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A QUANTITATIVE STUDY
OF
HOST AND PARASITE POPULATIONS

LINDA PENNYCUICK

A dissertation submitted for the degree of
Doctor of Philosophy
in the Faculty of Science, University of Bristol

March, 1970

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SUMMARY

A population of three-spined sticklebacks, Gasterosteus aculeatus, from Priddy pool in Somerset was found to be infected with three species of parasite: Schistocephalus solidus, Echinorhynchus clavula and Diplostomum gasterostei. The interactions between the host and parasite populations were studied by taking samples of the sticklebacks at frequent intervals and making a number of measurements on the fish and parasites.

The changes with time in the length-, weight- and age-structure of the fish population were determined. The relationships between pairs of these three parameters were represented by equations.

Schistocephalus was found to retard the growth rate of the fish and to cause predation or death when infections were heavy; it also interfered with the fish's breeding. Heavy infections of Echinorhynchus or Diplostomum also caused death or predation of the sticklebacks. This was less usual with Echinorhynchus as the numbers were reduced when the parasites died and passed out of the fish.

Frequency distributions and their associated parameters were determined for each species of parasite for each sample, and theoretical distributions were fitted. Schistocephalus was in general distributed as the log normal and Echinorhynchus and Diplostomum as the negative

binomial. The seasonal changes in the parasite populations are discussed in relation to their distributions in the fish population. Additional information about these changes was obtained from the size distributions of Schistocephalus and Echinorhynchus, and also from the distribution of weights of Schistocephalus amongst the fish, the sex ratio of Echinorhynchus and the percentage of females with shelled acanthors.

The distributions of the numbers of the three parasites, and the weights of the Schistocephalus, in fish of different sizes and ages were also considered.

The pattern of infection, and in particular the form of the frequency distribution, is related to the life cycle for each of the parasite species. It is shown how the life cycle and distribution are adapted to ensure survival of the parasite population and, in Echinorhynchus and Diplostomum particularly, how this includes causing the minimum ill-effects in the host population.

There was no tendency for any of the parasites to be associated, positively or negatively, with either of the others.

I N T R O D U C T I O N

This is a study of a population of three-spined sticklebacks, Gasterosteus aculeatus, and three species of parasite, Schistocephalus solidus, Echinorhynchus clavula, and Diplostomum gasterostei which were found in the fish. Sticklebacks from several localities near Bristol were examined and those from Priddy pool on the Mendip Hills in Somerset found to be the most suitable for this investigation. They were the most numerous and heavily parasitised and were the easiest to obtain. Also the three species of parasite they harboured had different life cycles making comparisons between them more interesting.

The aim was to investigate the structure of the fish and parasite populations and to determine how they interacted. Sampling at frequent intervals enabled changes in the populations to be followed and analysed.

M A T E R I A L S

The sticklebacks were caught from the bank using long-handled nets. Baited traps were also used with some success at certain times of year, particularly in autumn, but in summer no fish would enter the traps.

It was originally intended to collect 100 fish every two weeks, but this proved impracticable as it was difficult to obtain so many fish on one occasion at most times of year, and the examination of 100 fish took longer than two weeks. Hence about 70 fish were collected at two- to four-week intervals from October 1966 until April 1968. They were taken to the laboratory immediately and stored in a deep-freeze until they could be dissected. It would have been preferable to examine the sticklebacks shortly after killing, while the parasites were still alive, but this would have meant keeping them under unnatural conditions in an aquarium for some time.

S T A T I S T I C A L M E T H O D S

(i) FREQUENCY DISTRIBUTIONS

1. General description

Numerical data can often be classified by dividing them into a series of groups or classes, each with a certain frequency of occurrence: this is a frequency distribution. There are two main types of distribution, continuous and discrete. In the former the data consist of measurements (x) of a continuous characteristic, e.g. length or weight, which is divided into classes of an arbitrary size, depending on the number of observations, overall range of values and accuracy of measurement. In the discrete distribution there are no intermediate values and each class represents one possible value of the parameter, x ; for example, number of parasites per host. These classes can also be grouped into larger ones, but it is more usual to have one class per value of x .

There is a number of standard distributions and very often the data will fit closely to one of these. From the form of the distribution the way in which it arose can often be deduced, or at least a number of hypotheses can be set up. There are often very many causal factors which cannot be separated or described individually so that the frequency distribution acts as a useful empirical model, particularly when comparing similar situations. In most statistical

analysis it is assumed that the data follow a Gaussian or Normal distribution. If the data are distributed in a different but standard pattern they can often be transformed, for example by taking logarithms, to a Normal and then analysed.

The Normal is uncommon in biological data, though it does arise in measurements, such as length, of a homogeneous population. The mean length is the one which occurs most frequently and on either side of this the frequencies drop off symmetrically to produce a bell-shaped curve. Often distributions are discrete, being counts of individuals, for example number of parasites per host, individuals per species, individuals per unit area etc. Generally the means are low in these cases and there are many hosts with none or one parasite, etc., but still a few with large numbers. In other words there is a long right-hand tail which cannot be reproduced on the left-hand side without becoming negative. This is known as a positively skewed distribution.

The data are grouped into classes according to the value of x , each class having a frequency of occurrence, f_x . For a host-parasite distribution f_0 is the number of uninfected hosts, f_1 the number of hosts with one parasite and so on. A number of different parameters can be calculated from the raw data and these are then used to compute different theoretical distributions for comparison with the original.

2. Parameters

(a) Number of observations, N

The total number of observations made, for example number of hosts examined, is given by;

$$N = \sum_{x=0}^{x_{\max}} f_x \quad \dots(1)$$

This parameter is required for the calculation of all types of distribution. When comparing samples with different values of N the terms of the distributions can be expressed as proportions by dividing each by N, and as percentages by then multiplying by 100. The original calculation of the theoretical distribution should be based on the original numbers so that the goodness-of-fit can be tested.

(b) Mean, \bar{x}

The mean is the average number of parasites per host etc., but gives no indication of the probability of any one host having this number of parasites.

$$\bar{x} = \frac{\sum_{x=0}^{x_{\max}} f_x \cdot x}{N} \quad \dots(2)$$

The mean is also required in the calculation of all distributions. The value of the true mean of the population is μ , while that of the sample is \bar{x} .

(c) Variance, s^2

The variance is the average of the square of the deviation of each observation from the mean:

$$s^2 = \frac{\sum_{x=0}^{x_{\max}} f_x (x - \bar{x})^2}{N-1} \dots(3)$$

or

$$s^2 = \frac{1}{N-1} \left\{ \sum_{x=0}^{x_{\max}} f_x \cdot x^2 - \frac{\left(\sum_{x=0}^{x_{\max}} f_x \cdot x \right)^2}{N} \right\} \dots(4)$$

The variance gives some indication of the shape of the distribution: the larger the variance the longer the tail(s) and the smaller the frequency of the commonest class. Most, but not all, distributions are calculated using the variance. The true variance is σ^2 and the sample variance is s^2 .

(d) Percentage infection

This parameter is not applicable to all types of distribution but is relevant to host-parasite distributions and distributions of individuals in quadrats.

$$\% \text{ infection} = \left(\frac{N - f_0}{N} \right) \cdot 100 \dots(5)$$

It is a measure of the number of hosts infected, but not of how many parasites each contains. It is particularly important in host-parasite distributions as the number of uninfected hosts is meaningful: each host is a definite biological unit. In the case of quadrats the absence of organisms is not in itself

so significant as the size of the quadrat will affect the number of empty ones.

Williams (1964) considers that the zero term in host-parasite distributions from field observations should be treated with caution or even discounted altogether. He states that "it cannot be assumed that each of the hosts had an equal chance of being selected or rejected by a parasite. Small differences in the positions of the host might alter its chances of being discovered... Thus the zero term...might include hosts which were never liable to infection."

It might equally well be argued that hosts with large numbers of parasites should be ignored because they were in an area of high parasite concentration. The purpose of using a frequency distribution to analyse field observations is usually to obtain a complete picture of the situation. The fact that all hosts are not equally exposed to infection is a part of the situation and should not be discounted. In any case ignoring the zero term by no means eliminates this factor. It can be eliminated in laboratory experiments in which case the distribution will have arisen only from other factors, such as differing susceptibility of hosts and infectivity of parasites.

(e) Geometric mean, g

This is the mean of a discrete log-normal distribution.

The value of f_0 is ignored in its calculation as $\log 0 = \infty$.

$$g = N \sqrt{\prod_{x=1}^{x_{\max}} (x)^{f_x}} \quad \dots(6)$$

$$\text{or } \log g = \frac{\sum_{x=1}^{x_{\max}} f_x \cdot \log x}{N} \quad \dots(7)$$

It differs from the arithmetic mean in taking less account of single high values, but more of a general increase.

A computer program was written to calculate the mean and variance from the raw data. This was in the form of a procedure which could be used in conjunction with other programs. The flow diagram is shown in appendix 1 a.

3. Dispersion

Frequency distributions can be divided into three types according to the mean: variance ratio.

(a) mean = variance

This is a random distribution and is described by a Poisson with a single parameter, m .

(b) variance $>$ mean

This is an over-dispersed distribution and is common in biological data due to clumping for social or physical reasons, eggs laid in batches etc. There are many theoretical distributions of this type: Thomas, Fisher H^h , Neyman A, B, C, Polya-Aeppli, negative binomial, discrete log-normal, in order of increasing skewness and tail length.

(c) variance $<$ mean

This is an under-dispersed distribution and arises when organisms are evenly spaced, for example barnacles packed closely together on rocks, animals with equal-sized territories etc. This situation is described by the positive binomial.

4. Calculation

Different numbers of parameters are required for the calculation of the various theoretical distributions from the original data. The Poisson needs only the mean, the binomial only f_0 , and the Normal and Neyman A need only mean and variance. More often further information is required and a compromise may be necessary between simplicity of calculation and accuracy of fitting. The use of a computer enables lengthy calculations to be performed rapidly so that a better fit can be obtained. For example in the case of the negative binomial a rough fit can be obtained using only mean and variance, a better fit including f_0 , and an even better one using a reiterative procedure. Similarly the log series can be calculated from variance, mean and f_1 , but a better result is obtained by a reiterative method.

5. The Poisson distribution

This arises when the distribution of units amongst the groups is random. It is a discrete distribution with a single parameter, m , which is the mean and also the variance. The general formula is:

$$P_x = \frac{e^{-m} m^x}{x!} \quad \text{where } P_x \text{ is the probability of the value } x \text{ arising.} \quad \dots(8)$$

$$\phi_x = P_x N \quad \text{where } \phi_x \text{ is the frequency of occurrence of } x. \quad \dots(9)$$

It can be calculated from the following equations:

$$\phi_0 = N e^{-m} \quad \dots(10)$$

$$\phi_x = \frac{\phi_{(x-1)} m}{x} \quad \dots(11)$$

Conditions under which a host-parasite distribution is a Poisson are:

- (i) There is an equal chance of any parasite finding a host.
- (ii) Each host is equally susceptible to infection.
- (iii) The chance of infection is not altered by previous infections.

These are rarely all satisfied.

6. The negative binomial distribution

The negative binomial is an overdispersed distribution with two parameters, p and k . It is the expansion of $(q-p)^{-k}$,

$$\text{where } q = 1 + p \quad \dots(12)$$

$$\text{and } pk = \mu \quad \dots(13)$$

The general equation is

$$P_x = \frac{(k + x - 1)!}{x! (k - 1)!} \frac{p^x}{q^{k+x}} \quad \dots(14)$$

The mathematical derivation is given by Fisher (1941).

The negative binomial can be considered as an extension of the Poisson, with the mean not constant but varying continuously as x^2 throughout the sample. As the variance approaches the mean, or the overdispersion decreases, k tends to ∞ and p to zero, and the distribution approaches a Poisson. Cassie (1962) shows that $c (=1/k)$ is a measure of the overdispersion; $c=0$ in a random distribution.

Calculation

p and k cannot be calculated directly and there is a number of possible methods of approximation (Bliss and Fisher, 1953).

(a) The simplest and least accurate of these methods uses the calculated mean and variance, \bar{x} and s^2 :

$$k = \frac{\bar{x}^2}{s^2 - \bar{x}} \quad \dots(15)$$

and p is obtained from equation 13, above. This is inefficient over the range of p and k found in most biological situations.

(b) The second method is based on the zero term:

$$f_0 = \frac{N}{q^k} \quad \dots(16)$$

but $q = 1 + \frac{\bar{x}}{k}$ \dots(17)

These equations cannot be solved directly because the unknown (k) is an exponent of itself. An iterative solution to the equation

$$\hat{k} \log (1 + \bar{x}/\hat{k}) = \log (N / f_0) \quad \dots(18)$$

is obtained.

(c) The most efficient method is that known as "maximum likelihood". The calculation is time-consuming unless an electronic computer is available, as it was in this case. A first estimate of k , \hat{k}_1 , is obtained using method (a) above. This is used to calculate z_1 where

$$z_1 = \sum_{x=0}^{x_{\max}-1} \left[\frac{A_x}{\hat{k}_1 + x} \right] - N \left[\frac{1 + \bar{x}}{\hat{k}_1} \right] \quad \dots(19)$$

or, more accurately (Fisher)

$$z_1 = \sum_{x=0}^{x_{\max}-1} \left[\frac{A_x}{\hat{k}_1 + x} \right] - N \cdot \log \left[1 + \frac{\bar{x}}{\hat{k}_1} \right] \dots(20)$$

where A_x is the number of all units with more than x organisms. If z_1 is positive the new estimate of k , \hat{k}_2 , is made larger than \hat{k}_1 , and if z_1 is negative \hat{k}_2 is made smaller than \hat{k}_1 ; z_2 then has the opposite sign. \hat{k}_3 is obtained by linear interpolation between \hat{k}_1 and \hat{k}_2 . This can be continued until the value of z is as near zero as required.

A computer program based on the third method was written. Iterations were performed in which a diminishing increment was added to or subtracted from k , until $|z| \leq 0.001$. The flow diagram is shown in appendix 1b.

\hat{p} is obtained from the final estimate of k (equation 13) and the distribution can be calculated:

$$\phi_0 = \frac{N}{\hat{q}^{\hat{k}}} \dots(21)$$

gives the first value, and the reiterative formula

$$\phi_x = \frac{(\hat{k} + x - 1) \cdot R \cdot \phi_{x-1}}{x} \dots(22)$$

$$\text{where } R = \frac{\hat{p}}{\hat{q}} \dots(23)$$

is used for subsequent values.

R^2 and χ^2 were calculated to test the goodness-of-fit.

Truncated negative binomial

A method for calculating a truncated negative binomial is described by Brass (1958). It can be applied to upper or lower tail truncations. The ratio, L , of the frequency of the t th class, f_t , next to the point of truncation, to the frequency of all groups included, is calculated. The basic equation of the distribution is modified to:

$$P_x = \frac{w^k}{1 - w^k} \cdot \frac{(k + x - 1)! (1 - w)^x}{(k - 1)! x!} \quad \dots(24)$$

First approximations for w and k are calculated:

$$\hat{w} = \frac{\bar{x} (1 - L)}{s^2} \quad \dots(25)$$

$$\hat{k} = \frac{(\hat{w}\bar{x} - L)}{(1 - \hat{w})} \quad \dots(26)$$

and reiterations are used to solve a maximum likelihood equation for more accurate values.

(i) Lower tail

For a truncation of zeros ($t = 1$) the equations are:

$$L = f_1 / \sum_{x=1}^{x_{\max}} f_x \quad \dots(27)$$

$$\text{and } z = \frac{\bar{x} (\hat{k} + L)}{\hat{k} (\bar{x} - L)} \ln \left(\frac{\hat{k} + L}{\hat{k} + \bar{x}} \right) + \frac{I}{N} \sum_{j=1}^{x_{\max}} \left\{ \frac{\sum_{x=j}^{x_{\max}} f_x}{\hat{k} + j - 1} \right\} \dots(28)$$

The value of \hat{k} is adjusted until z has a low enough value and then \hat{w} is calculated from the final \hat{k} :

$$\hat{w} = \frac{\hat{k} + L}{\hat{k} + \bar{x}} \quad \dots(29)$$

The theoretical distribution, excluding the zero term, is calculated from equation 24. The expected value of the zero frequency, ϕ_0 , if there were no truncation and also the total sample size, N_t , can be calculated as follows:

$$\hat{p} = \frac{1 - \hat{w}}{\hat{w}} \quad \dots(30)$$

$$P_0 = \frac{1}{(1 + \hat{p})^{\hat{k}}} \quad \dots(31)$$

$$N_t = \frac{N}{1 - P_0} \quad \dots(32)$$

$$\phi_0 = N_t P_0 \quad \dots(33)$$

The remainder of the distribution can be calculated by the normal method.

(ii) Upper tail

For example if values above $x=6$ are to be ignored:

$$L = f_6 / \sum_{x=0}^6 f_x \quad \dots(34)$$

$$z = \frac{\bar{x} (\hat{k} + L)}{\hat{k} (\bar{x} - L)} \ln \left(\frac{\hat{k} + L}{\hat{k} + \bar{x}} \right) + \frac{1}{N} \cdot \sum_{j=0}^6 \left\{ \frac{\sum_{x=j}^6 f_x}{\hat{k} + j - 1} \right\} \dots(35)$$

The total sample size, N_t , is calculated by assuming that the values up to the point of truncation are accurate:

$$N_t = \frac{\sum_{x=0}^6 f_x}{\sum_{x=0}^6 P_x} \quad \dots(36)$$

The distribution can then be calculated

Computer programs were written for calculating both upper and lower tail truncations.

A host-parasite distribution is a negative binomial if there is a departure from randomness caused by any of the following factors:

1. The host is exposed to several waves of infection, each of which attacks randomly, giving rise to a series of Poissons.
2. The distribution sampled is not homogeneous but clumped.
3. The presence of a parasite increases or decreases the chance of further infection.

4. The sampling units are not equal, for example the hosts are of different ages.

5. The sampling units change during sampling, for example if the sampling takes a long time the ages of the hosts will change.

The negative binomial is the commonest distribution found in parasitological situations and is the most appropriate of the over-dispersed distributions.

The shape of the negative binomial

It would be useful when fitting the negative binomial to biological data to have a clearer picture of the relationships between the various parameters and the shape of the distribution. The chief parameters calculated from the original data are mean, variance and percentage infection (p. 5,6). The relationships between these and the values of p and k are investigated, as well as the effects of p and k on the shape of the distribution.

(a) $\mu = pk$. Thus for a given mean if either p or k increases the other must decrease; the values depend on the other parameters.

(b) $\sigma^2 = pkq$. Therefore increase in p has a greater effect on the variance than the same increase (multiple) in k .

(c) Percentage infection = $100 (1 - 1 / q^k)$. This can be ..(37)
more simply expressed in terms of the zero class: $P_0 = 1 / q^k$.

The zero class decreases for increases in both p and k , but for the same increase k has the greater effect. The percentage infection therefore increases with increases in p and k .

(d) $\sigma^2 / \mu = q$. This follows from (a) & (b). Hence q is a measure of the overdispersion, although Cassie (1962) uses $1/k$.

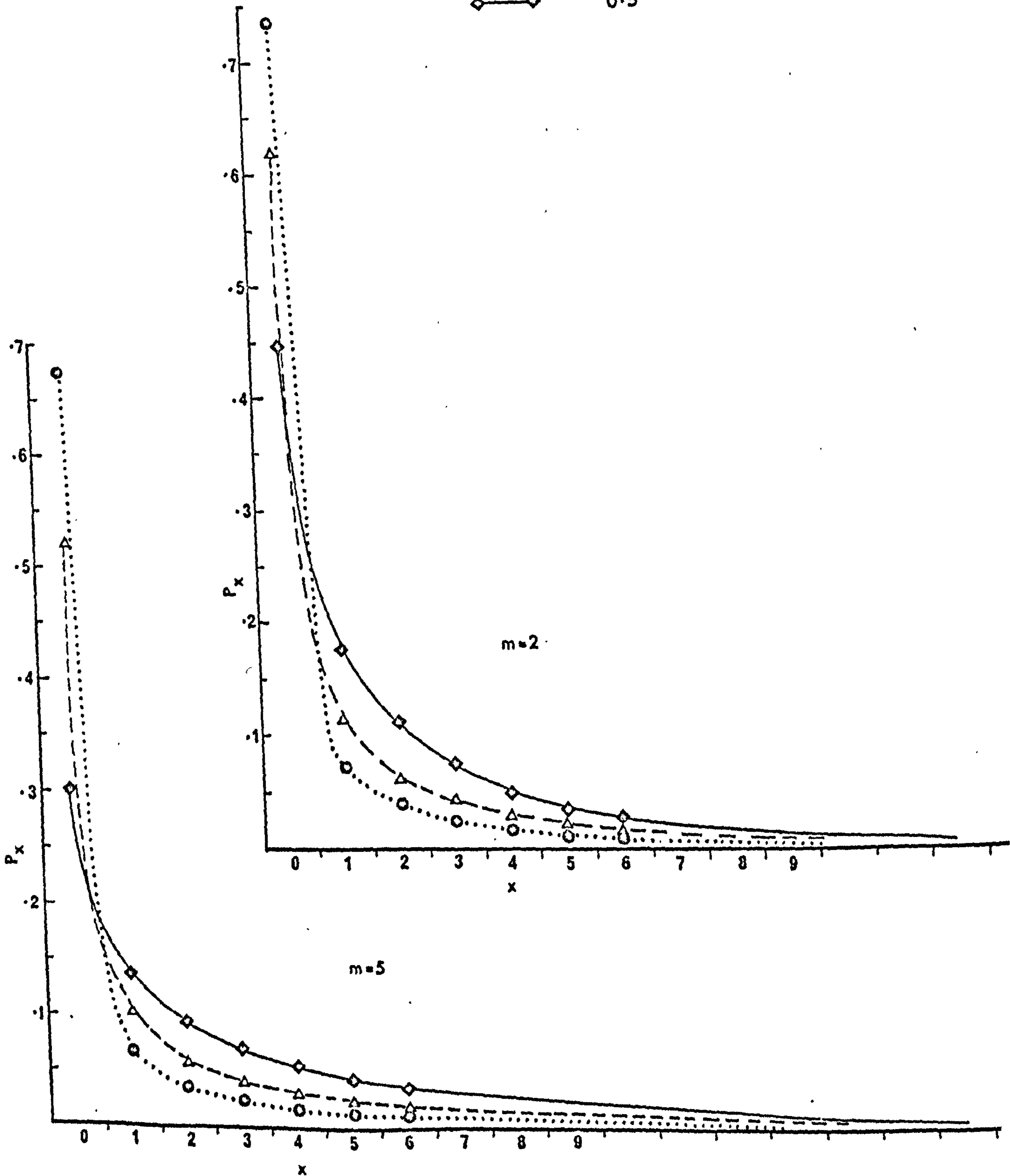
These points are illustrated in Fig. 1. For each of two different values of the mean (2 and 5) distributions are plotted for $k = 0.1, 0.2$ and 0.5 with corresponding values

FIG. 1: Negative Binomial

○.....○ $k = 0.1$

△---△ 0.2

◇—◇ 0.5



of p. The values of the different parameters for three of these curves are shown in Table 1.

Table 1

mean	p	k	Variance	% infection	overdispersion
2	10	0.2	22	38	11
5	25	0.2	130	48	26
5	10	0.5	55	70	11

When p is multiplied by 2.5 there is a large increase in the variance and smaller increases in the percentage infection and overdispersion. When k is multiplied by 2.5 there is a smaller increase in the variance, a larger one in the percentage infection, and no change in the overdispersion.

The effects on p and k of increases in mean, variance, and percentage infection in different combinations are shown below.

Table 2

	mean	variance	% infection	p	k
1.	inc			inc >	dec
2.		inc		inc ≈	dec *
3.			inc	dec ≈	inc *
4.	inc	inc		inc >	dec
5.	inc		inc	≈	inc
6.		inc	inc	inc =	dec
				or dec =	inc
7.	inc	inc		inc	inc
				=	inc

*The variance cannot increase without having some effect on at least one of the other two parameters. If the increase in p is greater than the decrease in k then the mean increases, while if the increase in p is equal to the decrease in k then only the percentage infection increases. Similarly if the percentage infection increases with constant mean then p must decrease as much as k increases and the variance will decrease, or if the variance is constant then the mean will alter.

The zero class is frequently the largest in distributions of biological data, but the negative binomial can also have the maximum frequency at a higher class. The values of p and k for differently shaped curves can be investigated by examination of the reiterative formula:

$$P_x = P_{x-1} \frac{(k + x - 1)}{x} \cdot \frac{p}{1 + p} \quad \dots(38)$$

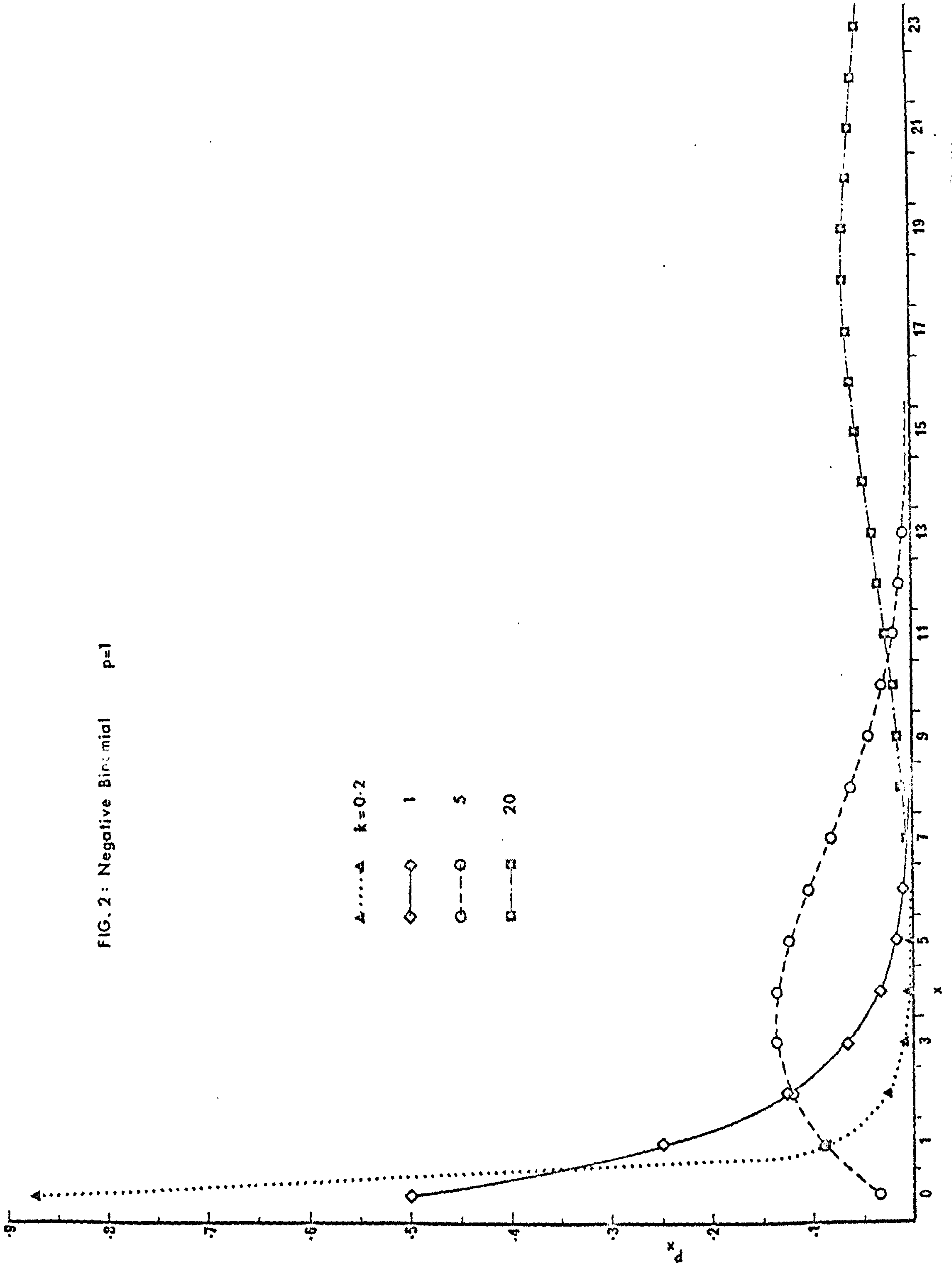
$$\text{where } \frac{k + x - 1}{x} = E \quad \dots(39)$$

$$\text{and } \frac{p}{1 + p} = R \quad \dots(40)$$

If the zero class is the largest then $P_x < P_{x-1}$ for all values of x . Hence $ER < 1$; $R < 1$, but approaches one as the value of p increases. Therefore usually $E < 1$, except for small p , so that $k+x-1 < x$ and $k < 1$.

The first case in which the zero class is not the largest is when it is equal to the one-class, i.e. $P_0 = P_1$. Therefore

FIG. 2: Negative Binomial $p=1$



$ER = 1$, but $R < 1$, so $E > 1$. As $x = 1$, $E = k$ and $k > 1$. Also $k = (1+p)/p$ or $pk = 1+p$, that is the mean is greater than one. In other words if the zero class is not the largest k must be greater than unity, and so must the mean. The converse is not true as a distribution with $k > 1$ may have the zero class the largest if the value of p is small.

The case when $k = 1$ is special:

$$E = \frac{k + x - 1}{x} = 1$$

therefore $P_x = P_{x-1} \cdot R$...(41)

As R is independent of x the curve falls exponentially, each value being obtained by multiplying the preceding one by the same amount.

The value of x for the maximum P_x increases as the value of k increases, that is the hump occurs further to the right (see Fig. 2).

The value of E (Fig. 3)

If $k > 1$ E approaches unity from $+\infty$ as x increases

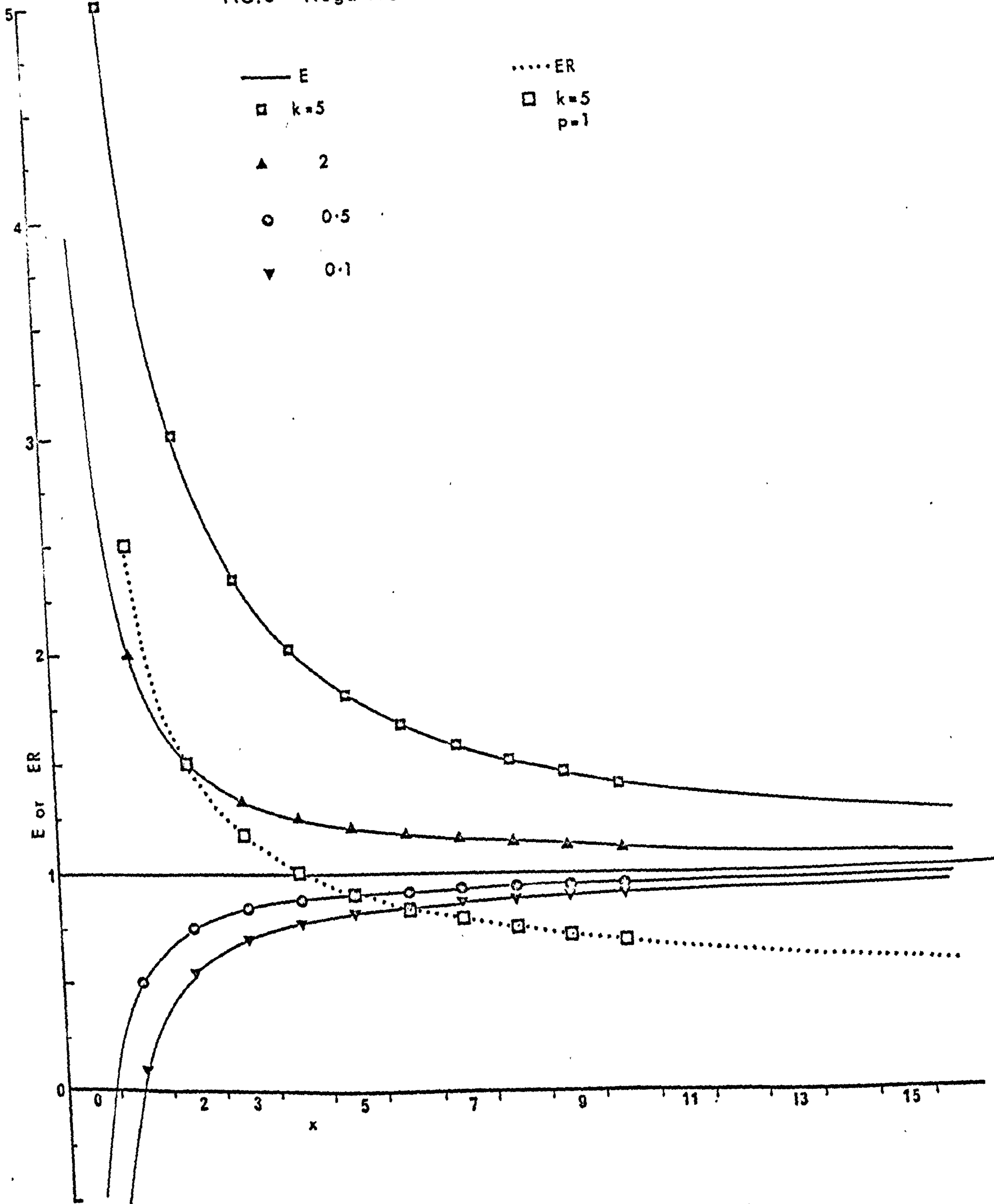
If $k < 1$ E approaches unity from $-\infty$ as x increases

If $k = 1$ $E = 1$ for all x .

The value of R

R is constant for all x . As p increases R approaches unity but is always below it.

FIG.3 Negative Binomial



The value of ER

If $k < 1$ ER is always less than one, but increases with increasing x , at a decreasing rate. If $k = 1$ then $ER = R$ for all x . If $k > 1$ then the value of ER may be less than unity if p is small, but if p is large the value will decrease from above one to below one as x increases (see Fig. 3).

The position of the hump for given values of p and k can be found as follows:

e.g. if $k = 5$ and $p = 1$:

$$E = \frac{5 + x - 1}{x} ; \quad R = 0.5$$

therefore $ER = 1$ when $\frac{(5 + x - 1)}{x} \cdot 0.5 = 1$

i.e. when $x = 4$

Thus $P_3 = P_4$ and the hump occurs between these two classes (see Fig. 2).

7. The log series distribution

The log series is described by Williams (1944). It was devised by Fisher to describe the distribution of species and individuals in samples of netted insects etc. It is the series:

$$f_1 \quad \frac{f_1 r}{2} \quad \frac{f_1 r^2}{3} \quad \frac{f_1 r^3}{4} \quad \dots \dots (42)$$

where r is a constant less than one: $r = 1 - \frac{f_1}{\text{sumx}} \dots (43)$

where $\text{sumx} = \sum_{x=1}^{x_{\text{max}}} f_x \cdot x \dots (44)$

α is a constant for any sample from the same population:

$$\alpha = \frac{f_1}{r} \dots (45)$$

also $N = - \alpha \log (1 - r) \dots (46)$

The value of r cannot be calculated directly; the first estimate, \hat{r} , is obtained from equation (43). The following equation is then equalised by an iterative method to find the best value of r:

$$\frac{N}{\text{sumx}} = \frac{(1 - \hat{r})}{\hat{r}} \cdot (-\ln(1 - \hat{r})) \dots (47)$$

If the right-hand-side is too large the value of r is increased

and vice versa, until the two sides are near enough equal.

The final value of \hat{r} is then used to calculate the distribution:

$$\phi_1 = \sum x (1 - \hat{r}) \quad \dots(48)$$

$$\phi_x = \phi_{x-1} \frac{(x-1) \hat{r}}{x} \quad \dots(49)$$

Williams (1944) describes the use of the log series parameter, α , as an "index of diversity", which is a useful concept when dealing with the distribution of individuals among species. This, together with the fact that there is no zero class in this type of distribution, makes the use of the log series very suitable. When dealing with host-parasite distributions, however, the "index of diversity" is meaningless while the zero term is biologically significant. The use of the negative binomial is therefore preferable in this case.

The log series is less versatile than the negative binomial as the first class is always the largest and each successive term is smaller than the last. As the negative binomial has two parameters there are many possible shapes for a given mean, whereas there is only one shape for the log series.

A computer program was written to calculate the log series distribution from the raw data. The flow diagram is given in appendix 1 c. The parameters were calculated and then used to obtain the theoretical distribution, which was

compared with the original by means of χ^2 and R^2 .

8. Neyman A distribution

This distribution was devised by Neyman (1939) to describe the distribution of larval insects hatching and dispersing from randomly distributed clumps of eggs. It is a generalisation of the Poisson. There are two parameters, m_1 and m_2 , calculated from the first two empirical moments, \bar{x} , the mean, and s^2 , the variance:

$$m_1 = \frac{(\bar{x})^2}{s^2 - \bar{x}} \quad \dots(50)$$

$$m_2 = \frac{(s^2 - \bar{x})}{\bar{x}} \quad \dots(51)$$

The general equation is given by Beall (1940):

$$P_x = e^{-m_1} \frac{m_2^x}{x!} \frac{d^x}{du^x} e^{m_1 e^{(u-m_2)}} \quad \dots(52)$$

where P_x is the probability of finding x insects on an area, u . The following equations are used to calculate the terms of the distribution:

$$P_0 = e^{-m_1(1-e^{-m_2})} \quad \dots(53)$$

$$P_{x+1} = \frac{m_1 m_2 e^{-m_2}}{x+1} \sum_{k=0}^x \left[\binom{m_2^k}{k!} P_{x-k} \right] \quad \dots(54)$$

A computer program was written to calculate m_1 and m_2 and hence the distribution. The flow diagram is shown in appendix 1d.

The Neyman A distribution may be polymodal.

9. Log normal distribution

If a distribution is converted to a normal by plotting x on a logarithmic scale then it is a log normal. The simplest method of testing whether a distribution is a log normal is to plot the data on log probability paper. The frequencies, f_x , are first expressed as percentages. The cumulative percentage for each value of x is then found by adding the percentages for all classes up to and including x . These are plotted against x on log probability paper and if a straight line results then the distribution is a log normal.

The best line is then drawn through the points and from this the parameters of the log normal can be determined. the value of x at a frequency of 50% gives the mean, and at 84% and 16% the mean multiplied by the standard deviation and the mean divided by the standard deviation respectively. The variance is obtained by squaring the standard deviation.

10. Other over-dispersed distributions

The Polya and Thomas distributions were also developed from aggregation models. The Polya arises if the habitat is initially colonised at random by the parent organisms, all arriving at once, and later producing clusters of offspring. The Thomas distribution is another which may be polymodal.

The Poisson-log-normal was devised by Cassie (1962) to describe the distribution of plankton. It is more skewed than the negative binomial, but less than the log normal. It arises because the distribution of plankton is dependent on the physical properties of the environment.

(ii) SIGNIFICANCE TESTS

The fit of the theoretical frequency distributions to the original was tested by calculating χ^2 and R^2 .

(a) χ^2

The value of χ^2 was calculated and then looked up in tables to find whether it was significant. If it was then the theoretical distribution was different from the original.

$$\chi^2 = \sum_{x=0}^{x_{\max}} \left\{ \frac{(f_x - \phi_x)^2}{\phi_x} \right\} \dots(55)$$

with $(x_{\max}-3)$ degrees of freedom. However, if for $x=i$, $\phi_i < 2$ then all subsequent values were taken together:

$$\frac{\left(\sum_{x=i}^{x_{\max}} f_x - \sum_{x=i}^{x_{\max}} \phi_x \right)^2}{\sum_{x=i}^{x_{\max}} \phi_x} \dots(56)$$

and χ^2 had $(i-2)$ degrees of freedom.

(b) R^2

The value of R^2 was calculated. As the fit becomes more nearly perfect so R^2 approaches one from less than one.

$$R^2 = \frac{\left(\sum f_x \phi_x - \frac{\sum f_x \sum \phi_x}{x_{\max}} \right)^2}{\left(\sum f_x^2 - \frac{(\sum f_x)^2}{x_{\max}} \right) \left(\sum \phi_x^2 - \frac{(\sum \phi_x)^2}{x_{\max}} \right)} \dots(57)$$

all sums from $x=0$ to $x=x_{\max}$.

Other tests were used to find whether there were significant differences between means and variances. (Bailey, 1959).

