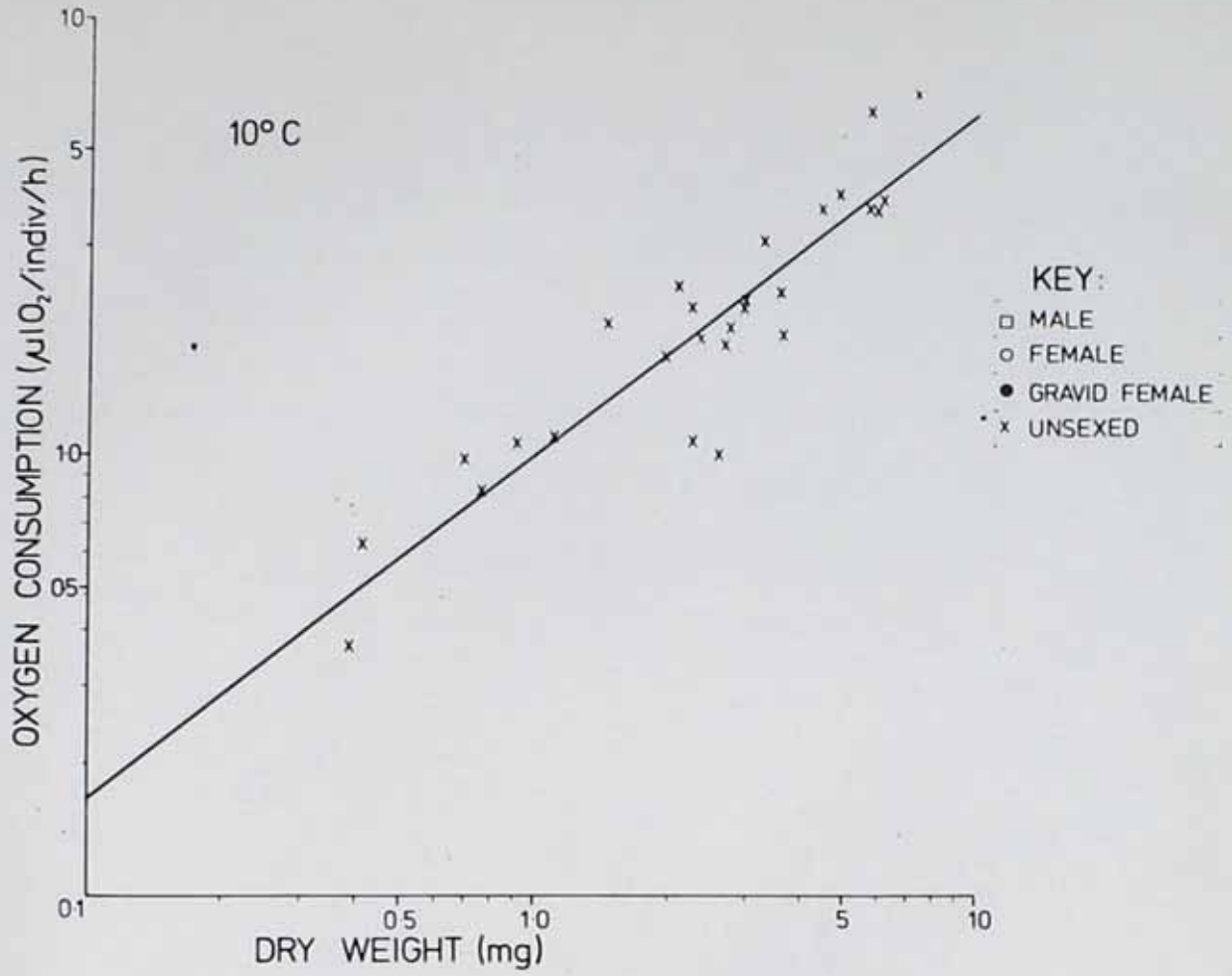

7°C
OXYGEN CONSUMPTION (μlO2/indiv/h)
DRY WEIGHT (mg)
10
5
1·0
0·5
0·1
0·5
1·0
5
10

Fig. 30 Oxygen consumption (μl O_2 ind^{-1} h^{-1}) against dry weight (mg) for A. aquaticus from Wistow Lake at 10°C (April) and 15°C (May). Data are plotted on a double log scale, and individual measurements with the fitted linear regression line are shown for each temperature. Linear regression for each temperature are given in Table 12.


10° C
KEY:
MALE
FEMALE
GRAVID FEMALE
UNSEXED
OXYGEN CONSUMPTION (µlO2/indiv/h)
DRY WEIGHT (mg)
10
5
1·0
0·5
0·1
0·5
1·0
5
10

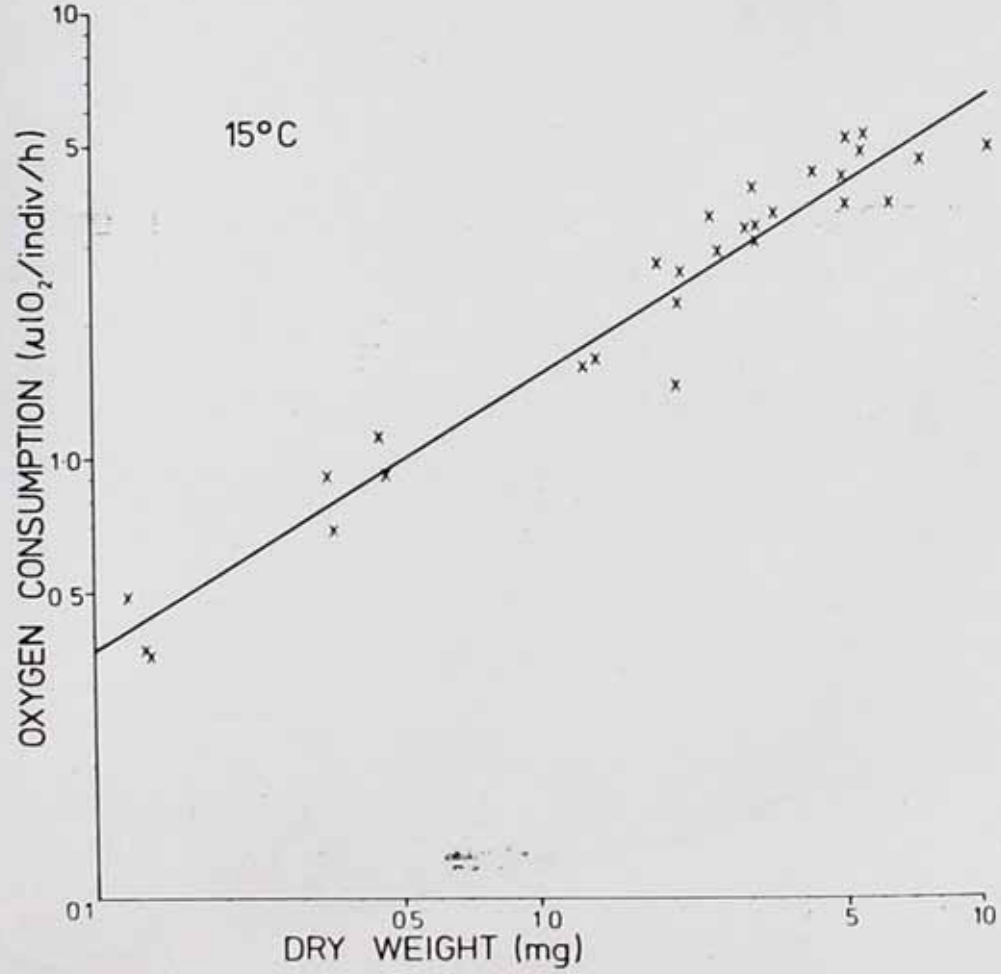

15° C
OXYGEN CONSUMPTION (µlO2/indiv/h)
DRY WEIGHT (mg)
10
5
1·0
0·5
0·1
0·5
1·0
5
10

Fig. 31A Oxygen consumption ($\mu l\ O_2\ ind^{-1}\ h^{-1}$) against dry weight (mg) for A. aquaticus from Wistow Lake at 18°C (July).

Linear regression is given in Table 12.

Fig. 31B Summary of oxygen consumption ($\mu l\ O_2\ ind^{-1}\ h^{-1}$) as a function of dry weight (mg) for A. aquaticus from Wistow Lake at the various temperatures investigated. Data are plotted on a double log scale and the linear regression line is shown for each temperature. The linear regressions are given in Table 12, and a summary of the tests for significance given in Table 13.

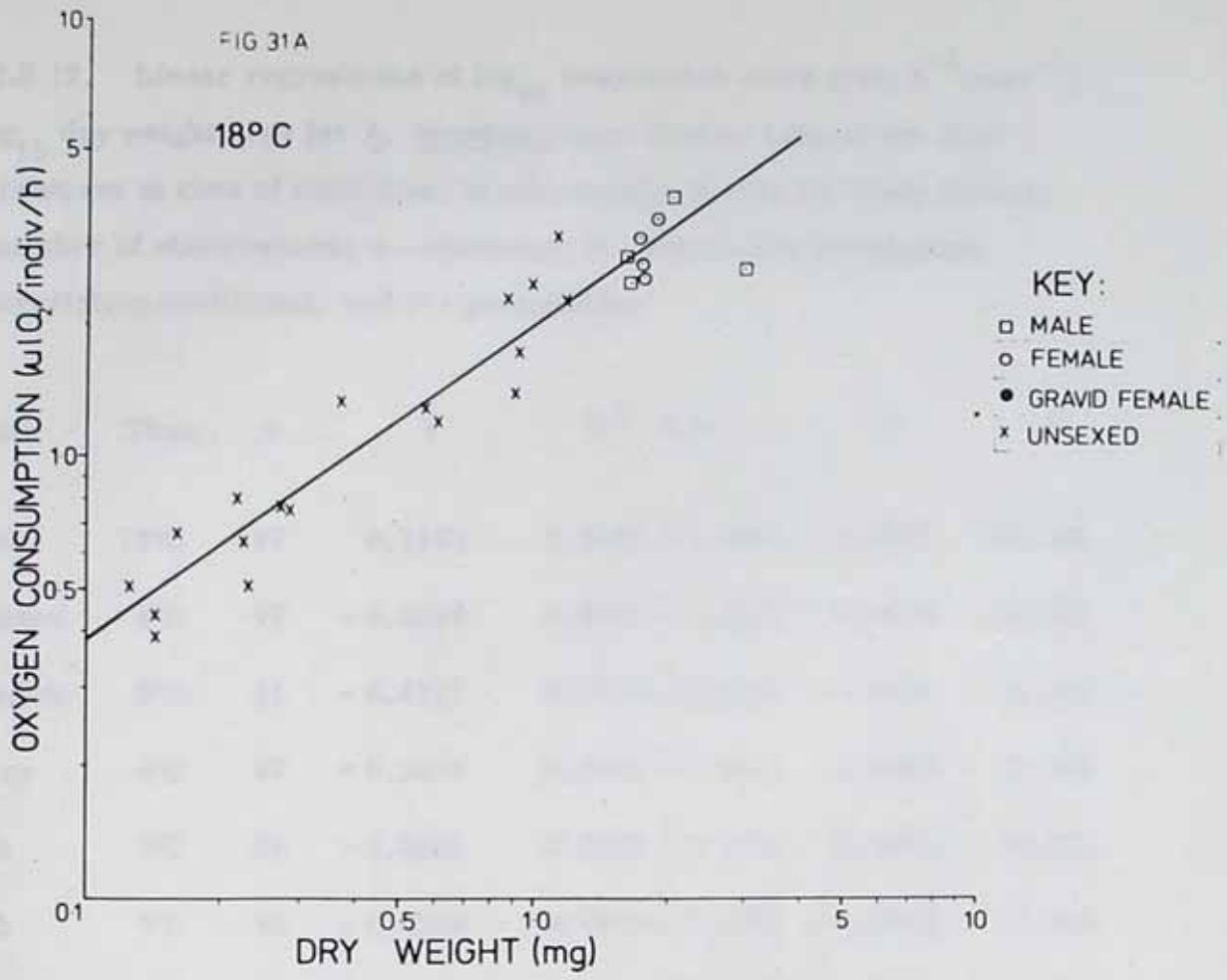


FIG 31A
18° C
OXYGEN CONSUMPTION (µl O2/indiv/h)
DRY WEIGHT (mg)
KEY:
MALE
FEMALE
GRAVID FEMALE
UNSEXED

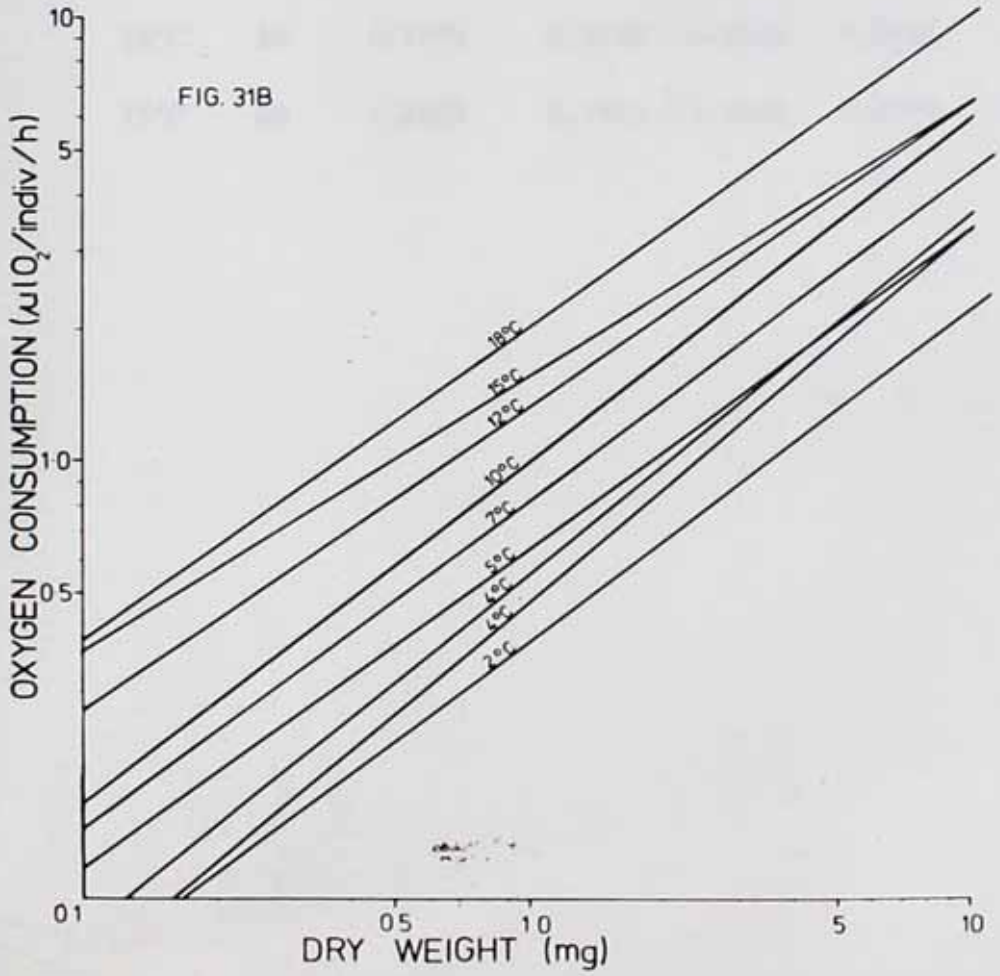


FIG. 31B
OXYGEN CONSUMPTION (µl O2/indiv/h)
DRY WEIGHT (mg)
18°C
15°C
12°C
10°C
7°C
5°C
4°C
3°C
2°C

TABLE 12. Linear regressions of $\log_{10}$ respiration rates ($\mu lO_2\ h^{-1}indiv^{-1}$) on $\log_{10}$ dry weight (mg) for A. aquaticus from Wistow Lake at the field temperatures at time of collection in nine months during the study period. (n = number of observations; a = intercept; b = regression coefficient; r = correlation coefficient, and P = probability).