(c) t-test

If the variances of the two means to be compared were not equal, but the number of observations in both cases was more than 30 then the following equation was used:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\frac{s_1^2}{N_1} + \frac{s_2^2}{N_2}} \dots(58)$$

and t had (N_1+N_2-2) degrees of freedom. If N_1 and N_2 were not greater than 30 then the number of degrees of freedom was

$$n = \frac{1}{\frac{u^2}{N_1-1} + \frac{(1-u)^2}{N_2-1}} \quad \dots(59)$$

where $u = \frac{s_1^2 / N_1}{s_1^2 / N_1 + s_2^2 / N_2} \quad \dots(60)$

The value of t was then looked up in tables to find the probability that it had arisen by random chance. If the probability was less than 0.05 then the means were considered to be significantly different.

(d) F-test

This was used to determine whether variances were significantly different from each other:

$$F = s_1^2 / s_2^2 \quad \dots(61)$$

where $s_1^2 > s_2^2$ so that $F > 1$. The degrees of freedom were (N_1-1, N_2-1) . Once again tables were used to find the probability that the ratio F had arisen by chance.

The statistical tables of Fisher and Yates (1963) were used in the determination of the levels of significance in these tests.

(iii) FITTING A POLYNOMIAL

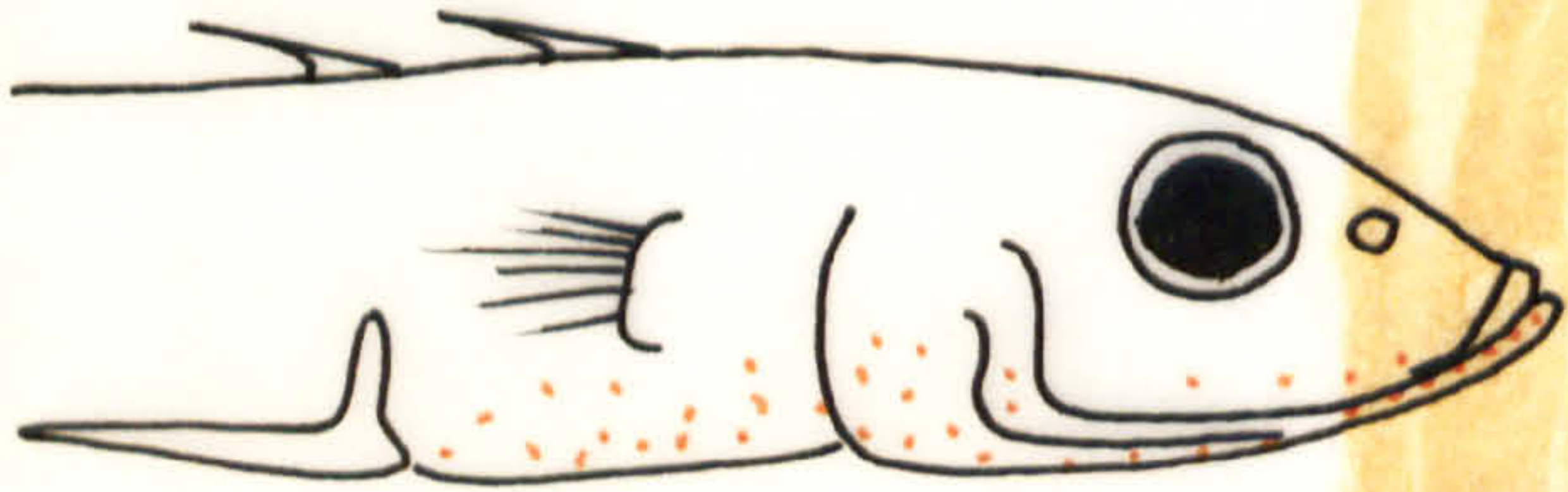
It is often useful to fit a curve to a set of points and this can be done using a polynomial. A polynomial can be fitted to any set of points if enough terms are used. If there are as many terms as points the fit will be perfect but the curve is no improvement on the raw data. In general as few terms as possible are used to obtain a reasonably close fit. Often it is useful to transform one or both of the ordinates, for example log, reciprocal etc.

A computer program was used to calculate curves by a method of least squares, as described by Snedecor (1946). This program calculated a curve of any order required, and could easily be modified to deal with different transformations. The equation of the curve was printed and a set of co-ordinates covering the same range as the original data. The original points and the calculated curve were also plotted. The closeness of the fit was tested by calculating R, which was less than one and approached one as the fit improved. The flow diagram of the program is given in appendix 1e.

Fig. 4 Redness
of male fish



I



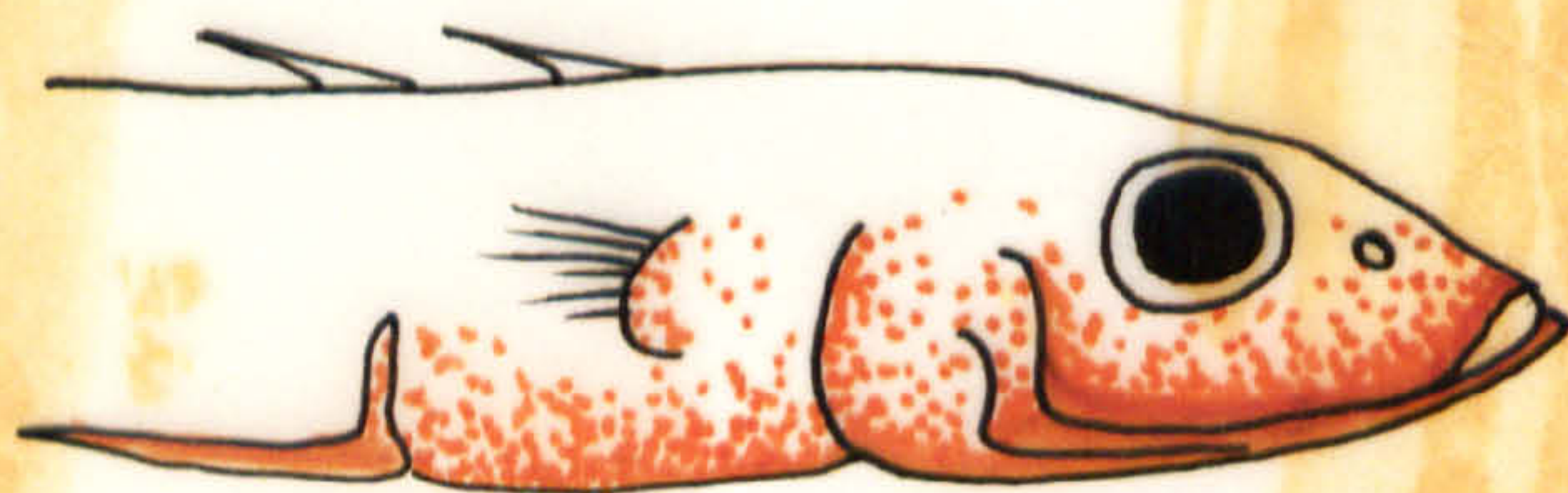
II



III



IV



V

M E T H O D S

The fish were thawed and then examined. They were dried on filter paper and then weighed; the total length was measured. The outside of the fish was examined for external parasites, but none was ever found. The body cavity was opened and if Schistocephalus solidus plerocercoids were present, as they often were, these were removed and counted. Each plerocercoid was measured by laying it on a slide over a ruler, and then weighed. The balance was accurate to only 0.01 g, so if there were several very small worms these were weighed together.

The fish was re-weighed and the gut was removed and examined. The acanthocephalan Echinorhynchus clavula was the only parasite found in the gut; if any were present they were removed, and measured using a graduated eyepiece on a dissecting microscope. The sex of the worm was noted, and the presence or absence of shelled acanthors in the females.

The sex of the stickleback was noted and a measure of the breeding condition obtained by examination of the gonads, and also the redness of the throat in males. The males were divided into six categories, from 0: no red coloration and testes undeveloped, to V: throat very red and testes developed with much black pigmentation. The degree of redness for the six categories is shown in Fig. 4. The females were more difficult to subdivide and only four categories were distinguished; 0: ovaries undeveloped, I: ovaries with yolk granules visible,

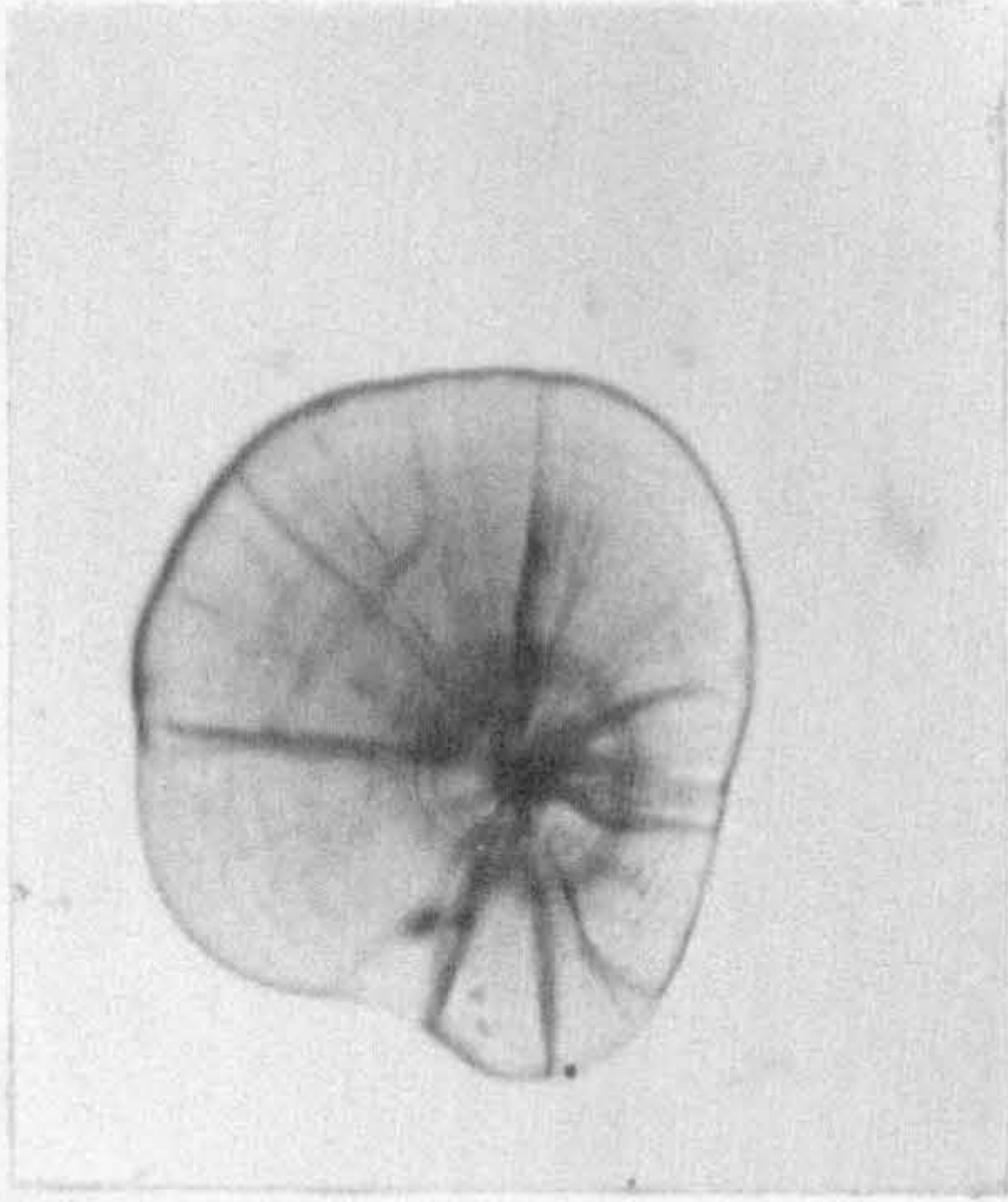
II: some eggs present, III: gravid.

The other internal organs of the fish were examined but no parasites ever found. The eyes were removed and the lenses and retinal layer examined for cercariae. None was found in the lens, but metacercariae of Diplostomum gasterostei were often present in the retinal layer. These were removed and those from each eye counted separately. Finally the brain of the fish was removed and examined; no parasites were found here.

In addition the ages of fish in samples from 21.8.67 onwards were determined by examination of the otoliths, using the method described by Jones and Hynes (1950). A slice was cut from the roof of the skull, from the region of the eyes back to the vertebral column. The brain was then carefully removed and the largest otolith, or sagitta, taken from both sides. These were placed on a slide and the surrounding membranes removed. They were then dehydrated in absolute alcohol for ten minutes, cleared in creosote oil for ten minutes and mounted in Canada balsam under a cover slip. They were later examined under the microscope and the growth rings counted to give the fish's age.

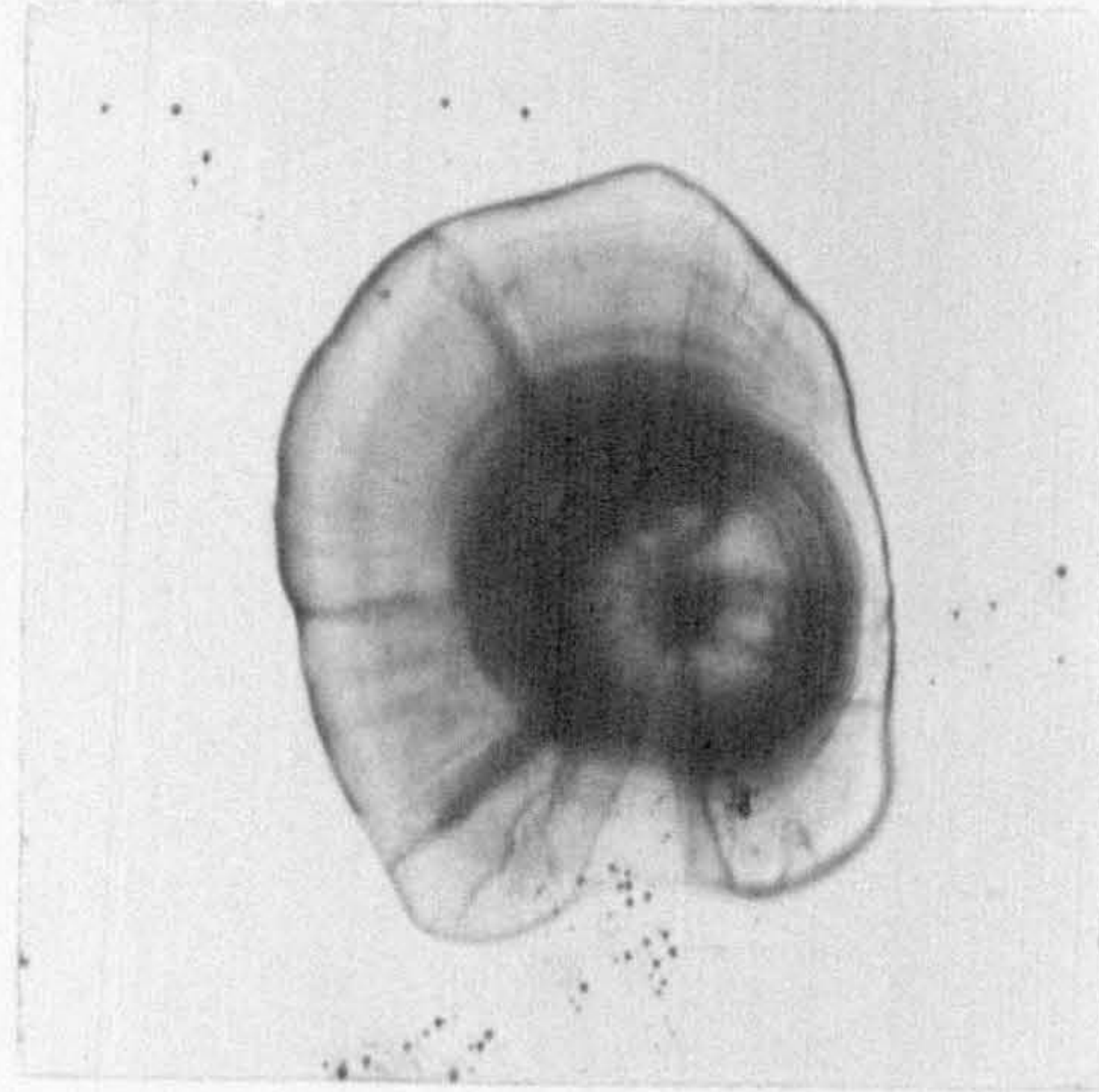
Young fish have an opaque or clear centre to the sagitta with an opaque outer ring. A transparent ring is added in late summer followed by an opaque one in autumn or winter. Transparent and opaque rings are then added alternately, one of each per year. Plate I shows photographs

PLATE 1: Otoliths from 6 fish of different ages



age-group I: centre only

scale:
0.1 mm
└───┘

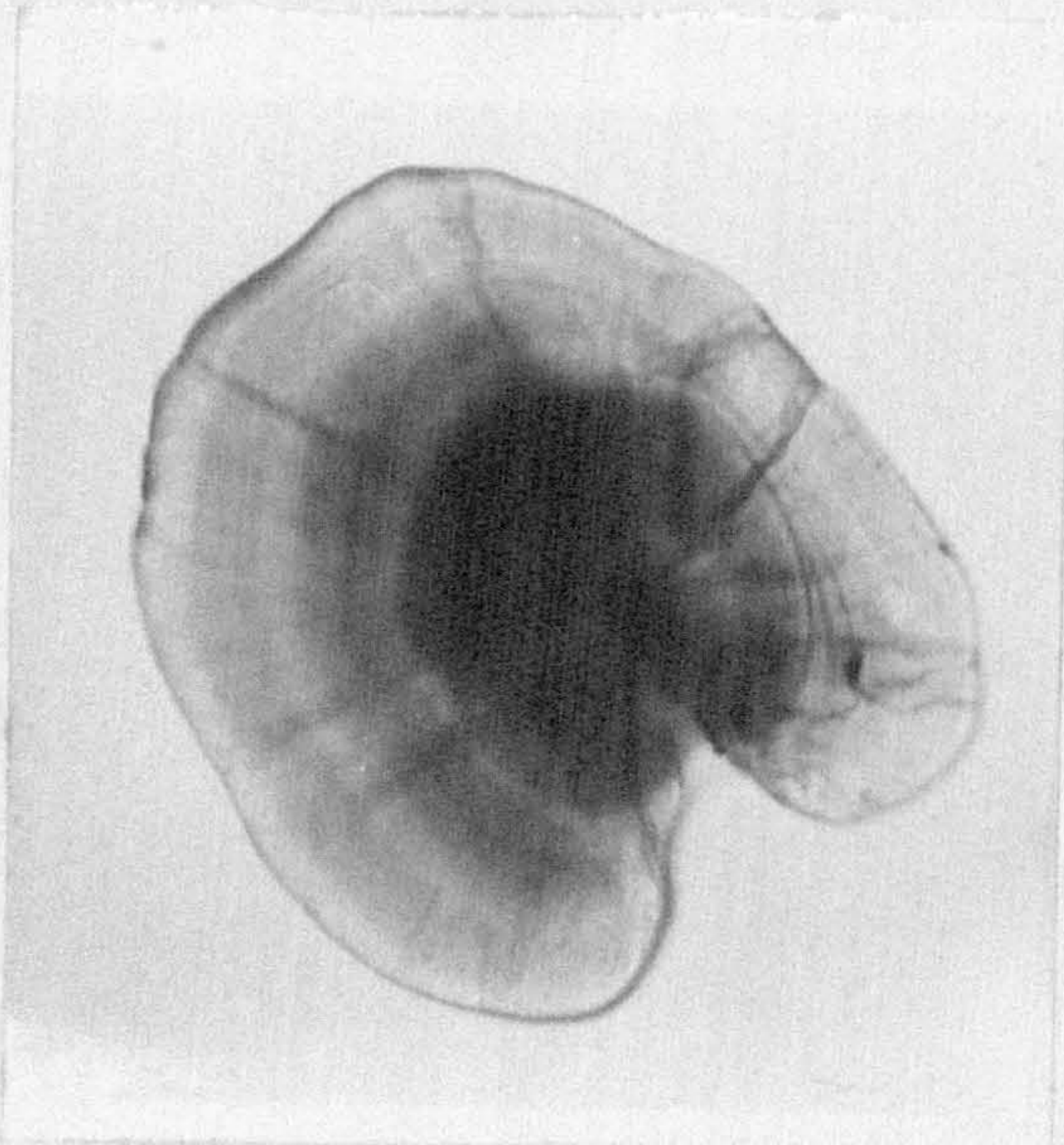


age-group I: 1 clear ring

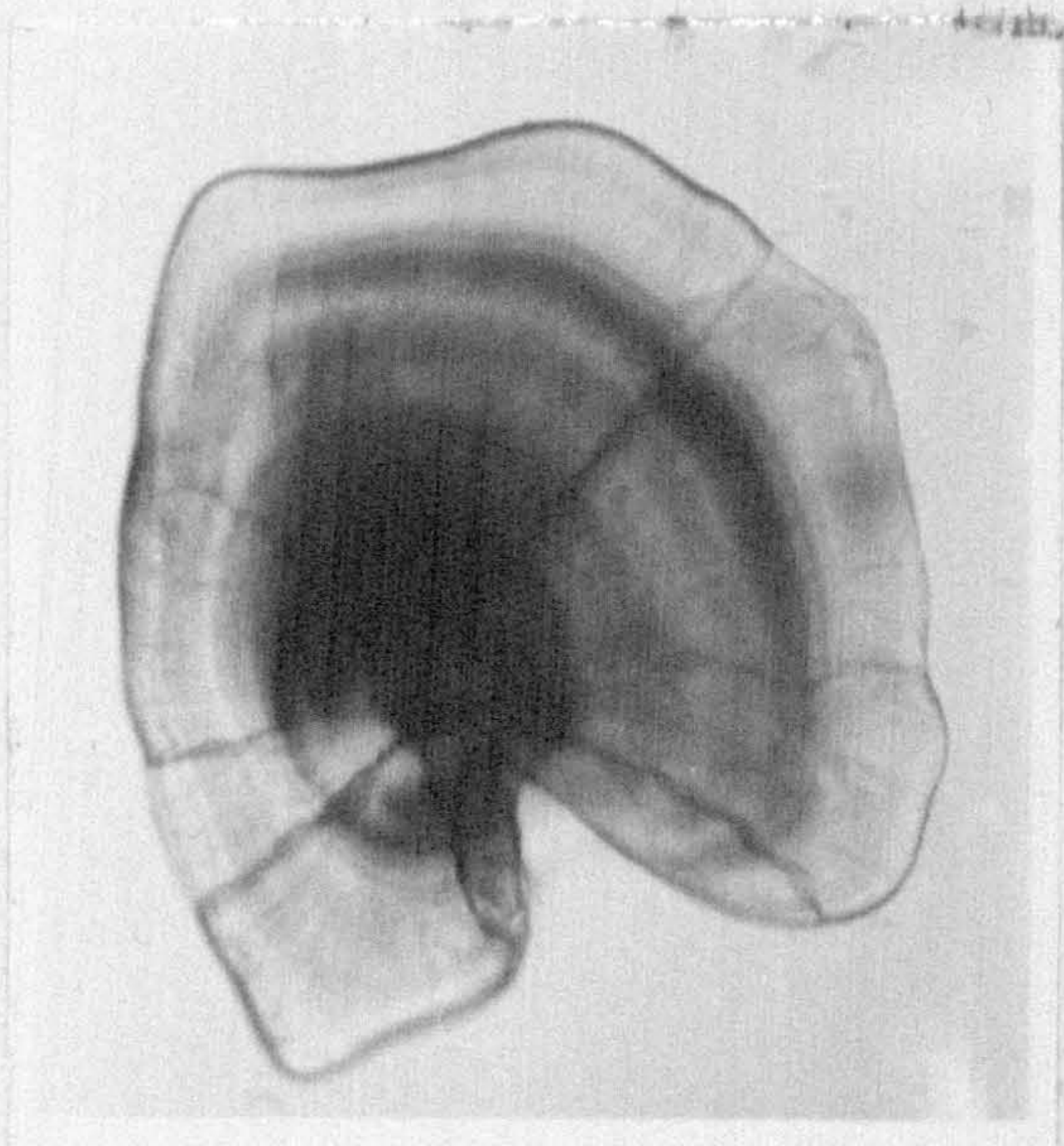


age-group II: 2 clear rings, 1 opaque

age-group II: 2 clear,
2 opaque rings



age-group III: 3 clear, 2 opaque



age-group IV: 4 clear, 3 opaque

of otoliths from fish of different ages. There were often intermediate rings as well, as can be seen, but it was generally clear which were the main ones on at least one of the pair of otoliths. Ages were reckoned from 1st June = 0.

Thus the following information was obtained for each stickleback:

1. Sex of fish and breeding condition
2. Age of fish
3. Length of fish, LF
4. Weight of fish with parasites, WF+WS
5. Weight of fish without Schistocephalus, WF
6. Total number of Schistocephalus, NS
7. Total weight of Schistocephalus, WS
8. Length of each plerocercoid
9. Weight of each plerocercoid, WP
10. Total number of Echinorhynchus, NE
11. Number of male Echinorhynchus
12. Length of each male Echinorhynchus
13. Number of female Echinorhynchus
14. Length of each female Echinorhynchus
15. Presence or absence of shelled acanthors in female Echinorhynchus
16. Total number of Diplostomum, ND
17. Number of Diplostomum in right eye
18. Number of Diplostomum in left eye

The data for each fish were punched on a card, omitting items 4, 8, 9, 10, 12, 14, 15 and 16. The figures could then be analysed in many different ways simply by reading the same cards as data for different computer programs. Any number of the items could be selected and used.



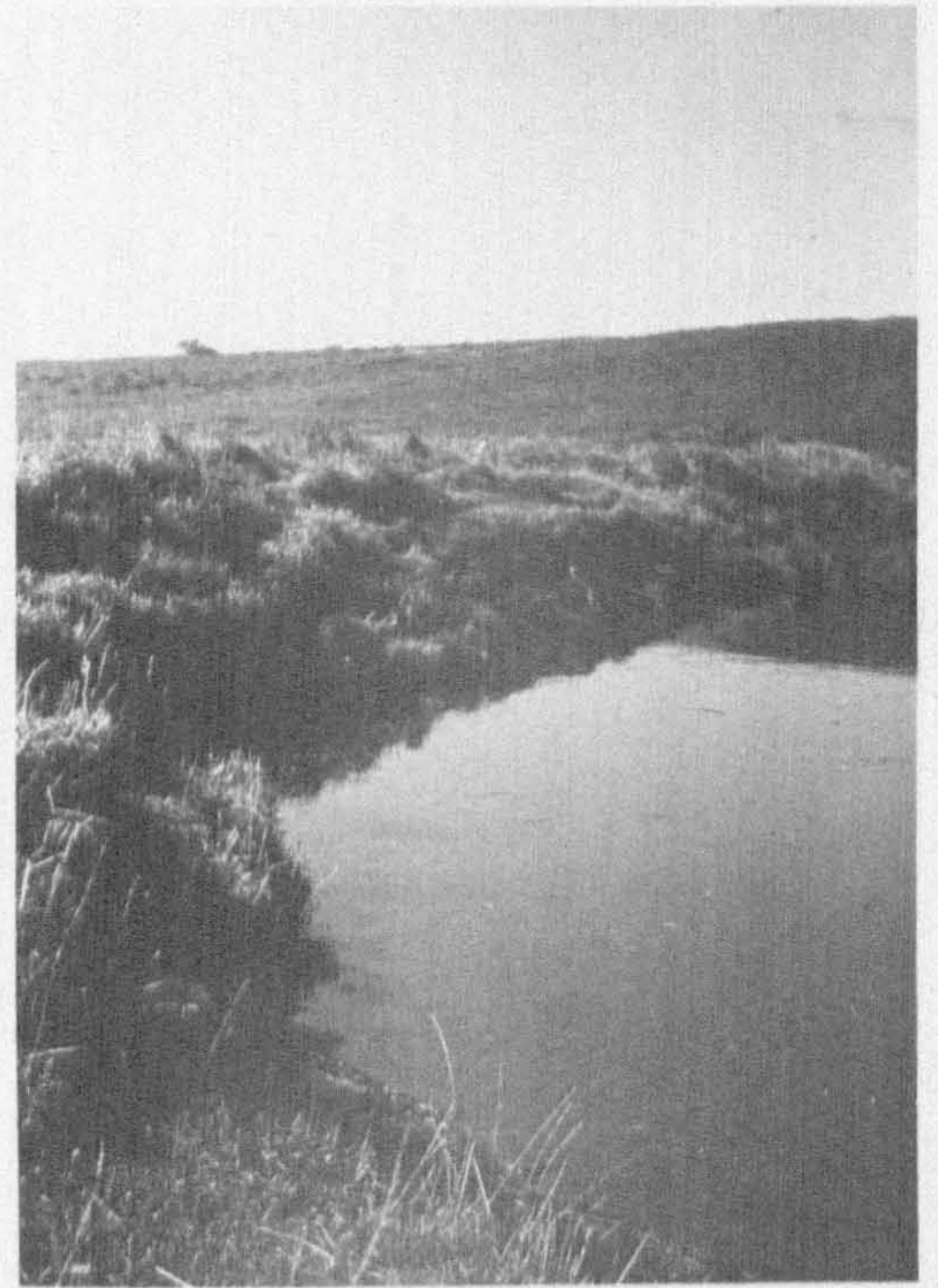
(a) August 1967



(c) October 1967

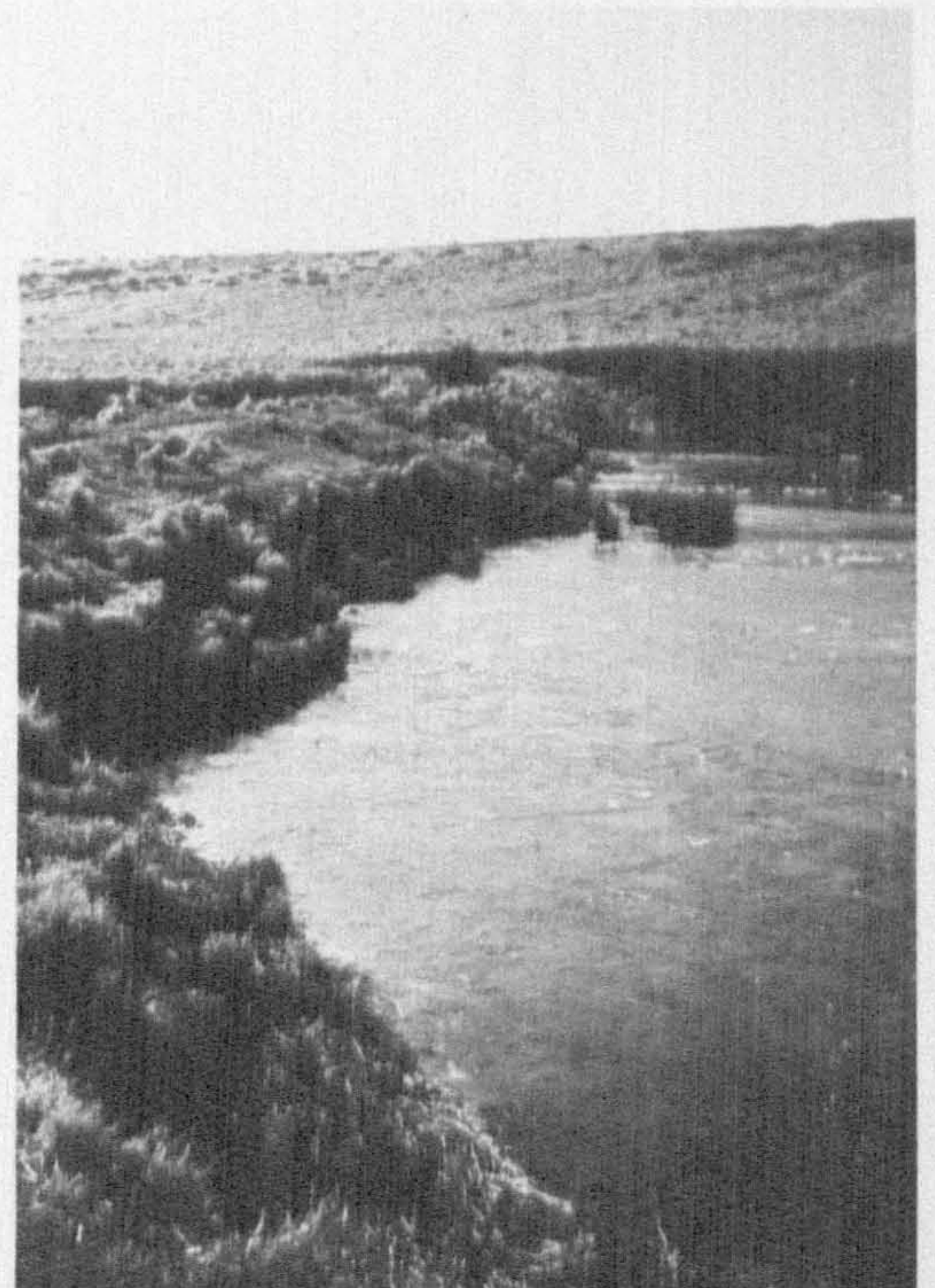


(d) February 1968



(b) August 1967

a, c, d: from the dam, looking
towards the inlet streams
b, e: the dam, from which most
of the fish were caught



(e) February 1968

H A B I T A T

Priddy pool is at 270m on the Mendip Hills, Somerset, in an exposed position so that it freezes frequently in winter. It is an artificial pond formed by damming a stream. The area fluctuates about an average of around 7000 m² and the maximum depth is about 2m. Most of the shoreline is marshy and overgrown, but the shore formed by the dam (see Plate 2b & c) is relatively free from vegetation.

There are very few submerged Angiosperms except for a little Potamogeton sp. In summer the water becomes very overgrown with Equisetum fluviatile L. (see Plate 2a) except for a small area near the dam. This dies back in autumn (see Plate 2c & d) and creates a large amount of debris which collects around the shores.

Avery (1968) has studied, throughout the year, the stomach contents of the two species of newt, Triturus helveticus (Razoumowsky) and T. vulgaris (L.), found at Priddy. He also examined sticklebacks in July and compared the invertebrates in the stomachs with those caught in the pond. He concluded that the fish were selecting Diptera larvae, Cladocera and Ostracoda, as there were higher percentages in the stomachs than in the water. Copepods, the most numerous invertebrate caught, and Ephemeroptera nymphs were also eaten by the fish. The same groups formed the main food of the newts at this time. Also eaten by the newts were Diptera pupae, Asellus, Gastropoda,

larval and adult Coleoptera, Hemiptera, Oligochaeta, Hydrachnellae, their own eggs, and Schistocephalus.

The stomach contents of the sticklebacks were not analysed in this study but small Crustaceans appeared to form the main bulk of the food while Diptera larvae were less important at most times of the year. No Asellus were found, either in the stomach contents or in the pond although Avery (pers. comm.) had found them in some numbers just prior to the start of this study.

Black-headed gulls (Larus ridibundus) and herons (Ardea cinerea) were seen at the pond occasionally; carrion crows (Corvus corone) were seen in trees near the pond, but not on the shore. All these birds probably preyed on the sticklebacks. Mallard (Anas platyrhynchos) were the only species of duck seen and these do not eat fish.

I GASTEROSTEUS ACULEATUS L.