Date	Temp.	n	a	b ± s.e.	r	P
October	12°C	17	0.1145	0.6903 ± 0.0997	0.8727	<0.001
November	4°C	77	- 0.2596	0.8128 ± 0.0236	0.9699	<0.001
December	2°C	41	- 0.4141	0.7530 ± 0.0242	0.9805	<0.001
January	4°C	37	- 0.3194	0.8471 ± 0.0565	0.9303	<0.001
March	5°C	26	- 0.2031	0.7221 ± 0.0747	0.8919	<0.001
March	7°C	40	- 0.0955	0.7469 ± 0.0351	0.9606	<0.001
April	10°C	28	- 0.0018	0.7746 ± 0.0669	0.9152	<0.001
May	15°C	29	0.1878	0.6232 ± 0.0319	0.9665	<0.001
July	18°C	29	0.2948	0.7151 ± 0.0062	0.9678	<0.001

TABLE 13. Summary of sums of squares and products and relevant tests described in text to test the significance of differences found in the effect of temperature on the equation $\log_{10} y = a + b \log_{10} x$, where x = respiratory rate ($\mu l\ h^{-1}$) and y = dry weight (mg) for A. aquaticus from Wistow Lake.

Temp °C	DF = (n - 1)	$\Sigma(x - \bar{x})^2$	$\Sigma(x - \bar{x})(y - \bar{y})$	$\Sigma(y - \bar{y})^2$	Residuals		
					SS	DF = (n - 2)	MS
2	40	8.33038	6.27258	4.91300	0.18990	39	0.00486
4 (Nov)	76	18.03127	14.92880	12.89976	0.76539	75	0.01020
4 (Jan)	36	6.98252	5.91466	5.78926	0.77916	35	0.02226
5	25	4.45279	3.21549	2.91900	0.59701	24	0.02487
7	39	5.63476	4.20867	3.40662	0.26312	38	0.00692
10	26	3.20595	2.48342	2.29679	0.37307	27	0.01434
12	16	3.43873	2.37381	2.15142	0.51274	15	0.03418
15	28	8.47100	5.27893	3.52192	0.23222	27	0.00860
18	28	4.86911	3.48181	2.65794	0.16817	27	0.00622
		Sum of residuals : S1 =			3.88078	307	0.01264
Within temps Σ=	314	63.41651	48.15817	40.55571	3.98571	313	0.01273
		Increase in sum of residuals: S2 =			0.10493	6	0.01749
Between temps	9	10.07926	-1.37869	6.97082	S_3: 6.78224	8	0.84778
Total:	323	73.49580	46.77948	47.52653	S_T: 17.75653	322	0.05514

Test for homogeneity: $VR = ((S_T - S_1)/15)/(S_1/307) = 0.92505/0.01264 = 73.18434$ ($P < 0.001$)

Test for identity of slopes: $VR = (S_2/6)/(S_1/307) = 0.01749/0.01264 = 1.3837$ N.S. ($P > 0.10$)

Test for linearity of temperature means: $VR = (S_3/8)/((S_1 + S_2)/313) = 0.84778/0.01273 = 67.07120$ ($P < 0.001$)

Fig. 32 Weight specific oxygen consumption ($\mu l\ O_2\ mg^{-1}\ h^{-1}$) as a function of dry weight (mg) for A. aquaticus from Wistow Lake at various temperatures. Data are plotted on a double log scale and the linear regression line is shown for each temperature.

Linear regression for each temperature is given in Table 14.

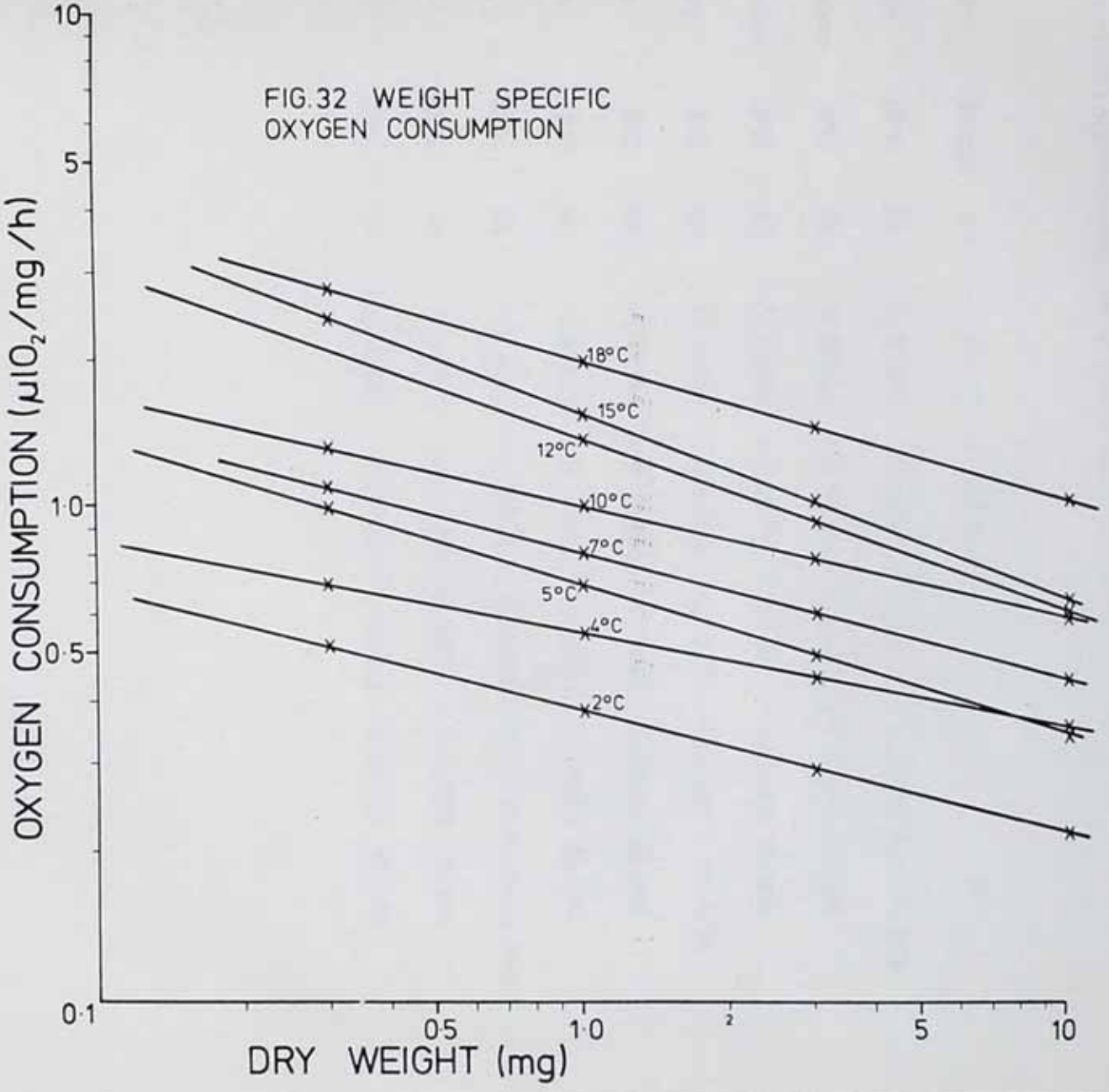


FIG. 32 WEIGHT SPECIFIC
OXYGEN CONSUMPTION
OXYGEN CONSUMPTION (μlO2/mg/h)
10
5
1·0
0·5
0·1
18°C
15°C
12°C
10°C
7°C
5°C
4°C
2°C
0·5
1·0
2
5
10
DRY WEIGHT (mg)

TABLE 14. Linear regressions of $\log_{10}$ weight specific respiration rates ($\mu l O_2 h^{-1} mg^{-1}$) on $\log_{10}$ weight (mg) for A. aquaticus from Wistow Lake at the field temperatures at the time of collection in nine months during the study period (Abbreviations as in Table 12).

Date	Temp.	n	a	b ± s.e.	r	P
October	12°C	16	0.13553	- 0.35515 ± 0.03467	- 0.64393	0.01-0.005
November	4°C	77	- 0.25916	- 0.18784 ± 0.01010	- 0.67905	<0.001
December	2°C	41	- 0.41408	- 0.24702 ± 0.00486	- 0.85324	<0.001
January	4°C	37	- 0.31942	- 0.15293 ± 0.02226	- 0.41627	0.02-0.01
March	5°C	25	- 0.16343	- 0.29703 ± 0.00782	- 0.81013	<0.001
March	7°C	40	- 0.09545	- 0.25308 ± 0.00692	- 0.76050	<0.001
April	10°C	28	- 0.00128	- 0.22573 ± 0.01440	- 0.55116	0.005-0.001
May	15°C	29	- 0.18777	- 0.37682 ± 0.0086	- 0.91552	<0.001
July	18°C	29	0.29480	- 0.28491 ± 0.00622	- 0.83757	<0.001

The salient feature of these relationships is that the larger animals show a higher respiration rate per individual but a smaller rate per unit weight. There is no observable difference between the data for males and females, or between gravid and non-gravid animals.

If the area of surface across which gaseous exchange occurs in A. aquaticus is the limiting factor governing metabolic rate, then the respiratory rate will vary as $\frac{2}{3}$ power of the body weight. Thus, in the relationship:

$$y = a + x^b$$

where y = respiratory rate ($\mu l\ O_2\ ind^{-1}\ h^{-1}$); x = body size; a = a constant, then b = 0.66 if this surface rule is applicable, (Bertalanffy 1957).

In the present study, the value of b varied from 0.623 to 0.8471, and thus Asellus approximates to the surface rule. Other crustaceans show similar b values, e.g. Armadillidium vulgare (0.66) (Muller 1943, as quoted in Bertalannfy 1957); Pachygrapsus crassipes Randall (0.664) (Roberts 1957); Uca pugnax (0.621) (Teal 1959); Diaptomus sp. (0.658) (Comita 1968).

Rao and Bullock (1954) suggested that b varies with temperature in poikilothermic animals and Akerlund (1967) supported this by showing lower b values above 20°C in the ampullariid snail, Marisa corrinarietus L. Berg and Ockleman (1959) showed that b varied seasonally in some freshwater Limnaea species. The present study does not support these authors, in that no significant change in b values was found, even though determinations were made throughout the year as well as at a range of field temperatures. Davies (1966) similarly found that b values were independent of temperature in Patella vulgata L.

2. Respiration rate and temperature. From the dry weight to length regression (Fig. 18), the dry weight of a median individual of 6 of the size classes used in the population study was calculated. The mean respiratory rate for each of these size classes could then be calculated from the regression equations for each temperature (Table 12) of $\log_{10}$ individual respiratory rate against $\log_{10}$ dry weight, for each of the experimental temperatures. Thus a linear regression equation was calculated for respiratory rate ($\mu l\ O_2\ ind^{-1}\ h^{-1}$) against temperature for each of the six size classes. This relationship for each size class is adequately described by a straight line and these are shown in Fig. 33. (Similarly, regressions of metabolic rate ($\mu l\ O_2\ mg^{-1}\ h^{-1}$) against temperature were calculated and these are shown in Fig. 34). From the data in Fig. 33, the temperature coefficients (Q_{10}'s) have been calculated for each size class in the temperature ranges 2° - $12^{\circ}C$ and 8° - $18^{\circ}C$ and these are given in Table 15.

The results show clearly that the individual rate of respiration shows a positive, linear correlation with temperature changes throughout the year. It was shown earlier (Table 13) that the regression coefficients of individual respiratory rate against dry weight were not significantly different. This means that the Q_{10} for different size classes is not significantly different.

However, when the individual respiratory rates for the selected size classes are plotted against temperature (Fig. 33), interesting trends in the Q_{10} values become apparent (Table 15). It can be seen that the smaller size classes show a greater response to temperature (as measured by Q_{10}) than do the larger Asellus. The calculated Q_{10} values vary from 1.90 - 5.8; similar values are obtained on both an individual and a weight specific basis. These coefficients are higher than the Q_{10} of 1.5 reported for Asellus for the

temperature range 10° - 20°C by Edwards and Learner (1960). However it is also noticeable that Q_{10} decreases with increased temperature, and if the present data are extrapolated to 20°C, then the Q_{10} (10 - 20°C) is 1.7. Thus the present data are not very dissimilar to those of Edwards and Learner.

Rao and Bullock (1954) analysed data from various sources and concluded that Q_{10} commonly increases with increasing size in poikilotherms within physiologically normal temperature ranges. The present results are in direct conflict with this conclusion, however, as the smaller size classes show the greater temperature response. In many cases, however, Rao and Bullock's conclusions are based on respiratory rates which, although often regarded as "physiologically normal", are outside the temperature range normally encountered by the animal. Sometimes also the experimental temperature differs from the field temperature, so that problems of acclimation are encountered. It may be that larger animals show greater response to changed or abnormal temperature conditions.

The present conclusions are in agreement with the more recent studies of Otto (1974) working with Potomophylax cingulatus (Steph.) (Trichoptera) and Nilsson (1974) for a laboratory population of Gammarus pulex L. (Amphipoda). Block and Tilbrook (1975) come to similar conclusions with the Antarctic collembolan Cryptopygus antarcticus (Willem). They showed that Q_{10} increased with smaller size classes and the range of Q_{10} for this species (1.99 - 4.42) is similar to that in the present study. They also showed that Q_{10} was smaller over the higher temperature ranges. As in the present study, the experimental temperatures were within the field ranges normally encountered by the organisms concerned during the season when the respiratory measurements were made.

Fig. 33 Effect of temperature on mean oxygen consumption ($\mu l\ O_2\ ind^{-1}\ h^{-1}$) of six size classes of A. aquaticus from Mistow Lake. Mean oxygen consumption calculated from the regression equations given in Table 12.

The equations of the linear regression lines are: -

2.5 - 3.0 mm: $y = 0.00422 + 0.02775\ x$ ($r = 0.98184$; $n = 9$)

3.5 - 4.0 mm: $y = 0.02983 + 0.04884\ x$ ($r = 0.99048$; $n = 9$)

5.5 - 6.0 mm: $y = 0.14818 + 0.10529\ x$ ($r = 0.99374$; $n = 9$)

7.5 - 8.0 mm: $y = 0.21615 + 0.21521\ x$ ($r = 0.96894$; $n = 9$)

9.5 - 10.0 mm: $y = 0.71571 + 0.26991\ x$ ($r = 0.97956$; $n = 9$)

10.0 - 12.0 mm: $y = 1.19419 + 0.37542\ x$ ($r = 0.96823$; $n = 9$)

$P = < 0.001$ in all cases

y = oxygen consumption ($ul\ O_2\ ind^{-1} h^{-1}$)

x = temperature (^{o}C)

FIG. 33

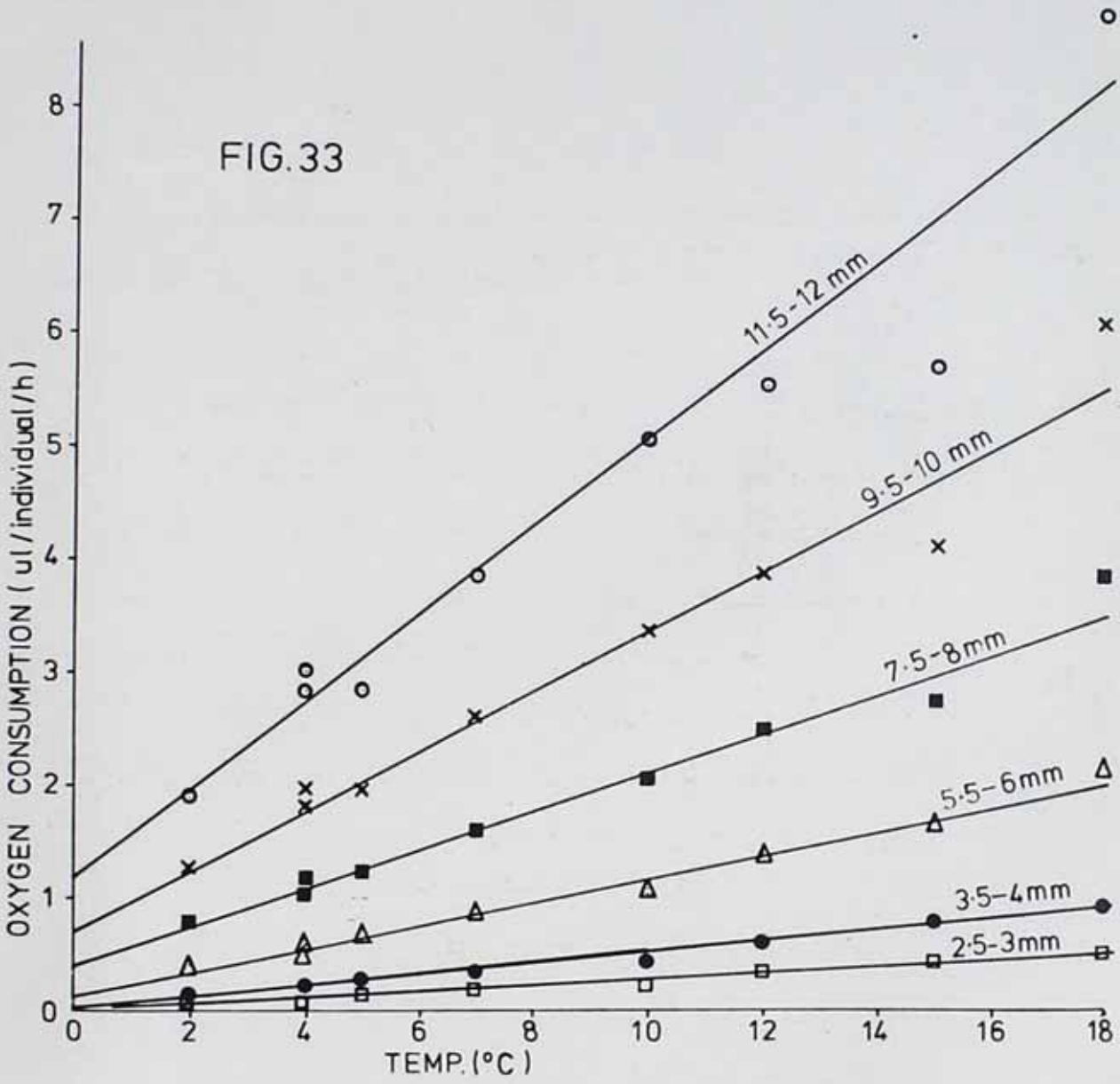

OXYGEN CONSUMPTION (ul / individual / h)
TEMP. (°C)
0
1
2
3
4
5
6
7
8
0
2
4
6
8
10
12
14
16
18
11·5-12 mm
9·5-10 mm
7·5-8mm
5·5-6mm
3·5-4mm
2·5-3mm

Fig. 34 Effect of temperature on the mean weight specific oxygen consumption of six size classes of A. aquaticus from Wistow Lake.

The equations of the linear regression lines are: -

2.5 - 3.0 mm: $y = 0.05517 + 0.19368\ x$ ($r = 0.97415$; $n = 9$)

3.5 - 4.0 mm: $y = 0.10861 + 0.14263\ x$ ($r = 0.98556$; $n = 9$)

5.5 - 6.0 mm: $y = 0.14432 + 0.09324\ x$ ($r = 0.99240$; $n = 9$)

7.5 - 9.0 mm: $y = 0.15192 + 0.07001\ x$ ($r = 0.98755$; $n = 9$)

9.5 - 10.0 mm: $y = 0.15295 + 0.05472\ x$ ($r = 0.97884$; $n = 9$)

11.5 - 12.0 mm: $y = 0.15066 + 0.04520\ x$ ($r = 0.96606$; $n = 9$)

$P < 0.001$ in all cases

y = oxygen consumption ($\mu l\ O_2\ mg^{-1}\ h^{-1}$)

x = temp ($^{\circ}C$)

FIG. 34

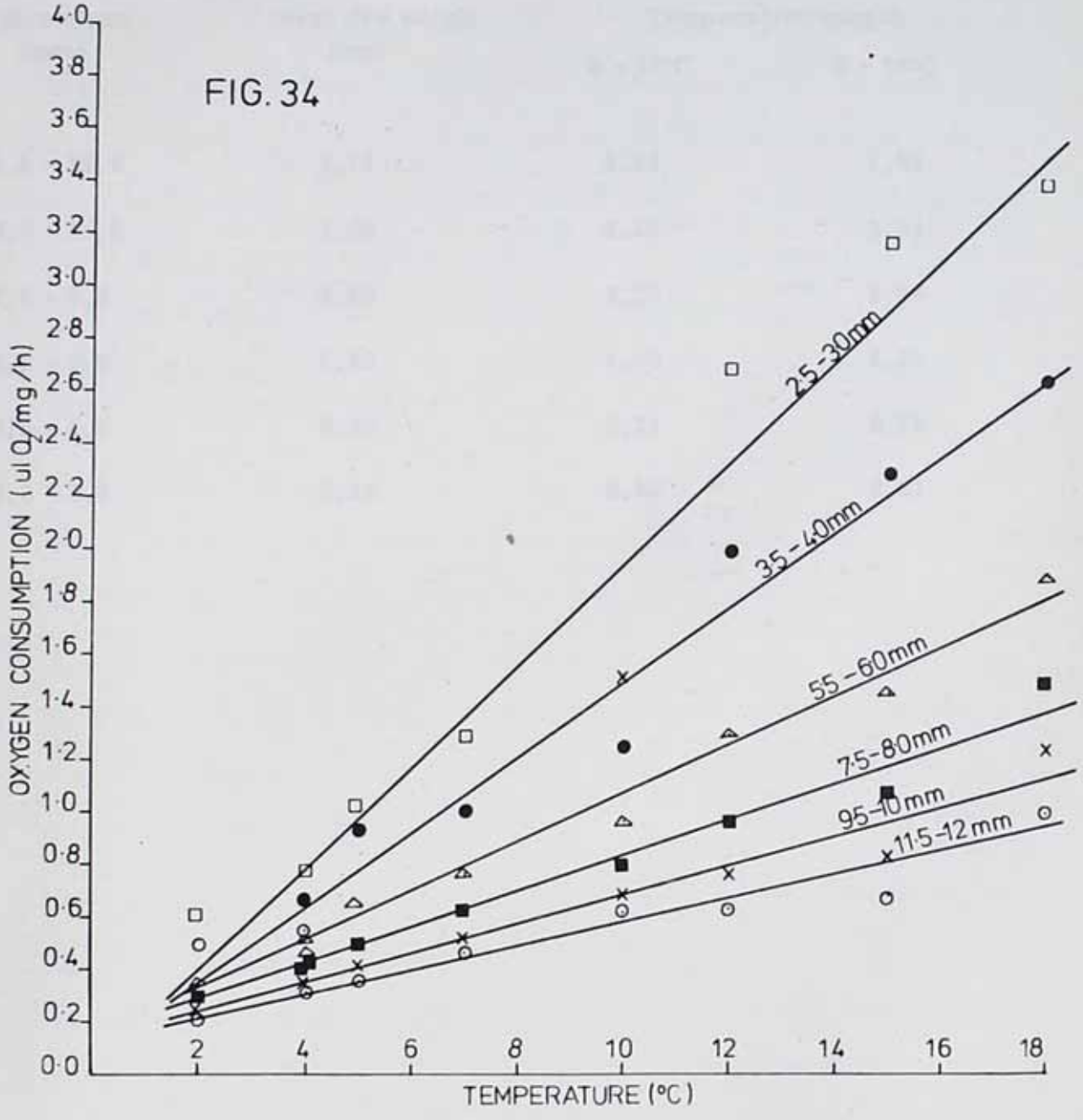

OXYGEN CONSUMPTION (ul O/mg/h)
4·0
3·8
3·6
3·4
3·2
3·0
2·8
2·6
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0·0
2
4
6
8
10
12
14
16
18
TEMPERATURE (°C)
25-30mm
35-40mm
55-60mm
7·5-80mm
95-10mm
11·5-12mm

TABLE 15. Temperature coefficients (Q_{10}) calculated for two temperature ranges for 6 size classes of A. aquaticus using the regression of respiration rate ($\mu l\ O_2\ indiv^{-1}\ h^{-1}$) against temperature (°C). (Fig. 31).

Size class (mm)	Mean dry weight (mg)	Temperature ranges	
		2 - 12°C	8 - 18°C
11.5 - 12.0	8.18	2.97	1.90
9.5 - 10.0	4.88	3.15	1.94
7.5 - 8.0	2.58	3.28	1.98
5.5 - 6.0	1.13	4.03	2.10
3.5 - 4.0	0.35	5.24	2.19
2.5 - 3.0	0.15	5.82	2.21

3.6 Population metabolism

From the foregoing data, an estimate of the total respiration of the Asellus population for the year can be made. This can be done by detailed computation taking into account the average population density at each sampling time, changes in population size class structure with time, respiratory rate in relation to size, changes in this respiration rate caused by temperature, and daily temperature changes in the field throughout the year. Such a computation would be extremely time-consuming, and in the present study it was carried out using a computer programme (Hodkinson 1971 as modified by Salmon. 1973). The computer input requires seven sets of data: -

1. The number of size classes in the population.
2. The total number of days for which the respiratory output is required.
3. Mean temperature of the lake for each day of the study.
4. The mean dry weight of each life cycle.
5. b and a in the regression equation $y = bx + a$ for each size class, where y = weight specific respiration rate ($\mu l\ O_2\ mg^{-1}\ h^{-1}$) and x = temperature (^{o} C).
6. The population density at each sample date and the day number on which the sample was taken.
7. The percentage size class composition at each sample date. The programme computes the total respiration of the population for each day and the cumulative total; hence the total for the year. The programme also plots daily total respiration against time (Appendix B).

Further estimates of the total population metabolism were made by two 'best estimate' methods. This term was first used by Phillipson (1962) in reference to the mean energy expenditure of a species per unit weight per unit time, calculated from laboratory respiration data covering all life stages. Phillipson further suggested that this best estimate could be used to estimate the annual energy loss due to respiration of a population by using the mean biomass of the population. Two methods of calculation have been proposed.

Method 1. Phillipson and Watson (1965) estimated the annual respiratory metabolism of Oniscus asellus L. by calculating the weight specific oxygen consumption, at the mean field temperature, of an individual corresponding to the mean weight of the population at each sampling time. Thus the oxygen uptake per mg per unit time was known and by multiplying by the mean biomass, it could be converted to oxygen uptake per unit area per unit time. The calculation for the Asellus population of Wistow Lake by this method is shown in Table 16.

Method 2. In later papers (Phillipson 1967, 1970) data were calculated on the respiratory rate of all instars or size classes in a population at the mean field temperature to obtain the average uptake of oxygen per mg per unit time. Again this could be used in conjunction with mean biomass data to obtain the annual oxygen comsumption per unit area. The calculation by this method is shown in Table 17.

The results are compared in Table 18, together with the data for three Fredericia populations (a soil dwelling enchytraeid), Melanotus rufipes Hbst (a log dwelling beetle), two populations of Pyrrhosoma nymphula (Sulz) (Odonata) and Oligolophus tridens (a litter dwelling phalangid) (Data modified from Phillipson 1970). The data for a population of Neobisium

muscorum (Leach) (a soil dwelling pseudoscorpion) (Salmon 1973) have been added.

The oxycalorific equivalent has been taken as 20.197 J ml^{-1} of oxygen (Brody 1945) taking the R.Q. of Asellus aquaticus as 0.82 (Will 1952) and 1 cal = 4.186 J.

The computed annual oxygen consumption is 5732 ml O_2 m^{-2} equivalent to an annual energy loss of 115.77 kJ. It can be seen that neither of the best estimate methods gives an estimate which is very close to the computer estimate for this population of Asellus. Method 2 gives an estimate 16% too small and method 1 an estimate 12.6% too large.

The discrepancy with method 2 is due to giving equal weighting to each of the size classes which are not equally important in the population. With Asellus, the larger size classes are thereby overweighted and these have a lower respiration rate mg^{-1} than the smaller animals. Phillipson (1970) recognised this problem and suggested that size class categories should not be selected on an arithmetic scale but on a scale approximating to a sigmoid curve resembling the growth curve. It is convenient, however, to use arithmetic size classes for other reasons (see section 2.5). Moreover, the growth curve is often not known at the start of an investigation. Some size classes are not present in the population throughout the year, and the estimate would clearly be better with a stable size class structure.

Method 1 appears to avoid the above objection, and so is potentially capable of yielding a better estimate, but nevertheless it still shows a 12.6% error, in this instance too high. A possible explanation is that the method overestimates respiratory rate in winter when temperatures were low, but this is not sufficiently compensated by summer rates as mean dry weight were smaller at this time.

TABLE 16. Calculation of annual respiration of Asellus aquaticus population in Wistow Lake (1973–4) by best estimate (method 1)

A) MALES:

SAMPLING TIME:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	TOTAL
Mean D.W./indiv(mg)	0.627	0.887	1.211	1.420	1.404	1.325	1.361	1.225	1.473	0.544	0.346	0.654	0.407	0.572	13.456 = A_1
μlO_2 mean indiv^{-1} h^{-1}	0.685	0.901	0.955	1.31	1.29	1.23	1.27	1.16	1.33	0.615	0.44	0.710	0.495	0.64	13.03 = B_1

B) FEMALES:

Mean D.W./indiv(mg)	0.522	0.689	0.948	1.080	1.172	1.065	1.474	1.494	1.860	0.734	0.318	0.945	0.572	0.434	13.307 = A_2
μlO_2 mean indiv^{-1} h^{-1}	0.600	0.745	0.955	1.05	1.12	1.04	1.33	1.35	1.61	0.788	0.400	0.960	0.641	0.518	13.107 = B_2

CALCULATION:

1. Sum mean weight indiv^{-1} at each census (mg) = $A_1 + A_2$
2. Sum total oxygen consumption h^{-1} for each of these individuals at the mean field temperature (10.1°C) = $B_1 + B_2$
3. Mean oxygen uptake for whole sampling period ($\mu l\ O_2\ mg^{-1}\ h^{-1}$) = $\frac{B_1 + B_2}{A_1 + A_2} = \frac{26.137}{26.763} = 0.97661$
4. Total oxygen uptake for year per mg of Asellus ($\mu lO_2\ mg^{-1}\ y^{-1}$) = 0.97661 x 24 x 365 = 8555.1036 = 8.555 ml $O_2\ mg^{-1}\ y^{-1}$
5. Total oxygen uptake per unit area ($mlO_2\ mg^{-1}\ y^{-1}$ x mean biomass) = 8555.1036 x 754.76 = 6457 $mlO_2\ m^{-2}\ y^{-1}$
6. Oxycalorific equivalent = 20.197 J ml^{-1} ∴ 6457 ml $O_2\ m^{-2}\ y^{-1}$ ≡ 130.41 KJ $m^{-2}\ y^{-1}$

TABLE 17. Calculation of best estimate of Asellus aquaticus population at Wistow Lake in 1973-74 by method 2.

Size class (mm)	Mean dry weight (mg)	μlO_2 indiv^{-1} h^{-1} at 10.1°C
1.0 - 1.5	0.0164	0.020
1.5 - 2.0	0.0417	0.035
2.0 - 2.5	0.0838	0.130
2.5 - 3.0	0.1461	0.225
3.0 - 3.5	0.2322	0.320
3.5 - 4.0	0.3452	0.435
4.0 - 4.5	0.4883	0.568
4.5 - 5.0	0.6646	0.724
5.0 - 5.5	0.8771	0.896
5.5 - 6.0	1.1286	1.10
6.0 - 6.5	1.4219	1.30
6.5 - 7.0	1.7600	1.54
7.0 - 7.5	2.1454	1.79
7.5 - 8.0	2.5809	2.08
8.0 - 8.5	3.0691	2.38
8.5 - 9.0	3.6127	2.70
9.0 - 9.5	4.2141	3.03
9.5 - 10.0	4.8760	3.40
10.0 - 10.5	5.6008	3.78
10.5 - 11.0	6.3911	4.20
11.0 - 11.5	7.2492	4.72
11.5 - 12.0	8.1775	5.10
12.0 - 12.5	9.1786	5.50
Total	64.3013	45.973

Best estimate = $\frac{\text{Total mean } O_2 \text{ uptake}}{\text{Total mean dry wt.}} = \frac{45.973}{64.3013} = 0.71496\ \mu lO_2\ mg^{-1} h^{-1}$ at 10.1°C

$\therefore$ Oxygen uptake in 24 h = 17.15904 μlO_2 mg^{-1} 24h^{-1} at 10.1°C

$\therefore$ Oxygen uptake in year = 6263.0496 μlO_2 mg^{-1} y^{-1}

$\therefore$ Oxygen uptake per unit area in year = 4,806,577 μlO_2 m^{-2} y^{-1} = 4,806.577 mlO_2 m^{-2} y^{-1}

$\therefore$ Oxycalorific equivalent = 23.19 k cals m^{-2}y^{-1} = 97.07 kJ.

TABLE 18. A comparison of best estimates of annual population respiration losses with estimates by detailed computation for a range of invertebrates. Data for A. aquaticus (present study), Neobisium muscorum (Salmon 1973). All other data modified from Phillipson (1970).