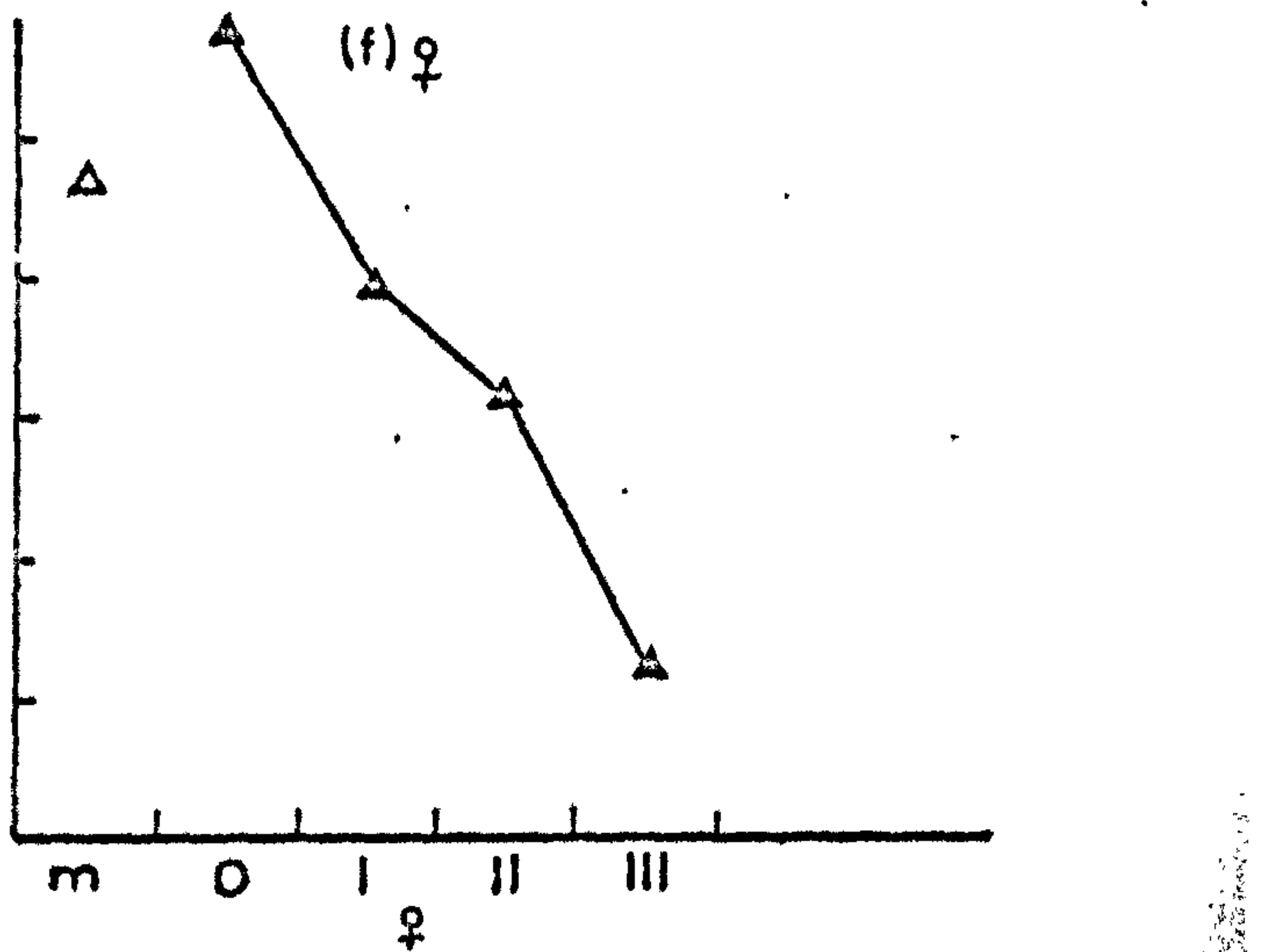
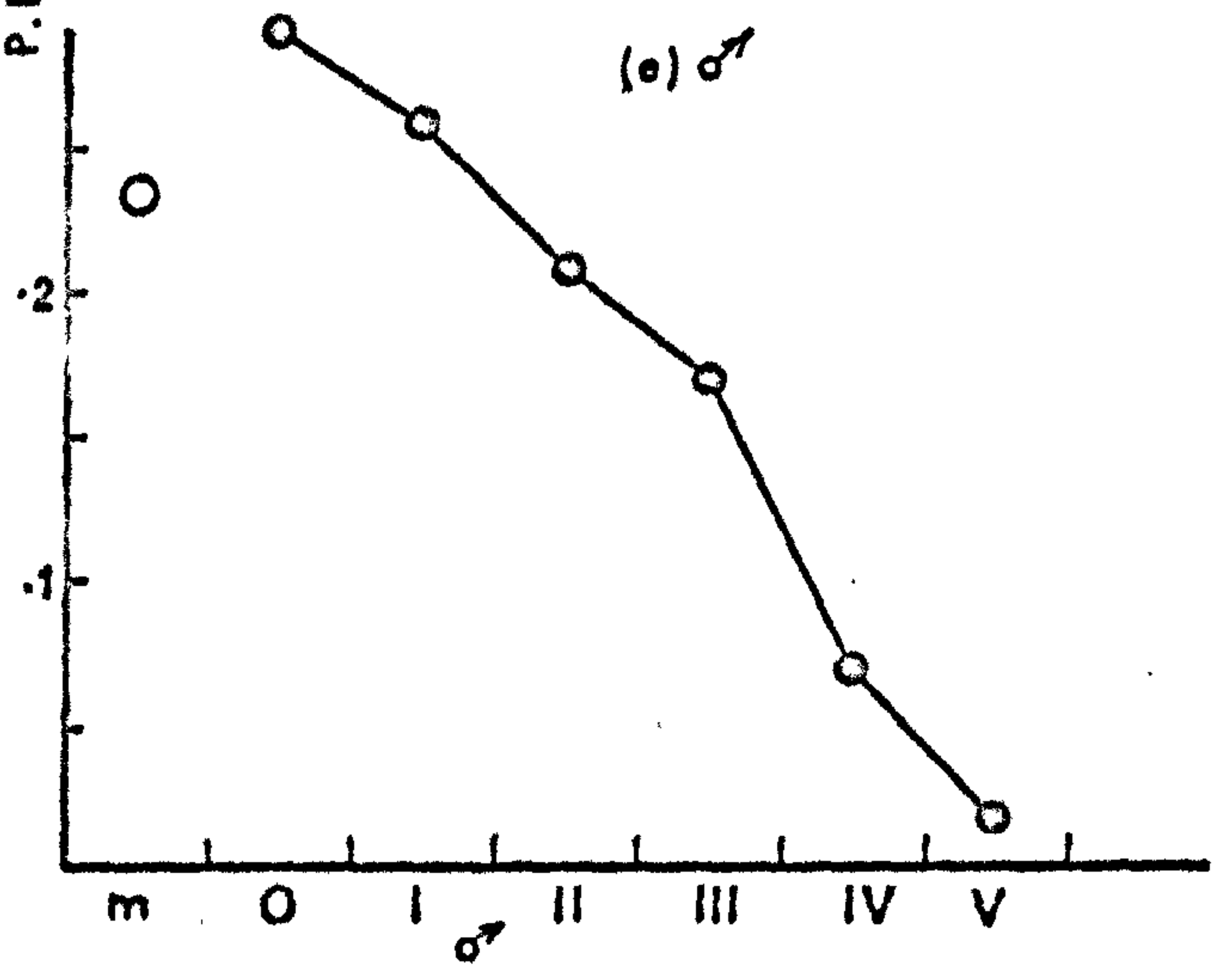
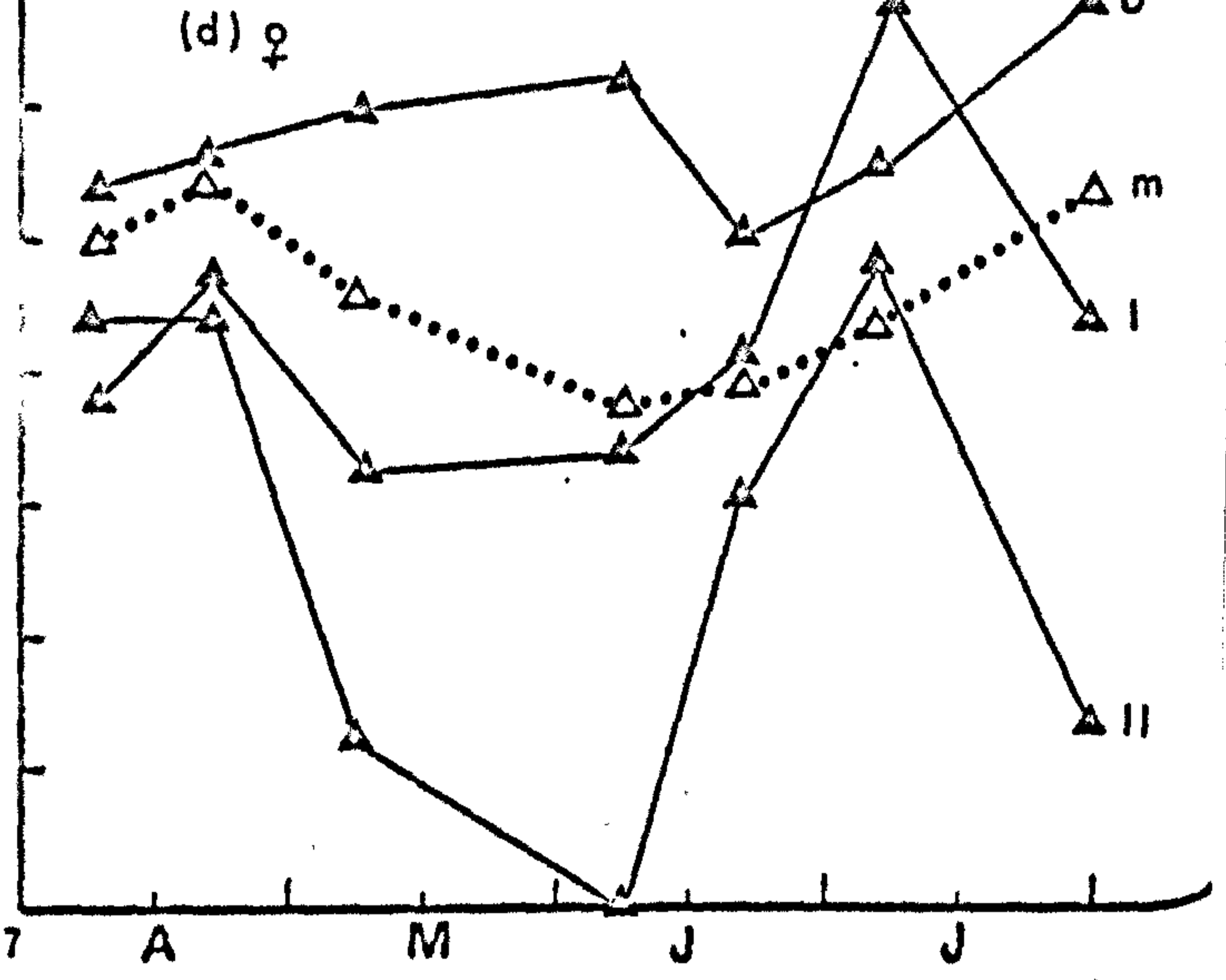
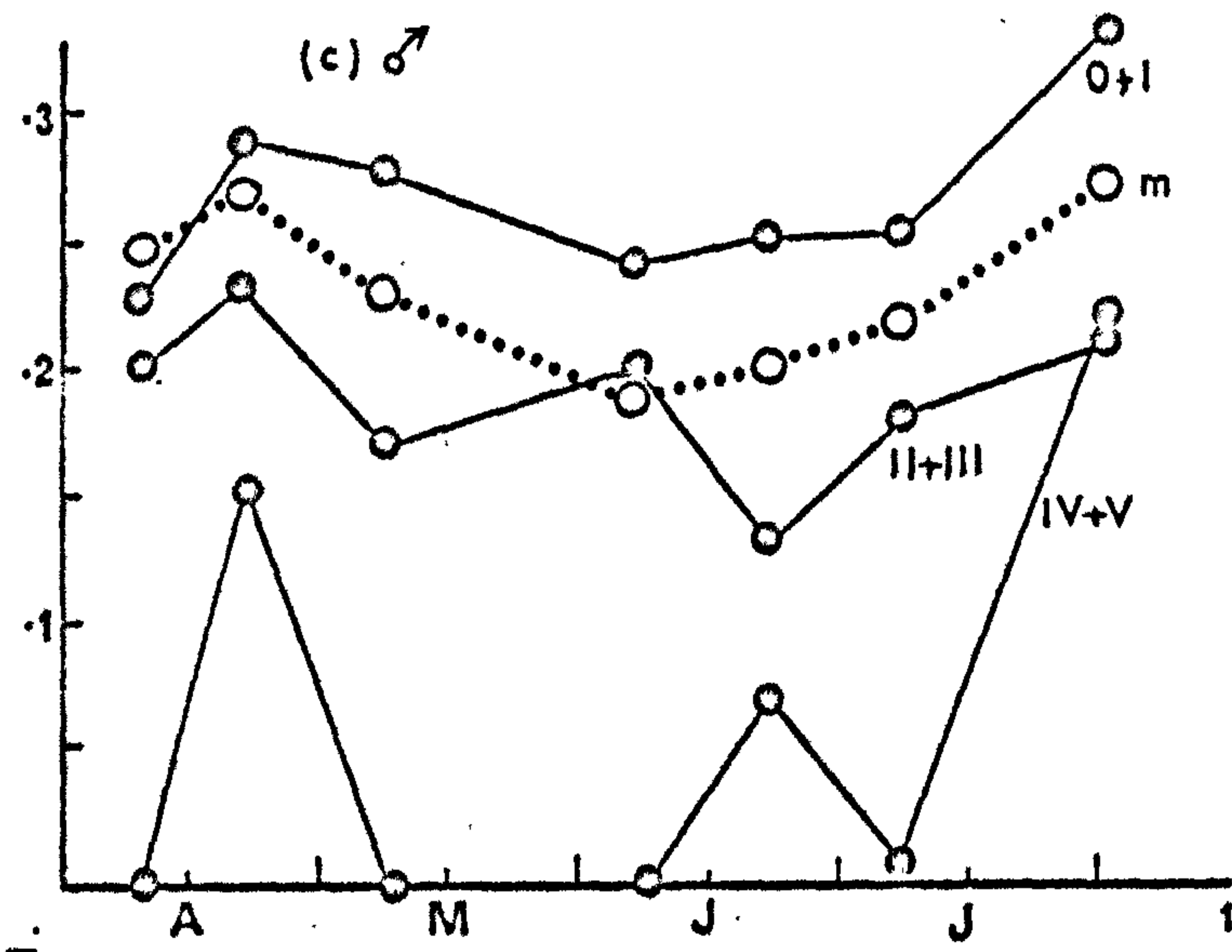
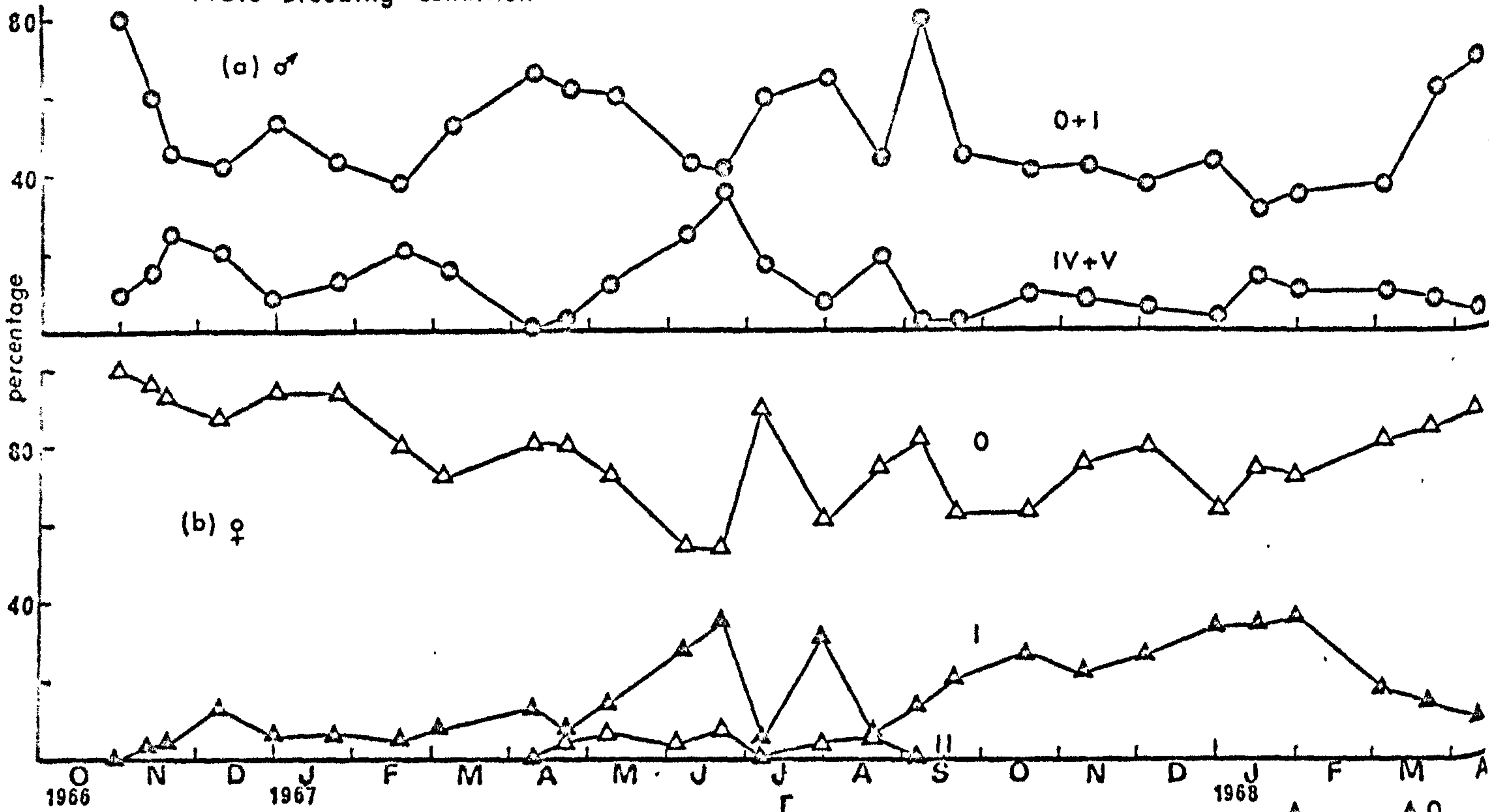
BIOLOGY OF FISH

The sticklebacks were of intermediate type, which Heuts (1947) describes as B¹ or A^m. According to the classification of Bertin (1925) they belong to the race gymnura.

The population was more or less self-contained as the streams which feed the pond do not provide a suitable habitat for the sticklebacks. The behaviour of the fish varied considerably throughout the year. In autumn they were sluggish and easy to catch and there were many dead or dying ones around the shore. Most fish were caught along the dam as they could be seen clearly in the water there. In winter more fish were found in the debris around the other parts of the shore, particularly in cold weather. When there was ice thin enough to be broken few fish were found near the shore - presumably they moved to deeper water.

During the spring the fish were found near the dam again and were moving more quickly. The fish bred in June and July and many males had territories and built nests along the dam. These breeding fish were very lively and difficult to catch; great efforts were not made as there was a danger of disrupting the breeding. Similarly large numbers of fry were not taken when they appeared in July and August. Breeding occurred later than is usual for Gasterosteus, probably due to the heavy Schistocephalus infection.

FIG.5 Breeding condition



BREEDING

The percentage of male and female fish in the different categories indicating breeding condition were calculated for each sample. Some of these are plotted in Fig. 5a & b. Some intermediate categories were omitted and in the case of male fish categories 0 + I and IV + V were added to increase clarity, as each group often contained only one or two fish.

Males

There was a considerable amount of fluctuation between samples, due largely to their small size. It can be seen however that between April and August 1967 there was a peak in the percentage of mature fish and a trough in the percentage of undeveloped fish. It was noticeable that there were never fewer than 40% of undeveloped fish (0 + I) during this breeding period, although from November 1967 to March 1968 the percentage did fall to between 30 and 40. Some fish were well-developed throughout the year. In the autumn and winter 1966-7 the percentage in groups IV + V was between 10 and 20, whereas in 1967-8 it was mostly under 10. This was probably due to the milder weather of the former year, and also to the lighter Schistocephalus infection.

Females

Fewer female fish came into breeding condition and although there were always some showing yolk development (I)

there were never fewer than 50% undeveloped (0), and usually at least 60%. Gravid fish (III) were found in small numbers from April - September 1967. It seems likely that in some of these the eggs did not mature until after breeding activity in the males had ceased: none was noted after July. Females with a few eggs were found until January 1968.

Effect of Schistocephalus on breeding

As such a small proportion of the fish population bred it seemed probable that the heavy Schistocephalus infection was having a deleterious effect. This was investigated by calculating the mean parasite index of fish in different stages of maturity. (Parasite index = $WS/(WS + WF)$, see p. 88). These means are plotted for each category of both sexes of fish during the breeding period April - July 1967, in Fig. 5e & f. This shows that there was a steady decrease of parasite index with increased sexual maturity. Many of the fully developed fish were uninfected with Schistocephalus although nearly all other fish were infected. This is contrary to the observations of Arme and Wynne Owen (1967) who found that Schistocephalus had no effect on the coloration of male sticklebacks.

Categories of male fish showed an increase in the mean parasite index as the breeding season proceeded, suggesting that more heavily infected fish came into breeding condition later, (Fig. 5c & d). This may, however, be partly a reflection of a general increase in the parasite index together

with retention of red coloration after breeding has occurred.

There was also an increase of mean parasite index in females with eggs, from June-July; this was not accounted for by an increase in the mean of the population, and does therefore show that more heavily-infected fish matured later.

Therefore Schistocephalus caused a delay in maturation in both sexes of fish, and prevented it altogether in many individuals.

SEX DIFFERENCES

(a) Numbers

A total of 1860 fish was examined, of which 847 were males, 946 females, and the rest young. This gives an average of 69 fish per sample with 31 males: 35 females. When these means were tested using an approximate t-test (see p.32) the result was a probability of 10-20%; in other words the sex ratio was not significantly different from 1:1.

(b) Length and Weight

Means and variances were calculated for lengths and weights of all males and all females. Those of the females were all slightly larger; mean length of males was 49.69 mm and of females 49.79 mm, mean weight of males was 0.882 g and of females 0.890 g. These means were subjected to a t-test and there was found to be no significant difference in length or weight between the two sexes.

The variances were tested with the F-test (see p. 33); the variances of the females' lengths and weights were both found to be significantly larger than those of the males' lengths and weights. This shows that the females are more variable in size than the males, in particular attaining a greater maximum length and weight, although this does not significantly increase the means.

(c) Age

Mean ages of males and females were calculated for

all fish which had been aged. Male = 2.07 yrs., female = 2.113 yrs. This difference was not significant. The variances are just significantly different, at the 5% level, which does not suggest a real difference.

Once again the females have higher values for mean and variance than the males. This indicates that the greater length and weight of females is due to greater age. This is borne out by the fact that there are more females than males.

DEAD FISH

Eighty-six dead fish were picked up from the pond, between October and April 1966-7 and September and March 1967-8. The largest numbers were found in November and December of both years except for an exceptionally large number in March 1968, probably due to heavy frosts in February and early March.

Many of the fish had been dead some time and were decaying and covered with fungus. This suggests that they were not eaten once dead, except for the eyes which were sometimes missing. Only 31 had the body wall intact and therefore still contained all the Schistocephalus they had harboured when alive. In some the gut was also decayed.

The fish and their parasites were dealt with in the same way as the living ones, as far as was possible.

(a) Length, weight and age of fish

Individual samples were nearly all too small to analyse separately. Means and variances of length and weight were calculated for all the fish. The mean length was 52.43 mm which was significantly greater than that of all the living fish (1% level, t-test). The mean weight was 0.899 g, not significantly greater than that of the living fish. Therefore the fish weighed less than would have been expected for their length; many were obviously emaciated. It was noticeable that the fish found in 1967-8 were on average longer and heavier than those found in 1966-7.

The ages of those in 1967-8 were determined and nearly all fish were in age-group IV showing that many fish died in their fourth winter.

(b) Schistocephalus

Plerocercoids were counted and measured even when the body wall of the fish was broken and it was apparent that some worms had escaped. A total of 206 plerocercoids was found, of which the mean weight was 0.115 g, as compared with 0.078 g for plerocercoids from living fish. This higher mean weight could be due to the fact that the average age of the dead fish was greater than that of the living ones rather than to a higher level of infection in dead fish.

The parasite indices of the 31 intact fish were calculated and the mean value was 0.355, significantly greater, at the 1% level, than the overall mean for living fish. This higher parasite index cannot be accounted for by the greater age of the dead fish as parasite index does not increase with age. Therefore death of fish was caused by heavy Schistocephalus infections.

(c) Echinorhynchus

The gut was intact in 70 dead fish. These contained an average of 0.76 male and 1.0 female Echinorhynchus per fish; these values were not significantly different from those for living fish. The male:female ratio of 0.757 was also very similar to that of worms from living fish.

(d) Diplostomum

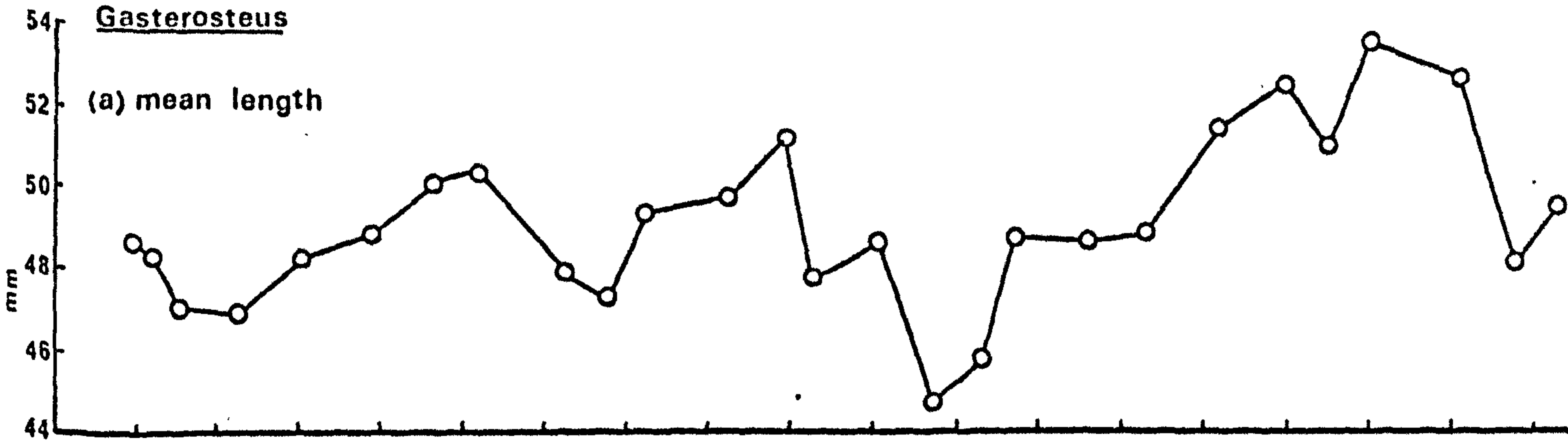
The 86 dead fish had 77 right and 75 left eyes between them. The mean numbers of Diplostomum were 5.62 per right eye and 4.43 per left eye; these were not significantly different from the means for living fish.

From these results it can be seen that the fish died mostly in autumn and winter when conditions were most severe and food shortest. Most of these fish were in their fourth year. Many were very emaciated and had died of starvation; this condition had very often been aggravated by a heavy infection with Schistocephalus. The presence of Echinorhynchus and Diplostomum did not generally affect the fish adversely, although in some samples there were individual fish with large numbers of one of these parasites, suggesting that they can cause death of the fish.

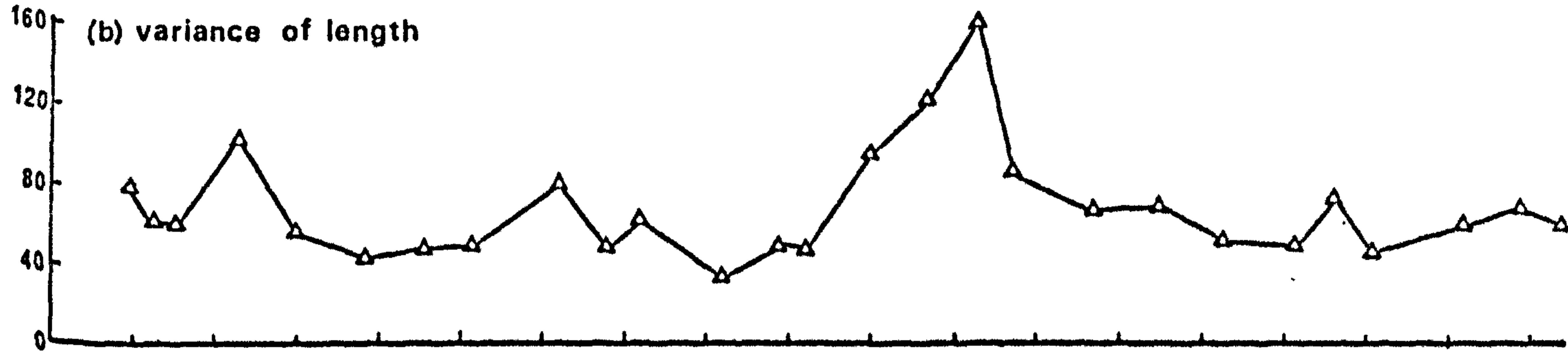
In spring and summer sticklebacks weakened by Schistocephalus would not have died of starvation as the food supply was plentiful, but were probably eaten by predators.

Gasterosteus

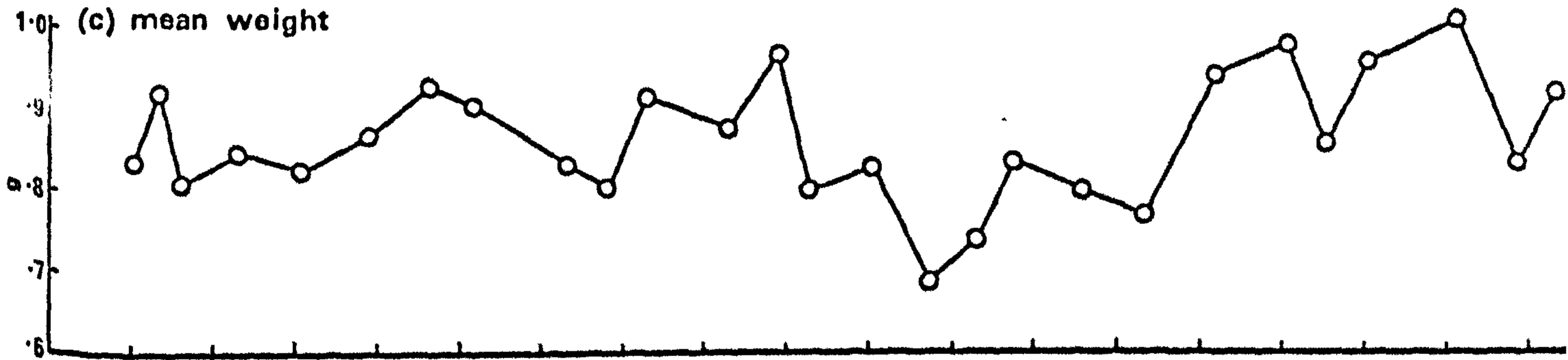
(a) mean length



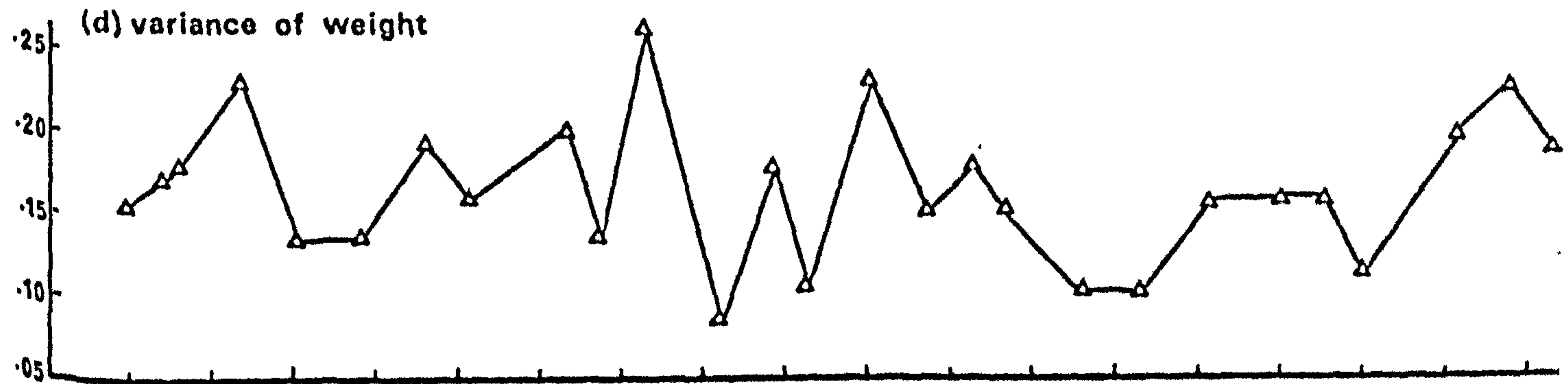
(b) variance of length



(c) mean weight



(d) variance of weight



O N D J F M A M J J A S O N D J F M A
1966 1967 1968

LENGTH OF FISH

Means and variances were calculated for each sample and for each age-group of each sample where ages were known. Graphs were plotted of mean and variance vs. date of sample and of mean vs. age of fish. The total distribution of lengths of all fish was plotted, and also the distribution for each age group of each sample.

A Samples (appendix 2 a)

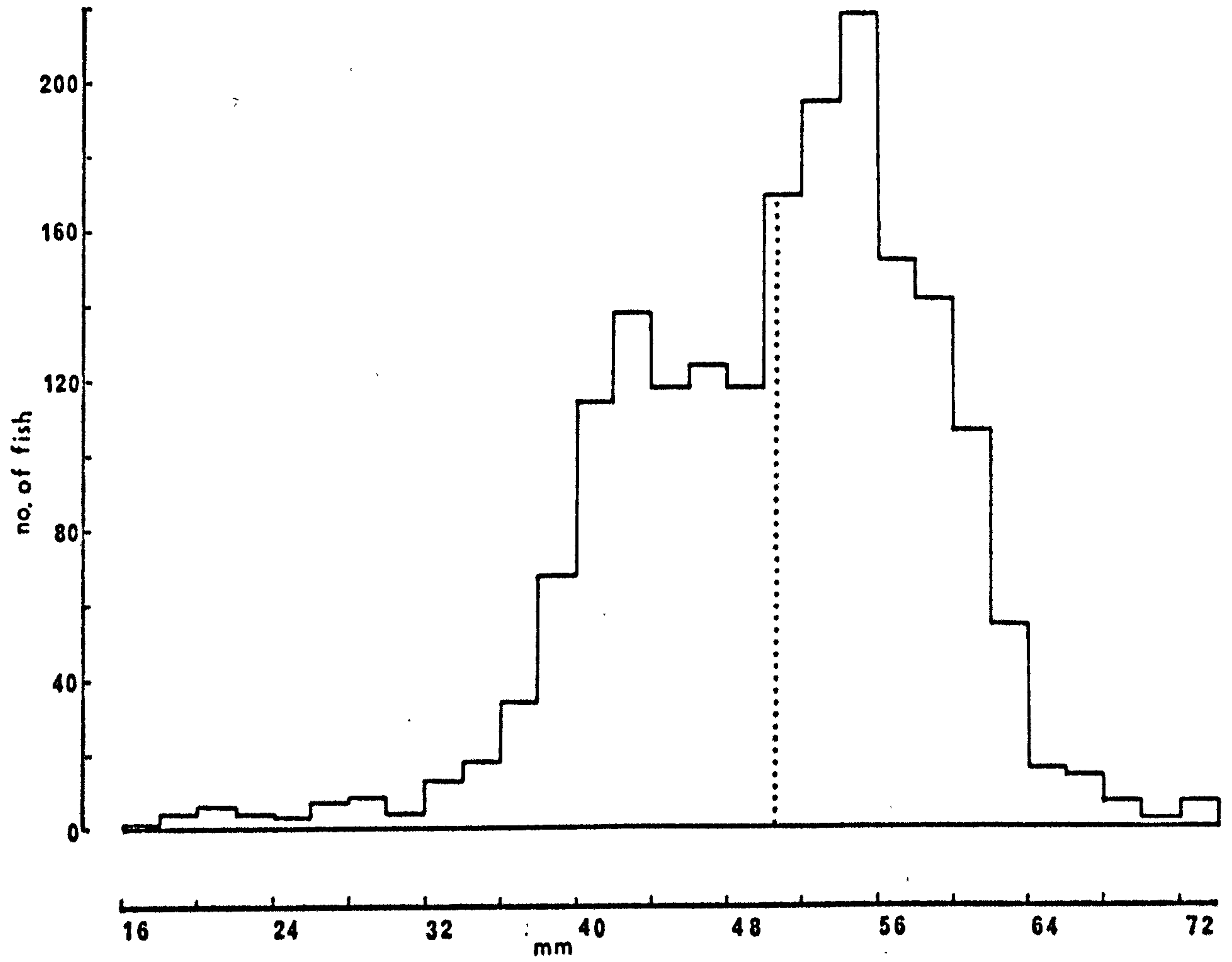
1. Mean (Fig. 6a)

The mean length of all fish was 49.1 mm. The value of the mean fell initially, from 48.7 mm on 29.10.66 to 47.0 mm on 10.12.66. It then rose fairly steadily, reaching 50.4 mm in March 1967. There was then a decrease, to 47.2 mm on 21.4.67 followed by an increase to 51.2 mm on 21.6.67, and another decrease to a minimum of 44.7 mm on 21.8.67. There was then a fairly steady increase to 53.6 mm on 1.2.68 and a final decrease to 49.5 mm on 9.4.68.

2. Variance (Fig. 6b)

The variance of the lengths of all fish was 69.25. The variance varied more or less inversely as the mean. The value decreased from 79 in the first sample to 59.4 on 19.11.66, then increased to 100.8 on 10.12.66. There was a decrease to about 44 during February 1967 followed by an increase to 80.9 on 9.4.67. The variance fell once more to 33.7 on 7.6.67 and then rose steadily, reaching 158.1 on 7.9.67. There was then

FIG. 7 Length frequency distribution



a more or less steady decline to 44.2 on 1.2.68 with a final increase to 58.3 on 9.4.68.

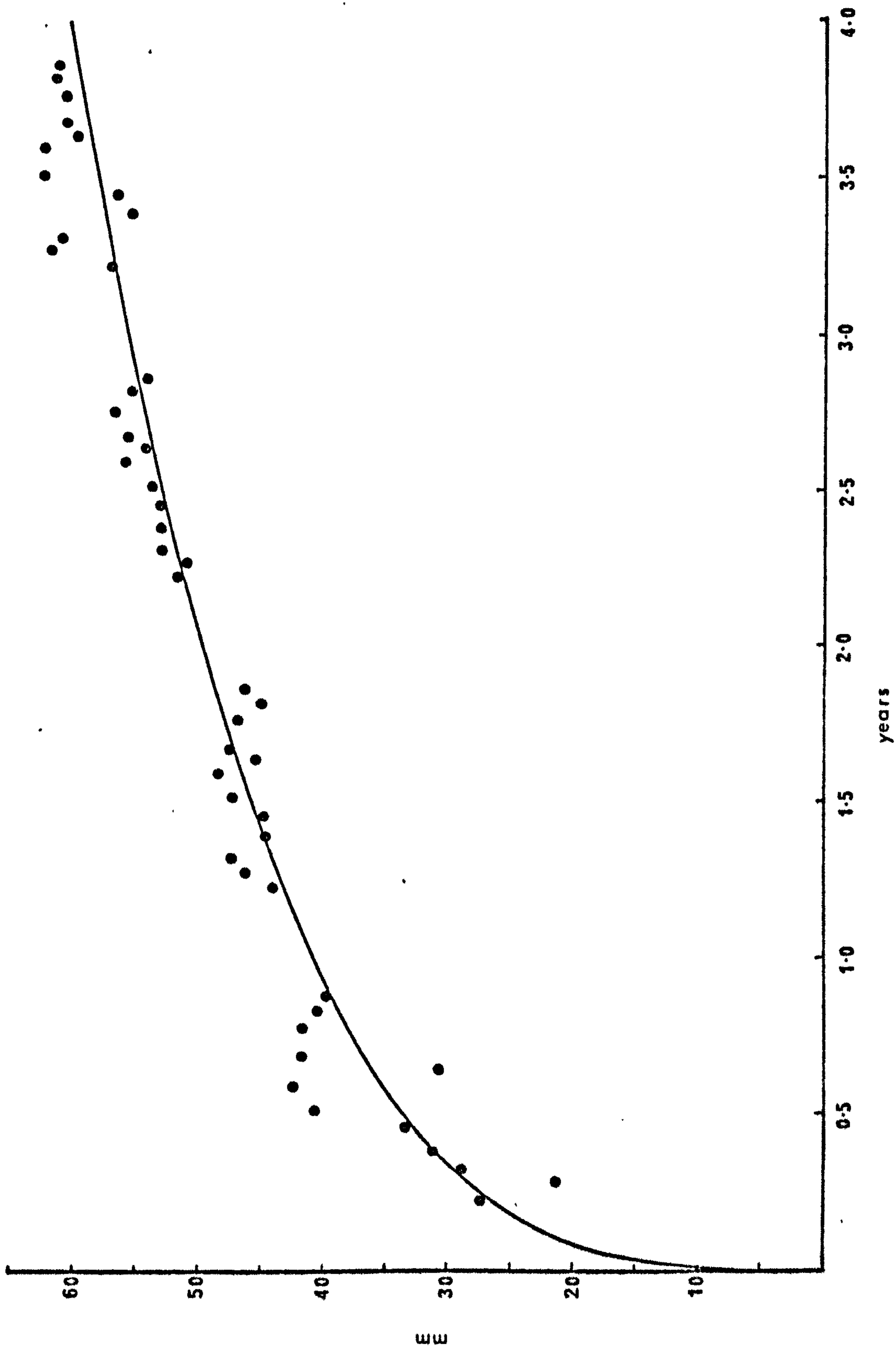
3. Total distribution (Fig. 7)

As would be expected from the lack of homogeneity in the age of the fish population the distribution was not normal. There were two peaks: at 42 and 54 mm. The lower tail was longer than the upper as only small numbers of very young fish were caught.

In general increases in mean length were due either to growth of fish - November 1966 to February 1967, April to June 1967, August 1967 to February 1968 - or to death of small fish - September 1967. Decreases were due to increases in numbers of small fish - July and August 1967 - or to death of old fish - November 1966, March to April 1967 and February to April 1968. The mean lengths were higher between October 1967 and April 1968 than in the same months of the preceeding year,

In general changes in the variance were small. Increases in mean due to growth of fish would not be expected to have very much effect on the value of the variance. Nor did decreases in mean due to death of large fish cause much, if any, decrease in the variance, as only small numbers of fish were involved. The only large changes in variance occurred between July and September 1967 when many small fish were entering the population, and then being removed again, largely through predation. These young fish were also growing rapidly which tended to decrease the variance.

FIG.8 Length vs age



B. Age-groups (samples 21.8.67-9.4.68; appendix 2 b)

1. Mean

The mean length of fish in each age-group of each sample is plotted against age in Fig. 8. This shows that there was a steady increase in length with age, more rapid at first and then becoming more or less linear from age one year onwards.

2. Distribution

Fig. 9 shows the length distributions of three samples: 21.8.67, 4.12.67 and 9.4.68. It can be seen that the length increased with age, but that there was considerable overlap between age-groups. There were few fish in groups I and IV so that the lengths of these were rather variable.

In Fig. 10 the distributions of the lengths of all fish in each age group are plotted. The means of the groups increased progressively but the overlaps were again large. These groups included fish caught over a period of seven months so that their ages varied and it would not be expected that the distributions were normal. Those for groups I and III were negatively skewed while those for groups II and IV were approximately normal.

3. t-tests

Mean lengths of successive age groups in each sample were tested to see whether they were significantly different. Between the mean lengths of the first two groups (I & II) there was a significant difference at the 0.1% level in four samples

FIG.9 Length distributions

age gp

I

4



II

4

21-8-67



III

no. of fish

6



IV

1



I

2

4-12-67



II

6



III

6



IV

2



I

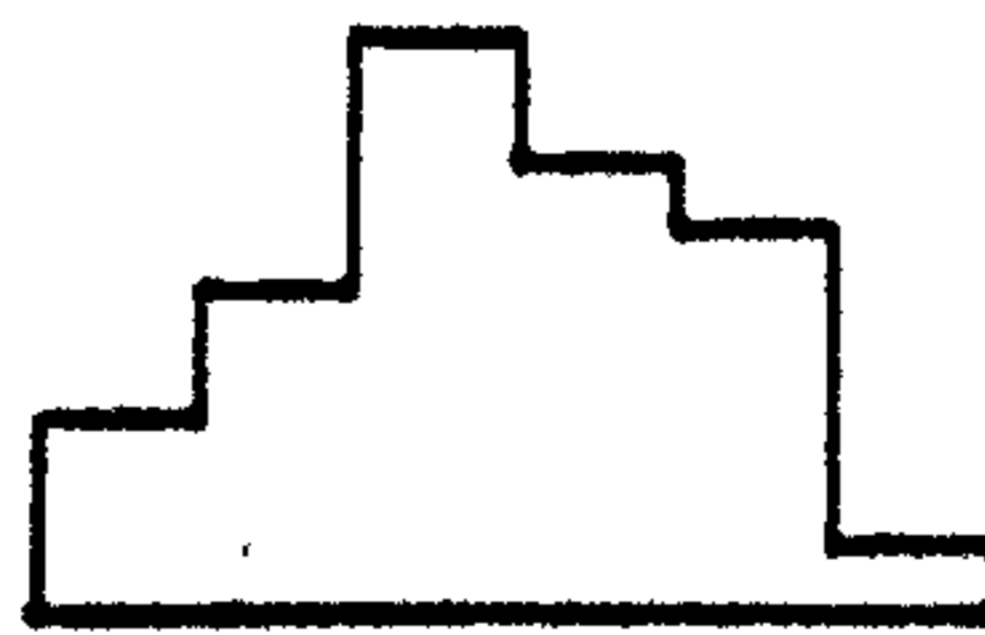
4

9-4-68



II

9



III

7



IV

3

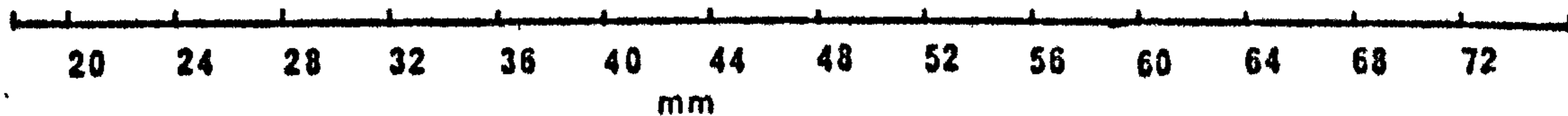
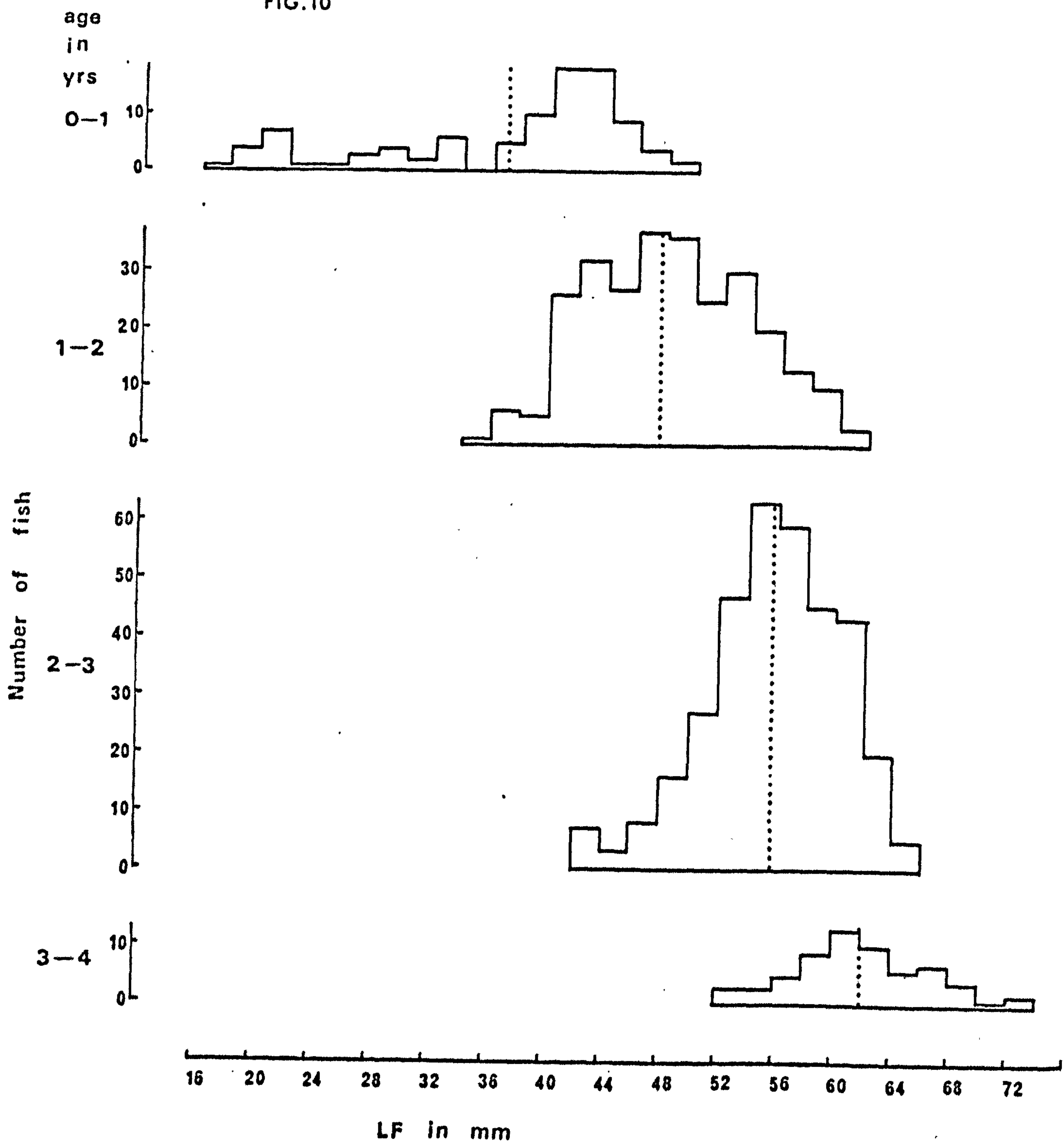


FIG.10



and at the 1% level in a further seven. The other sample did not show a significant difference. For the second two groups (II & III) there was a significant difference between the mean lengths at the 0.1% level in 11 groups and in the twelfth at 1%. Groups III and IV showed a significant difference between mean lengths at the 1% level in six samples and at the 5% level in another one. The other five were not significantly different.

Therefore the means of the first and second two groups were significantly different while those of the last two groups were not always. This means that the length distributions of the first three age groups could be separated by means of probability paper, using the method of Cassie (1954), but not of the last two.

WEIGHT OF FISH

The weights of the sticklebacks were treated in the same way as the lengths.

A. Samples (appendix 2 a)

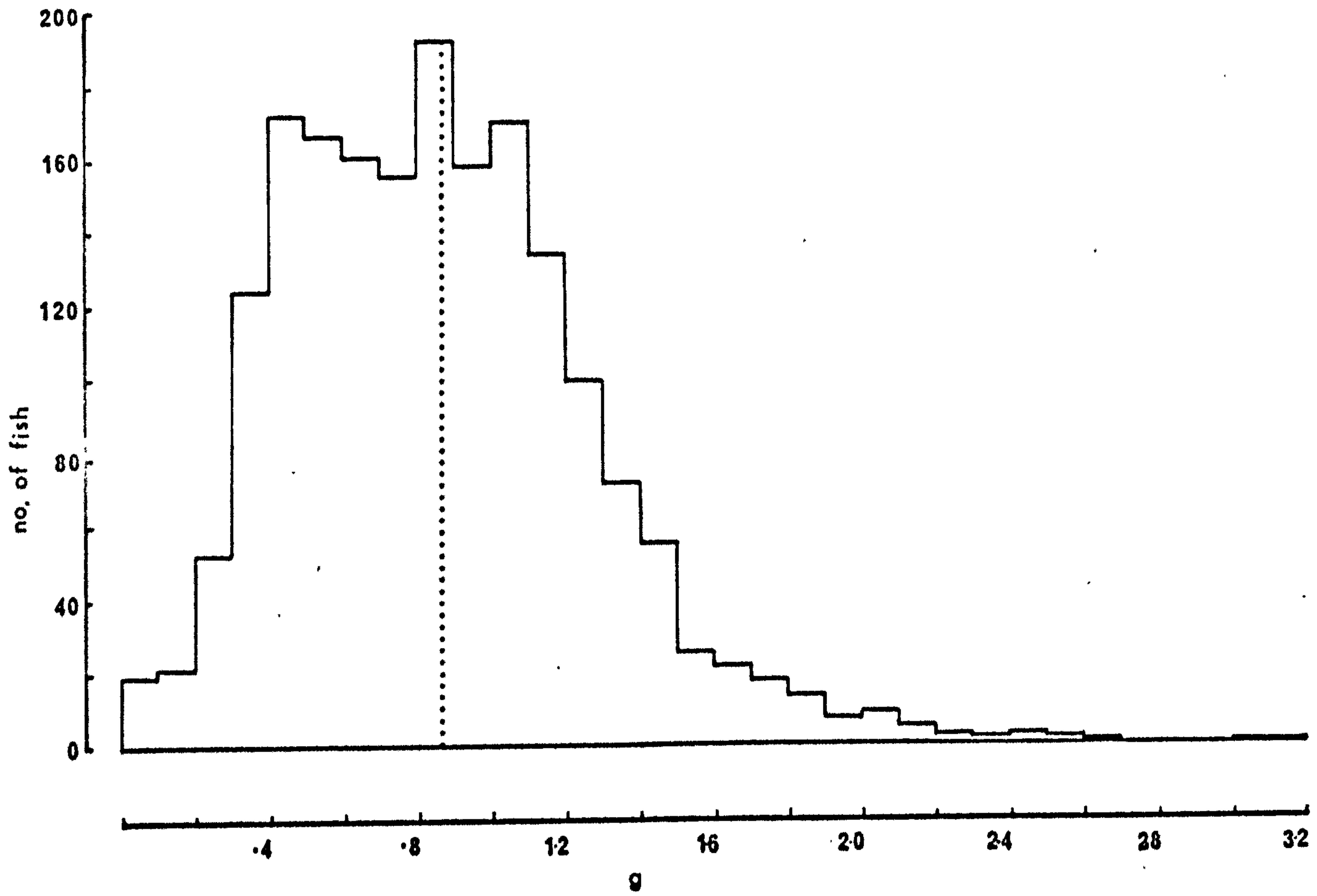
1. Mean (Fig. 6c)

The mean weight of all fish was 0.863 g. In general the mean weight varied as did the mean length. The first value was 0.83 g; there was then a slight rise to 0.92 g on 12.11.66, followed by a fall to 0.81 g on 19.11.66 and a fairly steady increase, to a value of 0.93 g on 18.2.67. There was a decrease to 0.80 g on 21.4.67 and then another increase to 0.97 g on 21.6.67. The mean weight then fell to 0.69 g on 21.8.67 and rose to 0.84 g on 21.9.67. There was a slight decrease to 0.77 g on 10.11.67 after which the value continued to rise, except for a low value of 0.86 g on 15.1.68, reaching 1.004 g on 4.3.68. Finally there was a decrease to 0.92 g on 9.4.68.

2. Variance (Fig. 6d)

The variance of the weights of all the fish was 0.166. The value tended to vary inversely as the mean, but not as markedly as with the mean and variance of the lengths. Initially there was a rise from 0.15 on 29.10.66 to 0.23 on 10.12.66. There was a decrease to 0.13 during January 1967 followed by a rise to about 0.175, around which level the value fluctuated until 8.5.67 when it had risen to 0.26. It then decreased to a minimum of 0.08 and rose again, with large

FIG 11 Weight frequency distribution



fluctuations, to 0.23 on 31.7.67. This was followed by a fall to 0.102 in October and November. The level then rose to 0.16 during December and January, decreased to 0.11 on 1.2.68 and increased to 0.224 on 25.3.68. The final value was lower again: 0.187

3. Total distribution (Fig. 11)

As with the lengths the total weight distribution was not normal, due to heterogeneity of the fish population. The frequency rose quite steeply at first, then stayed high for weights between 0.4 and 1.1 g and then fell slowly and steadily to about 1.5 g after which there was a fairly long tail. The maximum weight was 3.2 g.

Increase in mean weight can be caused by the same factors as increase in mean length: decrease in numbers of small fish, or growth of fish. The mean weight can decrease because of increase in numbers of small fish, decrease in numbers of large ones, or decrease in weights of individual fish.

Increases in mean weight occurred at about the same times as increases in the mean length: due to growth of fish between November 1966 and February 1967, April and June 1967, and November 1967 and February 1968, and to death of small fish in September 1967. Decreases also occurred more or less simultaneously with decreases in mean length: from June to August 1967 due to increase in numbers of young fish, and in November 1966, February to April 1967, October and November 1967,

and March to April 1968 due to death of large fish and decrease in weight of individuals. Fish found dead at these times were longer than average, but the weights were relatively low. It would therefore be expected that the decrease in mean length would be smaller than that in mean weight. As the weight decreases are as large, or larger (November 1967), they must be partly due to decrease in weight of each fish, caused by shortage of food very often aggravated by the presence of Schistocephalus. Once again the mean was higher between December 1967 and April 1968 than in the preceeding year.

Fluctuations in the value of the variance from sample to sample were relatively large. This was because the heaviest fish were much heavier than average whereas the longest fish were not very much longer than average. Hence the presence or absence of a single heavy fish caused large changes in the variance.

There were no very clear trends in the changes in the variance except for a steady decrease in August and September 1967 when young fish were dying and growing rapidly.

Both living and dead fish had higher mean lengths and weights during winter 1967-8 than they did in winter 1966-7. This shows that the age-structure of the population was changing and that there were more older fish in the second year. No fish older than their fourth year were found in August 1967 but there were still fish in age group IV in April 1968. This suggests that some might survive their fourth summer and

so enter their fifth year.

The age structure of the stickleback population is unlikely to remain constant; there would be continuous changes due to success of breeding, which is affected by level of Schistocephalus infection, severity of winter, availability of food etc. The very severe winter of 1962-3 must have caused a high mortality in the stickleback population. Evidence that cold weather causes the fish to die is provided by the fact that many dead ones were found after frosts in February and March 1968.

There would therefore have been few adults in the breeding season of 1963, but those that had survived would be the fittest and the most lightly infected with Schistocephalus so that breeding would have been successful. The young would have had relatively few adults to compete with and so survived well. Thus the population would gradually have built up and its average age increased once more. The increase in density of fish would have made it easier for the parasite populations to build up. Also the older fish, being heavier, could support a greater weight of Schistocephalus which would have speeded the build-up of this population. This in turn would have caused the breeding efficiency of the sticklebacks to decrease.

This is the situation prevailing at the time of the present study. Not more than half the adult fish bred in 1967 and the fairly small numbers of fish in age group II in 1967-8 suggests that breeding was also less successful in 1966 than

it had been in the previous three years. Fish in age groups III and IV would have been born in 1965 and 1964 respectively, both of which must have been successful years. The fish population was therefore decreasing, largely due to the increasing Schistocephalus infection. This fall in the density of the fish will lead to a decrease in the parasite populations once more.

There are thus cyclic changes in the stickleback and Schistocephalus populations which will be modified by other factors, both physical and biological.

A similar pattern is apparent in the fish studied by Arme and Owen (1967). In June 1962 they found 100% of sticklebacks infected with between 11 and 130 plerocercoids and the mean parasite index was 0.47. The fish were very large - about a third weighed more than 4 g. The size of the fish decreased steadily throughout the 3½ years of their study until at the end of 1965 all fish weighed less than 1 g. The parasite index and percentage infection also declined during the first 2½ years and then increased in the final year. The effects of the hard winter of 1962-3 would have been less marked in this case as there was a warm water inlet in the pond.

Again there is evidence of cyclic changes in the stickleback and Schistocephalus populations: a heavy infection was followed by death of large fish which in turn caused a decline in the level of infection; later the infection began to increase again.

FIG.12 Weight vs age

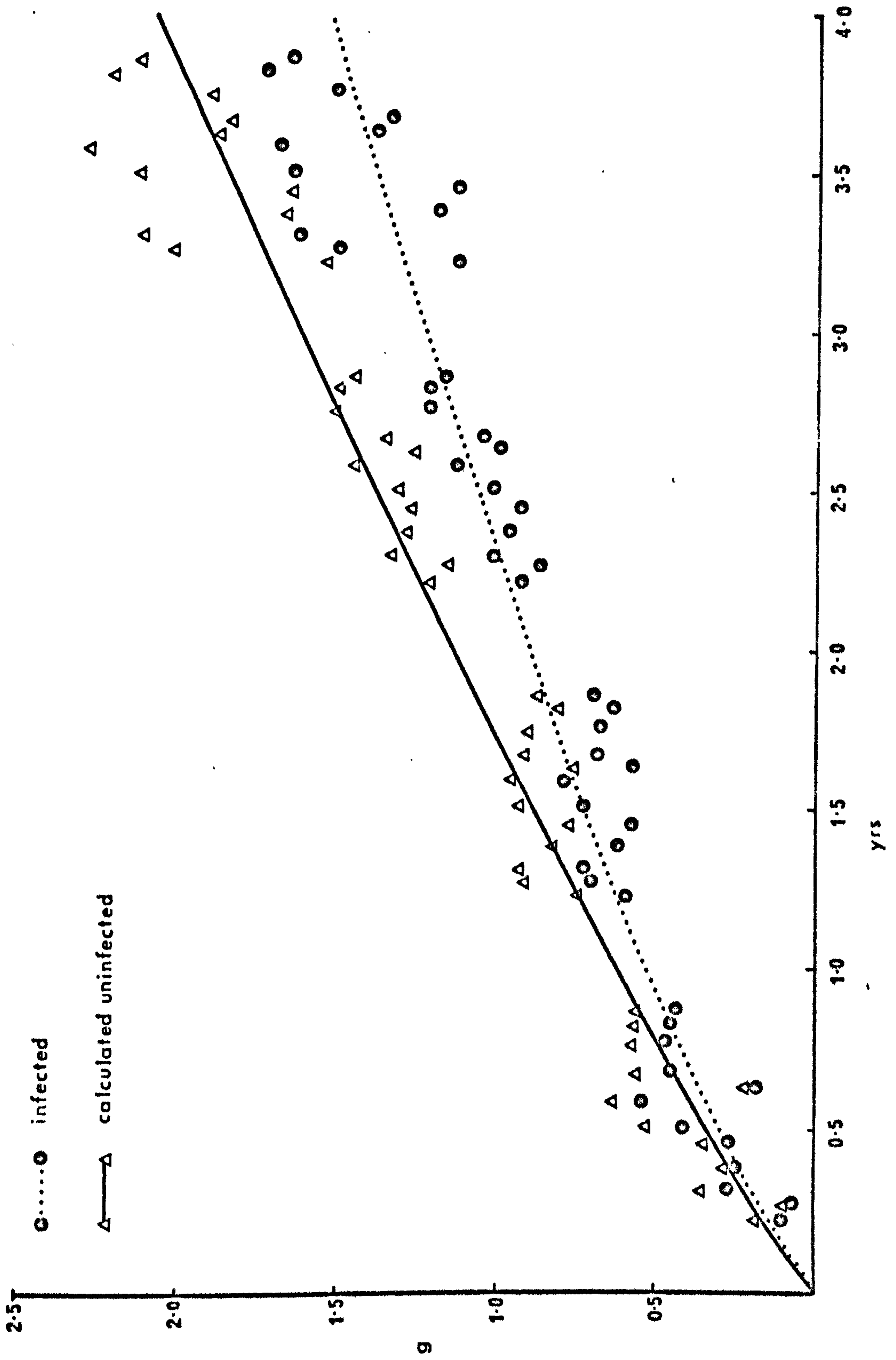
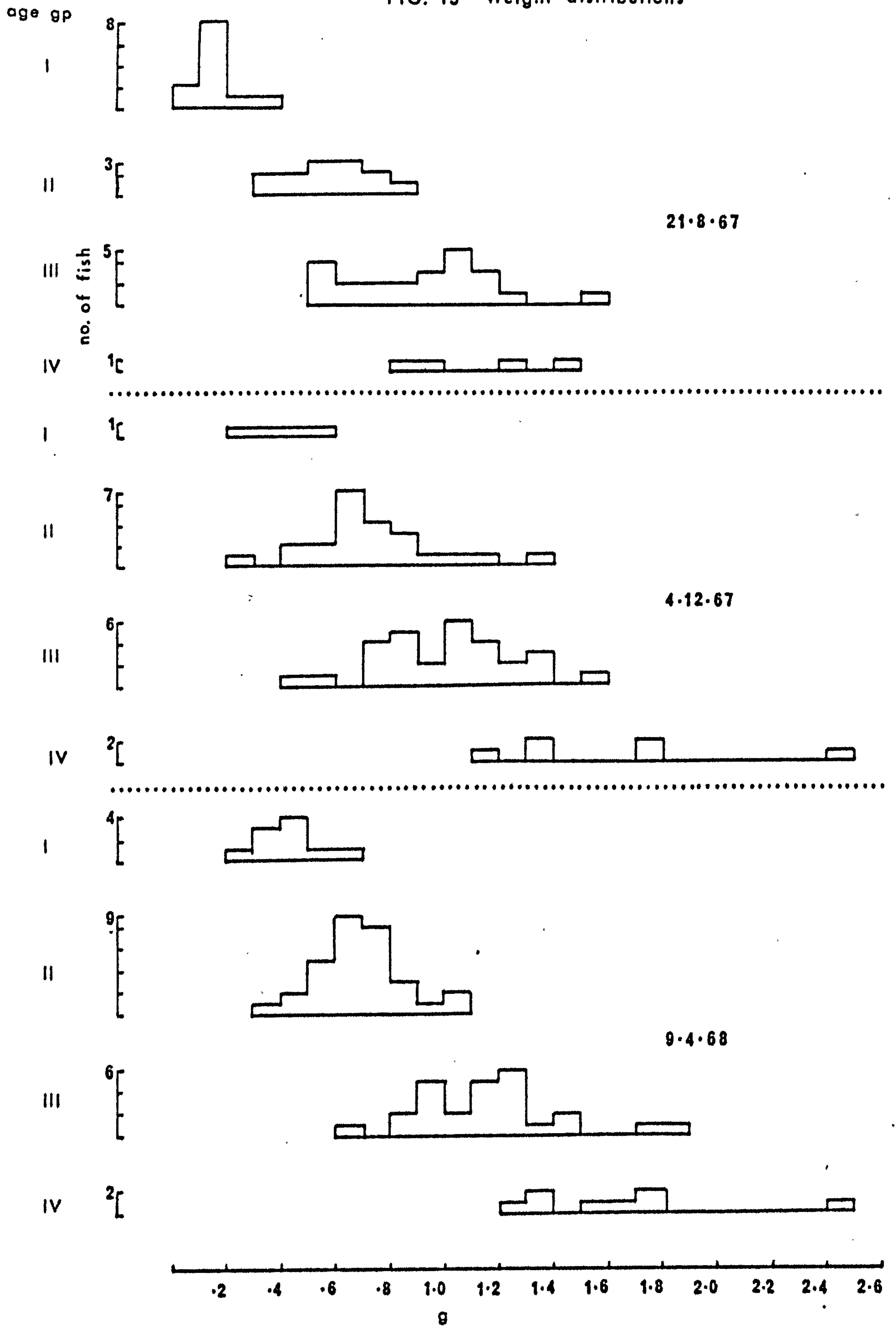


FIG. 13 Weight distributions



B. Age groups (appendix 2 b)

1. Mean (Fig. 12)

The mean weights (\bar{w}_t) of fish of each age group of each sample showed a steady increase with age. The rate of increase was slightly higher in small fish. These weights referred to fish which were often very heavily infected with Schistocephalus and might therefore be expected to be lower than those for uninfected fish.

2. Distribution

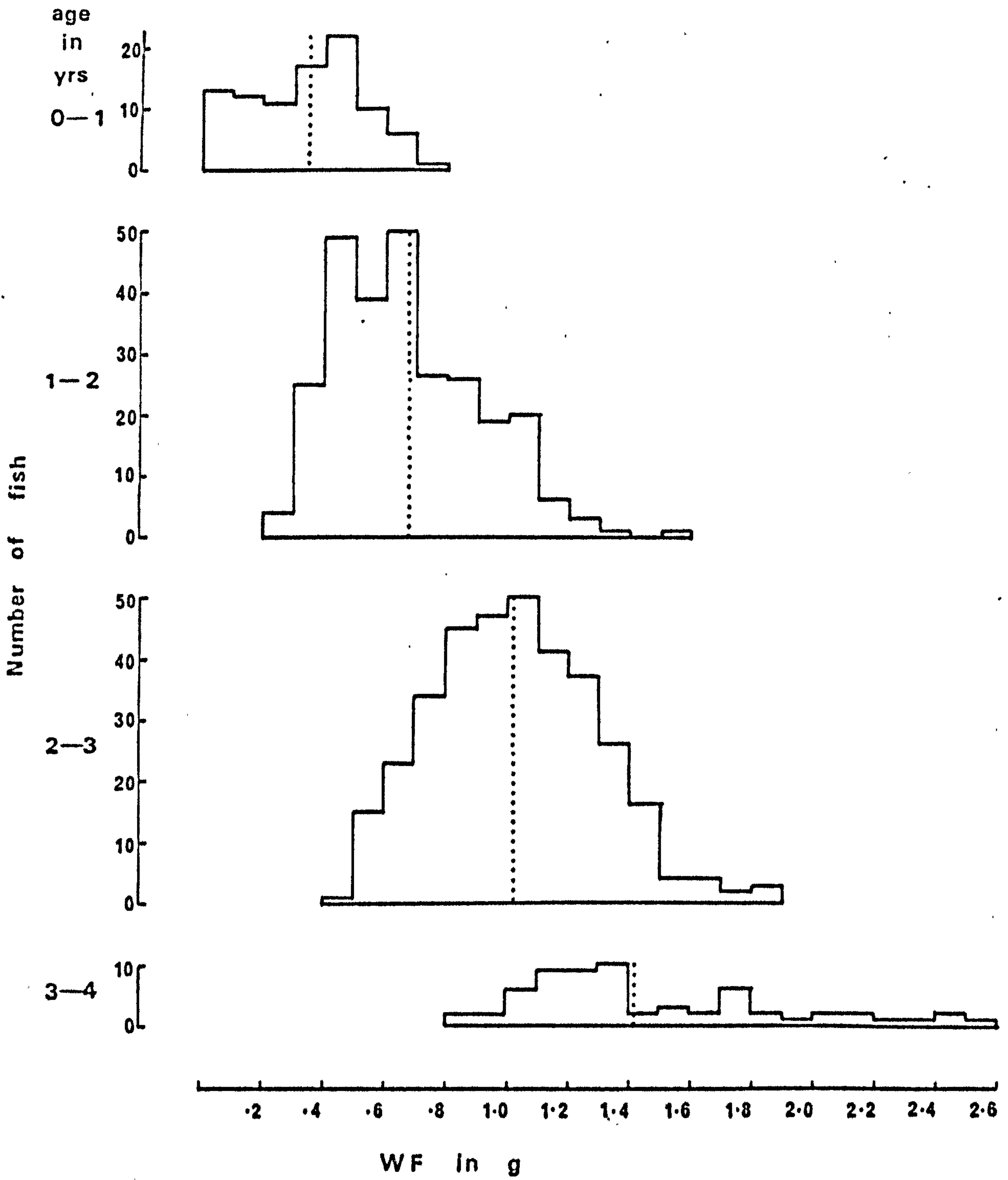
Fig. 13 shows the weight distributions of age groups of fish from three samples: 21.8.67, 4.12.67 and 9.4.68. It can be seen that the weight increased with age but that the overlap between age groups was large.

In Fig. 14 the distributions of the weights of all fish in each age group are plotted. There was a progressive increase of mean weight with age, but once again large overlaps between groups. The distributions were not normal but were all positively skewed due to the non-homogeneity of the groups.

3. t-tests

In eight out of the 12 samples there was a significant difference between the mean weights of groups I and II at the 0.1% level, and in another two at the 1% level. The other two samples did not have significant differences between the means. In ten samples the mean weights of groups II and III were significantly different at the 0.1% level, in one at the 1% and in one at the 2%. The mean weights of groups III and IV

FIG. 14



were significantly different, at the 5% level, in nine samples but not in the other three.

Therefore, as with the lengths, the weight distributions of the first three groups can generally be separated but not those of the last two.

4. Analysis of variance

The fish of each age group of each sample were grouped according to the weight of Schistocephalus they contained. As the Schistocephalus caused a loss of weight in the fish (p. 64) it was expected that the mean weight of fish would decrease with increasing Schistocephalus weight. However, the opposite was found: fish with higher weights of plerocercoids were heavier. Obviously the fish which were naturally heavier because of their genetic make-up were able to support a higher weight of Schistocephalus.

It was not therefore possible to carry out an analysis of variance to find out whether the Schistocephalus caused a significant change in the fish's weights.

GROWTH RATE

There are two ways of expressing the growth rate of an animal; by rate of increase either of weight (w) or of a linear dimension such as total length (l). If growth rate is constant with age

$$\frac{dw}{dt} \propto w \quad \dots(63)$$

$$\text{(or } \frac{dl}{dt} \propto l \text{)}$$

where t represents time. There is more often a decrease in growth rate with age, however, and Parker and Larkin (1959) have found that

$$\frac{dw}{dt} \propto w^x \quad \dots(64)$$

$$(x < 1)$$

is a better representation of growth in fishes. They observe that this is similar to equations representing many body functions in mammals.

In the case of the sticklebacks the ages of very few fish uninfected with Schistocephalus were known. Infections were often very heavy - up to 50% of the total fish weight being parasite - and it seemed highly probable that this was affecting the growth of the fish. The growth rate could not therefore be determined directly and the effect of the Schistocephalus had first to be investigated.

1. Infected fish (Fig. 12)

A curve was fitted to the points for mean weights (\bar{w}_t) of each age group of each sample against age in years (t), using the computer program for fitting a polynomial (p. 34). Natural logarithms were taken of both ordinate and abscissa and a first order equation of the form $\ln w = \ln k + a \cdot \ln t$ calculated. From this $w = k \cdot t^a$ was obtained and then the differential equation:

$$\text{from above} \quad \frac{dw}{dt} = k \cdot a \cdot t^{a-1} \quad \dots(64)$$

$$\text{but} \quad t = \frac{w^{1/a}}{k} \quad \dots(65)$$

$$\text{therefore} \quad \frac{dw}{dt} = k \cdot a \cdot w^{(a-1)/a} \quad \dots(66)$$

$$\text{The fitted curve had equation} \quad w = 0.514 t^{0.79} \quad \dots(67)$$

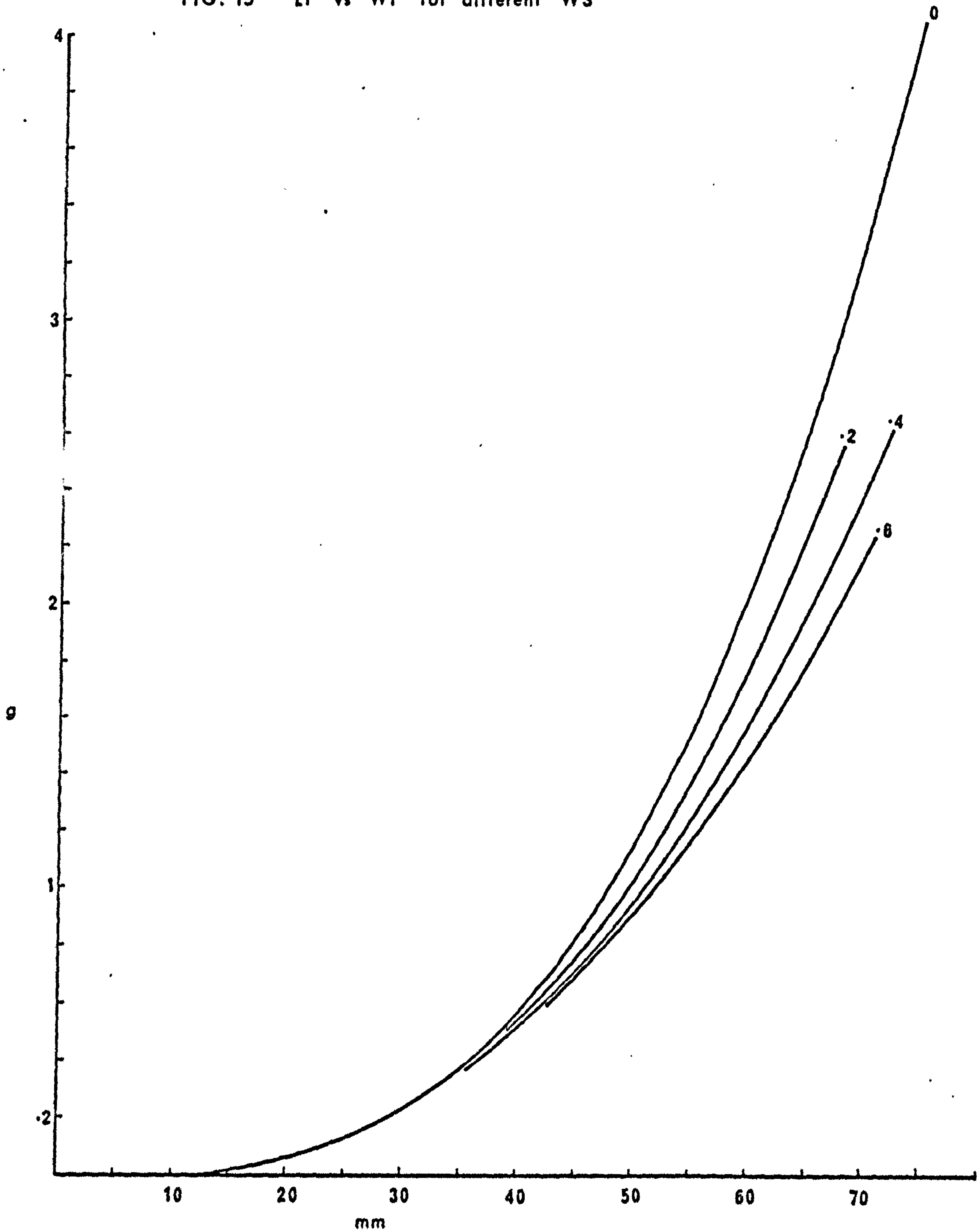
$$\text{or} \quad \frac{dw}{dt} = 0.619 w^{-0.266} \quad \dots(68)$$

This is plotted with the original points in Fig. 12 and can be seen to fit well

2. Length-weight curve

As the ages of few uninfected fish were known the length-weight relationship was used to calculate the growth curves. If the shape of an animal does not change with increase in size then the length-weight relationship will be constant, usually approximating to $w \propto l^3$.

FIG. 15 LF vs WF for different WS



(i) Uninfected fish

A curve for uninfected fish from all samples was calculated by fitting a polynomial to points representing fish with greatest weight for each length. Its equation was:

$$\ln w = -12.362 + 3.1912 \ln l \quad \dots(69)$$

$$\text{or } w = 4.28 \times 10^{-6} l^{3.19} \quad \dots(70)$$

$$\text{or } \frac{dw}{dt} = 0.066 w^{0.69} = 1.37 \times 10^{-5} l^{2.19} \quad \dots(71)$$

It can be seen that this is only slightly different from $w \propto l^3$. The curve is plotted in Fig. 15.

The maximum rather than the mean weight was used as there was considerable individual variation and it was found (p. 60) that light fish tended to have a smaller weight of Schistocephalus than heavier ones of the same length. Hence when comparing infected and uninfected fish it was often found that the uninfected ones were lighter than the infected; although the maximum weights did decrease with increasing Schistocephalus weight, as shown below.

Other curves were also fitted for the length-weight relationships for infected fish.

(ii) For fish with different weights of Schistocephalus.

The fish were divided into groups according to the weight of Schistocephalus which they were harbouring: up to 0.1 g, 0.11-0.2 g, ... 0.81-0.9 g, i.e. nine groups in all. For

each of these groups the maximum weight of fish for each length was plotted, and a curve fitted to the points. There were too few fish with more than 0.6 g of Schistocephalus for satisfactory curves to be calculated. The equation of the six curves for weights of Schistocephalus up to 0.6 g are given below:

1. $w_s \leq 0.1g$: $w = 1.23 \times 10^{-5} l^{2.87}$... (72)
2. $w_s = 0.11-0.2 g$: $w = 9.59 \times 10^{-6} l^{2.96}$... (73)
3. $w_s = 0.21-0.3 g$: $w = 6.69 \times 10^{-6} l^{2.98}$... (74)
4. $w_s = 0.31-0.4 g$: $w = 1.98 \times 10^{-5} l^{2.76}$... (75)
5. $w_s = 0.41-0.5 g$: $w = 1.15 \times 10^{-5} l^{2.89}$... (76)
6. $w_s = 0.51-0.6 g$: $w = 3.01 \times 10^{-5} l^{2.63}$... (77)

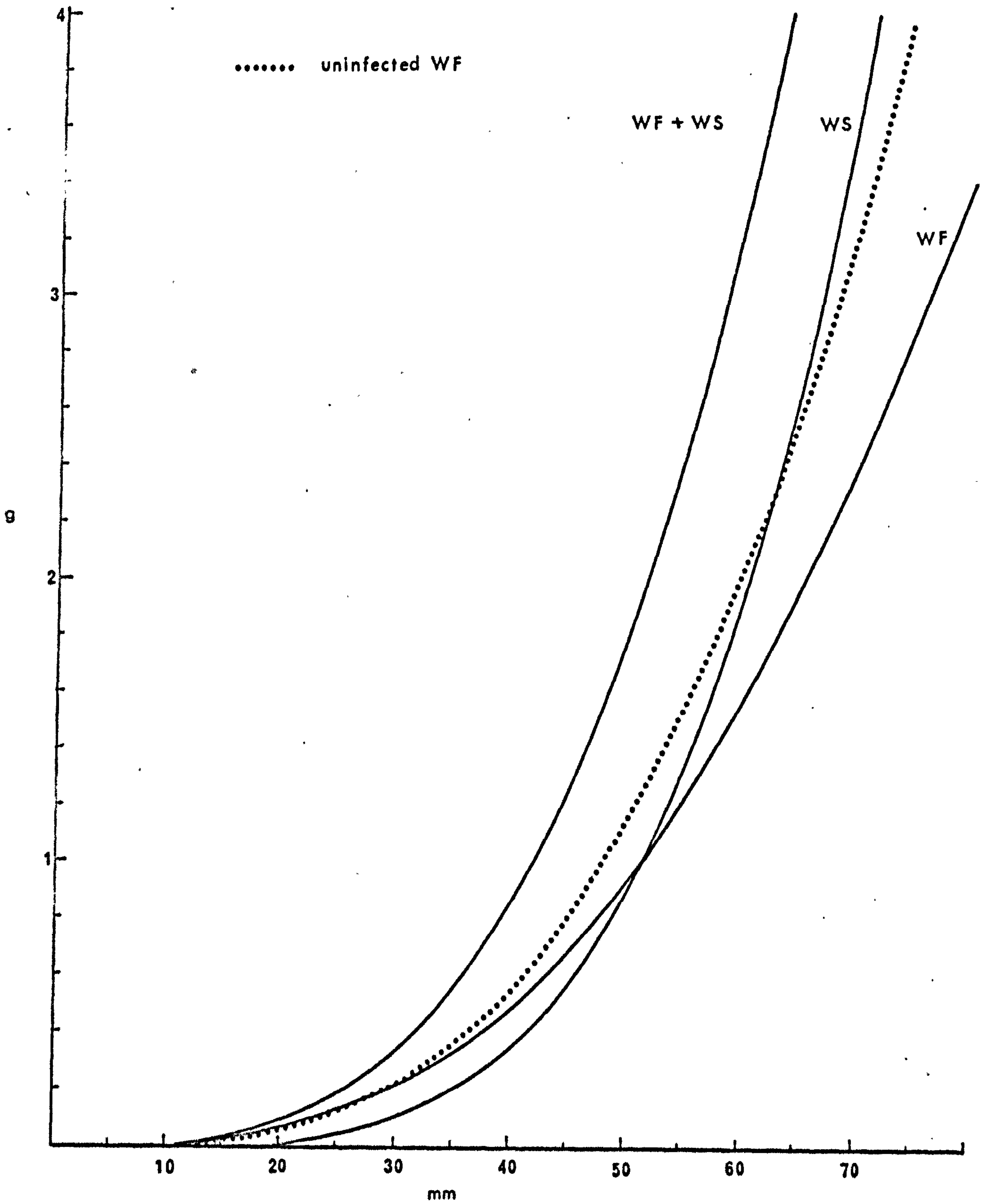
A series of divergent curves was produced in which the lower values were all similar but at higher lengths there was an increasingly large difference. Fig. 15 shows three of the curves: 73, 75 and 77, as well as the curve for uninfected fish. In general the exponent decreased and the constant increased with increasing weight of parasite. The higher the weight of Schistocephalus the lower was the weight of fish.