Population	Annual respiratory energy loss using 'best estimate'		Annual respiratory energy loss by detailed computation		% error of best estimate
	mlO_2	kJ (A)	mlO_2	kJ (B)	$\frac{A-B}{B}$ 100
Fridericia sp. (1)	8,919	180.1	7,000	142.2	+25.8
Fridericia sp. (2)	9,181	185.4	10,000	203.1	- 8.6
Fridericia sp. (3)	31,850	643.6	32,000	649.9	- 1.0
Melanotus rufipes	1,558	31.5	1,446	29.4	+ 7.2
Pyrrhosoma nymphula	675	13.65	660	13.4	+ 1.9
P. nymphula	805	16.24	767	15.5	+ 4.8
Oligolophus trideus	202	4.1	199	4.0	+ 3.7
Neobisium muscorum (1970 - 71)	8.436	170.37	9.183	185.48	- 8.1
Neobisium muscorum (1971 - 72)	3.897	78.53	4.041	81.59	- 3.75
Asellus aquaticus (method 2)	4,807	97.07	5,732	115.77	-16.1
Asellus aquaticus (method 1)	6,457	130.41	5,732	115.77	+12.6

Philoscia muscorum (Scopoli) Hassall (1976) 113-19

Porcellio scaber Latr. Watson (1966) 87-6

TABLE 19. A comparison of estimates of annual population respiratory losses for a range of detritivores and herbivores from various habitats.

Species	Reference	Respiratory Rate ($kJ\ m^{-2}\ y^{-1}$)
DETRITIVORES		
A. aquaticus L.	Present study	115.77
Armadillidium vulgare (Latreille)	Saito (1969)	118.88
Porcellio scaber Latreille	Saito (1960)	27.63
Ligidium japonicum	Saito (1969)	25.12
Tracheoniscus rathkei Brandt	White (1968)	3.88
Litter snails (all species)	Mason (1970)	29.69
Allolobophora rosea (Sav)	Bolton (1969) (in McNeill and Lawton 1970)	53.28
Limnodrilus hoffmeisteri Claraparede	Teal (1957)	2024.4
Total earthworms (limestone grassland)	Coulson and Whittacker (in press)	1130.2
Nematodes (limestone grassland)	"	25.1
Collembola (limestone grassland)	"	8.0
Tipulidae (limestone grassland)	"	334.0
Earthworms (blanket bog)	"	0.29
Enchytraeidae (blanket bog)	"	242.79
Nematodes (blanket bog)	"	12.98
Collembola (blanket bog)	"	7.12
Tipulidae (blanket bog)	"	66.14
HERBIVORES		
Cepea nemoralis L.	Richardson (1975)	1.8 - 5.6
Hazel defoliators	Smith (1972)	19.2
Total spittlebugs (in alfalfa)	Wiegart (1964)	94.6
Total grasshoppers (in alfalfa)	Wiegart (1965)	36.4
Orchelium fidicinum Rehm and Hebard	Smalley (1960)	77.9

Discussion. The role of population respiration in formulating the total energy budget will be discussed in section 5.

Respiratory measurements are a useful measurement of an animals activity and importance in a community as they overcome the limitations of estimating density of the population or measuring biomass. Thus it is of interest to compare the present respiratory data with other detritivores and other freshwater organisms in order to assess the importance of Asellus in freshwater habitats. Total respiratory figures for the population must, of course, be interpreted with caution as they clearly depend on the biomass of the population. However, the numbers and mean biomass of Asellus reported here do not appear to be abnormal (Anderson 1969; Fitzpatrick 1968).

A comparison with published data (Table 19) suggests that while the Asellus population in Wistow Lake has a much lower annual respiration than certain detritivores such as earthworms and enchytraeids in terrestrial ecosystems and tubificids, chironomids and nematodes in aquatic systems, its oxygen uptake is not insignificant. Its respiratory activity is greater than that of most terrestrial isopods, millipedes and snails, and may compare with earthworm populations. It has a higher oxygen uptake than any published data for an invertebrate herbivore other than marine molluscs.

4. FEEDING STUDIES

4.1 Introduction

Asellus aquaticus is capable of feeding on a wide range of plant and animal material (Dupey 1967). There appears to be little doubt, however, that its primary food source in lakes consists of decaying tree leaves, of which Alder (Alnus glutinosa (L)) is preferentially eaten (Levanidov 1949; Dupey 1967; Prus 1971). Its presence in streams containing few tree leaves

but mildly polluted with organic material such as sewage suggests that it may feed on other partially decayed organic matter also.

Thus the species is important in making the energy contained in allochthonous material available to other trophic levels of the lake ecosystem when Asellus is itself preyed upon by fish (Le Cren 1958). Reynoldson (1966) has also shown it to be preyed upon by Polycelis tenuis. Prus (1972) also suggests that by mechanically breaking down dead plant material the species accelerates decomposition by organisms such as bacteria. Matthews and Kowalczewski (1969) used the technique of placing leaves in fine and coarse meshed bags to assess the role of invertebrates on leaf decay in freshwater. They found that despite the presence of far greater numbers of invertebrates (including Asellus) in the coarse meshed bags, there was not a significantly greater rate of decomposition. They thus concluded that invertebrate animals are of no importance in litter breakdown in the aquatic situation. These workers, however, used oak (Quercus robur L.), willow (Salix sp.) and sycamore (Acer pseudoplatanus L.) in their experiments whereas Dupey (1967) showed that these species were much less preferred by Asellus than horse chestnut (Aesculus hippocastaneum L.) lime (Tilia sp.) and alder (Alnus glutinosa (L.)). Whatever the explanation, the conclusion is surprising, and it would be interesting to know the total consumption of leaves of a population of Asellus.

Feeding experiments are important in production studies in providing a check on production and respiration estimates. Thus assimilation can be calculated from: -

$$A = P + R$$

and also from: -

$$A = C - F$$

although problems in the application of these equations are discussed in section 5.

The studies reported in this section are based upon the latter equation, making the assumption that urine is an unimportant energy loss (Lawton 1971). Gravimetric methods were chosen as Prus (1971) had demonstrated the unreliability of the ash ratio method (Conover 1966), and there appears to be no way of using radioactive tracer techniques because of the problems of introducing tracer elements into decomposing material.

4.2 Methods

Animals for feeding experiments were collected in a pond net and transported to the laboratory in lake water, in a bucket, which was stored in a cold room at 10°C ± 2°C. They were subsequently sorted within a few days into size classes and the larger animals sexed. They were then kept in unisexual groups in 250 ml beakers containing 100 ml of lake water maintained at 10°C ± 0.1°C and fed on decayed alder leaves. Alder leaves were used as they are the predominant leaf on the lake bottom, and Dupey (1967) showed that they are the preferred food of Asellus. They were subsequently removed from the beakers and experiments carried out on individuals or small groups contained in 7.5 x 2.5 cm specimen tubes.

The experimental technique was as follows. 10 ml of filtered lake water were added to each specimen tube which was then maintained at 10°C ± 0.1°C in a water bath. Dust was excluded by covering each tube with a small, 3 cm diameter, petri dish lid.

Food material in the form of dead and slightly decomposed (but whole) alder leaves collected from the lake bottom in October and subsequently stored in lake water at 10°C ± 2°C was used. Discs of these leaves were cut with a 2 cm cork borer from the leaf lamina, avoiding the central midrib. The discs were then washed in distilled water (to remove small

particles and avoid errors due to deposition of mineral salts) and blotted dry by laying them on filter paper and pressing a further piece of filter paper on each one in turn. They were then stored in a petri dish lined with moist filter paper until they could be weighed.

The weighing procedure was as follows: -

a) A leaf disc was cut in half as exactly as possible, using a sharp scalpel and a template previously drawn on paper.

b) One half disc was replaced in the lined petri dish, whilst the other half was weighed in a foil pan, using either an electromicrobalance or a Mettler analytical balance, weighing to 0.01mg.

c) After weighing, the half disc was placed in one of the tubes of lake water which had been previously labelled.

d) The other half disc was similarly weighed and placed in a similar tube to act as a control.

The above procedures were carried out in one day and Asellus of the required size were also sorted into separate tubes and left with alder leaves as food overnight. It was thus hoped that the gut would be full at the start and at the end of the experiment. The animal was removed from the water onto a piece of tissue paper, and turned onto its dorsal surface, using a fine brush. Excess water immediately drained from the animal and it could be transferred to a deep foil pan and weighed (live weight). After weighing, each animal was added to an experimental tube as required, and allowed to feed for 2 - 6 days, according to the experiment. Daily inspection allowed the early termination of any replicate where food was used up rapidly. All experiments were conducted at $10^{\circ}C \pm 0.1^{\circ}C$, as this approximated to the mean temperature of the lake.

The water in the culture was changed and faeces removed every 72h, This was done by transferring the animal and uneaten food to a fresh tube. Faeces were separated and weighed as follows: -

a) Filter discs (nucleopore) were dried in a vacuum oven at 60°C; cooled in a desiccator and weighed.

b) Faeces were carefully examined and small pieces of food or exuviae removed. The faeces were then filtered in a sintered glass (Millipore) filter funnel and washed with distilled water.

c) The filter discs and faeces were then dried in the vacuum oven at 60°C overnight and subsequently cooled in a desiccator and weighed.

At the end of the feeding period, the faeces were separated in the same manner. Food and control leaf discs were removed from the lake water, washed, blotted dry (as above), and weighed (fresh weight). They were then vacuum dried and their dry weight determined.

In some later experiments (Tables 25 - 27) the initial live weight of the animals and final fresh weight of leaf discs was not recorded.

The animals were likewise blotted dry (as above) and their live weight measured. The animals were then anaesthetised to prevent them crawling out of the pans, rinsed in distilled water to remove anaesthetic, and vacuum dried at 60°C. Finally, the dried faeces, food, control leaf discs and animals were weighed to 0.01 mg.

Normally 20 experimental replicates were run at a time. The limiting factor was the number of weighings involved. With 20 replicates, a total of 420 separate weighings were performed.

Calculations.

Consumption. The initial dry weight of each food disc was calculated from the ratio of the final dry weight of the control disc to the initial fresh

weight of the control disc, assuming that the dry matter content of the two half discs was the same.

Assimilation and assimilation efficiency. Since the weight of the faeces (F) was known, assimilation (A) could be calculated from C = A + F and therefore the assimilation efficiency as $\frac{A}{C} \times 100$. In tables 20-23,24-27 individual assimilation efficiency was calculated on a dry weight basis. Consumption and faeces production and significance values were calculated on all replicates. Calorific values for consumption, faeces production, assimilation and mean assimilation efficiency were similarly calculated on the mean values for all the consumption and faeces replicates. Energy equivalents were taken from Prus (1972) and were 22.0259 J mg^{-1} (5.2618 cal mg^{-1}) for decaying alder leaves and 20.5131 J (4.9004 cal mg^{-1}) for Asellus faeces.

Production. Assuming the dry:live weight ratio of the animal was the same at the beginning and end of each experiment, the initial dry weight could be calculated and therefore the growth estimated.

4.3 Preliminary feeding experiments

These were conducted in order to ascertain the best gravimetric technique to use with Asellus. Animals were not sexed at the beginning of the experiment, so preliminary results are from mixed sex groups.

(i) Effect of state of decomposition of food on feeding rate. When conducting respiration experiments it was observed that Asellus fed with highly decomposed leaves (those showing partial skeletonisation) appeared to produce more faeces than animals fed with less highly decomposed leaves (wet and brown, but not skeletonised). As this could be a major source of variation in feeding experiments, this hypothesis was tested in the preliminary experiment.

The experiment was conducted as in section 4.2. Ten animals were fed on leaves showing partial skeletonisation, and ten on leaves which were brown but entire.

Results are shown in Table 20. A 't' test was conducted on the data transformed to $\sqrt{x + \frac{1}{2}}$ and there was a significantly greater amount ($P < 0.01$) of food eaten per 24h when the leaves were skeletonised, despite the large variation in food consumption in both cases. However, these animals also produced more faeces, so that total assimilation was lower but there was no significant difference in assimilation efficiency. Production (growth) of Asellus was very similar for both foods.

In a number of cases in this experiment assimilation could not be calculated as faeces production apparently exceeded food consumption. This was probably due to difficulties encountered with the use of Millipore filters which carried static electricity which was later found to affect the electro-microbalance. Faeces measurements may therefore be subject to error. Later experiments occasionally showed the same phenomena, so this is not the only explanation.

Conclusions. It is clear that quality of food is important in determining the level of food consumption in Asellus. Leaves collected for succeeding experiments were sorted according to two states of decay (skeletonised and unskeletonised), but it was impossible to categorise leaf decomposition more exactly.

Even within groups there was a wide range of levels of assimilation, consumption and faeces production. Possible causes of this were: -

a) It may reflect a wide variation of these parameters within the population.

b) There may also be variations within the individual animal at different times. It was noticed that there was considerable variation in faeces production between the first three days and the last three days of the experiment (Tables 20- 22).

c) There were experimental errors. Experience with this experiment indicated that the most important of these were: -

i) The estimation of initial dry weight of food material from final dry weight of controls. Although the procedure outlined in section 4.2 minimises this error, the heterogeneity of the leaf - especially variations in the mesophyll:vein ratio is particularly difficult to overcome. It is possible that these tissues contain different percentages of water. In all further experiments, care was taken to cut the leaf disc into half, at right angles to the veins. Discs with obvious differences between the two halves were discarded.

ii) Other workers (e.g. Prus 1971) have starved animals for 24h before experiments so that the gut was in a known state (i.e. empty) at the start of the experiment. The gut was then allowed to empty at the termination of the experiment. It was thought that the consumption rate in the experiment may be altered by this treatment, and it was therefore omitted. It does, however, introduce a possible source of error into the experiments.

An attempt to reduce experimental error by pre-drying the food material so that initial dry weights were known. Partially skeletonised leaves were used and the procedure was as described in section 4.2, except that in half of the 10 replicates the food discs were dried before the experiment, in order to find their initial dry weight. They were then allowed to soak in lake water for 24h before the feeding experiment began.

Nucleopore filter discs were used in this experiment as they were

thought to be non-static. Unfortunately they were later found to have static induced in them by contact with glass. This was overcome by washing the discs in water and placing them on filter paper for subsequent drying, etc. Filter paper was also placed between the disc and the sintered glass funnel during filtration. Results are shown in Table 21. It can be seen that assimilation efficiencies are higher in this experiment but comparable assimilation efficiencies were obtained by the two treatments, although the number of replicates were too small for this to be tested statistically. There was less variation in food consumption in the pre-dried samples, but the average consumption was less. The important thing that this experiment showed is that there was a loss in dry weight of the control leaves during the course of the experiment.

The loss of weight of control discs means that some materials diffused from the leaf (or were decomposed) during the experiment. Thus, if this method (pre-drying) was to be adopted, the control discs could not be dispensed with, as this loss must be estimated. There was variation in the amount of material diffusing from the disc, and difficulties also arose in calculating the diffusion from experimental as opposed to control discs.

As the criticism can also be made that the food was probably altered by this treatment, and as there is some evidence that pre-drying made the food less palatable to Asellus, this method was abandoned.

Effect of previous 24h starvation on food consumption.

Method. Ten replicates were treated as described in section 4.2, but a further ten replicates were starved for 24h before the experiment commenced. Gravid females were used in this experiment and it was found that these females gave an unusually high mortality during the experiments. Results are shown in Table 22. It can be seen that the consumption rate was not

significantly different between the two groups, although it was apparently lower in the starved animals. Assimilation and faeces production was not significantly different in the two groups. Pre-starvation did not reduce the variation between replicates.

Although there was no indication that pre-starved animals consumed more (indeed the evidence was to the contrary), this experiment gave no indication that it would reduce experimental errors. Variation was just as great in pre-starved animals and there was again one instance of faeces production apparently exceeding consumption. As this method also involves more weighings (faeces voided after the experiment ended had to be weighed) this method was also abandoned.