This shows that the length-weight relationship was changed by the presence of Schistocephalus. The parasite caused the fish to lose weight, or at least to stop increasing so rapidly in weight, rather than simply to grow more slowly.

(iii) Maximum weight of fish plus Schistocephalus

The maximum weight of fish plus parasites for each

FIG. 16 LF vs weights



fish length was plotted and a curve fitted. This had equation:

$$w = 4.42 \times 10^{-4} l^{3.3} \quad \dots(78)$$

It can be seen that this curve was above that for uninfected fish (Fig. 16), particularly for longer fish. In other words the weight of the fish plus Schistocephalus is greater than the weight of an uninfected fish of the same length. The weight of Schistocephalus was greater than the loss of weight it caused in the fish.

When the weight of Schistocephalus was subtracted the weight of infected fish alone was less than that for uninfected fish, as expected. The curve

$$w = 1.237 \times 10^{-5} l^{2.9} \quad \dots(79)$$

fitted these points. This is also plotted on Fig. 16.

It can be seen that the curve for infected fish was very similar to that for fish with 0.41-0.5 g of Schistocephalus. In fact the overall mean for all infected fish was 0.4 g which agrees closely.

This curve also fitted points for mean length and mean weight of each age group of each sample where ages were known. Most of these fish were infected; the mean weight of Schistocephalus was 0.45 g.

Finally the weights of Schistocephalus from the maximum (WF + WS) points were plotted for each length of fish and a curve fitted. This had equation

$$w = 4.67 \times 10^{-8} l^{4.3} \dots(80)$$

and is plotted in Fig. 16. The exponent was larger and the constant smaller than for the WF curves. The values were low at first, increasing rapidly with length of fish; the curve crossed the curve for weight of infected fish at LF = 52 mm. Therefore the weight of Schistocephalus was lower than the weight of fish in fish shorter than 52 mm, but greater in fish longer than this. In other words the parasite index was greater than 0.5 when LF > 52 mm.

The curve for maximum weight of Schistocephalus for each fish length followed the infected WF curve up to about 50 mm then continued along the above WS curve; for all lengths of fish between 35 and 65 mm the maximum parasite index was greater than 0.5. This suggests that fish shorter than about 52 mm will probably die if the parasite index exceeds 0.5, while those of greater size can survive a higher infection with Schistocephalus.

Therefore these length-weight relationships show that the weight of a fish of a given length was reduced by the presence of Schistocephalus, progressively more as the weight of parasite was greater. The weight of Schistocephalus was greater than the loss of weight it caused in the fish. This could be because the parasites were only taking part of their food from resources which would otherwise have been available to the fish, or because they made better use of the food. This

was probably the case as the metabolism of Schistocephalus is much simpler than that of sticklebacks and growth involves the formation of only a few types of tissue.

3. Calculated curve for uninfected fish

The theoretical uninfected growth curve was calculated by taking the mean lengths of each age group of each sample and finding the corresponding weights from the uninfected length-weight curve. As the ages of uninfected fish were not known it was assumed that the length was a reasonable indication of age. The weights were plotted against age and a curve fitted. This had equation

$$w = 0.619 t^{0.88} \quad \dots(81)$$

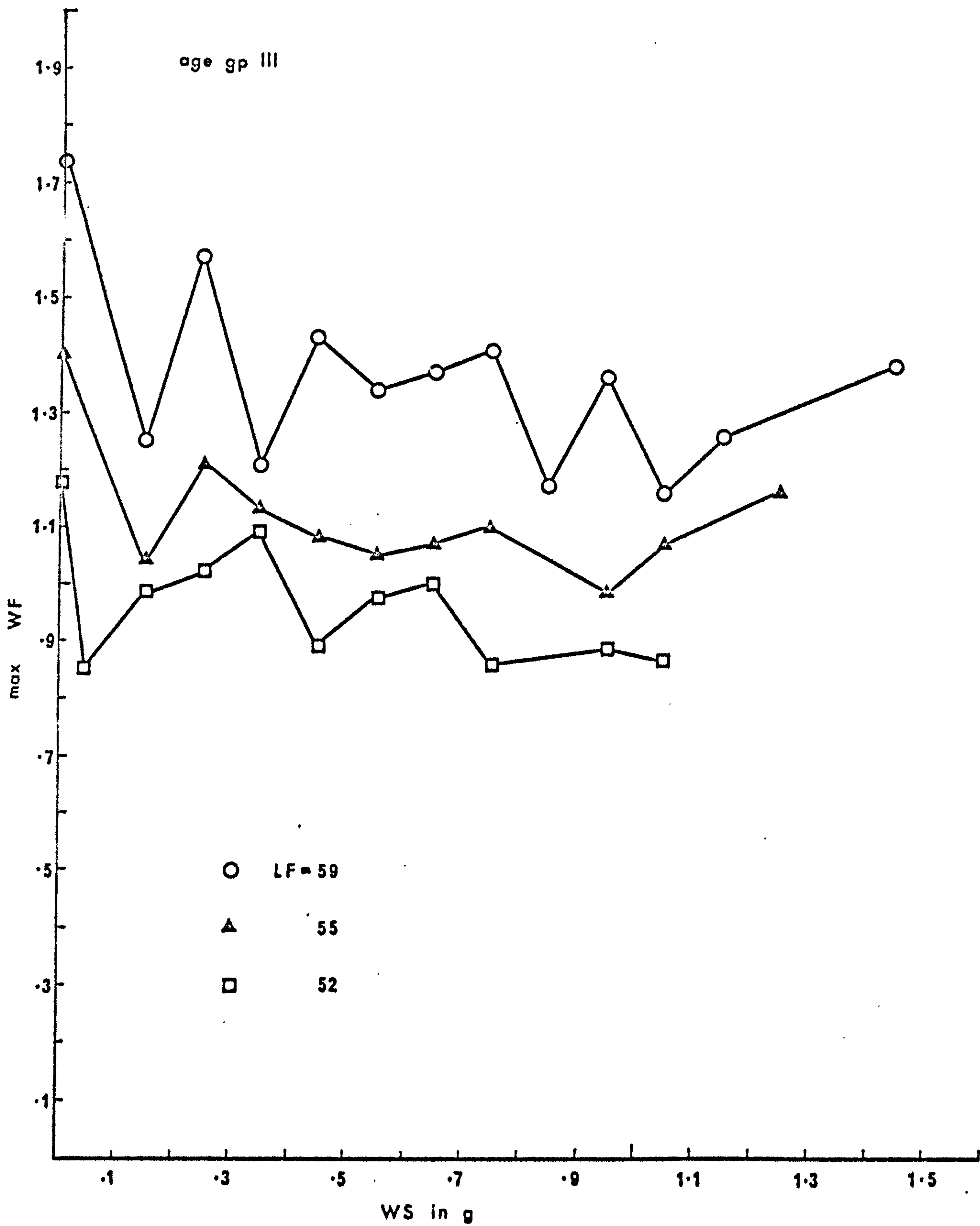
$$\text{or} \quad \frac{dw}{dt} = 0.507 w^{-0.14} \quad \dots(82)$$

The curve and points are plotted in Fig. 12. The constant is smaller and the exponent larger than in the curve for infected fish.

4. Weight of fish and weight of Schistocephalus

The effect of different weights of Schistocephalus on the weights of fish of different lengths and ages was investigated in more detail. The computer program whose flow diagram is shown in appendix 1f was used. The fish in each age group were divided according to length (groups of 1 mm interval) and then according to weight of Schistocephalus (groups of .1 g

FIG. 17



interval). The weight of the heaviest fish in each of these groups was printed, in matrix form. Each weight was then compared with the weight of an uninfected fish of the same length, and the difference (dw) printed in another matrix. Finally the loss of weight of fish equivalent to one gram of Schistocephalus (dw_1) was calculated and printed in a third matrix.

(i) Maximum weight of fish

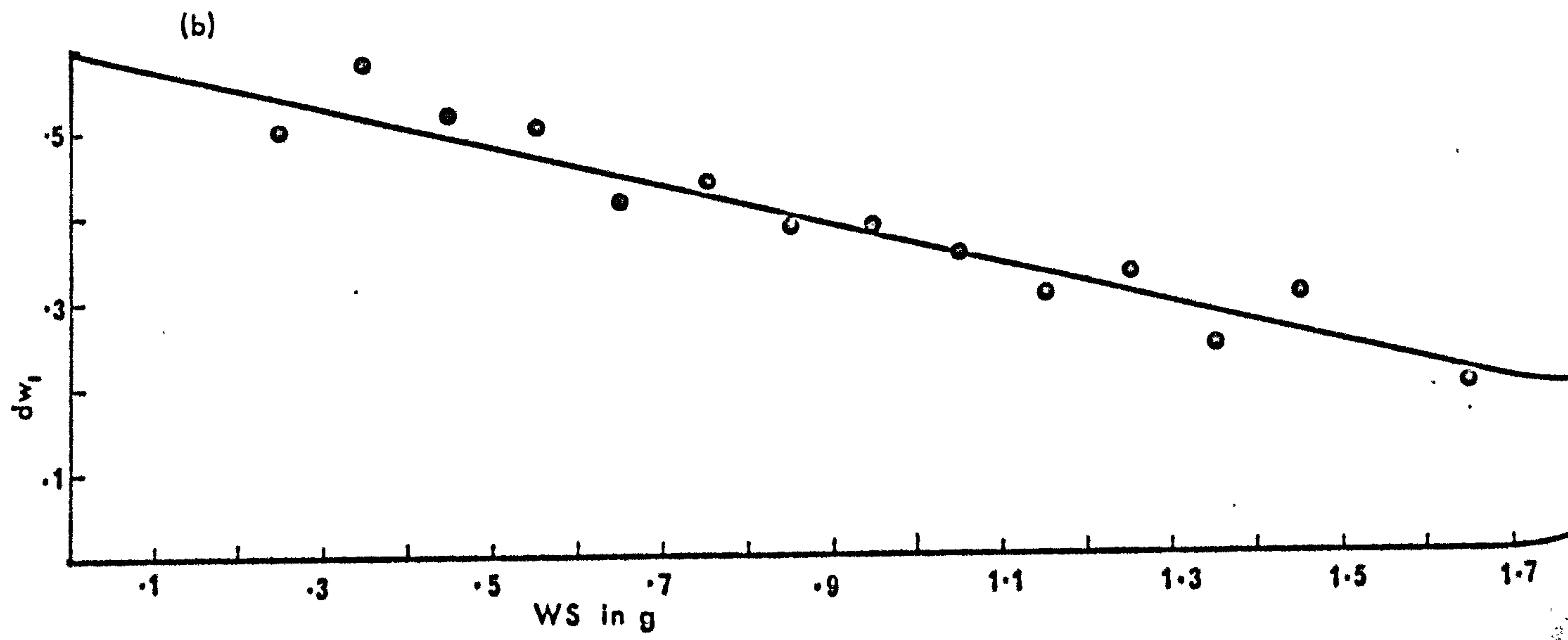
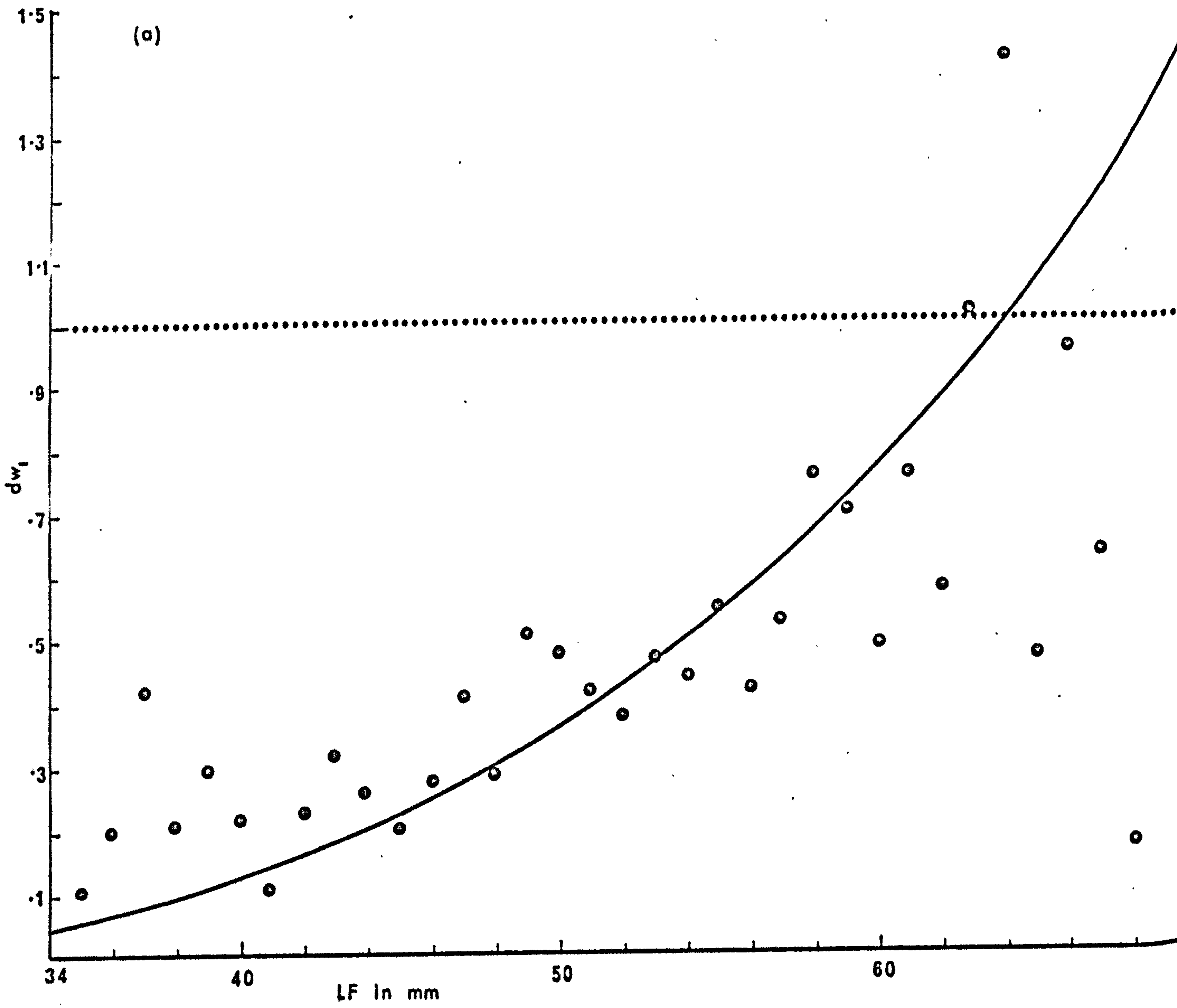
The maximum weight of fish tended to increase with length of fish, for a given WS, and to decrease with weight of Schistocephalus, for a given LF. An example of this is shown in Fig. 17 where the maximum weight of fish is plotted against weight of Schistocephalus for fish of lengths 52, 55 and 59 mm in age group III. In all cases the weight of fish was less than that of an uninfected one.

Older fish tended to have a higher maximum weight than younger ones of the same length, and weight of Schistocephalus.

(ii) Loss of weight of fish with length of fish

Fig. 18a shows the values of mean loss of weight equivalent to one gram of Schistocephalus (dw_1) for different lengths of fish of all ages. It can be seen that dw_1 increased with length, more rapidly at higher values. A curve to represent this interaction was calculated from the length-weight curves for uninfected fish and for fish with WS = 0.41-0.5 g, as the mean WS was 0.45 g.

FIG. 18



Uninfected: $\ln w_0 = -12.36 + 3.19 \ln l \dots(69)$

WS = 0.41-0.5: $\ln w_{0.5} = -11.38 + 0.29 \ln l \dots(83)$

$\therefore \ln w_0 - \ln w_{0.5} = -0.98 + 0.3 \ln l \dots(84)$

For WS = 1g $\ln w_0 - \ln w_1 = -1.96 + 0.6 \ln l \dots(85)$

or $\frac{w_0}{w_1} = 0.1409 l^{0.6} \dots(86)$

loss of weight caused by 1 g of Schistocephalus:

$$dw_1 = w_0 \left(1 - \frac{1}{0.1409 l^{0.6}} \right) \dots(87)$$

but $w_0 = 4.28 \times 10^{-6} l^{3.19} \dots(70)$

therefore $dw_1 = 4.28 \times 10^{-6} l^{3.19} - 3.04 \times 10^{-5} l^{2.59} \dots(88)$

This curve is plotted in Fig. 18a and fits the points fairly well except for low and high lengths, due to there being few fish of extreme lengths. $dw_1 = 1$ when $LF = 64$ mm so fish larger than this were reduced in weight more than the weight of Schistocephalus they contained; i.e. $WF+WS < WF_0$. This fits with the fact that the maximum parasite index was less than 0.5 in fish longer than 65 mm (p. 66).

(iii) Loss of weight of fish with weight of Schistocephalus

Fig. 18b shows the values of means loss of weight of fish equivalent to 1 g of Schistocephalus for different weights of Schistocephalus, for all ages of fish. The points

lie close to a straight line with equation

$$\overline{dw}_1 = 0.6 - 0.23 WS \quad \dots(89)$$

The proportional loss of weight of fish was smaller for larger weights of Schistocephalus.

(iv) Discussion

Although for any weight of Schistocephalus the maximum weight of fish increased with length, the loss of weight also increased. This was due to the slower growth rate of larger fish. The growth in length could not be slowed to such a large extent as in faster-growing smaller fish so that the decrease in weight was larger.

For fish of a given length the maximum weight decreased with increasing weight of Schistocephalus but the proportional loss of weight also decreased. This could be due to a number of factors. Firstly it was found that for fish of a given length the mean weight tended to increase with increasing weight of Schistocephalus: the heavier individuals were able to sustain a larger parasite burden. Also the mere presence of Schistocephalus in a fish may have caused some loss of condition due to an immune reaction. Thirdly a fish with a smaller weight of Schistocephalus was more likely to contain many small worms than one with a larger weight. These would have a higher growth rate and a larger surface-area: weight ratio and would therefore absorb larger

amounts of food for their weight. There would be considerable variation in this factor as the mean plerocercoid weight varied.

5. Length growth curve

The curve for rate of increase of length was obtained from the uninfected weight growth curve (81) and the length-weight relationship (69):

$$\ln w = -0.4842 + 0.8767 \ln t \quad \dots(90)$$

$$\ln w = -12.362 + 3.1912 \ln l \quad \dots(69)$$

$$\therefore \ln l = 3.7221 + 0.2747 \ln t \quad \dots(91)$$

$$l = 41.35 t^{0.275} \quad \dots(92)$$

$$\text{or } \frac{dl}{dt} = 2.16 \times 10^5 l^{-2.64} \quad \dots(93)$$

This is plotted in Fig. 8 and it can be seen that it fits the points for mean length of fish in each age group of each sample.

II SCHISTOCEPHALUS SOLIDUS (Muller, 1776)

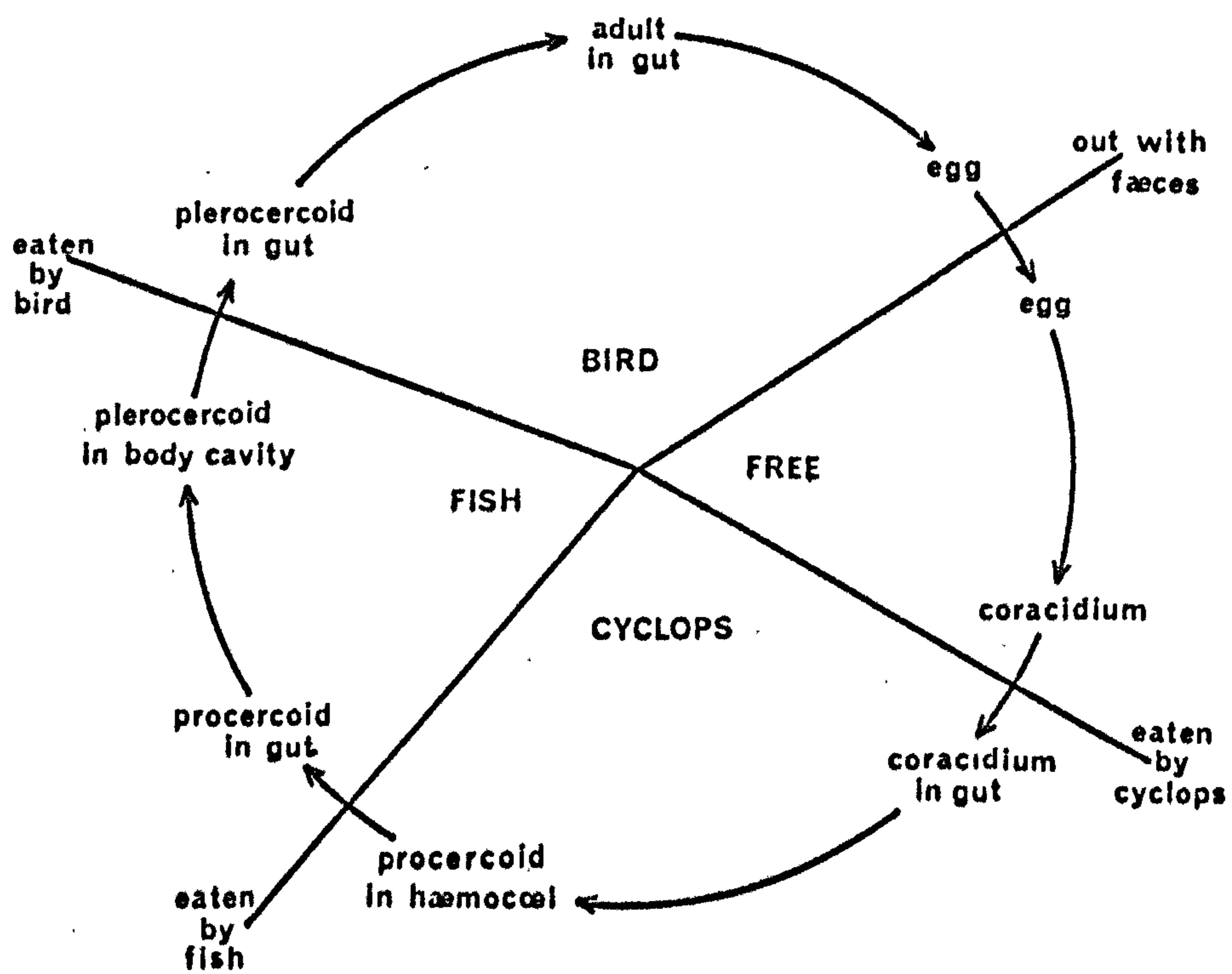
LIFE CYCLE

This is a Pseudophyllidean cestode belonging to the family Diphyllbothridae. The life cycle is described by Hopkins and Smyth (1951) and Clarke (1954). There are three hosts, of which Gasterosteus aculeatus is the second.

The adult Schistocephalus is found in the gut of a fish-eating bird. It lays eggs which pass out with the bird's faeces and hatch to free-swimming coracidia larvae. The hatching takes from 14 days to six months, depending on the temperature and also on the individual (Clarke). The coracidium can swim for five days and if eaten by a certain species of cyclops it bores through the gut and develops in the haemocoel to a proceroid larva. Clarke found that proceroids would develop in Cyclops serrulatus, C. bicuspidatus, C. viridis, and C. leuckarti. Development of the proceroid takes about 25 days, but the larva can survive for at least three months (Clarke).

If the cyclops is then eaten by Gasterosteus aculeatus the proceroid is released, passes through the fish's intestinal wall into the body cavity, taking about two hours, and then develops into a plerocercoid larva. Hopkins and Smyth cite Gasterosteus aculeatus as the only known host for the plerocercoid in this country. Clarke however states that Pygosteus pungitius, Blennius vulgaris and Atherina mochon are also hosts. Bråten

LIFE CYCLE of SCHISTOCEPHALUS



(1966) has studied the host-specificity of the plerocercoid and found that when surgically removed from Gasterosteus and inserted into the body cavities of a number of other species of fish the plerocercoid died. It survived insertion into Pygosteus, but did not grow. Orr, Hopkins and Charles (1969) fed infected cyclops to Gasterosteus and Pygosteus. Plerocercoids became established in both species, but grew faster in Gasterosteus. In Pygosteus the integument broke down and by the 14th day all plerocercoids had been rejected. Such a high degree of specificity is unusual in Diphyllbothridae.

Clarke states that cyclops are an unusual item in the diet of sticklebacks, particularly of larger ones, and that multiple infections with Schistocephalus are probably obtained from multiply-infected cyclops. He did, however, find new infections in all sizes of fish. At Priddy many cyclops were found in the guts of all sizes of sticklebacks.

The plerocercoid grows throughout its life in the stickleback, although no new proglottids are added. The largest plerocercoid found by Clarke weighed 560 mg; and up to 140 were found in one fish. Hopkins and Smyth suggest that small plerocercoids die within the fish as there are many more small than large worms. This could, however, be due to heavily infected fish dying. There is also some evidence that plerocercoids break out of the sticklebacks. Clarke found that this occurred, via the rectum, when the fish were handled,

without apparent damage to the fish. At Priddy free plerocercoids were often found in the water; Avery (1968) also noted this and found plerocercoids in the stomachs of three newts. These free plerocercoids may have escaped from dead fish only; dead fish often had no Schistocephalus, although they appeared to have been infected as the body wall was very extended. The plerocercoids may be eaten by birds directly from the water so that there would be an advantage to them in breaking out of dead fish.

If the stickleback is then eaten by a bird the Schistocephalus develops into an adult. Hopkins and McCaig (1963) found that worms weighing only 6 mg were capable of maturation, but that only a small proportion of worms under 30 mg became established. The high temperature in the bird's gut is the stimulus causing growth of the plerocercoid to cease and the gonads to mature (Smyth, 1952). Worms of all sizes take about 48 hours to mature in birds and slightly longer in mammals which have lower body temperatures (Hopkins and McCaig, 1963).

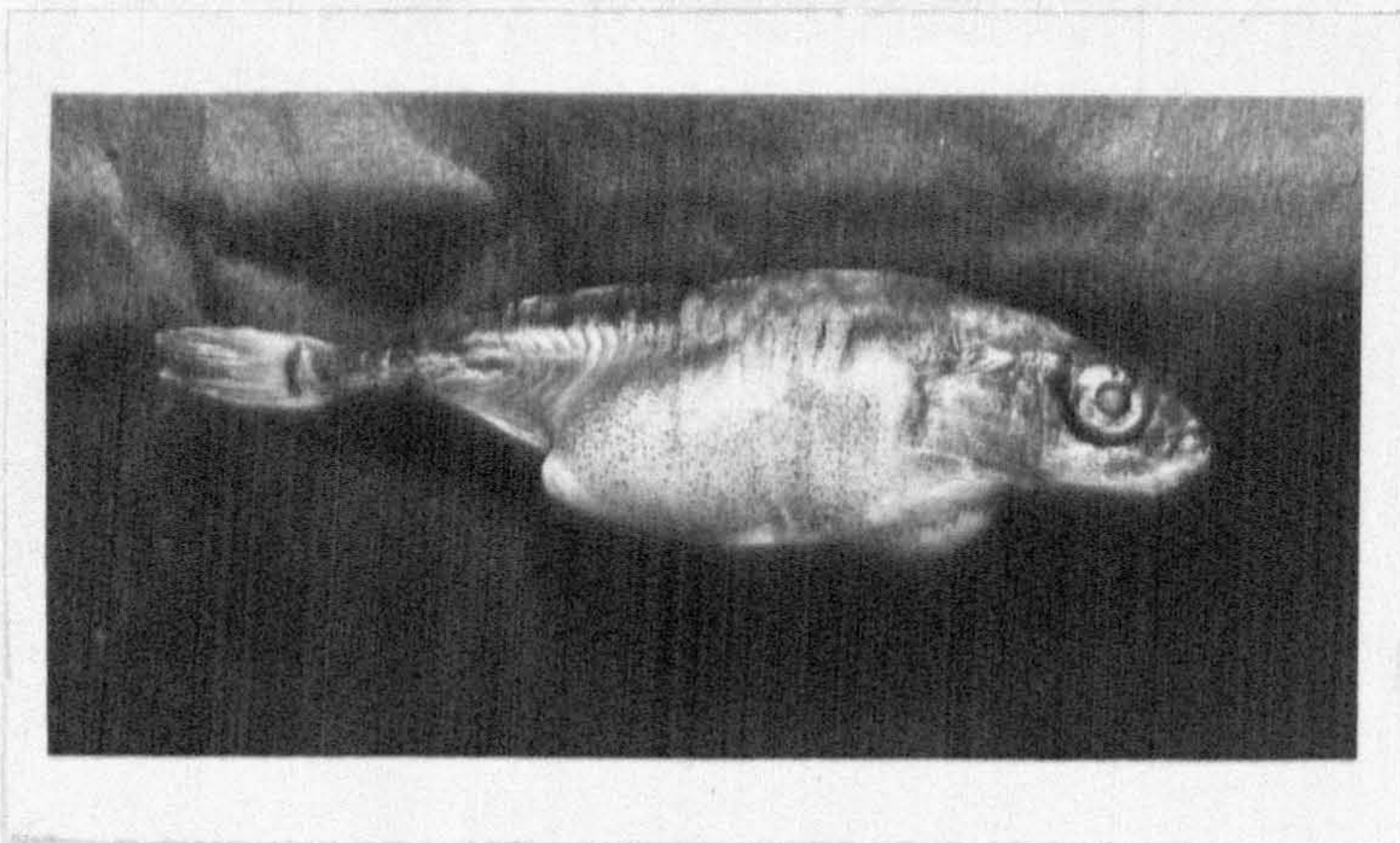
Unlike most Diphylobothridae the adult Schistocephalus has no bothria and is unable to attach itself to the intestine wall. Because of this it was thought for a long time that the worm passed passively through the gut and was unable to maintain its position. However McCaig and Hopkins (1963) showed that the worms lived for 6-18 days in different hosts, about

10-14 days in birds, and were found in different parts of the gut in different species. After this time the worm died, apparently of senility, as no immune reaction by the bird was found.

As there is little physiological interaction between the adult Schistocephalus and its host a wide range of species may act as the definitive host. Smyth (1962) says that any warm-blooded animal will do, but McCaig and Hopkins (1963) dispute this and suggest that a retention response must be triggered, and that the diameter of the gut must be such that the worm can maintain its position against peristaltic pressure. At Priddy hosts were principally black-headed gulls, with possibly some carrion crows. These gulls moved about between several ponds and lakes in the area so that the Schistocephalus population would not have been confined to Priddy. The birds would have carried infections to waters with different Gasterosteus populations, and brought infections from other fish to Priddy.

Thus the minimum time for the complete life-cycle is about 40-50 days. This can be considerably prolonged at several stages: hatching of the egg, and time of survival of the proceroid and plerocercoid larvae. The latter in particular can live for two or three years, probably as long as the fish host. This provides a reservoir of infection and a buffer against adverse conditions.

PLATE 3: Stickleback infected with Schistocephalus



intact fish

21.9.67: fish no. 37

♂ (I)

age group III

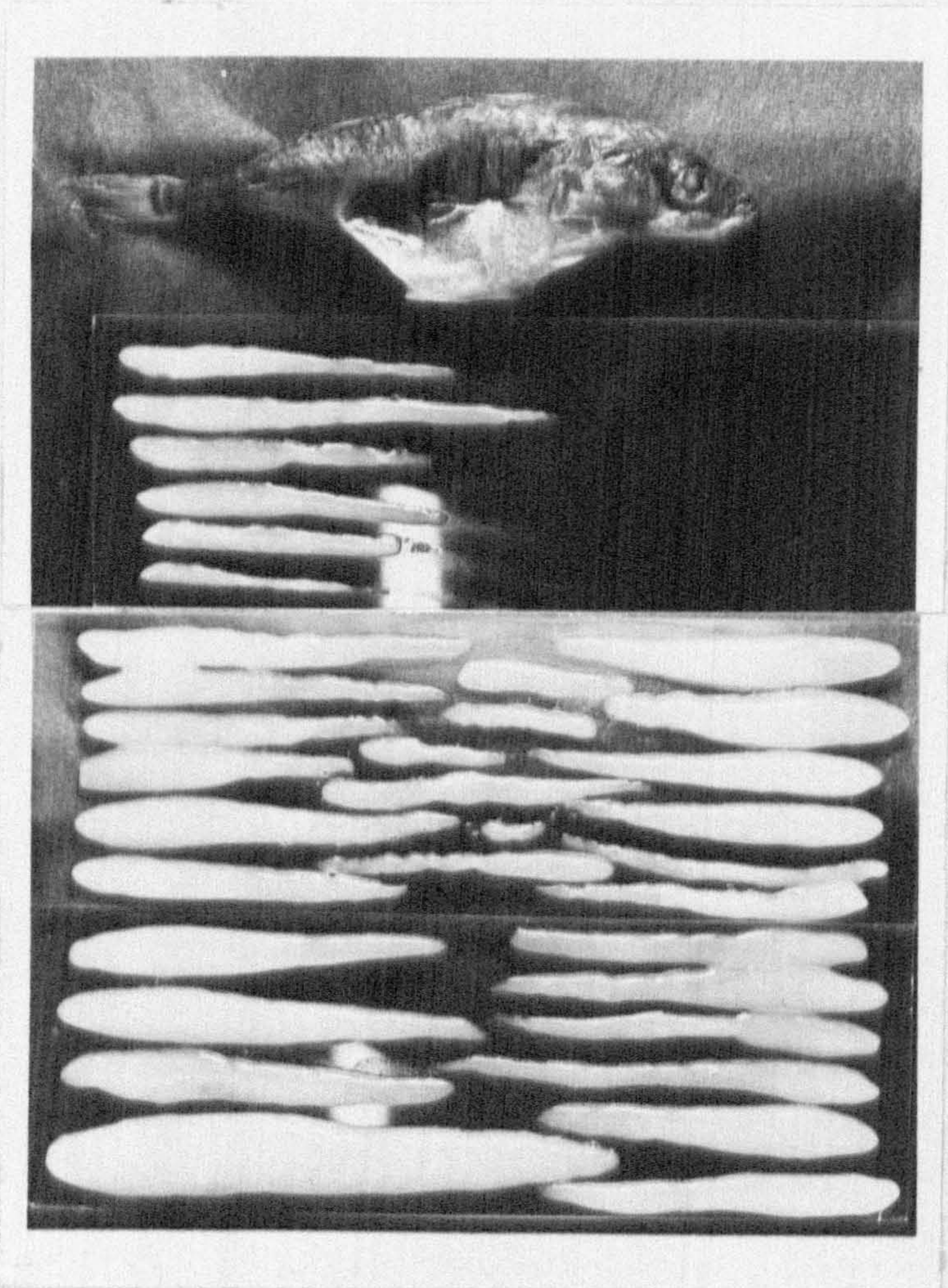
LF = 61 mm

WF = 1.40 g

WS = 1.54 g

P.I. = 0.52

scale : 10 mm

fish after removal
of plerocercoids

.03 the 34
.04 plerocercoids,
.02 with weights
.03 in grams
.02
.01

.04	.02	.05
.03	.02	.05
.03	.01	.05
.04	.02	.04
.06	.01	.02
.05	.02	.03
.06		.04
		.05
.08		.03
		.04
.06		.05
		.05
.34		.05

PLATE 4: Stickleback infected with Schistocephalus

intact fish

21.9.67: fish no. 35

♀ (0)

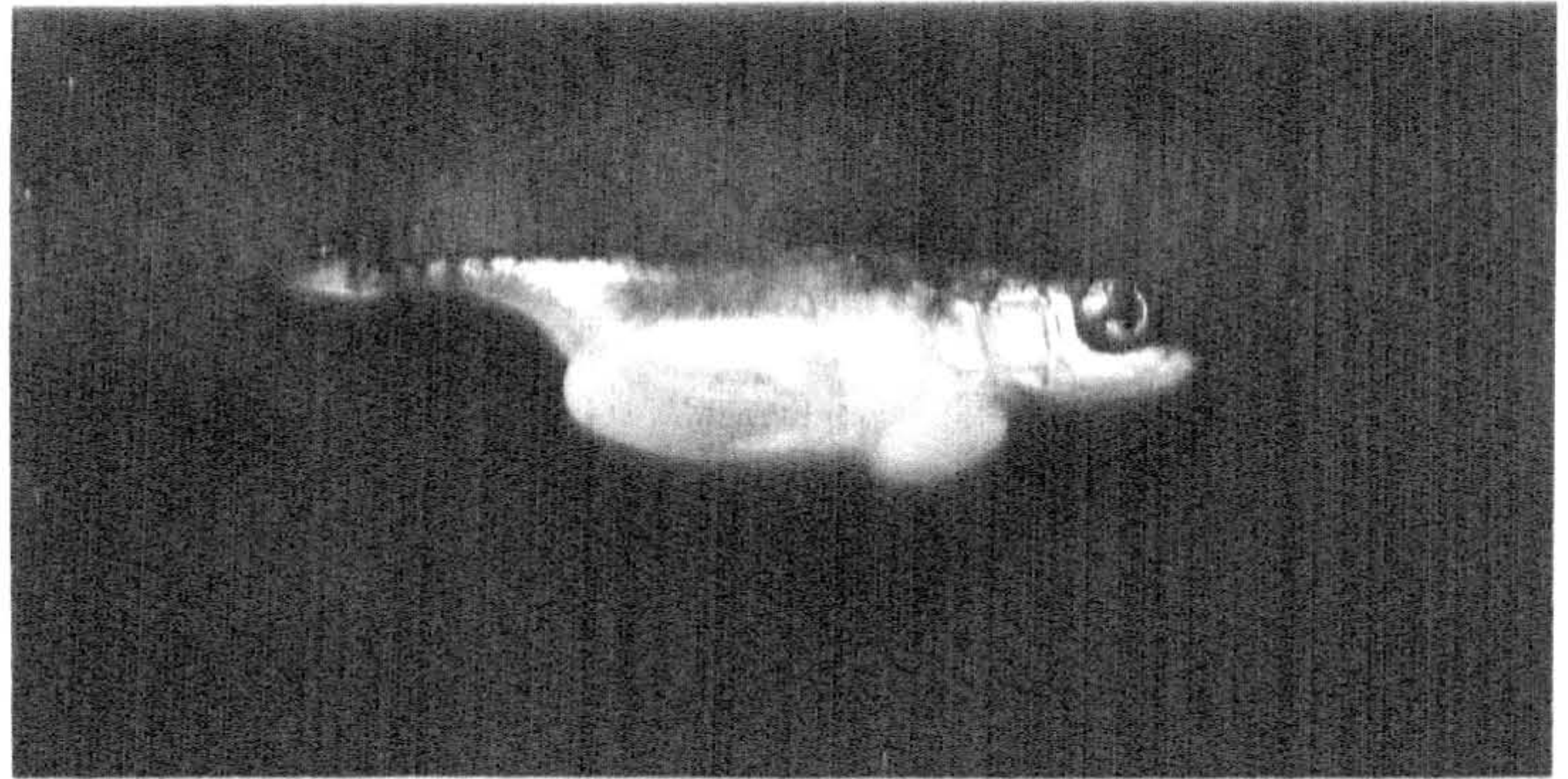
age group II

LF = 48 mm

WF = 0.68 g

WS = 0.63 g

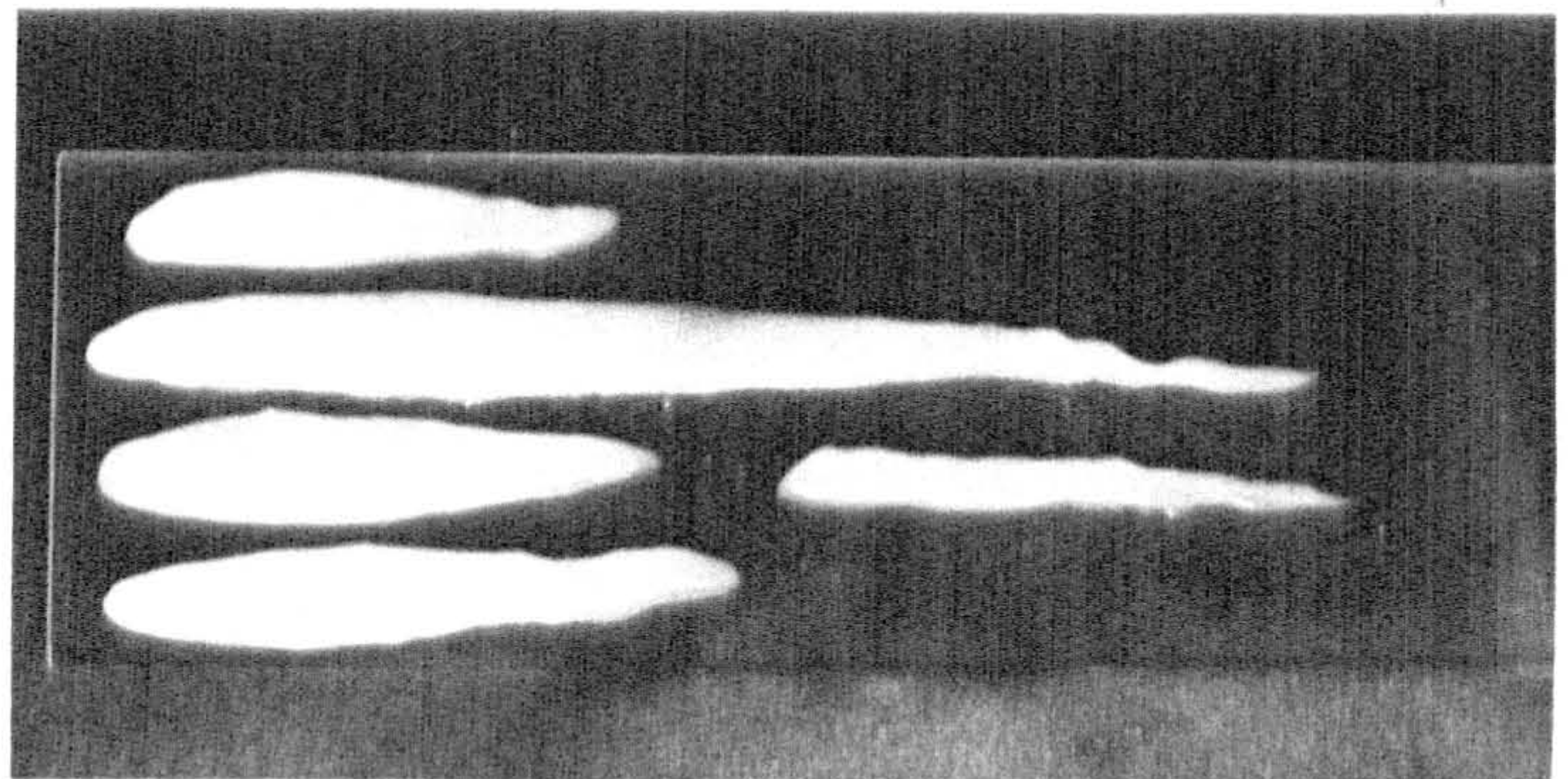
P.I. = 0.48



scale: 10 mm
└───┘

the 5 plerocercoids
with weights in grams

.08
.25
.14 .04
.12



PATHOLOGY

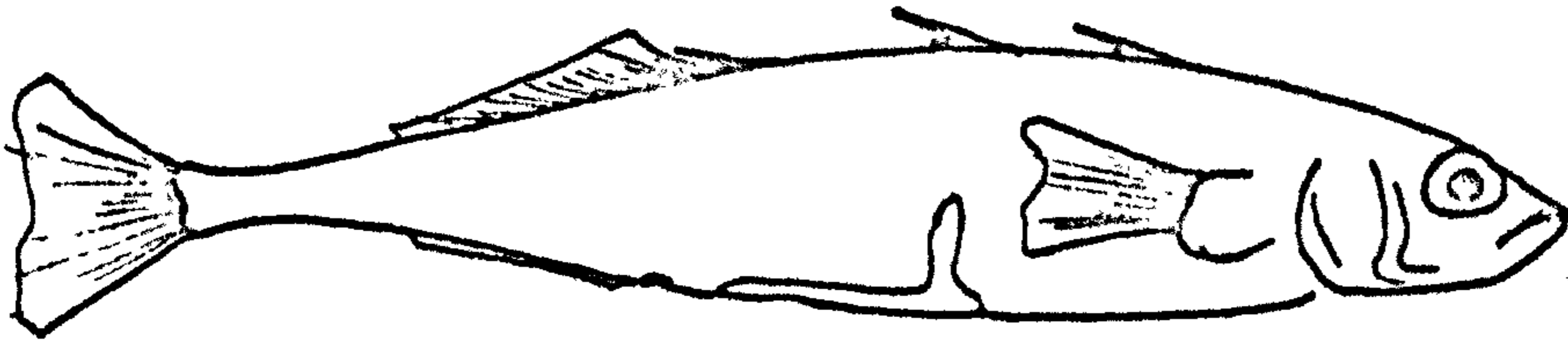
Of the three parasite species found in the Priddy sticklebacks Schistocephalus undoubtedly had the greatest pathological effects. The most heavily infected fish supported a weight of worms considerably greater than their own weight and the parasites must have been taking much food which would otherwise have been available to the fish. This is discussed further on p. 99 .