From the preliminary experiments, it can be seen that consumption, faeces production and assimilation efficiencies varied considerably between similar sized animals. From the faeces collections, it would appear that these parameters varied in the same animal at different times. This does not preclude the possibility of experimental errors from the sources already discussed. Indeed the fact that occasional replicates showed greater final dry weight of food than was calculated for initial dry weight, or a greater weight of faeces than food consumed, suggests that such errors are very real. These results also show that the state of decay of the food material was an important factor in determining the total food consumption. However, with greater consumption, the assimilation efficiency was reduced so that the food assimilated remained much the same. Gere (1956) showed the same phenomena with Glomeris hexasticha (Diplopoda) and Chromatoiulus projectus (Isopoda) which when fed on slightly decomposed and strongly decomposed oak litter, consumed larger amounts of the latter, but assimilated a greater proportion of the former. This was presumably related to the rate

TABLE 20. A comparison of consumption and assimilation efficiency when alder leaves in two states of decay were used as food by Asellus aquaticus. Date: 2.11.73 Sex: Mixed Average dry weight (mg) = 2.66

A) SKELETONISED LEAVES:

No.	Duration (days)	Asellus Production P (mg)	Consumption C (mg)	Faeces Day 1 - 3 (mg)	Faeces Day 4 - 6 (mg)	Total Faeces F (mg)	Assimilation A = C - F (mg)	Assimilation Efficiency $\frac{A}{C} \cdot 100\%$
1	6	0.153	2.859	0.945	1.505	2.45	0.409	14.31
2	6	0.016	2.369	1.155	0.585	1.74	0.629	26.55
3	6	0.433	0.761	0.380	0.640	1.02	-	-
4	6	0.286	1.974	1.145	0.455	1.60	0.374	18.95
5	6	0.132	4.987	2.180	1.550	3.73	1.257	25.21
6	6	0.175	3.987	1.305	1.575	2.88	1.107	27.76
7	6	0.188	1.257	0.755	0.925	1.68	-	-
8	6	- 0.385	3.731	1.945	1.495	3.44	0.291	7.80
9	6	0.382	6.603	2.520	3.600	6.12	0.483	7.32
10	6	0.658	1.010	0.102	0.868	0.97	0.040	3.96
Mean 6 days^{-1}		0.20392	2.9538	1.243	1.320	2.563	0.574	16.48
Mean indiv^{-1}day^{-1}(mg)		0.0340	0.4923	0.2072	0.2200	0.0828	0.0956	-
Standard error		0.0146	0.2430	0.4081	0.4081	0.4272	0.0243	3.36
Mean indiv^{-1}day^{-1}(J)		0.4219	10.84335	4.2626	4.5129	8.7626	2.0808	19.189

B) NON-SKELETONISED LEAVES:

1	6	0.471	1.181	0.000	0.230	0.23	0.951	80.52
2	6	0.159	0.693	0.310	0.160	0.47	0.223	32.18
3	6	0.210	0.157	0.000	0.126	0.126	0.031	19.74
4	6	0.461	1.291	1.120	0.37	1.49	-	-
5	6	0.189	1.073	0.055	0.535	0.59	0.483	45.01
6	6	0.212	0.457	0.270	0.100	0.37	0.083	18.16
7	6	0.916	0.653	0.820	0.33	1.15	-	-
8	6	0.651	0.000	0.655	0.045	0.70	-	-
9	6	0.187	1.485	0.915	0.505	1.42	0.065	4.38
10	6	0.202	1.528	0.1935	0.405	1.34	0.188	12.30
Mean 6 day^{-1}		0.2938	0.8518	0.508	0.281	0.7890	0.289	30.33
Mean indiv^{-1}day^{-1}(mg)		0.0490	0.1420	0.0847	0.0468	0.1315	0.0482	-
Standard error		0.0089	0.0285	0.0203	0.0091	0.0272	0.0207	9.75
Mean indiv^{-1}day^{-1} (J)		0.6081	3.1277	1.7375	0.9600	2.6974	0.4295	13.74

TABLE 21. A comparison of consumption and assimilation efficiency of A. aquaticus with and without pre-drying of food (alder leaves). Date: 22.1.74 Sex: Mixed Mean dry weight (mg) = 2.66

A) SKELETONISED LEAVES:

No.	Duration (days)	Asellus Production P (mg)	Consumption C (mg)	Faeces Day 1 - 3 (mg)	Faeces Day 4 - 6 (mg)	Total Faeces F (mg)	Assimilation A = C - F (mg)	Assimilation Efficiency $\frac{A}{C}$. 100%
1	6	- 0.049	3.49	1.33	0.89	2.22	1.27	36.45
2	6	0.481	0.71	0.05	0.50	0.55	0.16	22.17
3	6	- 0.955	6.70	2.47	2.36	4.83	1.87	27.93
4	6	0.820	3.42	0.64	2.50	3.14	0.28	8.19
5	6	0.313	1.18	0.32	0.12	0.44	0.74	62.71
Mean 6 days^{-1}		0.122	3.10	0.962	1.274	2.2360	0.864	31.49
Mean indiv^{-1}day^{-1}(mg)		0.0203	0.5167	0.1603	0.2123	0.3727	0.1440	-
Standard error		0.0506	0.1772	0.0722	0.0813	0.1375	0.0531	9.06
Mean indiv^{-1}day^{-1}(J)		0.2519	11.3808	3.2882	4.3549	7.6446	3.7362	32.83
B) WITH PRE-DRYING								
6	6	0.271	2.06	0.16	1.00	1.16	0.90	43.69
7	6	- 0.048	2.31	0.58	1.11	1.69	0.62	26.84
8	6	- 0.242	2.10	0.19	1.25	1.44	0.66	31.43
9	6	0.473	1.39	0.13	0.85	0.98	0.41	29.50
10	6	0.095	2.36	0.07	1.51	1.58	0.78	33.05
Mean 6 days^{-1}		0.110	2.044	0.226	1.144	1.37	0.674	32.90
Mean indiv^{-1}day^{-1}(mg)		0.0183	0.3407	0.0377	0.1907	0.2283	0.1123	-
Standard error		0.0206	0.0289	0.0151	0.0188	0.0220	0.0137	2.88
Mean indiv^{-1}day^{-1}(J)		0.2271	7.5042	0.7733	3.9118	4.6831	2.8211	37.59

TABLE 22. A comparison of consumption and assimilation efficiency of A. aquaticus with and without prior 24h starvation using alder leaves as food. Date: 18.2.74 Sex: Gravid females Mean dry weight = 3.733 mg

A) WITHOUT STARVATION:

No.	Duration (days)	Asellus Production P (mg)	Consumption C (mg)	Faeces Day 1 - 3 (mg)	Faeces Day 4 - 6 (mg)	Total Faeces F (mg)	Assimilation A = C - F (mg)	Assimilation Efficiency $\frac{A}{C} \cdot 100\%$
1	6	0.507	0.886	0.127	0.589	0.716	0.170	19.19
3	6	0.301	0.410	0.054	0.356	0.410	0.000	0.0
6	6	0.322	-			-	-	-
7	6	0.213	1.620	1.128	0.366	1.494	0.126	7.78
8	6	0.409	2.737	0.220	2.165	2.385	0.352	12.86
10	6	- 0.001	1.930	0.484	1.186	1.670	0.260	13.47
Mean 6 days^{-1}		0.292	1.517	0.403	0.932	1.335	0.181	10.66
Mean indiv^{-1}day^{-1}(mg)		0.0486	0.2527	0.0672	0.1553	0.2225	0.0302	-
Standard error		0.0119	0.0676	0.0326	0.0572	0.0587	0.0100	3.22
Mean indiv^{-1}day^{-1}(J)		0.6031	5.5675	1.3785	3.1857	4.5642	1.0033	18.02
B) WITH STARVATION:								
12	6	0.225	0.705	0.488	0.131	0.619	0.086	12.20
14	6	0.071	3.354	0.707	1.930	2.637	0.141	35.88
15	6	- 0.105	0.393	0.071	0.181	0.252	0.141	35.88
17	6	- 0.453	0.401	0.145	0.346	0.491	-	-
18	6	0.302	0.440	0.157	0.229	0.386	0.054	12.27
20	6	0.058	0.499	0.400	0.045	0.445	0.054	10.82
Mean 6 days^{-1}		0.0163	0.96533	0.328	0.477	0.80500	0.210	18.51
Mean indiv^{-1}day^{-1}(mg)		0.0027	0.16089	0.0547	0.0795	0.1342	0.0350	-
Standard error		0.0184	0.0800	0.0168	0.0489	0.0616	0.0213	4.73
Mean indiv^{-1}day^{-1}(J)		0.0335	3.5438	1.221	1.6308	2.7522	0.7916	22.33

TABLE 23. A comparison of consumption and assimilation efficiency between male and female A. aquaticus using alder leaves as food. Date: 6.5.74 Mean dry weight (males) 2.50 mg Mean dry weight (females) 2.22mg

A) FEMALES. 2 animals/culture.

Replicate No.	Duration (days)	Consumption (mg)	Total Faeces (mg)	Assimilation (mg)	Assimilation Efficiency
F5/1	3	3.749	3.146	0.603	16.08
F5/2	3	2.136	1.056	1.056	50.56
F5/6	2	3.334	3.432	-	-
F5/7	2	4.380	4.048	0.332	7.580
F6/1	3	2.279	1.573	0.706	30.98
F6/2	3	1.176	1.144	0.032	2.72
F6/5	3	2.917	2.574	0.343	11.76
F6/6	3	2.621	1.683	0.932	35.79
F6/7	3	2.059	1.661	0.398	19.33
Mean 3 days^{-1}	3.16756	3.16756	2.673	0.553	21.65
Mean indiv^{-1}day^{-1}(mg)		0.5279	0.4455	0.0922	-
Standard error		0.0936	0.1003	0.0204	5.69
Mean indiv^{-1}day^{-1}(J)		11.6281	9.1386	2.4895	21.41

B) MALES. 2 animals/culture.

F5/3	3	2.747	2.574	0.173	6.298
F5/4	3	2.574	2.024	0.550	21.37
F5/5	3	3.014	3.307	-	-
F5/8	3	1.894	1.507	0.387	20.43
F5/9	3	3.331	2.926	0.405	12.16
F5/10	3	2.487	2.353	0.134	5.38
F6/3	3	1.298	0.957	0.341	26.27
F6/4	2	1.418	1.500	-	-
F6/8	3	1.499	1.452	0.047	3.13
F6/9	3	2.261	1.584	0.677	29.94
F6/10	2	4.359	3.201	1.158	26.57
Mean 3 days^{-1}		2.706	2.3396	0.430	16.83
Mean indiv^{-1}day^{-1}(mg)		0.45106	0.38993	0.0717	-
Standard error		0.0708	0.0538	0.0188	3.42
Mean indiv^{-1}day^{-1}(J)		9.9350	7.9987	1.9363	19.49

TABLE 24. Summary of preliminary feeding experiments with Asellus aquaticus using different treatments.

Treatment	Consumption mg ind^{-1} 24h^{-1}	Consumption J ind^{-1} 24h^{-1}	Significance	Assimilation Efficiency
Skeletonised	0.4923	10.8433	)	19.19
			) P<0.01	
Non-skeletonised	0.1420	3.1277	)	13.74
Pre-dried food	0.3407	7.5042	)	37.59
			) N.S.	
No predrying	0.5167	11.3808	)	32.83
Without starvation	0.2527	5.5674	)	18.02
			) N.S.	
Prior starvation	0.1609	3.5440	)	22.33
Males	0.4511	9.935	)	19.49
			) N.S.	
Females	0.5279	11.6281	)	21.41

of passage of food through the gut. Prus (1971) has suggested that when ingestion is slow in A. aquaticus, the food passes more slowly and therefore enzymatic action will be more complete.

Nilsson (1974) showed that food consumption in Gammarus pulex increased with the time of immersion of the food leaves in water. However, this increase was for immersion times of up to 40 days, whereas even the non-skeletonised leaves in the present study had been immersed for longer than this.

With the above variables, it would have been desirable to conduct the feeding experiments with a large number of replicates. However, the time-consuming nature of this methodology precluded this in the present study.

4.4 The effect of sex and size on consumption and assimilation efficiency.

In these experiments the number of animals per culture was increased to 5 for the smallest size classes, and 2 for the largest size class. This was done in order to complete the experiments in a shorter time period and yet still obtain sufficient weight differences for reliable results. Otherwise, the method was as described in section 4.2.

After the first two experiments in this series, the animals were not sexed, as no significant difference was found between males and females.

The effect of sex onfood consumption and assimilation efficiency is shown in Table 23, and size class estimations are given in Tables 25 - 27 . Results are summarised in Table 28 . There were no significant differences in consumption or assimilation efficiencies between the sexes, or between non-gravid and gravid animals (Table 24).

Larger individuals consumed more food than the smaller animals, consumption ranging from 0.2236 mg ind^{-1} $24h^{-1}$ for animals 4.5 - 5.5 mm long, to 0.4895 mg ind^{-1} $24h^{-1}$ for animals 8.0 - 9.0 mm long. On a weight specific basis, however, the smaller animals consumed more food per mg live

weight. Assimilation efficiencies do not show significant differences or obvious trends between size classes.

Discussion. In the present study, consumption data are similar to those reported by Prus (1971) but assimilation efficiencies are generally lower. Prus found a total variation from 26.32% assimilation efficiency (large males) to 43.62% (gravid females) and calculates an average of 30% for a whole population (New Hinksey Stream, near Oxford). The present study showed a total range from the various experiments of 13.74% to 37.59% and an average figure of 23% on the basis of the mean value of the four size classes investigated.

Consumption figures in this study ranged from 0.142 mg ind^{-1} $24h^{-1}$ for animals fed on less well decayed leaves to 0.5279 mg ind^{-1} $24h^{-1}$ for females in May. This latter figure, however, is not significantly different from mixed groups of larger animals. Prus' data ranged from 0.25 mg ind^{-1} $24h^{-1}$ to 0.8430 mg ind^{-1} $24h^{-1}$ for males in June.

The range of estimations of assimilation efficiency on individual animals is greater in the present study, and Prus did not report any instances where the calculation of assimilation is not possible due to estimation of faeces production greater than that of food consumed.

Levanidov (1949) reported assimilation efficiencies of 56% in Asellus aquaticus. Faeces, however, were collected after several months, and it is likely that the losses due to disintegration and decay of faecal material (Pavlyutin 1970; Prus 1971) were underestimated.

Table 29 compares the present data with those published for terrestrial isopoda, detritivores and three aquatic detrivores. It is clear that there is a considerable range in assimilation values within and between species, but detritivores generally have low assimilation efficiencies in laboratory

estimations. This may reflect the quality of the food eaten but the data of Hubbell, Sikora and Paris (1965) are interesting in that they suggest assimilation efficiencies in the field are much higher, due to less abundant food. This argument probably does not apply to Asellus in Wistow Lake, which appear to have abundant food on the lake bottom throughout the year. McDiffett (1970) criticised the usual gravimetric techniques of estimation of assimilation efficiency as he found that the stonefly, Potomophylax cingulatus fragmented a lot of food which was not consumed, and this fragmented portion was estimated with the faeces. By using a modified technique, he showed a very low assimilation efficiency.

Both Nilsson (1974) and Otto (1974) showed that consumption and assimilation are affected by temperature. No attempt has yet been made to study the effect of this parameter on Asellus aquaticus. Both these authors also show that size affects consumption and assimilation efficiency. The present study confirms the effect on consumption, but not on assimilation efficiency, but the full range of sizes has not been investigated. Both of these parameters (size and temperature) vary throughout the year and make it difficult therefore to estimate an annual budget.

It is also likely that the size of an animal reflects its state of development, and that the developmental stage is likely to be important in feeding studies. The present experiments were conducted before the population analysis had revealed the distinct growth patterns of the various cohorts. In order to produce an accurate estimate of feeding parameters by the field population, more detailed studies are required, particularly studies which link feeding experiments with the growth curve(s) of the field population.

One way of achieving this is to monitor food consumption, faeces production and growth (production) of a number of individuals throughout the

TABLE 25. Estimation of consumption and assimilation efficiency of A. aquaticus 8 - 9 mm in length, using alder leaves as food. Date: 13.5.74 Sex: mixed. Mean dry weight = 3.499 mg. 2 animals/culture.

No.	Duration	C (mg)	F (mg)	Λ (mg)	%
F5/1	3	3.749	3.146	0.603	16.08
F5/2	3	2.136	1.056	1.080	50.56
F5/3	3	2.747	2.574	0.173	6.298
F5/4	3	2.576	2.024	0.550	21.37
F5/5	3	3.014	3.307	-	-
F5/6	2	3.334	3.432	-	-
F5/7	3	4.380	4.408	0.332	7.580
F5/8	3	1.894	1.507	0.387	20.43
F5/9	3	3.331	2.926	0.405	12.16
F5/10	3	2.487	2.353	0.134	5.38
F6/1	3	2.279	1.573	0.706	30.98
F6/2	3	1.176	1.144	0.032	2.72
F6/3	3	1.298	0.957	0.341	26.27
F6/4	2	1.418	1.500	-	-
F6/5	3	2.917	2.574	0.343	11.76
F6/6	3	2.621	1.683	0.932	35.79
F6/7	3	2.059	1.661	0.398	19.33
F6/8	3	1.499	1.452	0.047	3.13
F6/9	3	2.261	1.584	0.677	29.94
F6/10	2	4.359	3.201	1.158	26.57
Mean 3 days^{-1}		2.937	2.489	0.488	19.20
Mean indiv^{-1}day^{-1}(mg)		0.4895	0.41771	0.0813	-
Standard error		0.04	0.1055	0.0136	3.1851
Mean indiv^{-1}day^{-1}(J)		10.7815	8.5685	2.2129	20.52

TABLE 26. Estimation of consumption and assimilation efficiency of A. aquaticus 6 - 7 mm in length, using alder leaves as food. Date: 18.5.74 Sex: Male and Female Mean dry weight = 1.681 mg. 3 animals/replicate.