The large bulk of worms can be seen in Plates 3 and 4 where two fish and the plerocercoids they contained are shown. The sticklebacks' body cavities were much distended, both in front of and behind the ventral bony plate, to accomodate this great bulk. This is illustrated in Fig. 19 where the shapes of two heavily infected fish are compared with that of an uninfected one. The skin was not simply stretched as it retained its shape after removal of the plerocercoids (see Plate 3).

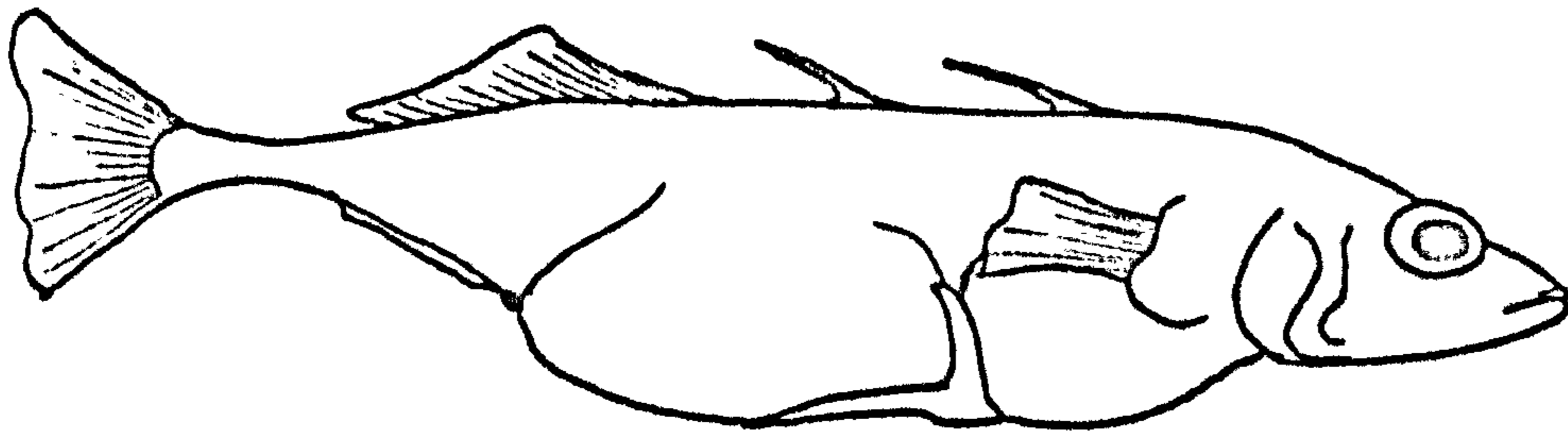
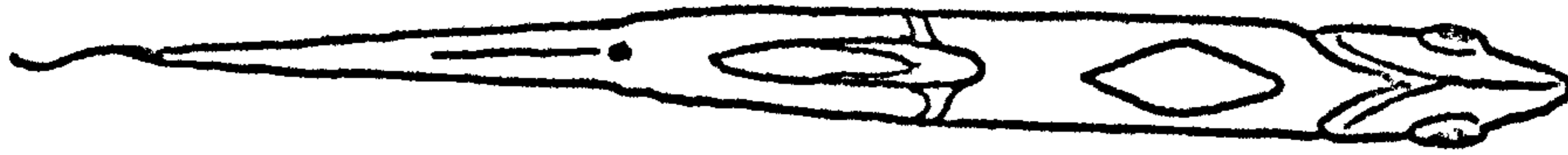
This distension affected the swimming performance of the fish, both by restricting movement and by decreasing the stream-lining and hence the hydrodynamic efficiency. Arme and Owen (1967) found that infected fish moved slowly and often rested on the bottom. They were capable of short bursts of rapid movement, but must nevertheless be more susceptible to predation. The food-finding capacity may also be reduced which would be important at times of food shortage in autumn and

FIG. 19 Distortion by Schistocephalus

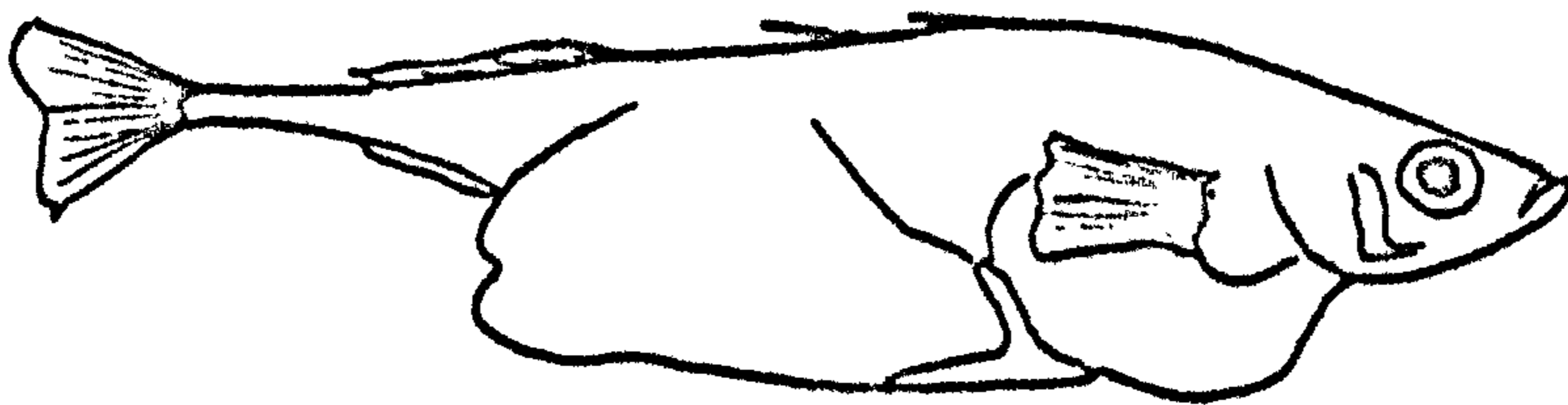
1 cm



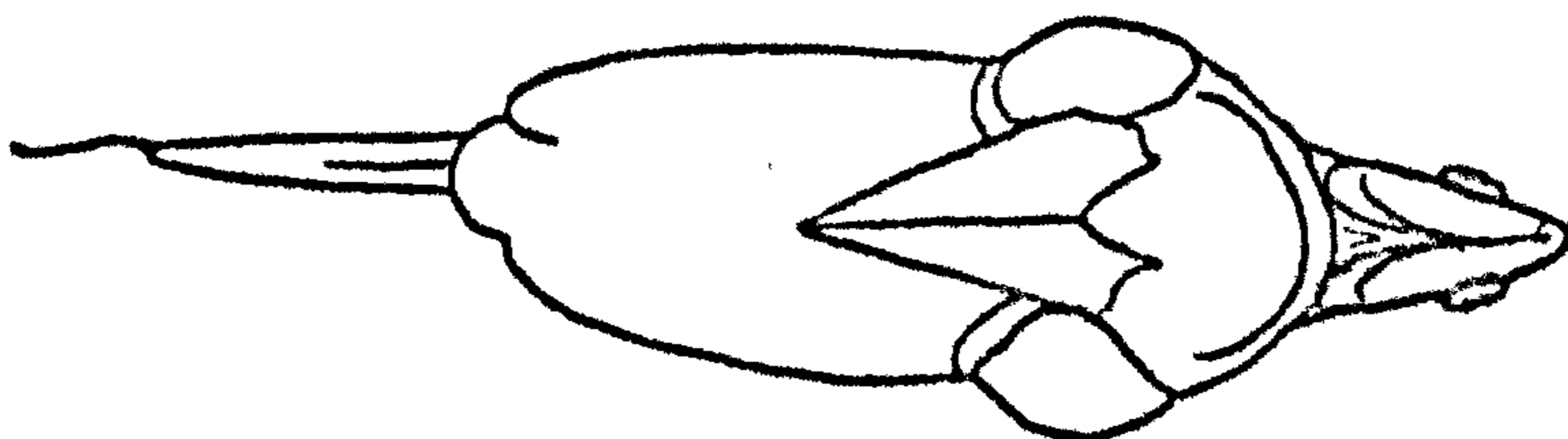
uninfected



P.I. = 0.47



P.I. = 0.58



winter. It is of course to the Schistocephalus's advantage that an infected fish should be eaten by a bird so that the life cycle can be completed.

Other effects found by Arme and Owen were a reduction in the packed cell volume of erythrocytes and a decrease in liver weight. Reproduction was not affected so greatly as in roach (Rutilus rutilus) infected with Ligula intestinalis where the pituitary malfunctions (Kerr, 1948). In sticklebacks Arme and Owen found no histological difference between the pituitaries of infected and uninfected fish at any time of year. The testes developed normally and the sexual coloration of the males was not affected. There was however a delay in oocyte maturation in females. Breeding behaviour was also disrupted as grossly distended males were unsuccessful at building nests, and one distended female was observed attempting to spawn in a nest and totally destroyed it. At Priddy there was greater interference with breeding; heavy Schistocephalus infections delayed maturation in both sexes of fish and less than 50% of the population bred, as described on p. 43 .

SEASONAL DISTRIBUTION

Three measurements were made on the Schistocephalus of each fish: total number of plerocercoids, length and weight of each plerocercoid. As the weight of individual plerocercoids varied greatly their total weight must be more significant than their numbers when considering the effects on the stickleback. The lengths varied greatly in worms of the same weight and depended to a large extent on the state of contraction of the muscles. Hence weight was used as a measure of size, rather than length. The figures are shown in appendix 2 c.

I Percentage infection (Fig. 20a)

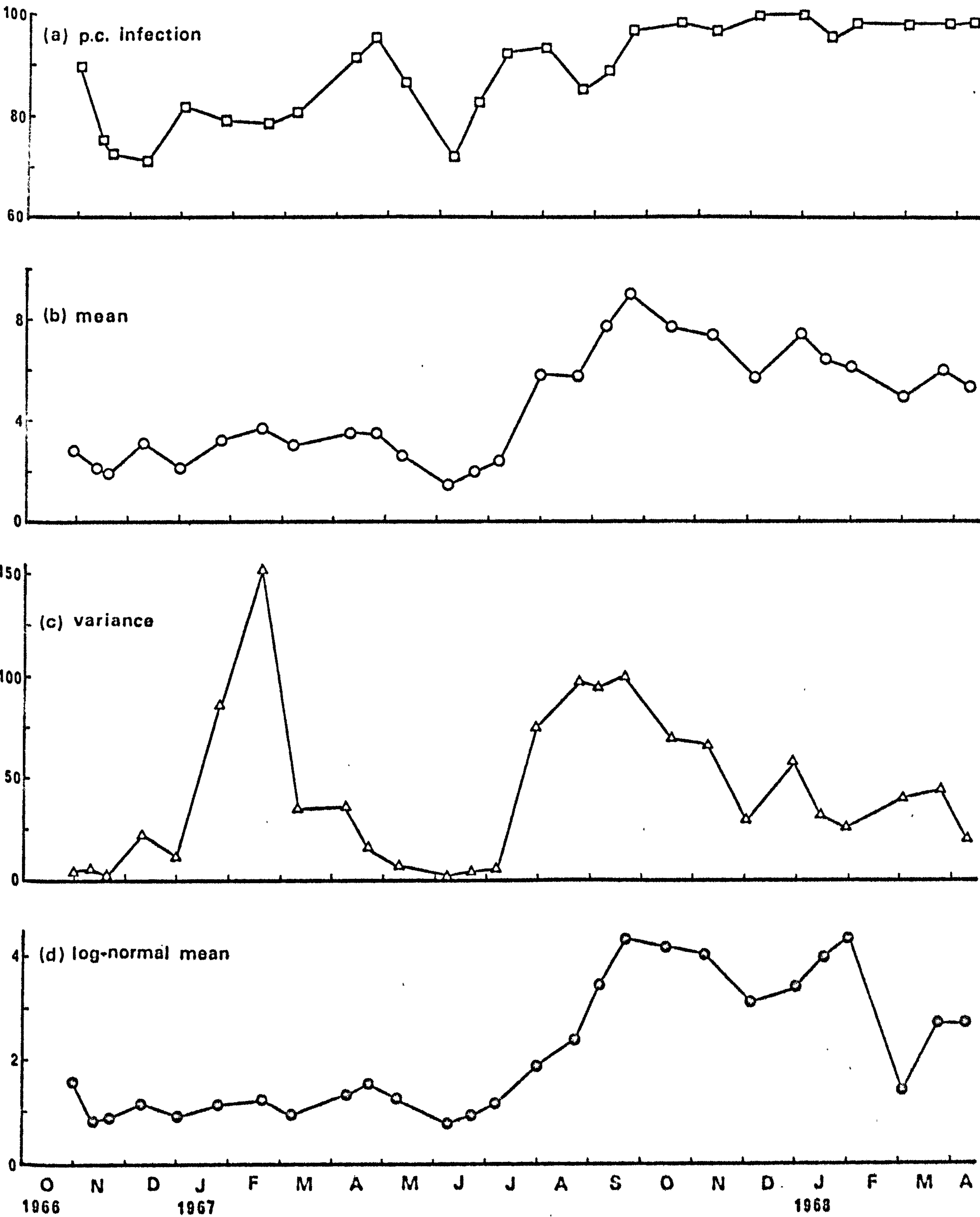
88.3% of all fish were infected. The percentage of fish infected with Schistocephalus fell from 89% on 29.10.66 to 70.5% on 10.12.66. It then rose to 82% on 1.1.67 and remained at about this level until April when it had risen to 96% by 21.4.67. There was then a decrease to 71% on 7.6.67, followed by a rise to 93% on 31.7.67. There was then another decrease, to 85% on 21.8.67, and an increase to 97% on 21.9.67. This high level of infection was maintained for the rest of the study period; between 97 and 100% of fish being infected.

II Numbers of Schistocephalus per fish

The figures for each sample were fed into the computer as data for the program calculating mean and variance (see p.5-6 and appendix 2 c). They were also collected into frequency

FIG. 20

Schistocephalus : no. per fish



distributions. These were arranged in log x2 classes, 0, I, II, III ... with class centres at 0, 1,2,4... and plotted. Five samples are also plotted on a numerical scale along with various theoretical distributions for comparison. These were picked as being representative of the differently shaped curves which occurred.

1. Mean (Fig. 20b)

The overall mean was 4.4 plerocercoids per fish. The mean number of plerocercoids per fish fell from 2.8 on 29.10.66 to 1.87 on 19.11.66. There was then a steady increase to 3.7 on 18.2.67, except for a high value of 3.1 on 10.12.66. The value then remained between 3.0 and 4.0 until 21.4.67. There was a decrease to 1.4 on 7.6.67 followed by a steady increase to 9.0 on 21.9.67. The mean fell to 5.7 by 4.12.67, rose to 7.4 on 1.1.68, then fell steadily, reaching 4.9 by 4.3.68. There was a slight increase to 5.9, then a decrease to 5.3 in the final two samples.

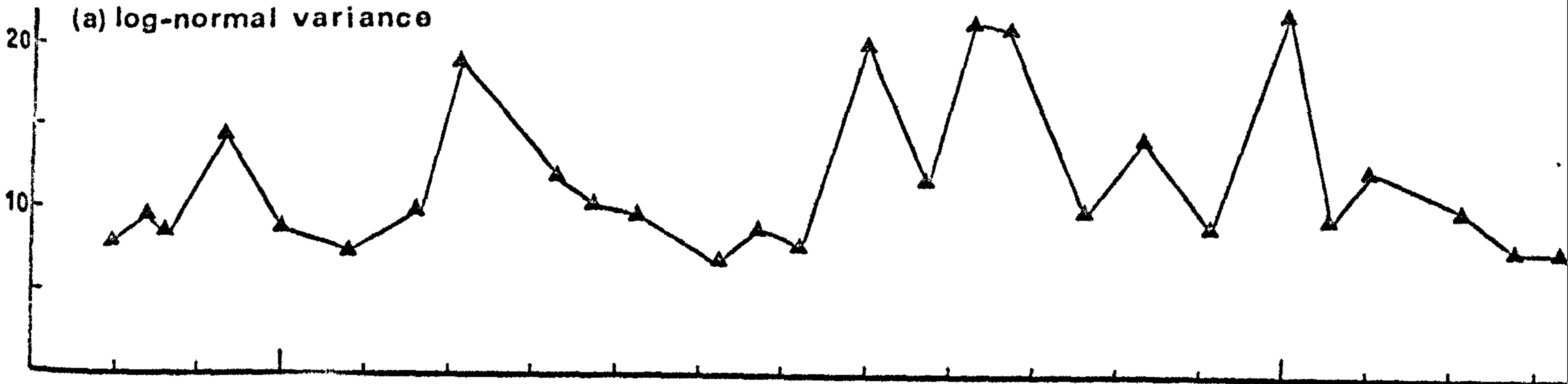
2. Variance (Fig. 20c)

The variance for all fish was 45.1. The variance was low initially, 5.5 on 29.10.66, but increased fairly steadily to a maximum of 154 on 18.2.67. There was then a large decrease to 36.5 on 5.3.67 followed by a slower fall to a minimum of 2.3 on 7.6.67. There was a slow increase until 6.7.67 when the value was 4.9, followed by a more rapid increase

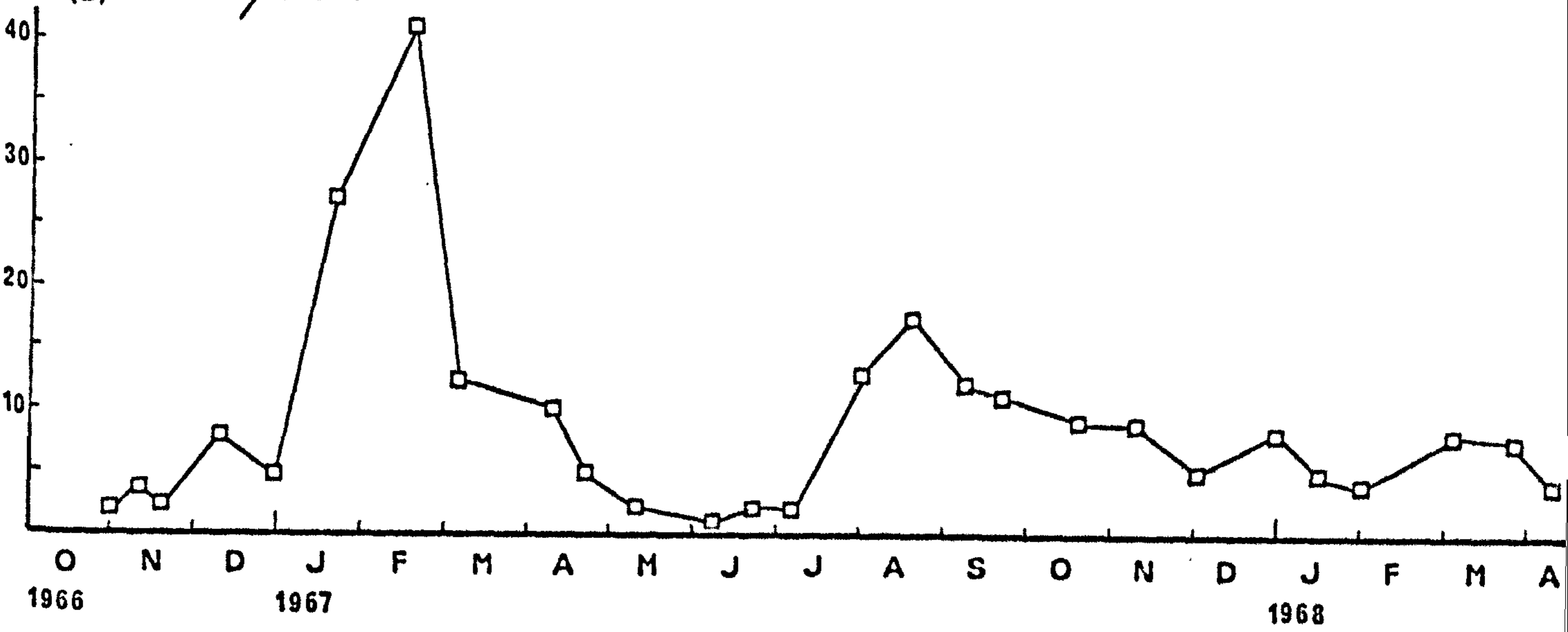
FIG. 21

Schistocephalus

(a) log-normal variance



(b) variance / mean



to 98.3 on 21.8.67. The level remained at around 100 until 21.9.67; there was then a fairly steady decrease to 30.6 on 4.12.67. The level remained more or less the same in the rest of samples, between 23 and 46, except for a value of 61 on 1.1.68.

3. Overdispersion (Fig. 21b)

The overall value of the variance: mean ratio was 10.26. The overdispersion rose fairly steadily from 1.87 on 29.10.66 to a maximum of 41.2 on 18.2.67. It fell suddenly to 12.16 on 5.3.67, then more slowly to a minimum of 1.61 on 7.6.67. It rose slightly to 2.09 on 6.7.67, then rapidly to 17.35 on 21.8.67. There was a steady decrease, to 5.38 on 4.12.67, with a higher value of 8.26 on 1.1.68, then a further decrease to 4.22 on 1.2.68. The value rose to 8.51 on 4.3.68 then finally fell to 4.29 on 9.4.68.

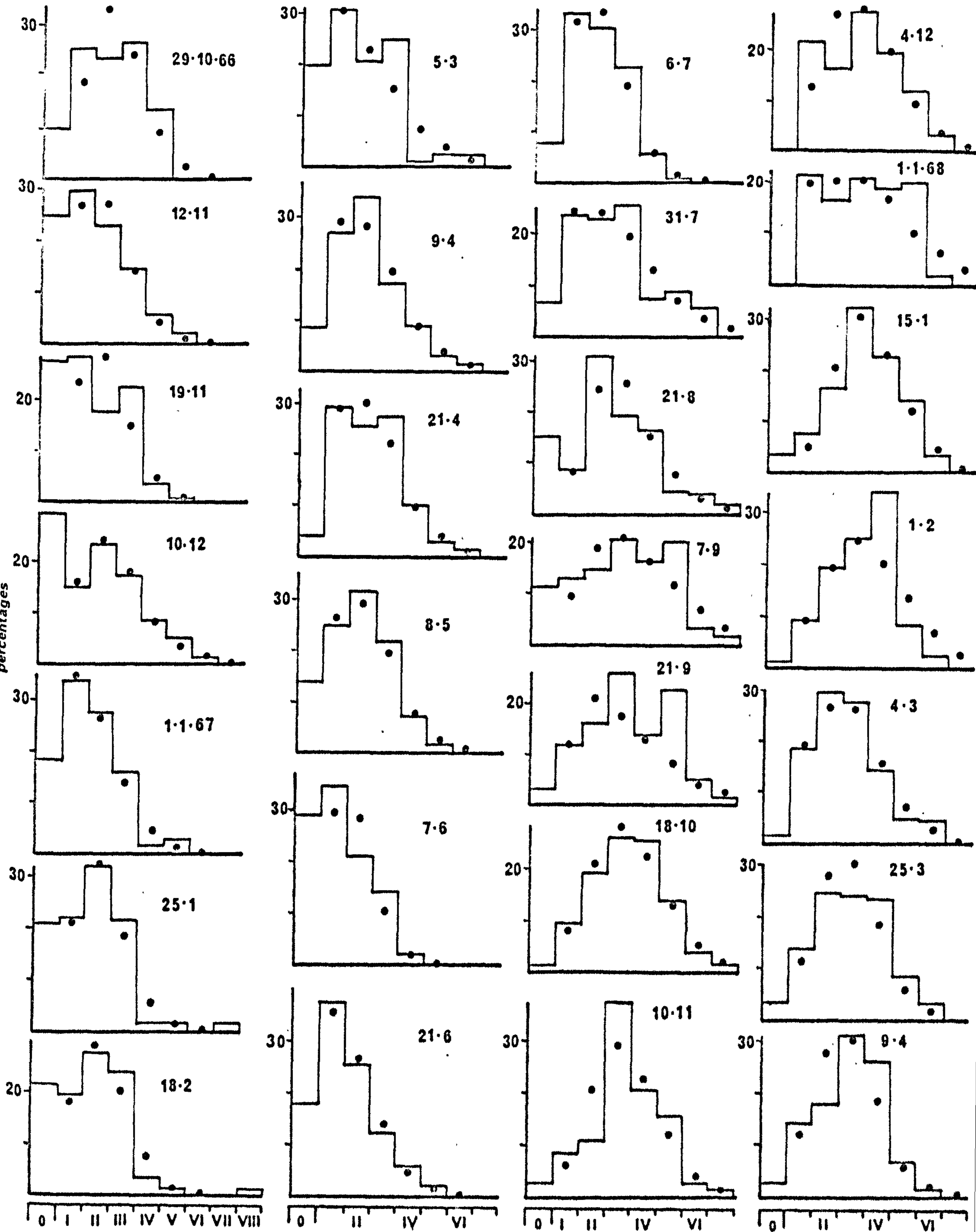
In general the pattern of the overdispersion was very similar to that of the variance; during the first nine months the increases and decreases were of about the same sizes, but from July onwards the overdispersion was lower.

4. Frequency distributions (Fig. 22)

Initially most fish had very few plerocercoids, the maximum number in one fish being 10. During November and December 1966 there was an increase in the proportion of fish with none or one plerocercoid and a decrease in the number of more heavily infected fish, although the maximum number of

FIG. 22 *Schistocephalus* log x 2 classes

• log-normal



worms was higher. Most fish still had few Schistocephalus in January and February 1967 although on 25.1.67 the maximum number was 70 and on 25.1.67 106, the two highest values recorded. There was a decrease in the zero class in March and April, but otherwise little change. In June and July there was an increase in the numbers of fish with many parasites. This was followed by a gradual decrease in numbers of heavily infected fish during October and November. There was a further rise in the numbers of fish with many plerocercoids in January and February 1968, followed in March and April by a gradual fall once again.

Negative binomial, log series and Neyman A distributions were fitted to the data by means of computer programs (see pp. 12, 24, 27 and appendix 1). The Neyman A was always a very poor fit. The negative binomial fitted poorly in most cases as the calculated frequency of zeros was too high, and of ones too low. The log series fitted fairly well when the percentage infection was low, but not at all when it was high.

A negative binomial truncated at the zero end was then tried (see p. 15). It was thought that as uninfected fish moved faster and may have been difficult to catch there might have been too few zeros. The distribution fitted better than the log series, which also takes no account of the zero class. However the theoretical number of zeros was very large, too large to be accounted for by difficulty of catching,

as lightly infected fish would also have been under-represented.

A truncation at the upper end was tried also, but the fit was poor. This could have arisen if fish with large numbers of Schistocephalus were dying. The situation was however complicated by the variability in the weight of plerocercoids and the fact that it was weight rather than numbers which was the factor causing death of fish.

Finally cumulative percentage frequencies were plotted on log probability paper and in many cases fell fairly close to a straight line showing that a log normal was a reasonably good fit. A line was drawn through the points and the values of mean and standard deviation of the distribution obtained from it (see p. 15).

The theoretical log normal distributions, in $\log x^2$ classes, are plotted in Fig. 22 with the original distributions. In a large proportion of the samples the fit was good. In some cases, particularly when the infection was high, the upper tail of the original distribution was too short, suggesting that there was a truncation due to heavily infected fish dying.

The mean and variance of the log normal distributions are plotted against date of sample.

Mean: (Fig. 20d). The overall mean was 2.14.

The value of the mean was low from October 1966 to June 1967, varying between 1.6 and 0.7. It then rose steadily until 21.9.67 when the value was 4.4. It fell to 3.1 on 4.12.67,

then rose to 4.4 again on 1.2.68; there was finally a decrease to 2.75 in the last two samples.

The geometric mean was thus considerably lower than the arithmetic mean, the overall value being approximately half as great.

Variance: (Fig. 21a). The value of the variance rose from 7.9 on 29.10.66 to 14.3 on 10.12.66, then fell to 10 on 25.1.67, rose to 19 on 5.3.67 and fell again to 6.8 on 7.6.67. There was then an increase to a higher level during July, which was maintained until January 1968, with large fluctuations between 22.1 and 9.2. From February to April the value fell from 12.4 to 7.7.

The variance of the log normals was also lower than the actual variance, the level being about a quarter as high, as would be expected from the mean being half as large.

The patterns of the two means were very similar and so were those of the variances, except for the high values of the calculated variance on 25.1.67 and 18.2.67. These were both due to single high values which had a large effect on the calculated value, but would have virtually no effect on the shape of the distribution and therefore on the log-normal variance.

The distributions of five selected samples are described in more detail below:

FIG. 23 12-11-65

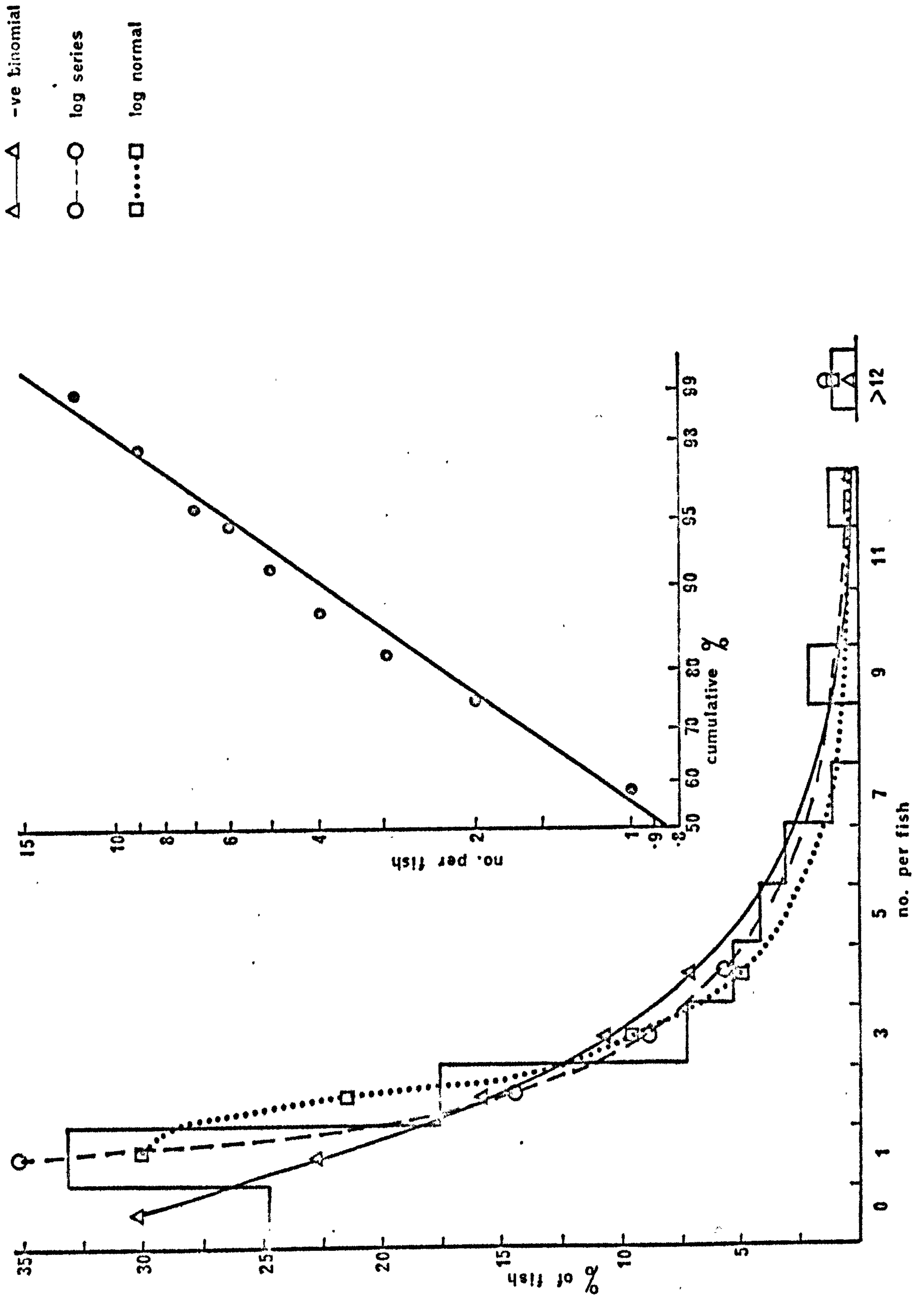
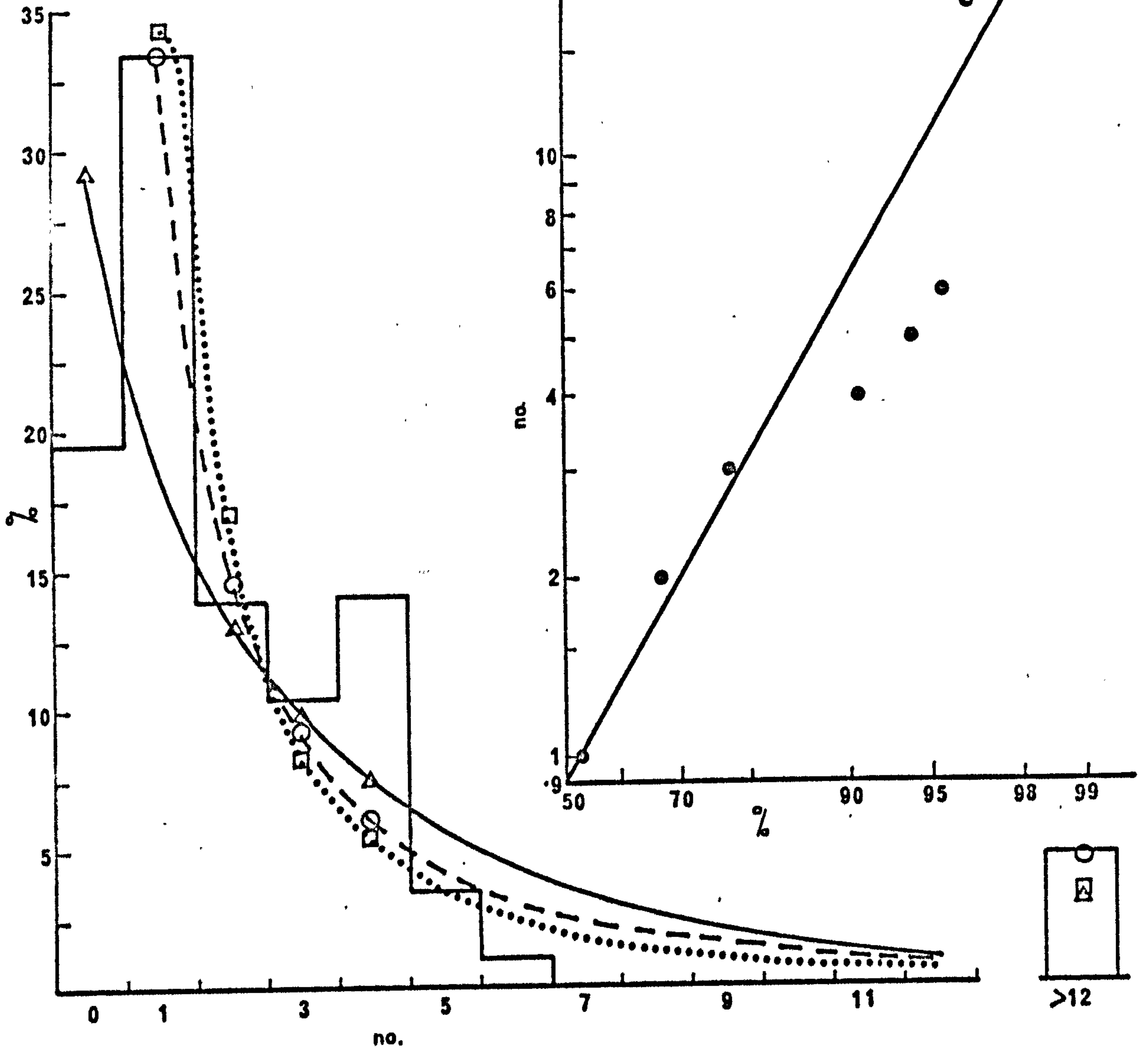


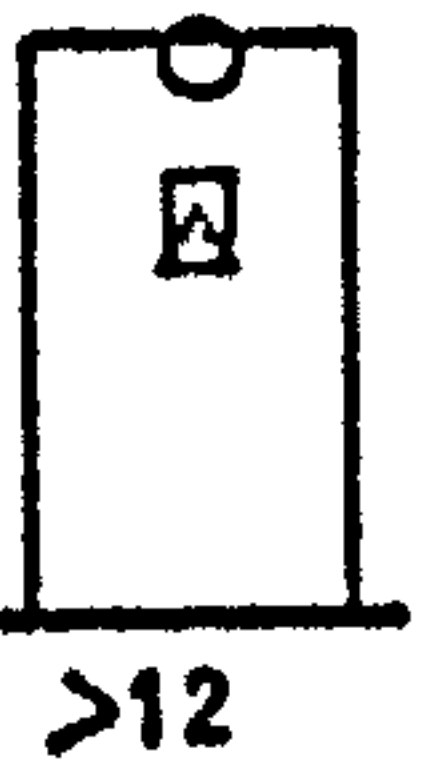
FIG. 24 5-3-67



△—△ -ve binomial

○—○ log series

□.....□ log normal



(i) 12.11.66 (Fig. 23)

This distribution had a fairly low percentage infection, large one-class and short tail. Negative binomial, log series and log normal distributions all fitted quite well and none was found to be significantly different from the original distribution, using the χ^2 test. The negative binomial was the worst fit, due largely to the inclusion of the zero class. The log normal was better, but it can be seen from the plot on log probability paper that a curve would fit the points better than a straight line. The log series distribution was the best fit.

(ii) 5.3.67 (Fig. 24)

This distribution was similar in shape to the previous one, but had a shorter tail; there were no fish with 7-12 parasites although more had over 12. The theoretical distributions did not fit well because of the high frequencies of the lower classes. The negative binomial was again the worst, with χ^2 significant at the 0.1% level. The log series was little better although it fitted classes 1-3 quite well; χ^2 was significant at the 1% level. The log normal was the closest but χ^2 was still significant at 2%. The probability plot showed that the ends of the distribution fitted well but the centre did not.

(iii) 21.8.67 (Fig. 25)

This distribution was a very different shape, with a

FIG. 25 21-8-67

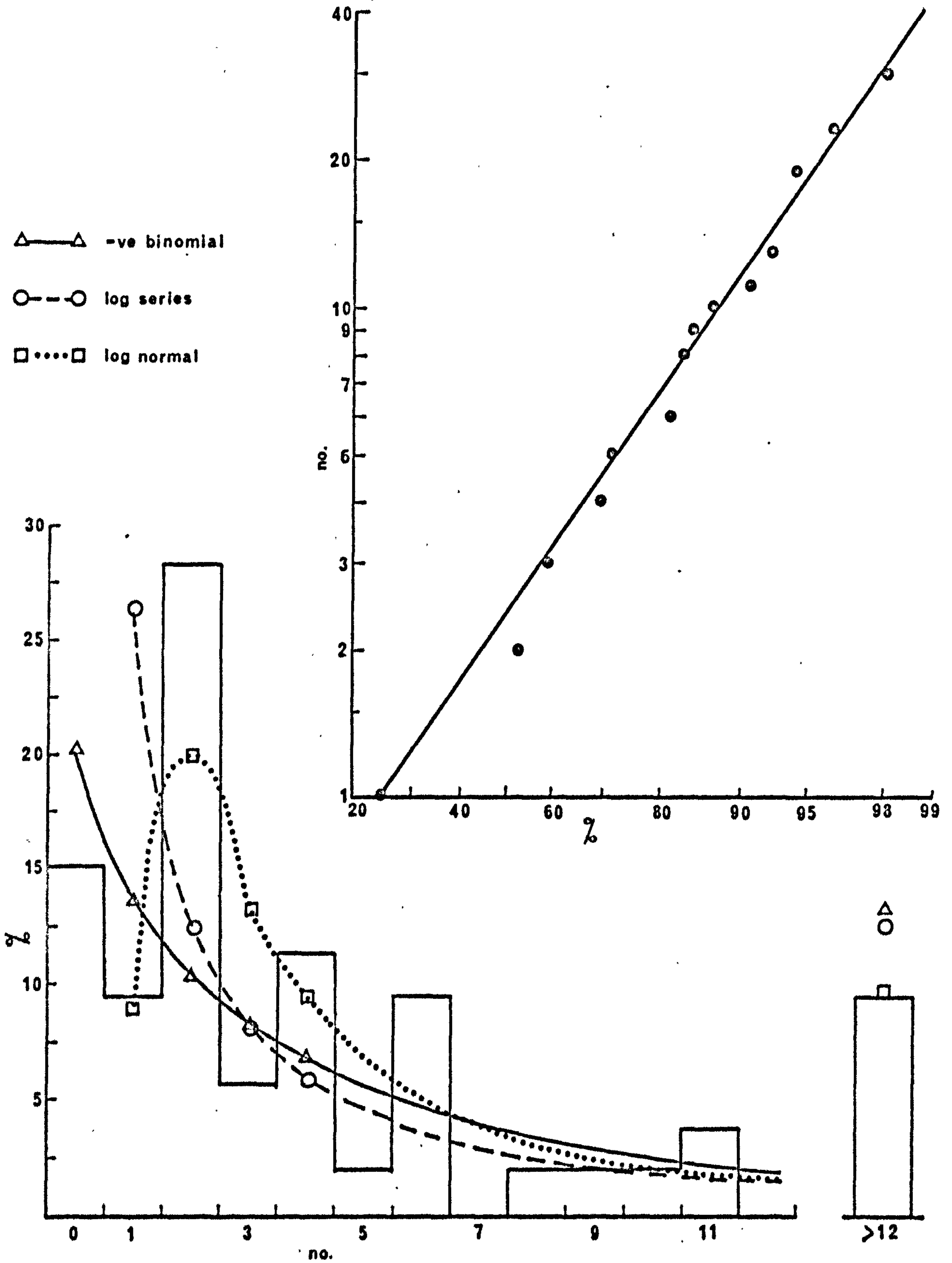
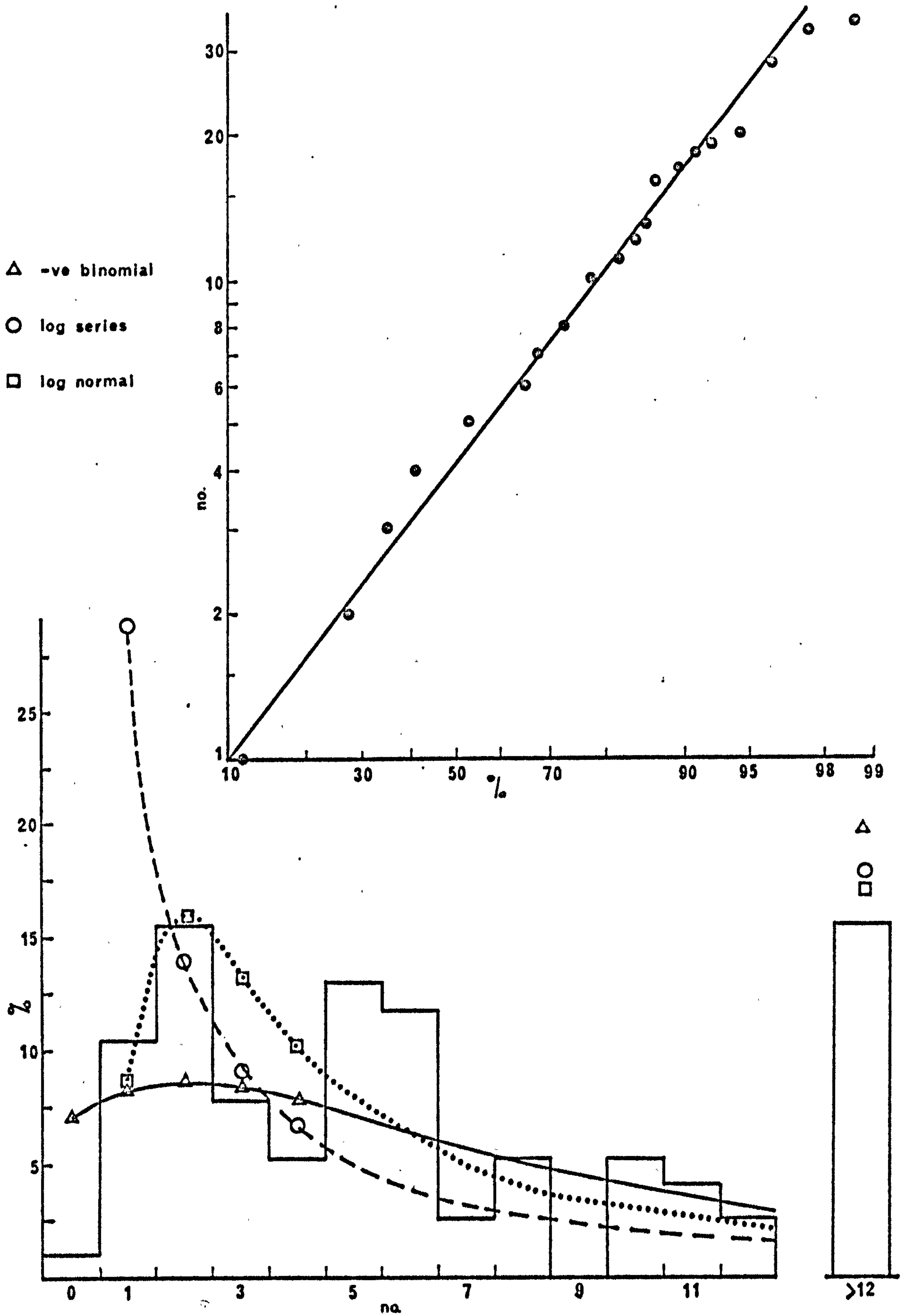


FIG. 26 18-10-67

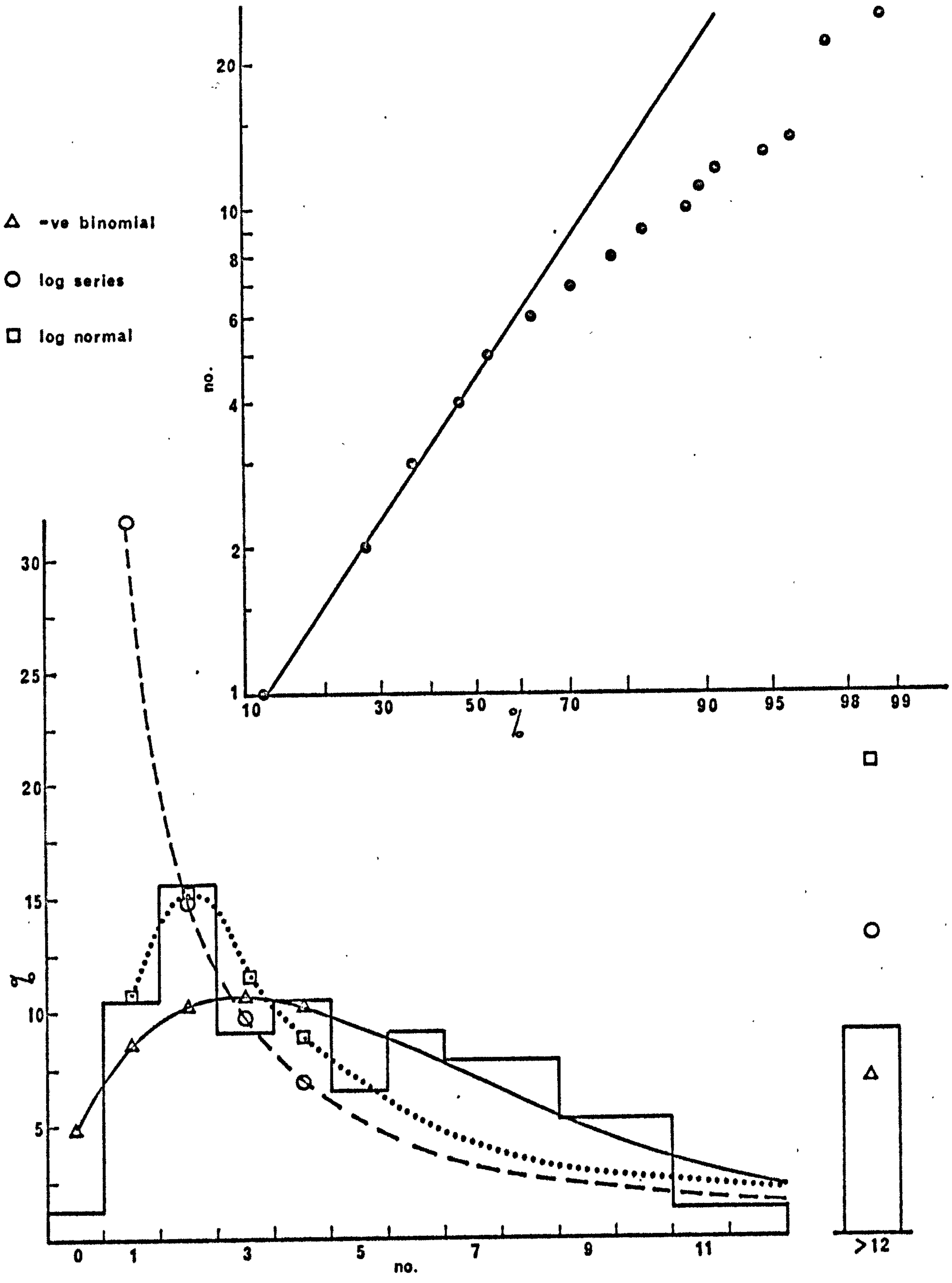


higher percentage infection and the maximum frequency at the 2-class; the tail was longer, continuing well beyond 12. The log series was a poor fit as it had a high value for the one-class and a low one for the 2-class. χ^2 was significant at 0.1%. The negative binomial also had χ^2 significant at this level as the frequency of the 2-class was very far out. It was similar to the log series distribution from class 2 onwards. The log normal fitted better although χ^2 was still significant at 1%. It had the maximum frequency at class 2, although the value was too low, and the tail fitted quite well. The probability plot was close to a straight line.

(iv) 18.10.67 (Fig. 26)

This was similar to the previous distribution; the 2-class had the highest frequency, the tail was slightly longer but the percentage infection was much lower. The log series was the worst fit with χ^2 significant at 0.1%. The one-class always has the highest frequency in a log series distribution so this was much too large and the values for classes 5-12 too low. The negative binomial was better and the 2-class was the largest. However the fit was not good at the lower end as the shape was too flat and the zero value too high. χ^2 was significant at the 5% level. The log normal fitted much better with the maximum frequency at the 2-class and the tail quite close. The probability plot gave a reasonably straight line. χ^2 was not significant.

FIG. 27 1-2-68



(v) 1.2.68 (Fig. 27)

Again the 2-class was the largest and the percentage infection was low; but the tail was not so extended and classes up to 10 had higher frequencies. The log series was a very poor fit as the one-class was much too large: χ^2 was significant at 0.1%. The log normal fitted classes 1-3 well, but then the tail dropped away too quickly and flattened out so that it was too extended. The probability plot showed that the points curved off at the upper end indicating truncation. The negative binomial was a good fit except for the 2-class; the hump was more abrupt but the 3-class not the 2-class had the maximum frequency. χ^2 was not significant for the log normal or negative binomial.

Thus it can be seen that each distribution fitted the data in some cases. Which of the three fitted most efficiently depended upon the level of infection and length of tail. In general, however, the log normal, sometimes truncated, was better than the negative binomial or log series.

III Weights of Schistocephalus

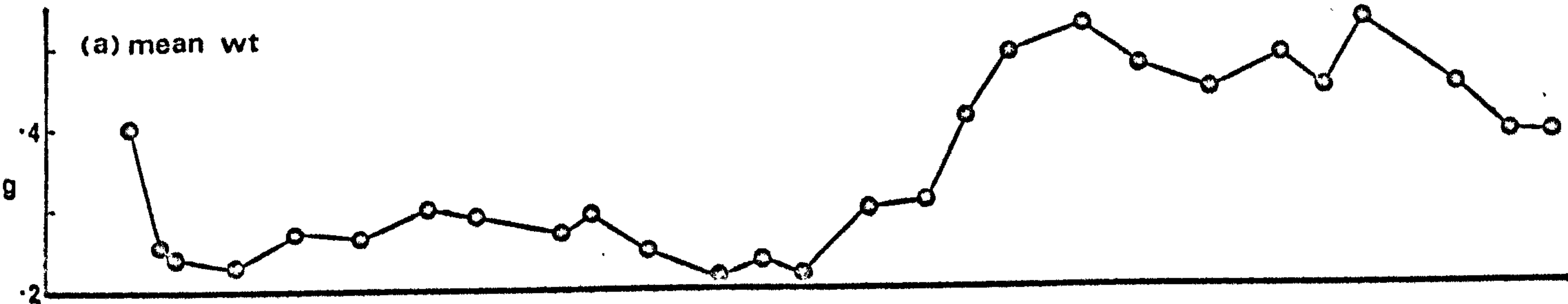
A. Weight per fish

The figures for the total weight of Schistocephalus (WS) per fish were treated in a similar way to those for numbers per fish. The mean weight and its variance were calculated for each sample, and the fish grouped into classes of 0.05 g

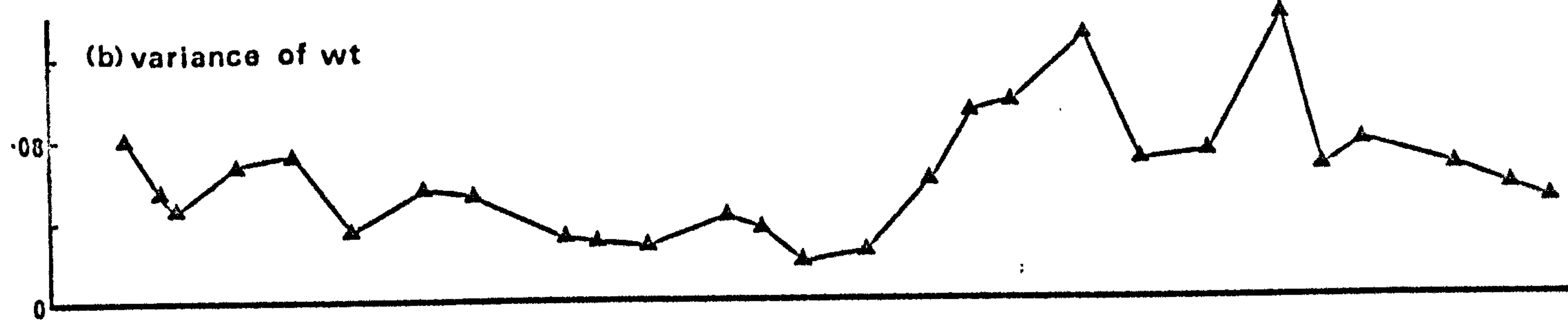
FIG. 28

Schistocephalus: weights

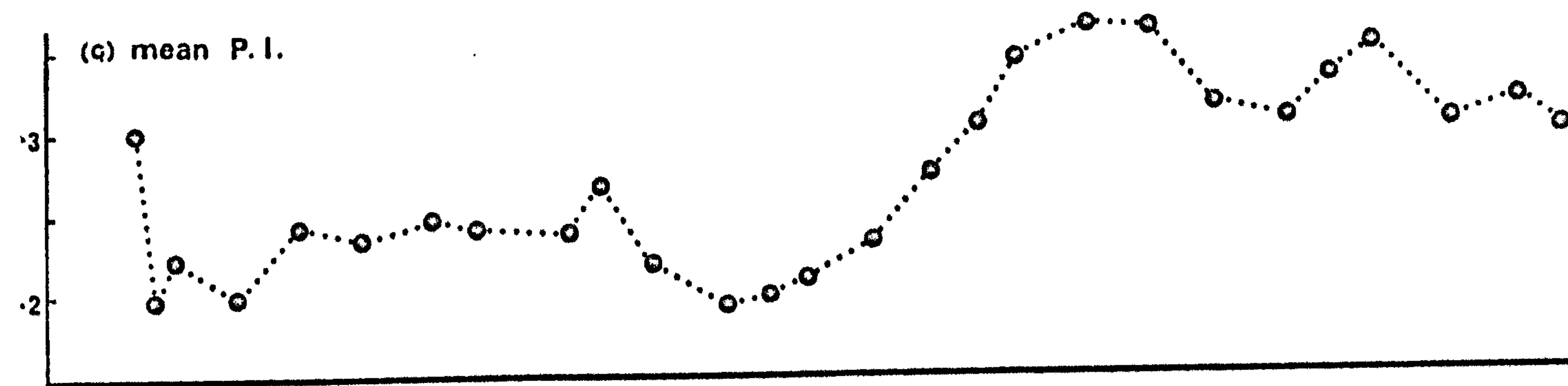
(a) mean wt



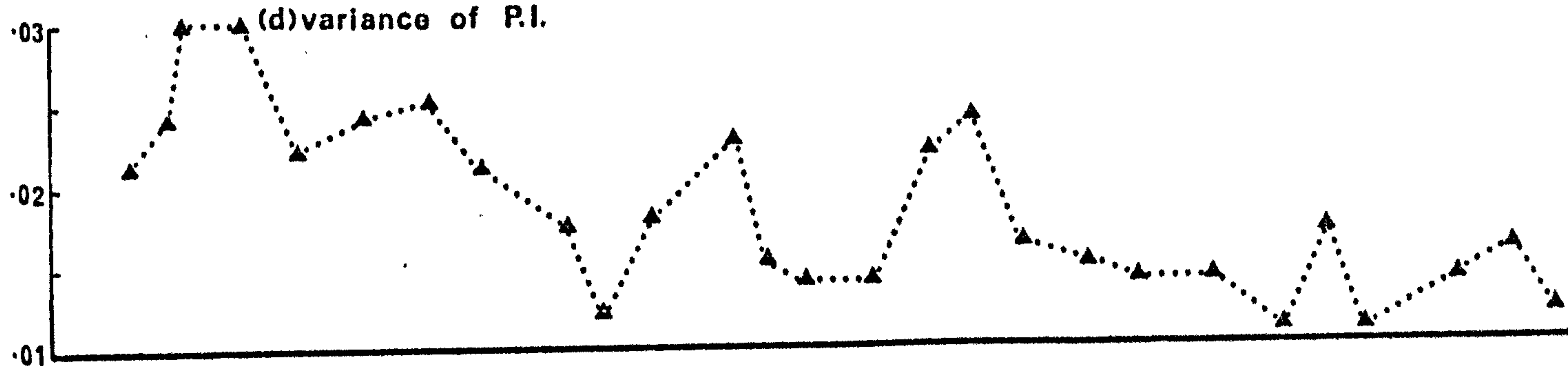
(b) variance of wt



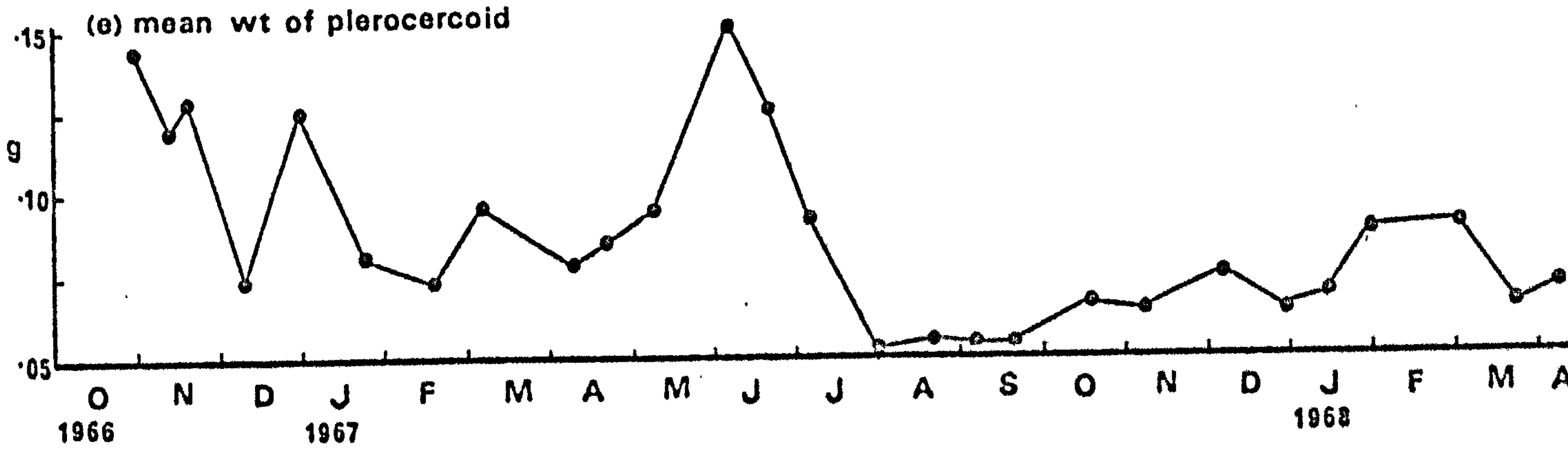
(c) mean P. I.



(d) variance of P. I.



(e) mean wt of plerocercoid



interval to form a distribution.

1. Mean (Fig. 28a)

The mean for all fish was 0.343 g.

The mean weight of Schistocephalus fell from 0.41 g per fish on 29.10.66 to 0.23 g on 10.12.66. There was then a gradual rise to around 0.29 g by February, this level being maintained until 21.4.67 after which there was a decrease to 0.22 g on 6.7.67. The value then rose steadily, reaching 0.52 g by 18.10.67. The mean fluctuated between 0.44 g and 0.53 g until 1.2.68, after which it fell steadily to 0.38 g on 9.4.68.

2. Variance (Fig. 28b)

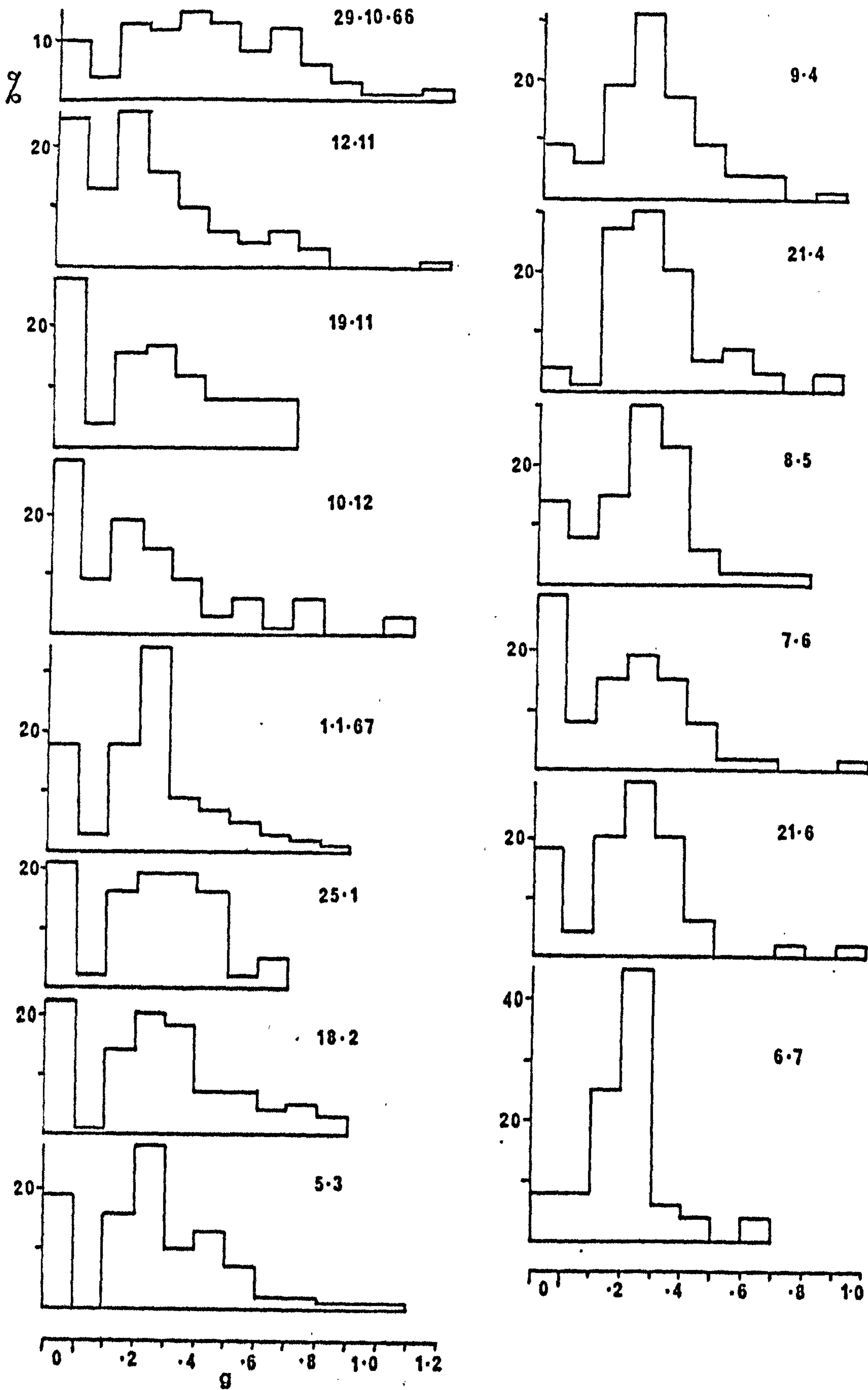
The variance for all fish was 0.071.

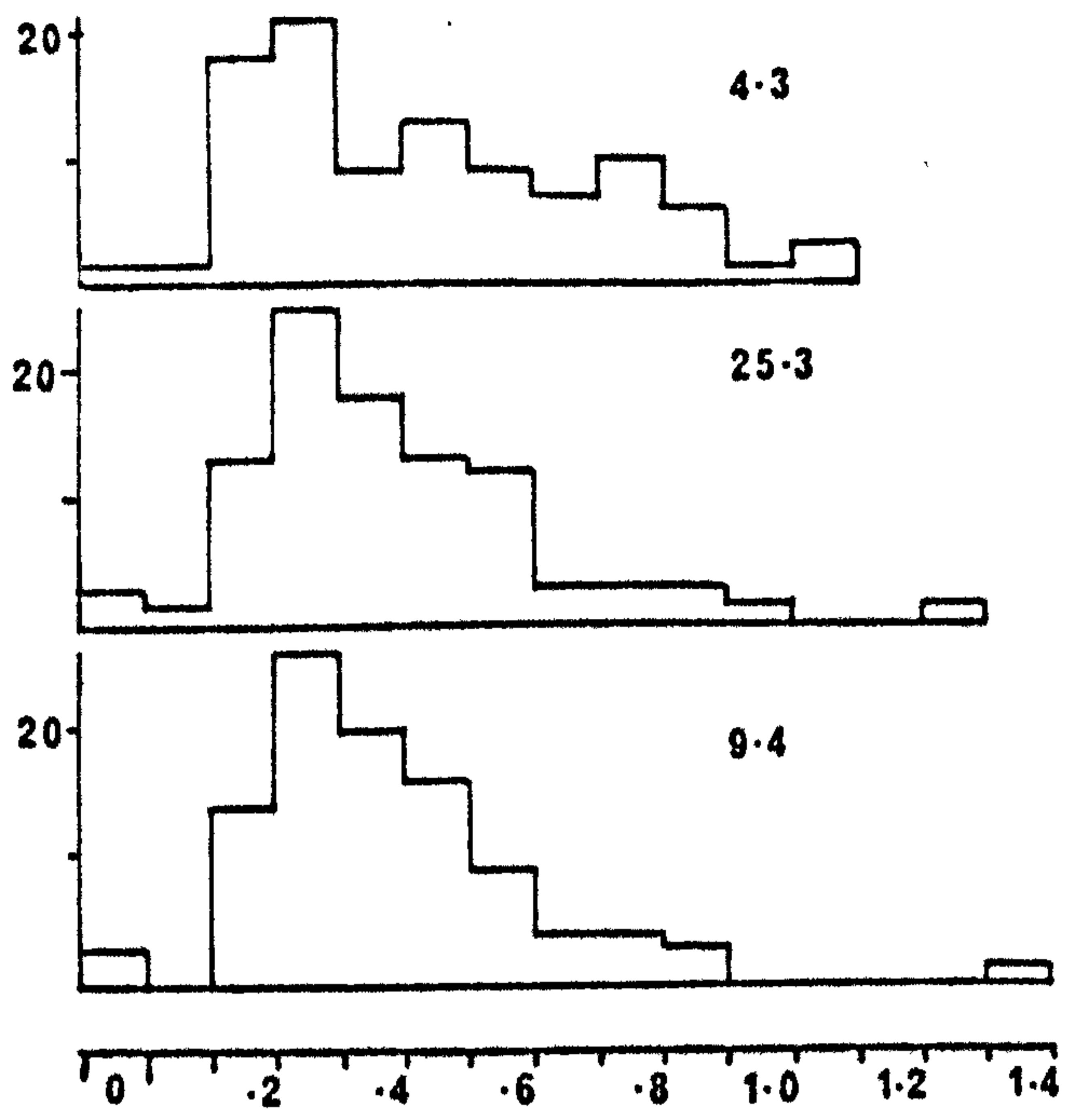
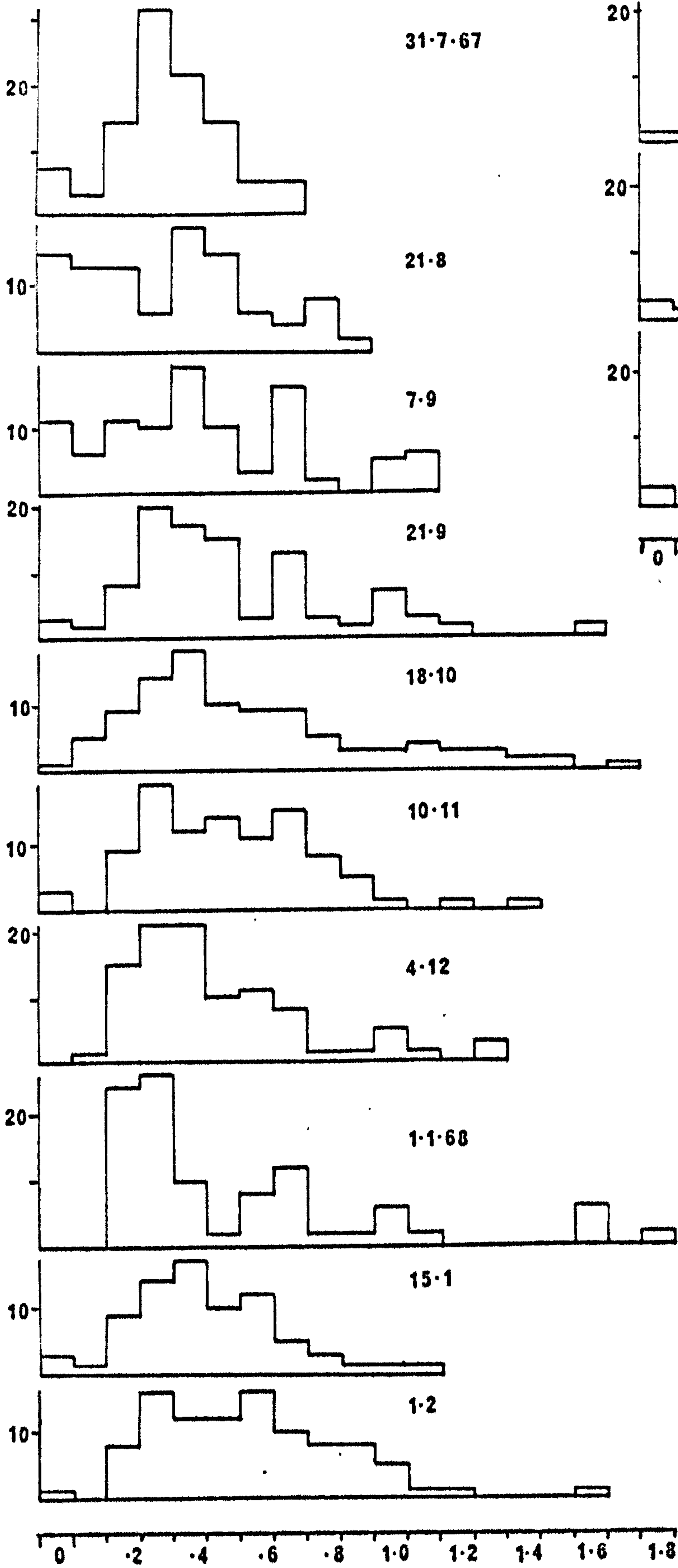
The variance of the weights was initially 0.08. It then fell to 0.045 on 19.11.66, rose to 0.071 on 1.1.67, and fell again, to 0.03 on 25.1.67. The value then decreased steadily from 0.055 on 18.2.67 to 0.026 on 8.5.67. There was a slight rise to 0.042 on 7.6.67 followed by a decrease to 0.019 on 6.7.67. The variance then increased steadily, reaching 0.129 on 18.10.67. There were two low values of 0.07 in November and December followed by a maximum of 0.149 on 1.1.68. The value then decreased fairly steadily to 0.047 on 9.4.68.

3. Frequency distributions (Fig. 29)

Initially most fish harboured quite high weights of

FIG. 29 Schistocephalus wts per fish





Schistocephalus; there were approximately equal numbers of fish with from 0.2 to 0.7 g. During November and December 1966 there was a tendency for the numbers of fish with large weights of Schistocephalus to decrease. There was then a progressive increase in weights until February 1967. There was little change until July when the numbers of fish with heavier worm burdens increased, and continued to do so until November. During December and early January 1968 there was an increase in the numbers of fish with smaller weights. In late January and February there was an increase in the proportion of heavily infected fish, followed by a gradual decline in March and April.

B. Parasite index (P.I.)

This is similar to the "parasitisation index" of Arme and Owen (1967). Here it is defined as

$$P.I. = \frac{WS}{WF + WS} \quad \dots(94)$$

If the parasite index equals 0.5 then the weights of fish and Schistocephalus are equal.

The parasite index was calculated for each fish and the means and variances for each sample were worked out and plotted.

1. Mean (Fig. 28c)

The mean for all fish was 0.266.

The mean parasite index fell from 0.30 on 29.10.66 to 0.20 on

12.11.66. It had increased to 0.24 by 1.1.67, after which there was little change until 21.4.67 when the value was 0.27. This was followed by a decrease to 0.19 on 7.6.67 and then a steady increase, the value reaching 0.37 on 18.10.67 and 10.11.67. The mean decreased to 0.31 on 1.1.68, increased to 0.35 on 1.2.68, then decreased to about 0.3 in the final three samples.