Replicate No.	Duration (days)	C (mg)	F (mg)	A (mg)	%
F5/11	3	2.889	2.596	0.293	10.14
F5/12	3	2.366	2.27	0.096	4.06
F5/13	3	4.283	3.86	0.423	9.88
F5/14	3	2.692	2.376	0.316	11.74
F5/15	3	2.420	2.101	0.319	13.18
F5/16	3	1.627	1.023	0.604	37.12
F5/17	3	0.891	1.22	-	-
F5/18	3	2.946	2.112	0.834	28.31
F5/19	3	1.719	1.782	-	-
F5/20	3	3.251	2.98	0.270	8.31
F6/11	3	2.121	1.804	0.317	14.95
F6/12	3	2.955	2.552	0.403	13.64
F6/13	3	1.024	0.561	0.463	45.22
F6/14	3	2.156	1.595	0.561	26.02
F6/15	3	0.603	0.69	-	-
F6/16	3	3.659	2.596	1.063	29.05
F6/17	3	0.751	0.726	0.025	3.33
F6/18	3	2.105	1.43	0.675	32.07
F6/19	3	5.654	2.68	2.970	52.53
F6/20	3	1.821	1.11	0.710	38.99
Mean 3 days^{-1}		2.397	1.9032	0.608	22.26
Mean indiv^{-1} day^{-1} (mg)		0.2663	0.21147	0.0676	-
Standard error		0.0308	0.0215	0.0179	3.66
Mean indiv^{-1} day^{-1} (J)		5.8652	4.3379	1.5273	26.04

TABLE 27. Estimation of consumption and assimilation efficiency of A. aquaticus of A) 7.0 - 8.0 mm in length, and B) 4.5 - 5.5 mm in length, using alder leaves as food.

A) 7.0 - 8.8 mm in length: Date: 17.6.74 Sex: Mixed Mean dry weight = 2.188 mg. 3 animals/culture

Replicate No.	Duration (days)	Consumption C (mg)	Faeces F (mg)	Assimilation A = C - F (mg)	Assimilation Efficiency %
11	4	0.090	0.48	-	-
12	4	3.545	2.048	0.597	16.8
13	4	0.682	1.160	-	-
14	4	1.462	1.27	0.186	12.72
15	4	2.567	1.83	0.637	25.82
16	4	2.171	1.99	0.181	8.34
17	4	1.696	1.254	0.442	26.00
18	2	3.722	2.728	0.994	26.71
19	4	2.390	2.563	-	-
20	2	7.466	5.313	2.153	28.84
Mean 4 days^{-1}		3.6879	2.8677	0.741	20.74
Mean indiv^{-1}day^{-1} (mg)		0.30733	0.2390	0.0618	-
Standard error		0.1168	0.0802	0.0215	3.04
Mean indiv^{-1}day^{-1}(J)		6.76922	4.90222	1.86700	27.58

B) 4.5 - 5.5 mm in length. Date: 17.6.74 Sex: Mixed Mean dry weight = 0.831 mg. 5 animals/replicate

1	4	3.702	3.322	0.382	10.26
2	4	3.903	3.564	0.339	8.68
3	2	3.381	3.322	0.059	1.75
4	2	3.180	3.102	0.078	2.45
5	2	3.669	2.651	1.018	27.75
6	4	3.474	3.014	0.460	13.24
7	4	1.900	1.353	0.547	28.79
8	4	2.097	2.03	0.062	2.96
9	4	4.524	3.861	0.663	14.65
10	4	-	0.88	-	-
Mean 4 days^{-1}		4.45111	3.6174	0.401	12.28
Mean indiv^{-1}day^{-1}(mg)		0.2226	0.1809	0.0201	-
Standard error		0.0329	0.0309	0.0053	3.39
Mean indiv^{-1}day^{-1}(J)		4.90808	4.02221	0.87987	17.95

TABLE 28. Summary of feeding experiments using Asellus aquaticus of different sizes from Wistow Lake.

Length (mm)	Mean dry weight (mg)	Consumption (mg $ind^{-1} 24h^{-1}$)	Consumption (J $ind^{-1} 24h^{-1}$)	Significance	Assimilation efficiency	Consumption (mg $mg^{-1} 24h^{-1}$)	Consumption J $mg^{-1} 24h^{-1}$
8 - 9	3.499	0.4895	10.7815	)	20.56	0.1399	3.0813
				) N.S.			
7 - 8	2.188	0.3688	6.7692	)	27.58	0.1686	3.0937
6 - 7	1.681	0.2967	5.8652	)	26.04	0.1765	3.4891
				) N.S.			
4.5 - 5.5	0.831	0.2226	4.9030	)	17.95	0.2679	5.9001
Means		0.3444	7.0797		23.0	0.1882	3.8911
			8 - 9 mm	)			
				) *P<0.02			
			4.5 - 5.5 mm	)			

TABLE 29. Comparison of assimilation efficiencies for a range of isopods and freshwater detritivores.

	Species	Reference	Lowest recorded value	Mean	Highest recorded value	Comments
ISOPODS	Asellus aquaticus	Present study	13.74	23.0	32.83	
	Asellus aquaticus	Prus 1971	26.32	30.0	43.62	
	Oniscus asellus	Watson 1966	24.74	27.2	40.49	
	Porcellio scaber	Watson 1966	16.04	29.3	39.58	
	Tracheoniscus rathkei	White 1968	–	33.0	–	
	Armadillidium vulgare	Hubbell, Sikora and Paris 1965	19 59	– –	27 84	Laboratory Field
FRESHWATER DETRITIVORES	Gammarus pulex	Nilsson 1974	33.00	35.0	37.00	
	Potomophylax cingulatus	Otto 1974	29 21	– –	36 29	15°C 5°C
	Pteronarcys scottii	McDiffett 1970		10.6		

life cycle at temperatures simulating those found in the field or, if possible, actually under field conditions.

For the purposes of the present study, it would seem reasonable to accept an overall consumption figure of 0.1882 mg^{-1} $24h^{-1}$ and an assimilation efficiency of 23.0% for A. aquaticus from Wistow Lake. This is equivalent to an energy uptake of 3.8911J mg^{-1} $24h^{-1}$.

5. ENERGY BUDGET

From the data presented in the previous sections, it is possible to calculate both a daily energy budget for any given size of individual and also an annual population budget.

Calorific values have not been determined in the present study, but have been taken as follows: -

Asellus males: 11.6078 J mg^{-1} (Fitzpatrick 1968)

Asellus females: 13.8054 J mg^{-1} (Fitzpatrick 1968)

Asellus mixed sexes: 12.3838 J mg^{-1} (Prus 1972)

Decayed Alnus glutinosus leaves: 22.0259 J mg^{-1} (Prus 1971)

Asellus faeces: 20.5131 J mg^{-1} (Prus 1971)

5.1 Daily individual energy budget.

This is a budget for a single individual at 10°C and can be calculated from the results of laboratory experiments. Here an individual weighing 2.75 mg dry weight (12.81 mg live weight) is arbitrarily chosen. Using the equations

$$C = A + F$$

and

$$A = P + R$$

as defined in section 1; consumption = 8.48 J $24h^{-1}$ (Table 28), and with an assimilation efficiency of 23.0%, A is calculated as 1.95 J $24h^{-1}$ and F as 6.53 J $24h^{-1}$.

Assimilation rates can also be estimated from respiration and production measurements. From the respiratory data the respiration rate of an animal of this size at 10°C = 52.32 µl O_2 $24h^{-1}$. Taking the R.Q. of Asellus aquaticus as 0.82 (Will 1952) and the oxycalorific equivalent as 20.197 J ml^{-1} of oxygen (Brody 1945) this is equivalent to 1.0567 J $24h^{-1}$.

Production was only estimated in the preliminary feeding experiments, but the average of all replicates gives a daily production of 0.0298 mg $24h^{-1}$ = 0.368 J $24h^{-1}$.

Thus the equation can be quantified to: -

C	=	P	+	R	+	F	
8.480		0.368		1.057		6.530	(All figures in J $24h^{-1}$).

Clearly there is some discrepancy in the two independently derived values for the assimilated energy (1.95 J $24h^{-1}$ and 1.425 J $24h^{-1}$). Either P or R has been underestimated, or the assimilation efficiency has been overestimated. There is a 20% error in the two estimates, but the equation illustrates clearly the fate of consumed energy. A very much greater amount of energy is passed on as faeces to the decomposers than as production to predators.

Prus (1972) gave a budget for the same sized animal of A. aquaticus as:

C	=	P	+	R	+	F	
8.28		0.44		2.07		5.78	(All figures in J $24h^{-1}$).

There is obviously close similarity between the two sets of data, the differences arising in the estimated assimilation efficiency and a much higher respiratory rate. Prus determined respiratory rates at 22°C, however, which is an abnormally high temperature for most Asellus, and may give an inflated estimate of energy used in respiration.

5.2 Annual production budget

Annual production of the male population (Table 10) was 1073 mg $m^{-2}y^{-1}$ in Wistow Lake, which is equivalent to 12.455 k J $m^{-2}y^{-1}$. The female production was 1651 mg $m^{-2}y^{-1}$ = 22.792 kJ $m^{-2}y^{-1}$. This gives a total production of 35.247 kJ $m^{-2}y^{-1}$.

Similarly, the total annual population respiration is calculated as 5732 ml O_2 = 115.77 kJ $m^{-2}y^{-1}$ (Table 18).

Thus $A_f = P_f + R_f$

$A_f = 35.25 + 115.77 = 151.02$ kJ $m^{-2}y^{-1}$

Where A_f = estimate of assimilat energy in the field.

These figures can be accepted with some confidence, as the ratio $\frac{R}{A} = 0.761$. Fitzpatrick (1968) gave the value of this ratio as 0.758.

Accepting the value for assimilation efficiency for Asellus in the present study as 23%, then field consumption can be calculated from: -

$$C_f = \frac{A_f}{A/C} = \frac{151.02}{0.23} = 656.61 \text{ kJ } m^{-2}y^{-1}$$

The annual population energy budget can therefore be quantified as: -

$C_f = P_f + R_f + F_f$

656.61 35.25 115.77 505.59 (All figures in kJ $m^{-2}y^{-1}$)

It is also possible to calculate field consumption from laboratory experiments, by calculating population consumption using Phillipson's (1963) best estimate method. The calculation is shown in Table 30. It can be seen that the consumption (1296 kJ $m^{-2}y^{-1}$) is nearly twice that estimated above. As production calculations are based on the same biomass data as population consumption, it must be assumed that either respiration is underestimated in the above equation, consumption is overestimated, or the estimated assimilation efficiency is too high.

TABLE 30. Calculation of annual consumption of A. aquaticus in Wistow Lake (1973 - 74) by best estimate (method 1).

A) MALES

SAMPLING TIME	1	2	3	4	5	6	7	8	9	10	11	12	13	14	TOTAL
Mean dry wt indiv^{-1} (mg)	0.627	0.887	1.211	1.420	1.404	1.325	1.361	1.225	1.473	0.544	0.346	0.654	0.407	0.572	13.456 = A_1
Consumption (mg indiv^{-1})	0.212	0.225	0.243	0.255	0.255	0.250	0.250	0.245	0.260	0.210	0.205	0.215	0.206	0.215	3.246 = B_1

B) FEMALES

Mean dry wt indiv^{-1} (mg)	0.522	0.689	0.948	1.080	1.172	1.065	1.474	1.494	1.860	0.734	0.318	0.945	0.572	0.434	13.307 = A_2
Consumption (mg indiv^{-1})	0.210	0.220	0.230	0.240	0.243	0.235	0.255	0.260	0.285	0.220	0.200	0.230	0.213	0.210	3.251 = B_2

Calculation

1. Sum mean weight per individual at each census (mg) = $A_1 + A_2$
2. Sum total food consumption per day for each of these individuals at mean field temperature (10°C) = $B_1 + B_2$
3. Mean consumption per mg for whole sampling period (mg mg^{-1} day^{-1}) = $\frac{B_1 + B_2}{A_1 + A_2} = \frac{6.497}{26.763} = 0.24276$
4. Therefore uptake per mg for whole year = 88.6074 mg mg^{-1} y^{-1}
5. Uptake per m^2 for whole year = 88.6074 x 754.76 (biomass) = 66.8773 g m^{-2} y^{-1}
6. Energy equivalent of decayed alder leaves = 22.0259 kJg^{-1} = 1473.0327 kJm^{-2} y^{-1}
7. But respiratory estimate was 12% too high by this method = 1296.27 kJ m^{-2} y^{-1}

Consumption measurements in laboratory experiments have been reported elsewhere as being too high (Lawton 1971; Smith 1972), but usually in the order of an increase of 10%. Otto (1974) reports greater growth of Potomophylax in the laboratory than in the field, even at lower temperatures. This has often been explained as due to greater availability of food in the experimental situation. This explanation may not apply to Asellus aquaticus in Wistow Lake, for the areas where the animal is found are covered with abundant decaying alder leaves. Animals living in the algae may not be in direct contact with alder leaves, however, and it would be of interest to observe or otherwise determine their feeding habits.

McDiffet (1970) claimed that consumption of leaf material is often overestimated because of the fragmentation of leaves by the detritivores. He also believes assimilation efficiency is overestimated for this reason. Thus it appears that the errors in the above energy budget are most likely to arise from one or more of the following: -

1. Overconsumption by animals in the laboratory, when excess food material is provided.
2. Overestimation of consumption in feeding experiments.
3. Overestimation of assimilation efficiencies.

5.3 Discussion

There are two main reasons for carrying out a population energy study. The first is to allow an assessment of the role which the species plays within the ecosystem. The second is that energy studies allow the role of animals in different ecosystems and in different trophic levels to be compared.

a) The role in the ecosystem. Energy budget parameters allow direct comparison of different species in terms of their function within the ecosystem. The problem here is that there is no base-line with which to evaluate the present data on Asellus aquaticus. It is estimated that the population in Wistow Lake consumed 656 kJ $m^{-2}y^{-1}$. This is equivalent to about 35g dry weight m^{-2} of leaf material annually. About 77% of this energy is voided as faeces, about 18% is respired, and 5% is made available to other organisms. Thus Asellus plays a larger role in breaking down leaf material and producing food for other detritivores than it does in passing material to carnivores.

Unfortunately, we do not know how much allochthonous material is deposited in the lake annually. Neither can the breakdown of this substrate due to Asellus be compared with other lake detritivores, as no comparable studies have been made. The material consumed by Asellus in Wistow is equivalent to twice the amount of allochthonous material falling into the River Thames (Mann et al. 1972) and about one-ninth of the leaf litter fall in Meathop Wood (Satchell 1970). It is likely, therefore, that the role of Asellus will be a significant one in the lake ecosystem.

b) Comparison with other ecosystems and trophic levels. The number of complete studies of energy budgets for field populations is still small (but increasing at the present time) and there are now sufficient data available for tentative generalisations to be attempted. Table 31 compares some published data for detritivores, herbivores and carnivores.

Saito's data show a surprisingly high assimilation efficiency (49.9 - 51.5%) compared with other studies (Table 31), and should perhaps be treated with some caution. Most detritivores show a lower assimilation efficiency than herbivores, especially when compared with those herbivore species with

TABLE 31. A comparison of the energetic efficiencies of some herbivores, detritivores and carnivores.

	Subject	Reference	% Assimilation consumption	% Production assimilation	% Production consumption	Respiration Production
DETRITIVORES	Asellus aquaticus (L.)	Present study	23.0	23.0	7.5	3.19
	Armadillidium vulgare Latreille	Saito (1965)	49.9	18.9	9.53	4.2
	Porcellio scaber Latreille	Saito (1965)	50.0	15.6	8.75	5.5
	Ligidium japonicum	Saito (1965)	51.5	13.0	6.52	6.7
	Potomophylax cingulatus Steph.	Otto (1974)	20.2	42	9.4	3.3
	Pteronarcys scottii Ricker	McDiffett (1970)	10.6	34.2	3.6	-
HERBIVORES	Cepea nemoralis L.	Richardson (1975)	33.6	41	13.0	1.8
	Hazel defoliators	Smith (1972)	41.7	57.4	23.9	0.65
	Philaenus spumaris L.	Wiegart (1964)	39 - 58	8 - 42	4.8 - 16	1.4 - 10.8
	Grasshoppers	Wiegart (1965)	37	34 - 38	13 - 14	1.6 - 1.9
CARNIVORES	Pyrrhosoma nymphula (Sulz)	Lawton (1971)	89.8	51.8	46.5	0.8
	Pardosa lugubris (Walckenaer)	Edgar (1971)	100	21.4	21.4	2.7

a short larval period characterised by rapid growth (Richardson 1975), or hemipterans feeding directly on cell contents (Wiegert 1964). This is not surprising. Macfadyen (1967) pointed out that detritivores are consuming material already rejected by herbivores. As the material is dead, and therefore probably older, it will contain a higher proportion of relatively indigestible cellulose and lignin. Carnivores, at the other extreme, have extremely high assimilation efficiencies although many do not consumeall that they kill.

Similarly, $\frac{P}{A}$ ratios are low in detritivores. Defoliators and spittle-bugs are relatively sedentary feeders. Respiration is therefore comparatively low. Asellus and other isopods are more active. It is interesting that Potomophylax has a relatively high $\frac{P}{A}$ ratio, but being a case living caddis, it is relatively sedentary. Also, Otto's (1974) production data are for a single individual, whereas in a population study, predation and other mortality factors will reduce the total production. Otto regarded food as a limiting factor in the growth of this case forming trichopteran, perhaps a reflection of its relative immobility. $\frac{P}{C}$ is therefore low in all detritivores. Slobodkin (1962) believed that this ratio is unlikely to exceed 15%, and it can be seen that it does so only in the case of defoliators. The $\frac{R}{P}$ ratio is higher in detritivores than defoliators. Active herbivores such as grass-hoppers and snails occupy an intermediate position. The two carnivores included here show very different $\frac{R}{P}$ values, probably reflecting their differing food catching behaviour.

McNeil and Lawton (1970) have compared animals of different taxonomic groups in terms of their annual population production and respiration. They found that the linear regression of annual production on annual respiration for homiotherms is significantly different from that of short-lived poikilotherms (less than 2 years) when plotted on a double $\log_{10}$ scale.

Fig. 35 The relationship between annual production (P) and annual respiration (R) (k cals m^{-2} y^{-1}) in animal populations. Regression lines from McNeill and Lawton (1970) and the two A. aquaticus populations added from the present study (A) and Fitzpatrick (1968) (B).

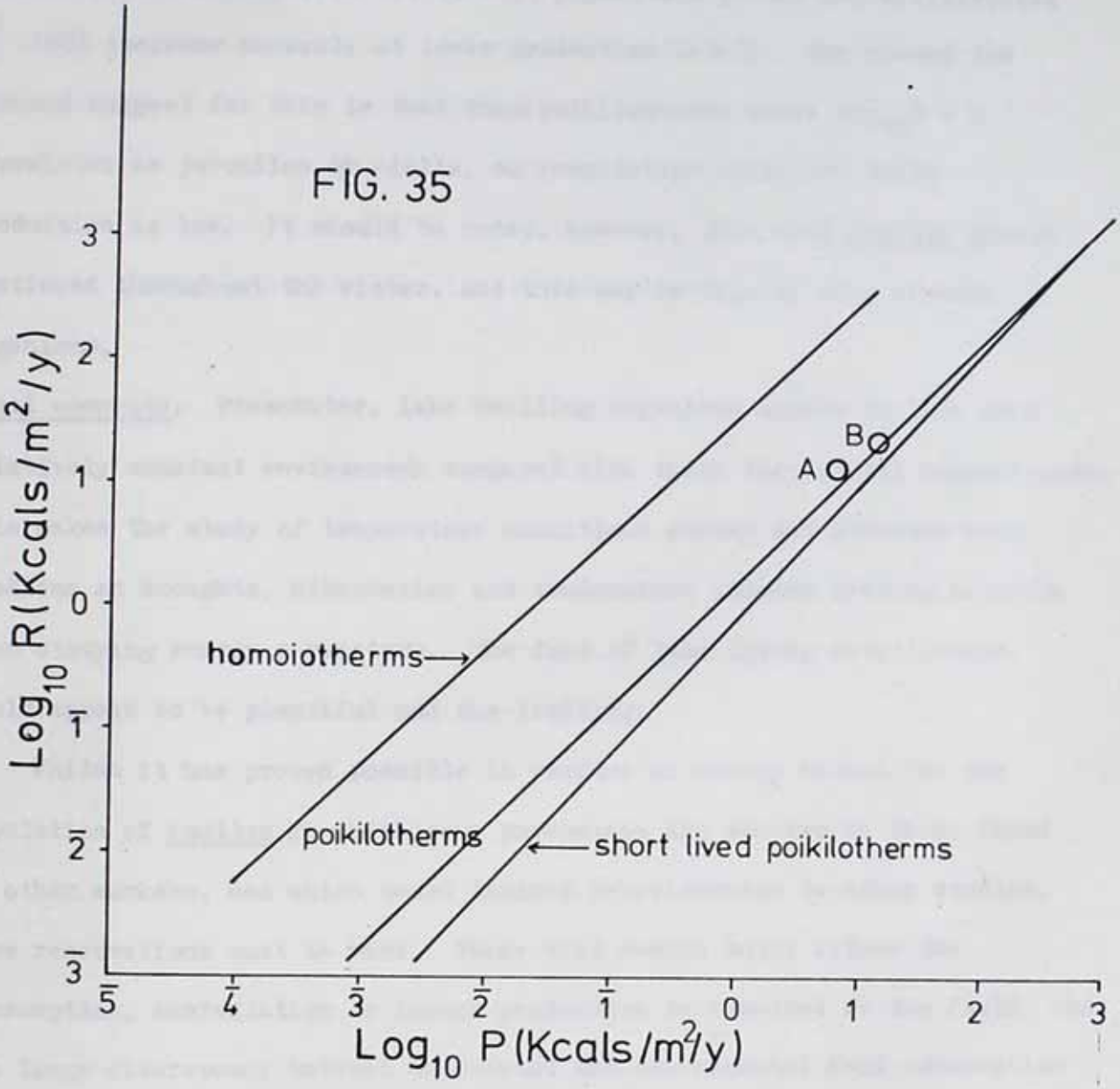
Regression equations for these lines (McNeill & Lawton 1970) are: -

All poikilotherms: $\log P = 0.8233 \log R - 0.2367$

Short-lived poikilotherms: $\log P = 0.8262 \log R - 0.0948$

Homoiotherms: $\log P = 1.0137 \log R - 1.7761$

FIG. 35


Log10 R (Kcals/m2/y)
3
2
1
0
1
2
3
A
B
homoiotherms
poikilotherms
short lived poikilotherms
5
4
3
2
1
0
1
2
3
Log10 P (Kcals/m2/y)

The present study shows that Asellus aquaticus fits this regression relationship quite well (Fig. 35). The slope of the regression line differs significantly from 1.0 so that population production efficiencies ($\frac{P}{A}$ .100) increase markedly at lower production levels. One reason the authors suggest for this is that those poikilotherms above $\log_{10}P = 0$ overwinter as juveniles or adults, so respiration continues while production is low. It should be noted, however, that with Asellus growth continued throughout the winter, and this may be true of many aquatic organisms.

Final comments. Freshwater, lake dwelling organisms appear to live in a relatively constant environment compared with their terrestrial counterparts. This makes the study of temperature conditions easier and obviates such problems as droughts, hibernation and temperature induced feeding activity when studying energy parameters. The food of lake living detritivores would appear to be plentiful and non-limiting.

Whilst it has proved possible to produce an energy budget for the population of Asellus in which some parameters are similar to those found by other workers, and which bears logical relationships to other studies, some reservations must be made. These will remain until either the consumption, assimilation or faeces production is measured in the field, and the large discrepancy between calculated and experimental food consumption figures explained.

However, the study has provided data to assess the role of A. aquaticus in the lake ecosystem. The animals are clearly of some importance in the breakdown of allochthonous material and this can now be quantified. The conclusions of Mathews & Kowalczewski (1969) that invertebrates are unimportant in the decomposition of allochthonous material are therefore difficult to

reconcile with the present study. Furthermore, by the production of faeces Asellus provides food for other members of the community, and this appears to be more important, in terms of energy flow, than the energy passed to predators. The data gathered in this study will be of value in determining the functional importance of Asellus aquaticus in the lake ecosystem, but similar studies of lake detritivores (and of other trophic levels) will be necessary before the importance of the detritus food chain, and of the individuals within it, can be fully assessed.

6. SUMMARY

1. Field sampling of a population of *Asellus aquaticus* (L.) in Wistow Lake at four weekly intervals showed that the population decreased from a mean density of 2,000 m^{-2} in September 1973 to 300 m^{-2} in September 1974. During the year there were two breeding periods producing spring and autumn cohorts. The length/frequency curves of the two cohorts were separated mathematically, which allowed their production to be estimated.

2. Annual production of the field population was 2,725 mg m^{-2} from a mean biomass of 734 mg m^{-2}. This gave a higher $\frac{P}{B}$ ratio than populations of *A. aquaticus* in Sweden.

3. Nine sets of respiratory data were collected at field temperatures throughout the year. Linear regressions were calculated for $\log_{10}$ oxygen uptake on $\log_{10}$ dry weight. The mean rates of respiration at the various temperatures were significantly different ($P < 0.001$), but the slopes of the regression lines were not. Thus in the equation $y = a + bx$, where $y = \log_{10}$ oxygen uptake and $x = \log_{10}$ body size; a increased with temperature, and b varied from 0.623 to 0.847.

4. The annual population metabolism as calculated using a computer programme was 115.77 kJ m^{-2}. Two best estimate calculations gave estimates 16% above and 13% below the computed figure and possible reasons for this are discussed.

5. Feeding experiments using alder leaves gave variable data for food consumption and faeces production. It is not clear whether variation between replicates is due to variation within the population; variation in food material or experimental error. A consumption rate of 3.891 J $mg^{-1} 24h^{-1}$ was calculated and a mean assimilation efficiency of 23%.

6. An annual energy budget for the field population was calculated as:-

Consumption = 656.61 kJ $m^{-2}y^{-1}$

Production = 35.25 kJ $m^{-2}y^{-1}$

Respiration = 115.77 kJ $m^{-2}y^{-1}$

Faeces = 505.59 kJ $m^{-2}y^{-1}$

Laboratory experiments gave a consumption rate approximately twice this figure, and possible reasons for this are discussed.

The budget has been compared with published data for other detritivores, herbivores and carnivores, and the possible significance of A.aquaticus in the lake ecosystem discussed.

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Last, but not least, to my family who have been quite patient with me throughout the study.

APPENDIX

APPENDIX A. Number of A. aquaticus in each sample from Wistow Lake on each sampling date, 1973 - 74.

a) Non-algal samples. Mean, standard errors and fiducial limits are detransformed from logarithms.

Date	15th Sept	15th Oct	12th Nov	10th Dec	7th Jan	4th Feb	4th Mar	1st Apr	29th Apr	3rd June	24th June	22nd July	19th Aug	18th Sept
	1	37	3	3	1	5	0	0	0	3		0	3	5
	5	7	32	18	0	11	2	1	0	1		0	0	39
	2	10	5	2	0	4	8	0	0	0		0	0	87
	3	3	20	9	0	2	0	0	0	0		0	1	0
	0	2	0	4	8	2	0	0	Lost	10		0	0	0
	17	8	30	14	4	3	6	0	2	8		0	1	0
	0	35	12/2	8	0	0	0	1	0	7		0	2	0
	0	25	69/26	16	2	0	4	7	0	0		0	19	0
	0	1	1/0	13	6	0	0	2	0	0		7	0	1
	5/38	0/26	7/0	1	15	0	7	7	2	1		0	0	0
Mean	3.35	8.57	6.95	7.70	2.81	2.58	2.44	1.94	1.28	2.57	-	1.23	1.99	2.90
x Standard ÷ error	1.4588	1.4522	1.4733	1.2850	1.3941	1.3306	1.3661	1.3046	1.1752	1.3685	-	1.2311	1.3560	1.7117
Upper 5% fiducial limit	5.38	19.69	16.04	13.57	5.95	4.92	4.94	3.55	1.85	5.23	-	1.97	3.96	9.78
Lower 5% fiducial limit	1.28	3.73	3.01	4.37	1.32	1.35	1.20	1.06	0.88	1.27	-	0.77	1.00	0.86

NO SAMPLES TAKEN

APPENDIX A. Number of A. aquaticus in each sample from Wistow Lake on each sampling date, 1973 - 74.

b) Algal samples. Mean, standard errors and fiducial limits are detransformed from logarithms.

Date	15th Sept	15th Oct	12th Nov	10th Dec	7th Jan	4th Feb	4th Mar	1st Apr	29th Apr	3rd June	24th June	22nd July	19th Aug	18th Sept
	312	280	80	116	84	440	82	3	7	16	2	4	3	2
	225	316	128	128	176	184	104	80	59	2	13	2	10	4
	237	324	152	312	15	162	34	11	20	9	18	298	86	19
	54	184	180	80	236	96	82	84	3	11	94	6	23	0
	150	92	86	125	128	248	18	56	43	78	130	1	30	24
	62	63	460	156	112	64	236	114	27	7	2	2	212	8
	46	206	288	808	26	72	56	35	2	72	2	8	3	4
	117	124	138	11	288	36	11	2	1	2	2	2	122	3
	38	-	100	100	36	15	15	32	36	51	25	9	42	40
	-	-	40	35	50	16	39	11	3	13	2	5	12	5
Mean	121.93	173.60	161.65	110.33	81.06	82.90	46.75	24.93	11.60	15.10	10.77	7.05	26.44	7.11
x Standard ÷ error	1.2950	1.2361	1.2293	1.4298	1.3567	1.4201	1.3450	1.5048	1.4893	1.4542	1.6082	1.5668	1.5407	1.4179
Upper 5% fiducial limit	224.42	286.28	163.12	247.53	161.52	183.16	91.35	62.77	28.53	35.20	31.51	19.46	70.22	15.66
Lower 5% fiducial limit	66.25	105.27	99.31	49.17	40.68	37.52	23.93	9.90	4.72	6.48	3.68	2.56	9.95	3.23

APPENDIX A. Number of A. aquaticus in each sample from Wistow Lake on each sampling date, 1973 - 74.

c) Edge samples. Mean, standard error and fiducial limits are detransformed from logarithms.

Date	15th Sept	15th Oct	12th Nov	10th Dec	7th Jan	4th Feb	4th Mar	1st Apr	29th Apr	3rd June	24th June	22nd July	19th Aug	18th Sept
	115	3	124	5	13	5	8	2	0	4	NO SAMPLES	0	12	14
	-	24	70	7	16	4	34	3	11	1		26	16	152
	-	108	-	26	9	4	10	16	25	16		13	31	8
		140												
Mean		55.3		10.90	13.35	5.31	15.13	5.89	6.78	15.10	-	7.23	19.19	27.44
x Standard		1.6346		1.5856	1.17	1.0626	1.5269	1.7104	2.6721	1.4542	-	2.7378	1.3061	2.3913
÷ error														
Upper 5% fiducial limit		184.33		79.13	26.00	6.90	93.39	59.18	464.32	35.20	-	549.53	60.51	1165.34
Lower 5% fiducial limit		16.49		1.50	6.86	4.09	2.45	0.59	0.99	6.48	-	0.09	6.09	0.65

APPENDIX B

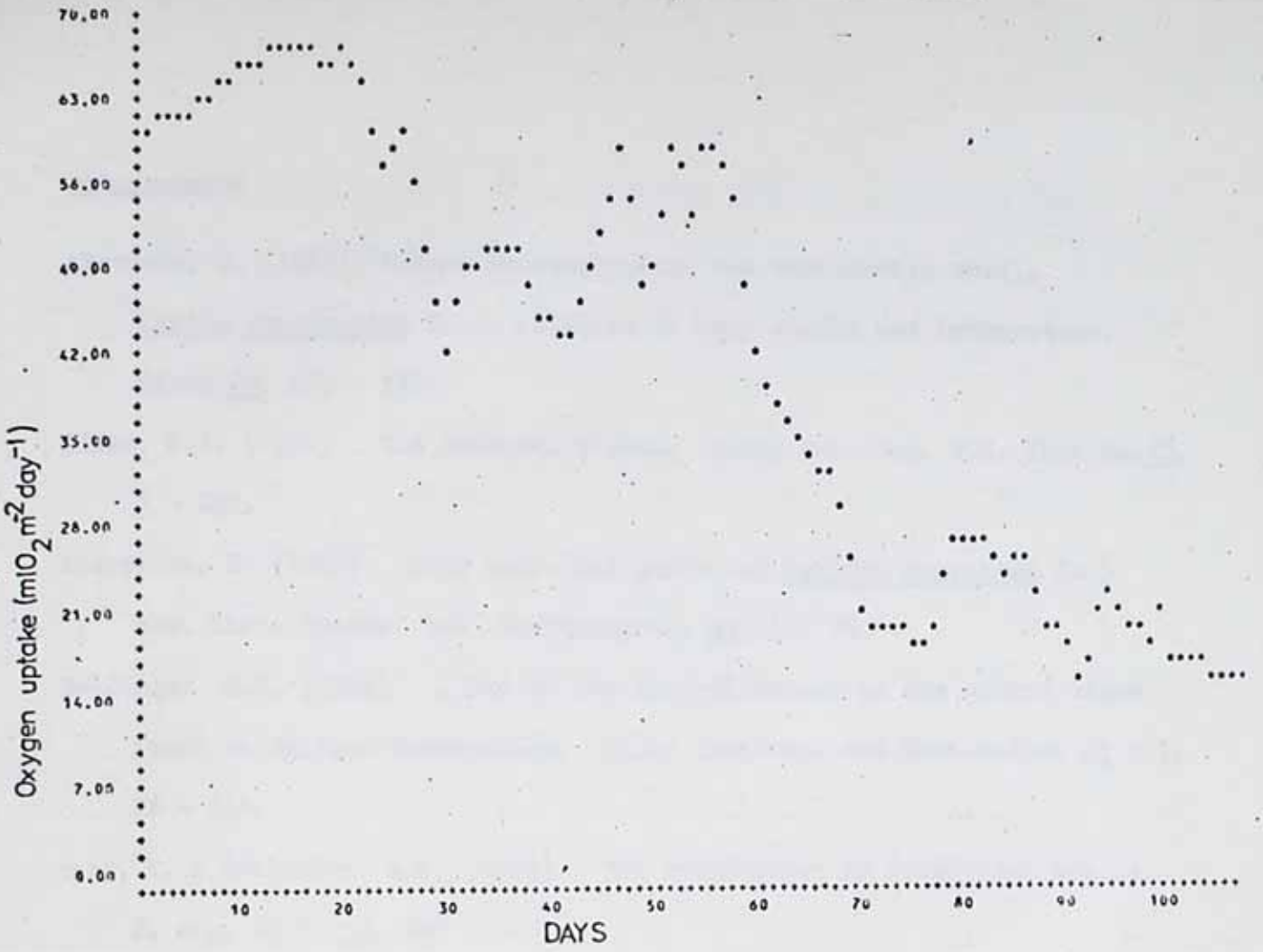
i) The computer programme for the calculation of population metabolism.

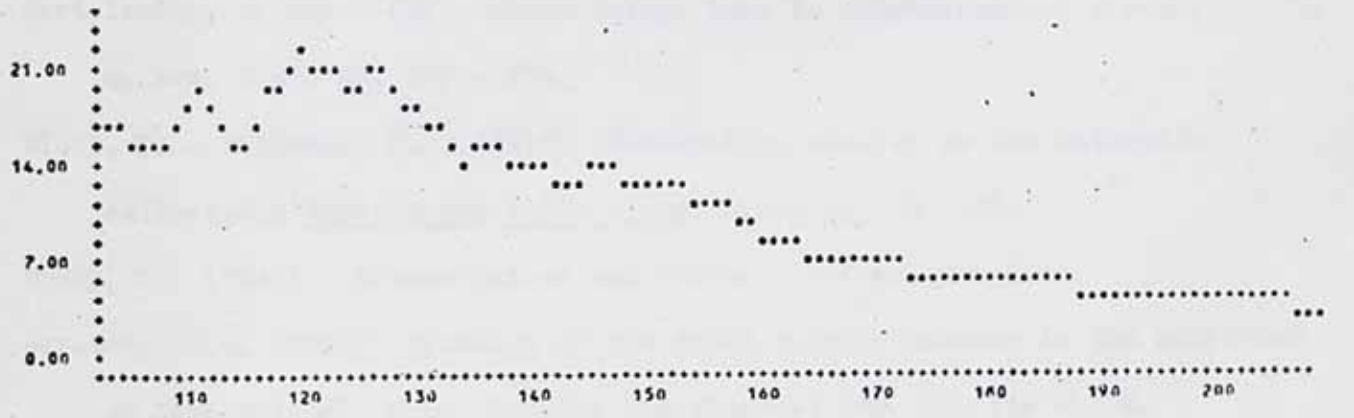
ii) Computer output for daily population metabolism (ml O_2 m^{-2} day^{-1}).

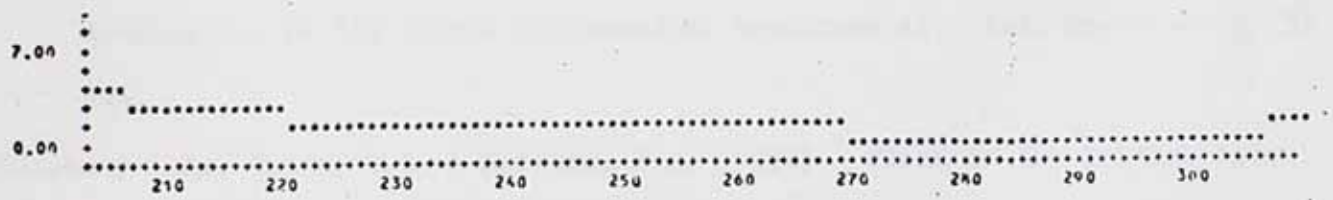
```
LINE STATEMENT
   9     0        'TRACE' 0
  10     0        'BEGIN''INTEGER''ARRAY'DAY[1:2];'INTEGER'NDAYS,N,NSTAR,I,J,K,SECOND,
                BLOCK     1
  11     2            FIRST,PDAY;
  12     2            'INTEGER'KK;
  13     3            'REAL'SUM,POP;
  14     4            'PROCEDURE'PLOT(F,YJUM,NO,N,OR,XJUM,NL,NS,CH);
                BLOCK     2
  15     6            'VALUE'YJUM,NO,N,OR,XJUM,NL,NS; 'REAL''ARRAY'F;
  16     8            'INTEGER'YJUM,NO,N,OR,XJUM,NL,NS; 'STRING'CH;
  17    10            'BEGIN''REAL'DP,DH,MAX,MIN,X; 'INTEGER'K,P,I,J,M,PLUS,STAR,STEP,ZX,ZN
  18    11               ,ZR;
  19    11               PLUS:=CODE('('+')'); STAR:=CODE(CH);
  20    14               'IF'YJUM<2'THEN'YJUM:=NL'/'10;
  21    15               'BEGIN'
  22    15                  'INTEGER''PROCEDURE'MAIN(A,B);'VALUE'A,B;'INTEGER'A,B;
                BLOCK     3
                BLOCK     4
  23    18                   MAIN:='IF'A>B'THEN'A'ELSE'B;
  24    18                   'INTEGER''PROCEDURE'UP(X);'REAL'X;UP:=-DOWN(-X);
                BLOCK     5
  25    21                   'INTEGER''PROCEDURE'DOWN(X);'REAL'X;
                BLOCK     6
  26    24                   DOWN:='IF'X'GE'0'THEN'ENTIER(X)'ELSE'ENTIER(X+8-50);
  27    24                   MAX:=MIN:=F[NO];
  28    26                   'FOR'I:=NO+1'STEP'1'UNTIL'N'DO'
  29    27                   'IF'MAX<F[I]'THEN'MAX:=F[I]'ELSE''IF'MIN>F[I]'THEN'MIN:=F[I];
  30    28                   X:=LN(10);ZR:=DOWN(LN((MAX-MIN)/3)/X);
  31    30                   ZX:='IF'MAX=0'THEN'0'ELSE'UP(LN(ABS(MAX))/X);
  32    31                   ZN:='IF'MIN=0'THEN'0'ELSE'UP(LN(ABS(MIN))/X);
  33    32                   'IF'ZX-ZR>5'THEN'ZR:=ZX-5;X:=10.0↑(-ZR);DP:=10.0↑(ZR);
  34    35                   MAX:=DP*UP(MAX*X); MIN:= DP*DOWN(MIN*X);
  35    37                   DP:=(MAX-MIN)/NL; DH:=DP/2;
  36    39                   ZX:=MAIN(ZX,MAIN(ZN,1));ZN:=MAIN(3-ZR,1);ZR:=ZN+7N+4;
  37    42               'END';
  38    43               NS:=NS-ZR-6;J:='IF'N<NS'THEN'N+1'ELSE'NS:STEP:=NS'/'J;M:=NO;
  39    47               XJUM:='IF'XJUM<1'THEN'10'/'STEP 'ELSE'XJUM;
  40    48               'IF'XJUM*STEP>78'THEN'XJUM:=0;
  41    49            P3:'IF'10.0↑(XJUM*STEP-3)'LE'OR+N'THEN'
  42    49               'BEGIN'XJUM:=XJUM*2;
  43    51                  'GOTO'P3
  44    51               'END';
  45    52               K:=XJUM;
  46    53            P4:PAPERTHROW; NEWLINE(4);
  47    55               P:='IF'M+NS<N'THEN'M+NS'ELSE'N;
  48    56               X:=MAX-DH;STEP:=STEP-1;
  49    58               'FOR'I:=0'STEP'1'UNTIL'NL'DO'
  50    59               'BEGIN''IF'I'/'YJUM*YJUM=I'THEN'
  51    60                  PRINT('IF'X+DH=0'THEN'ABS(X+DH)'ELSE'X+DH,ZX,ZN)
  52    60                  'ELSE'SPACE(ZR);
  53    61                  PRINTCH(PLUS);
  54    62                  'FOR'J:=M'STEP'1'UNTIL'P'DO'
  55    63                  'BEGIN'
  56    63                     'IF'F[J]<X+DP'AND'F[J]'GE'X'THEN'PRINTCH(STAR)
  57    64                     'ELSE'SPACE(1);
  58    65                     SPACE(STEP);
  59    66                  'END';
  60    67                  NEWLINE(1);X:=X-DP;
  61    69               'END';
  62    70               STEP:=STEP+1; SPACE(ZR);
  63    72               'FOR'I:=1'STEP'1'UNTIL'NS+1'DO'PRINTCH(PLUS);
  64    74               NEWLINE(1); I:=YJUM*STEP-3;
  65    76               'IF'M>NO'THEN'SPACE(ZR+4+F-M-XJUM)'ELSE'SPACE(ZR+4-NO*STEP);
  66    77               'FOR'K:=K'STEP'XJUM'UNTIL'P'DO'PRINT(I+OR,I,0);
  67    79               'IF'P<N'THEN''BEGIN'M:=J-6;'GOTO'P4'END';
  68    82            'END' OF PLOT;
  69    82         SELECT INPUT(5);          SELECT OUTPUT(4);
  70    85         DST:NINSTAR:=READ;
  71    86            'IF'NINSTAR=0'THEN''GOTO'END;
  72    87            NDAYS:=READ;
  73    88            'BEGIN''REAL''ARRAY'TEMP[1:NDAYS],MNT,M,C[1:NINSTAR],INSTAR[1:2,
                BLOCK     7
  74    88             1:NINSTAR],INC[1:NINSTAR];
  75    88             'PROCEDURE'READ DAY;
                BLOCK     8
  76    89             'BEGIN'DAY[SECOND]:=READ;
  77    91                POP:=READ ;
  78    92                'FOR'I:=1'STEP'1'UNTIL'NINSTAR'DO'INSTAR[SECOND,I]:=READ*POP
  79    93                /100;
  80    94             'END' OF READ DAY;
  81    94             'PROCEDURE'RESP(J);'INTEGER'J;
```

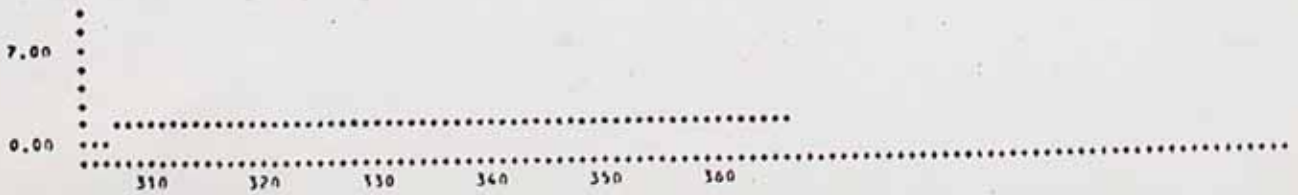
```
                BLOCK     9
 82    97                 'BEGIN'SUM:=0.0;
 83    99                    'FOR'I:=1'STEP'1'UNTIL'NINSTAR'DO'
 84   100                    'BEGIN'
 85   100                       POP:=RWT[I]*(C[I]+M[I]*TEMP[J])*INSTAR[FIRST,I];
 86   102                       'IF'POP'GT'0.0'THEN'SUM:=SUM+POP;
 87   103                    'END';
 88   104                    TEMP[J]:=SUM*24;
 89   105                 'END' OF RESP;
 90   105                 'PROCEDURE'GRAD;
                BLOCK     10
 91   106                 'BEGIN'
 92   106                    J:=DAY[SECOND]-DAY[FIRST];
 93   108                    'FOR'I:=1'STEP'1'UNTIL'NINSTAR'DO'
 94   109                    INC[I]:=(INSTAR[SECOND,I]-INSTAR[FIRST,I])/J;
 95   110                    'FOR'K:=DAY[FIRST]+1'STEP'1'UNTIL'DAY[SECOND]'DO'
 96   111                    'BEGIN'
 97   111                       'FOR'I:=1'STEP'1'UNTIL'NINSTAR'DO'
 98   113                       INSTAR[FIRST,I]:=INSTAR[FIRST,I]+INC[I];
 99   114                       RESP(K);
100   115                    'END';
101   116                 'END' OF GRAD;
102   116                 'FOR'I:=1'STEP'1'UNTIL'NDAYS'DO'TEMP[I]:=READ;
103   119                 'FOR'I:=1'STEP'1'UNTIL'NINSTAR'DO'RWT[I]:=READ*4-3;
104   121                 'FOR'I:=1'STEP'1'UNTIL'NINSTAR'DO'
105   122                 'BEGIN'M[I]:=READ;
106   124                    C[I]:=READ;
107   125                 'END';
108   126           'FOR'KK:=1'STEP'1'UNTIL'2'DO'
109   127           'BEGIN'
110   127                 SECOND:=1; FIRST:=1;
111   130                 READ DAY; RESP(1); FIRST:=2; PDAY:=DAY[SECOND]-1;
112   134           CHECK:'IF'DAY[SECOND]=NDAYS'THEN''GOTO'ENDPR;
113   135           START:SECOND:=3-SECOND; FIRST:=3-FIRST;
114   137                 READ DAY; GRAD;
115   139                 'GOTO' CHECK;



116   140           ENDPR:SUM:=0.0;
117   141                 WRITETEXT('('''('P2C')'DAY%NUMBER'('10S')'RESPIRATION'('10S')'
118   141                 RUNNING%TOTAL'('2C')''')');
119   142                 'FOR'I:=1'STEP'1'UNTIL'NDAYS'DO'
120   143                 'BEGIN'PRINT(I+PDAY,4,0); SPACE(14);
121   146                    PRINT(TEMP[I],0,6);
122   147                    SPACE(11); SUM:=SUM+TEMP[I];
123   149                    'IF'I=1'THEN''GOTO'MIS;
124   150                    PRINT(SUM,0,6);
125   151                 MIS:'IF'I'/'7*7=I'THEN'NEWLINE(1);
126   152                     'IF'I'/'49*49=I'THEN'PAPERTHROW;
127   153                     NEWLINE(1);
128   154                  'END';
129   155                  PLOT(TEMP,5,1,NDAYS,0,10,50,120,'('*')');
130   156           'END';
131   157                 'GOTO'DST;
132   158              'END';
133   159           END:'END';
SEGMENT GENA             LENGTH  1544
NO OF BUCKETS USED        59
```

COMPUTER OUTPUT - DAILY POPULATION METABOLISM









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