2. Variance (Fig. 28d)

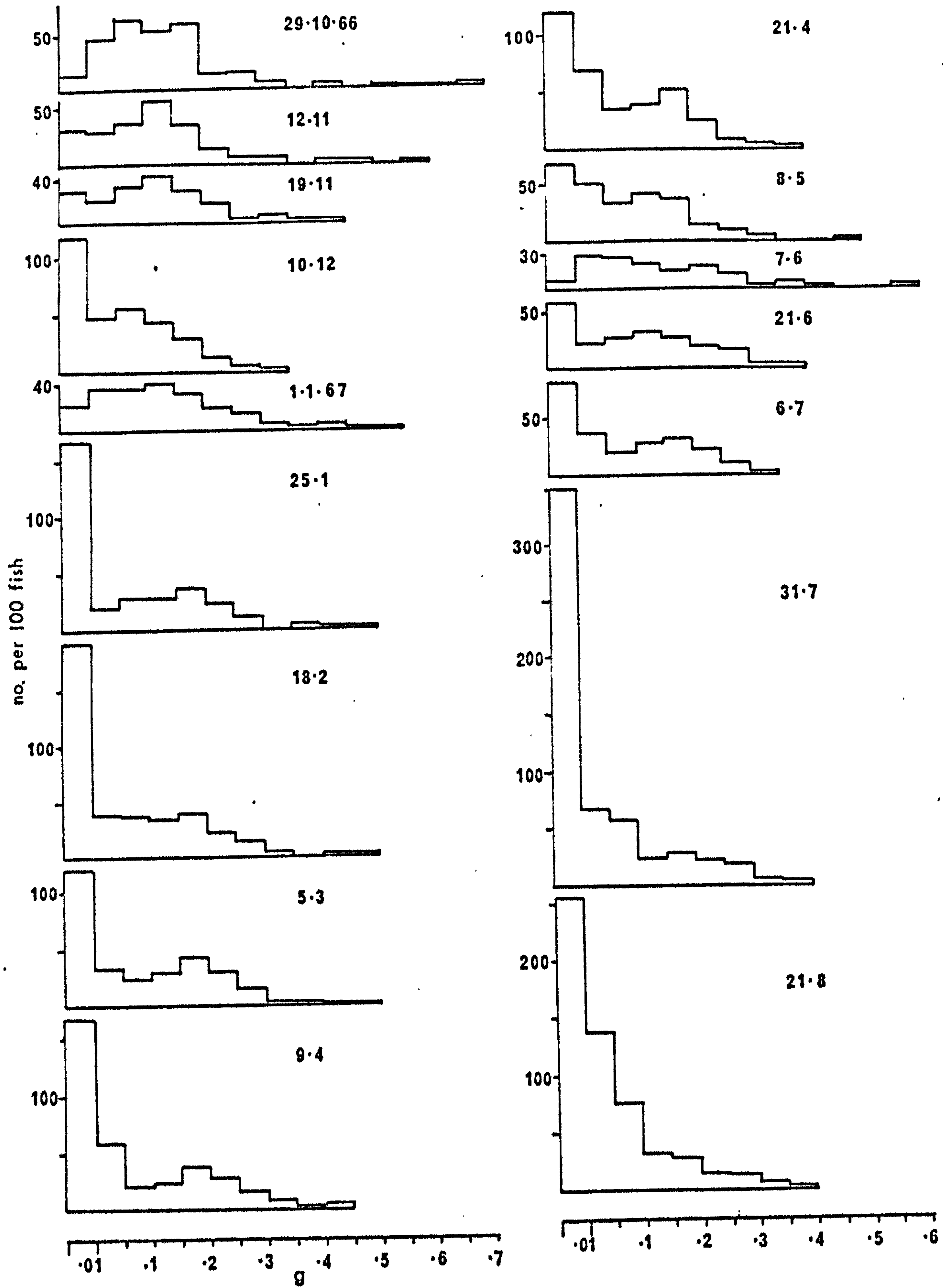
The variance for all fish was 0.024.

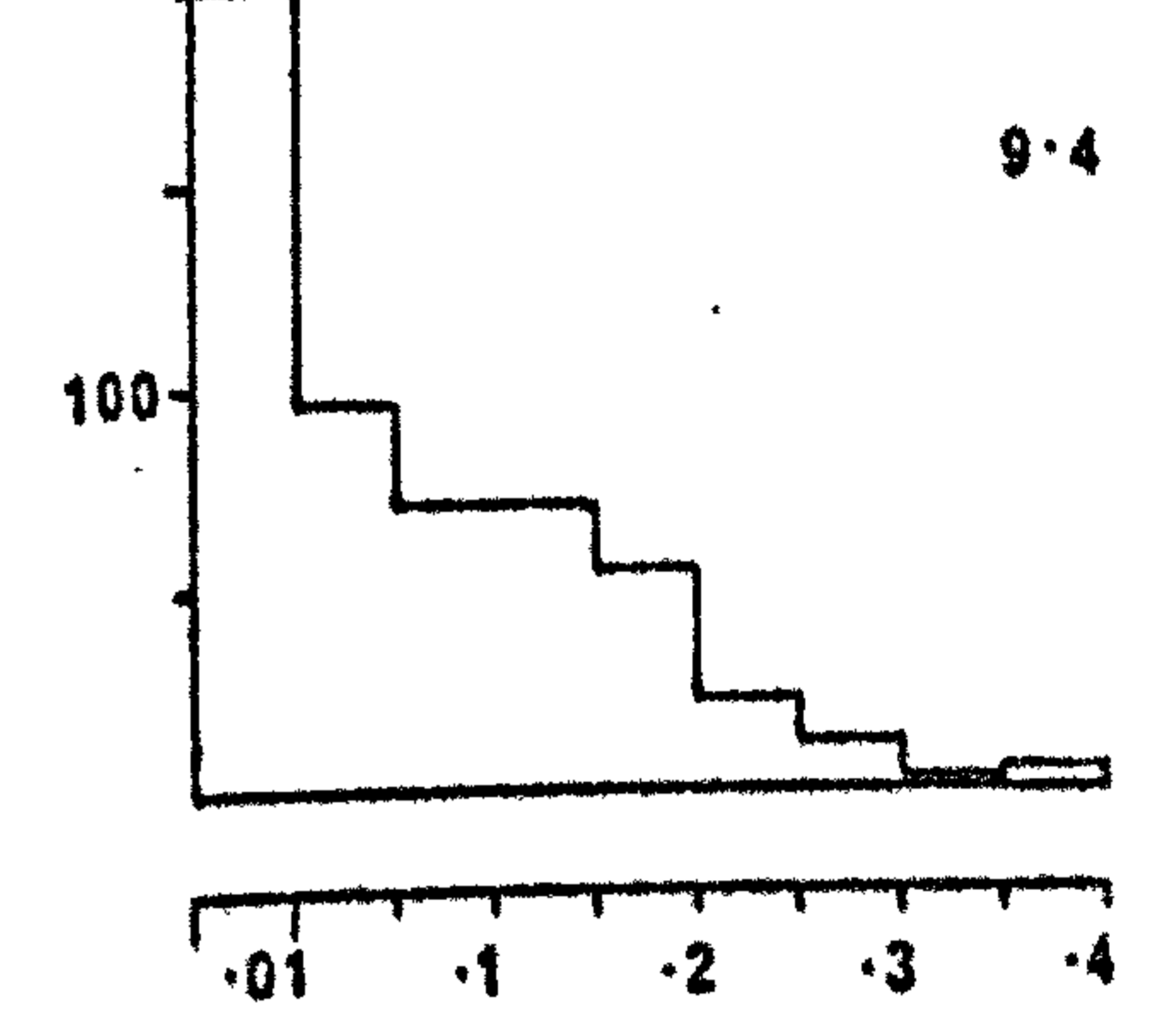
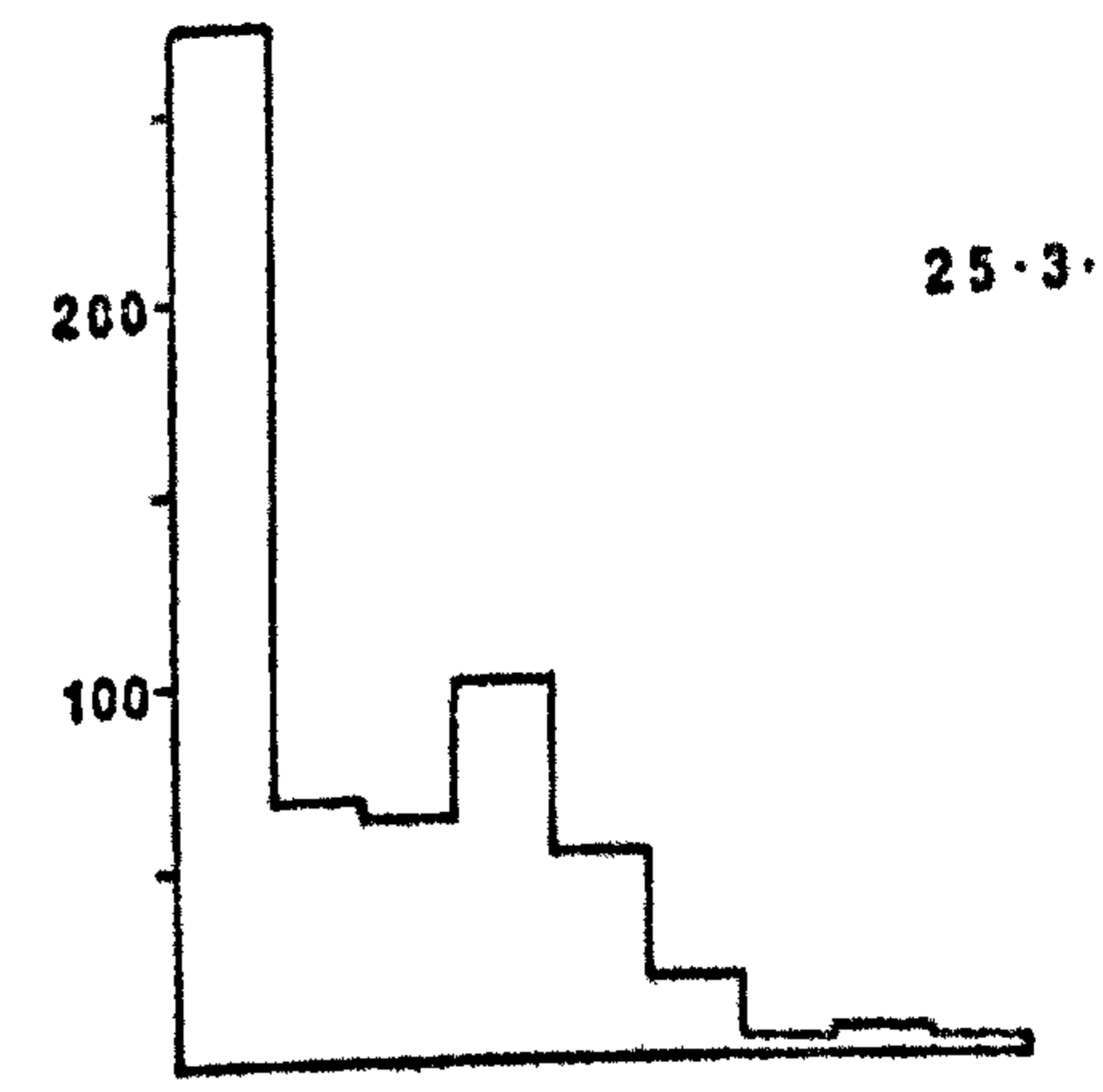
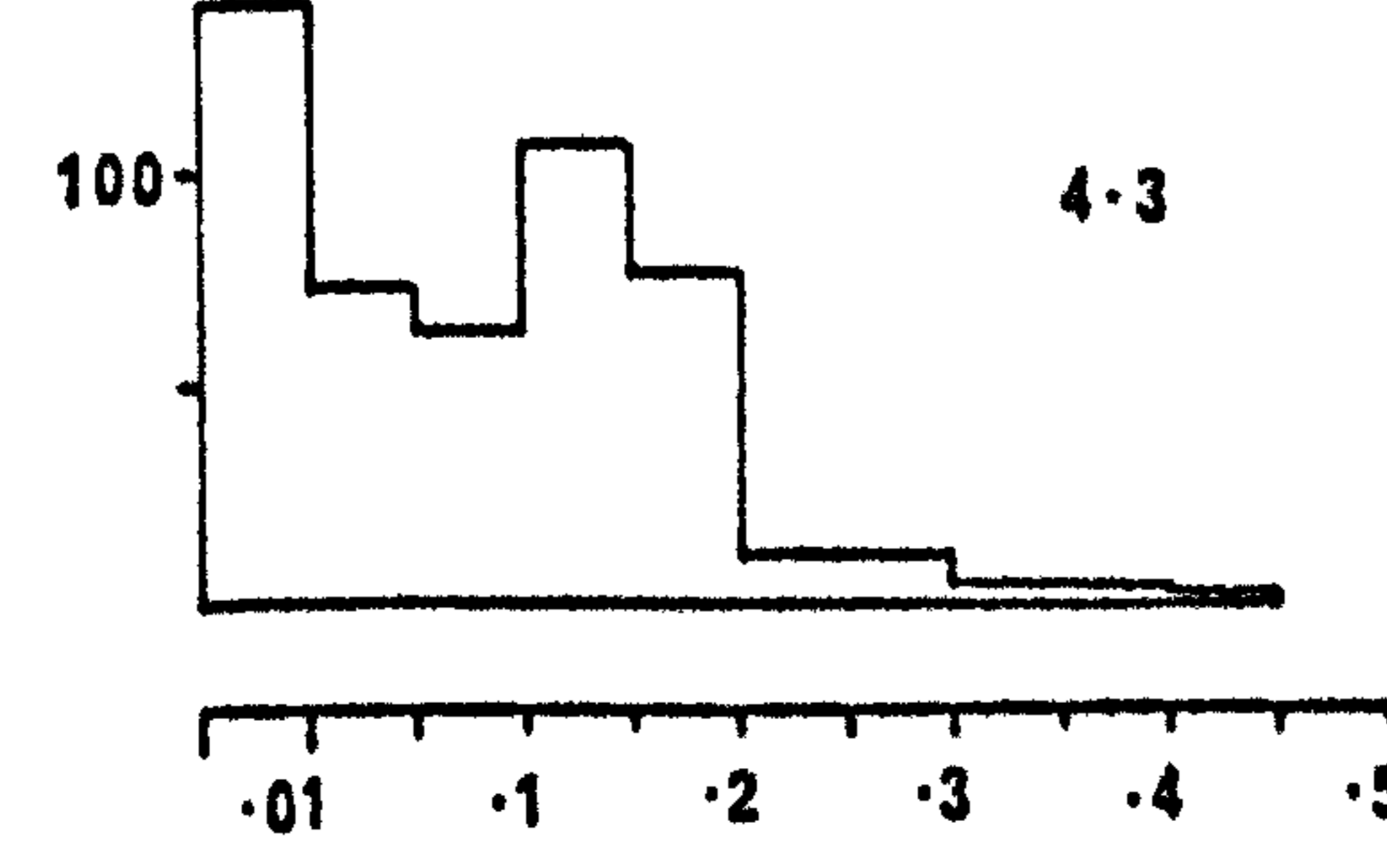
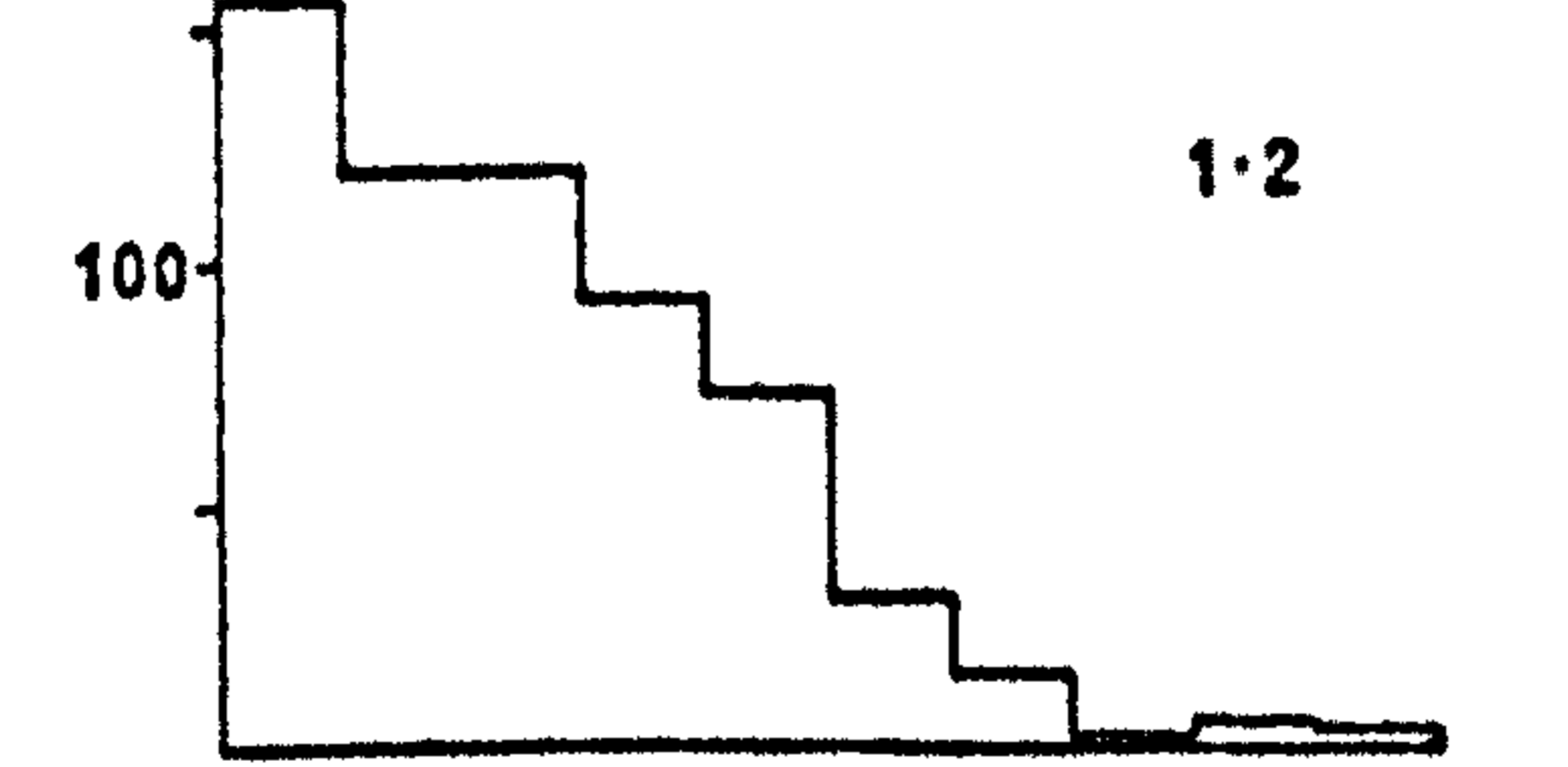
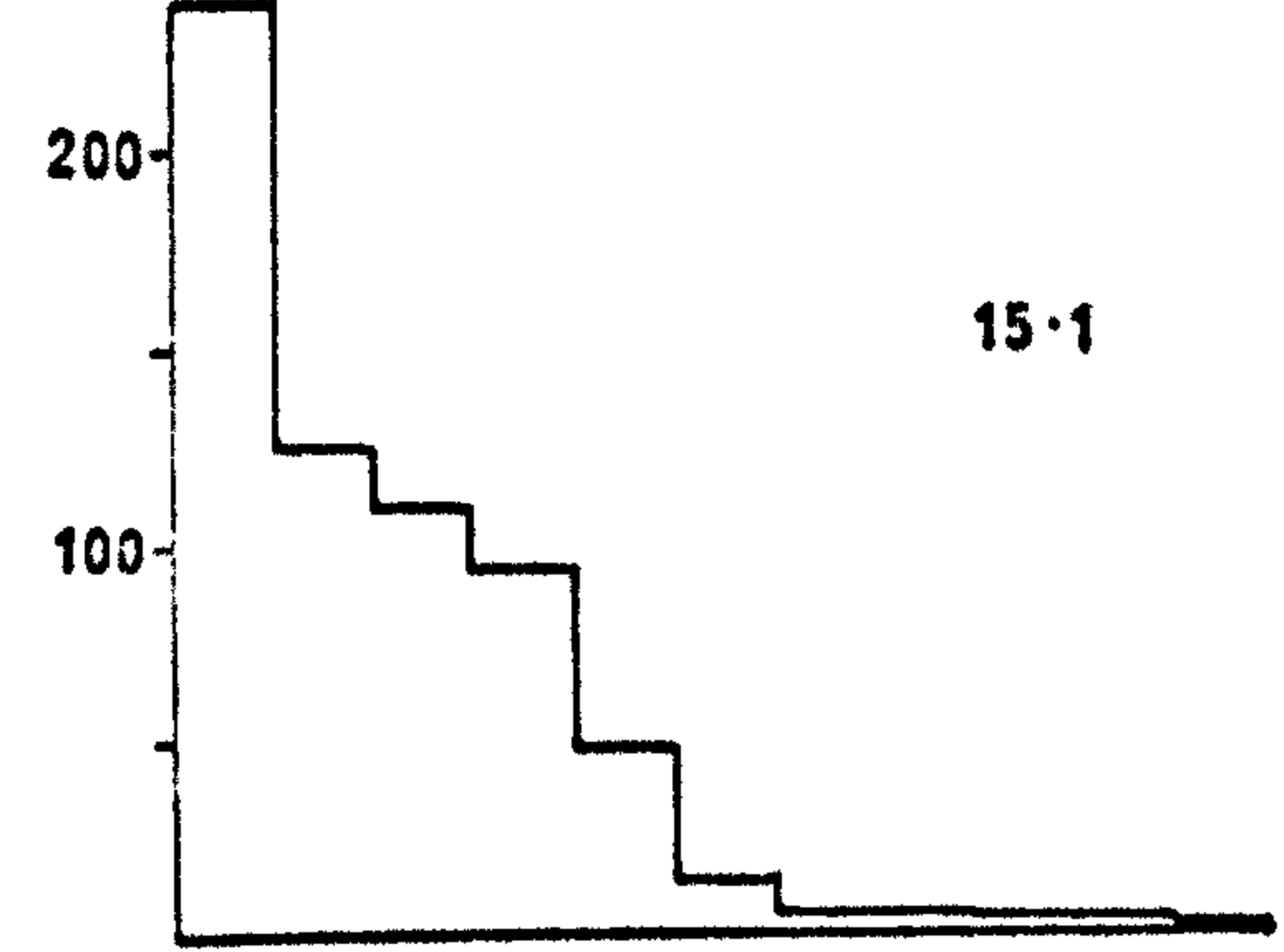
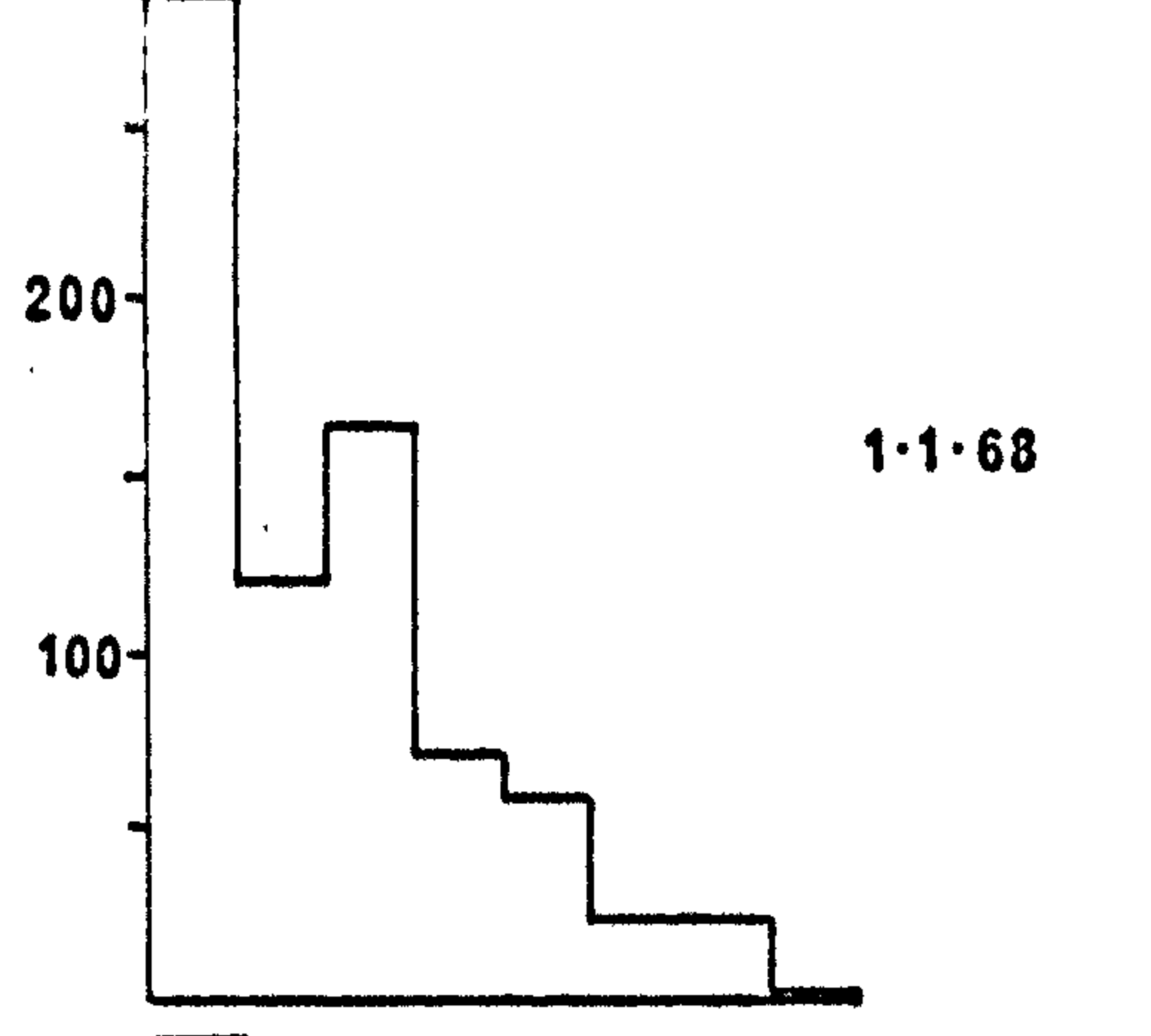
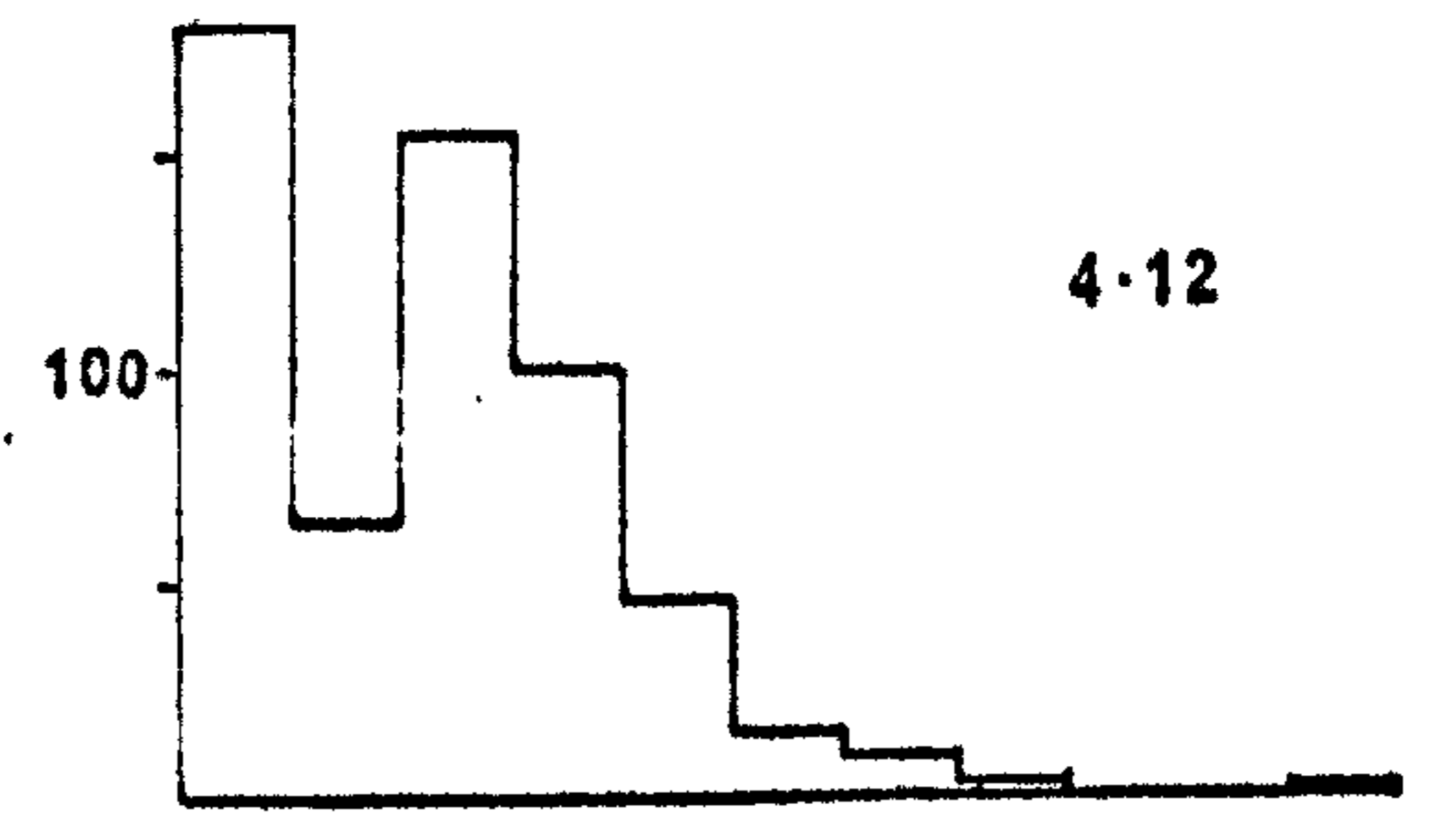
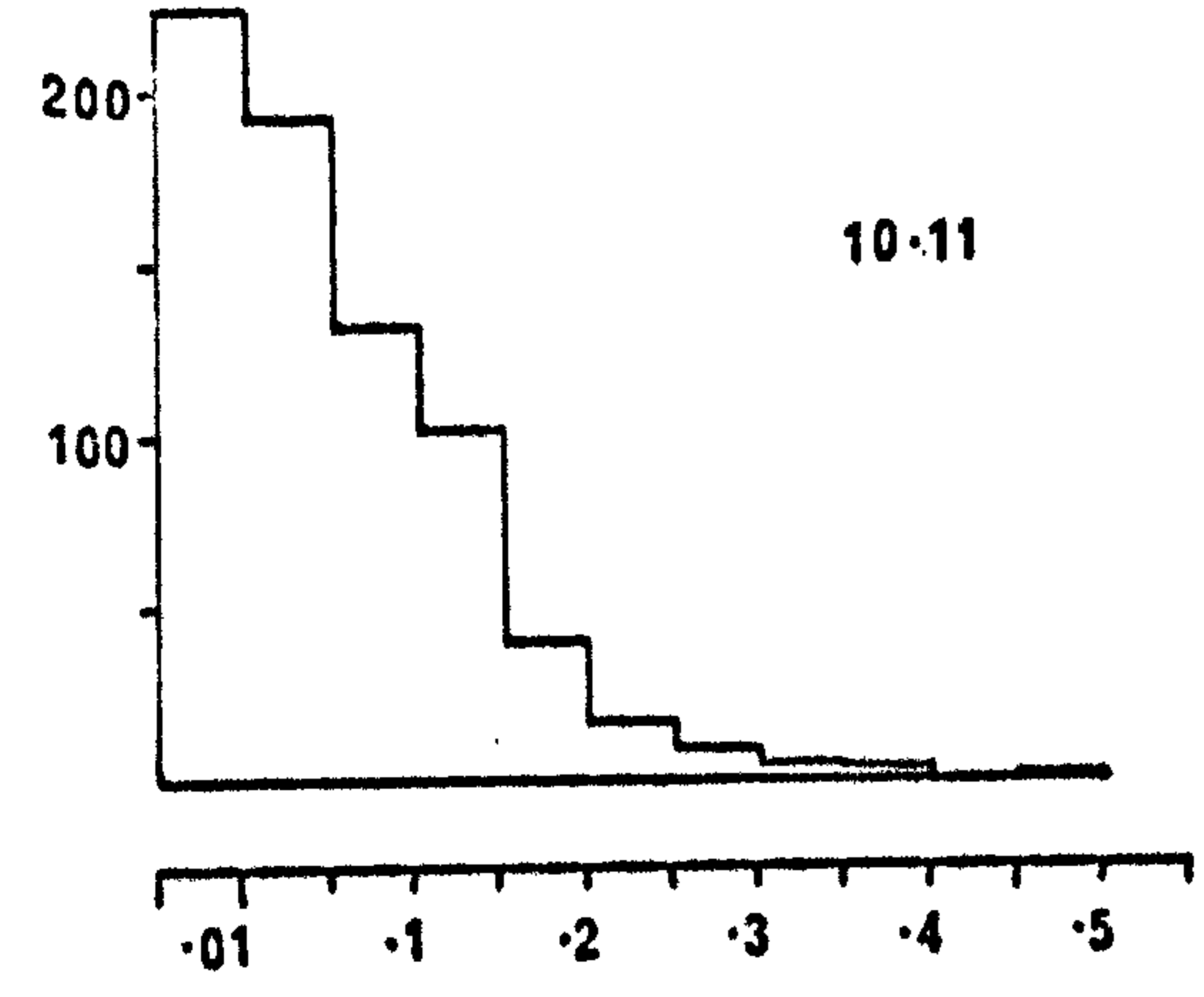
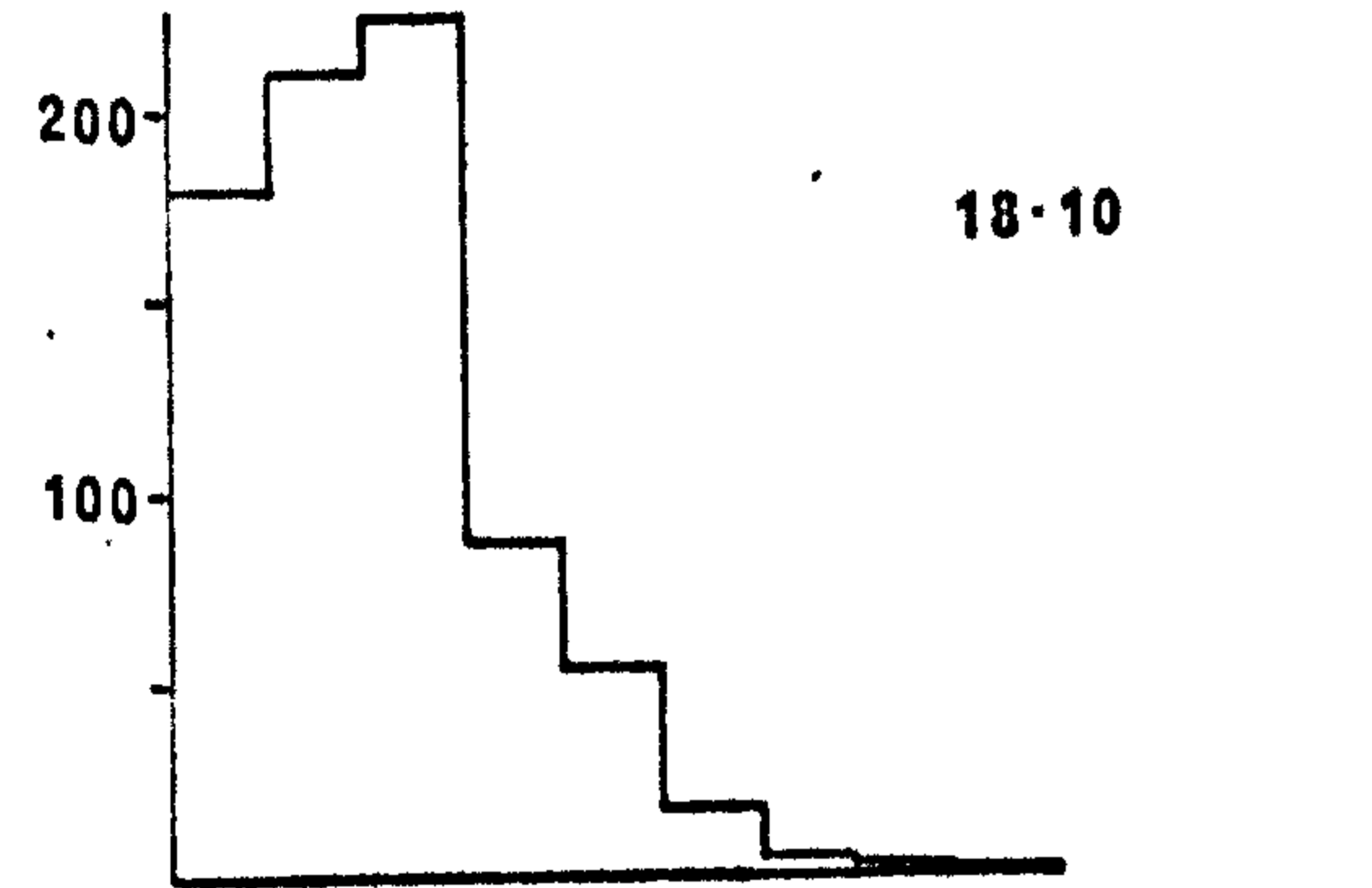
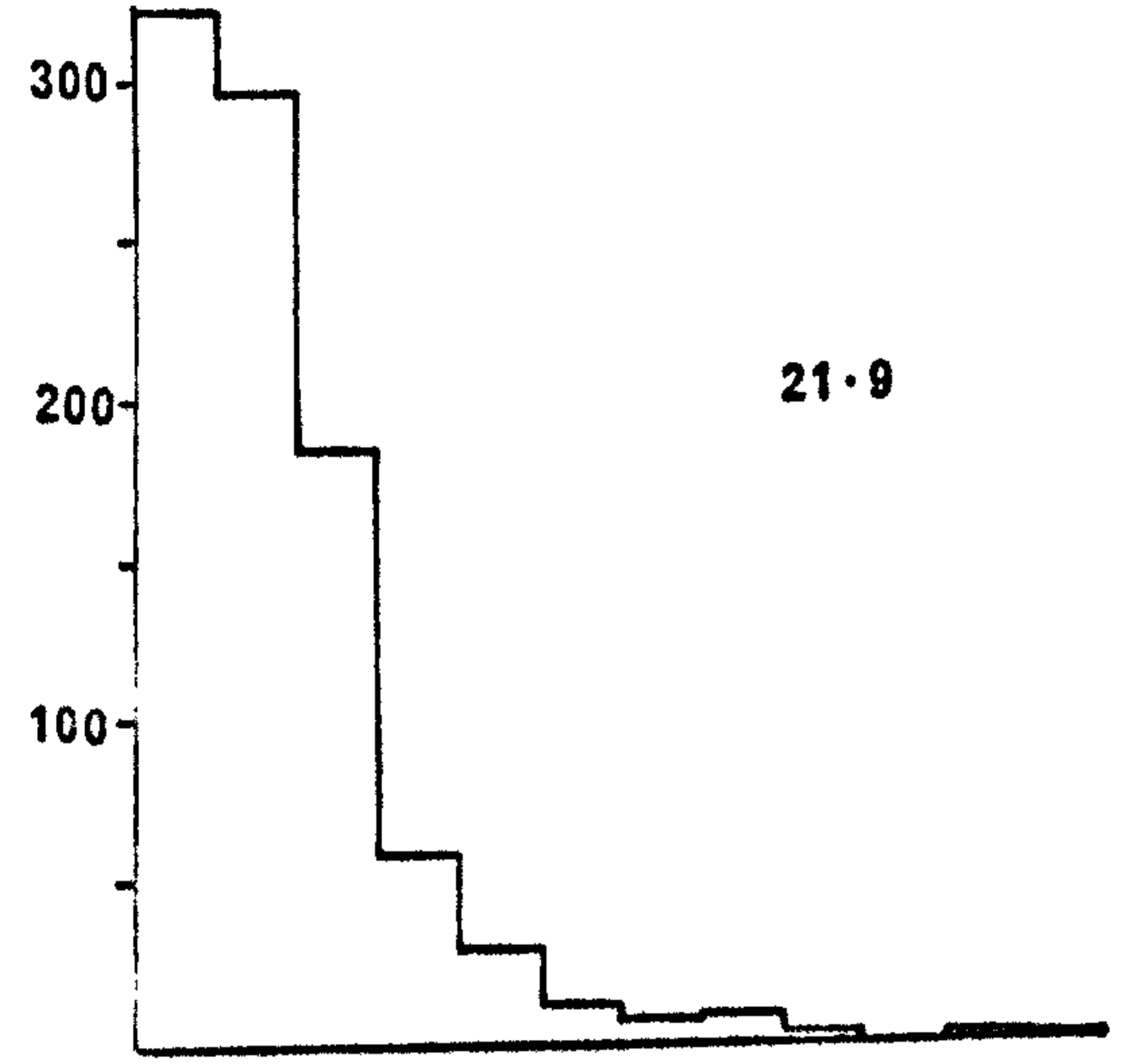
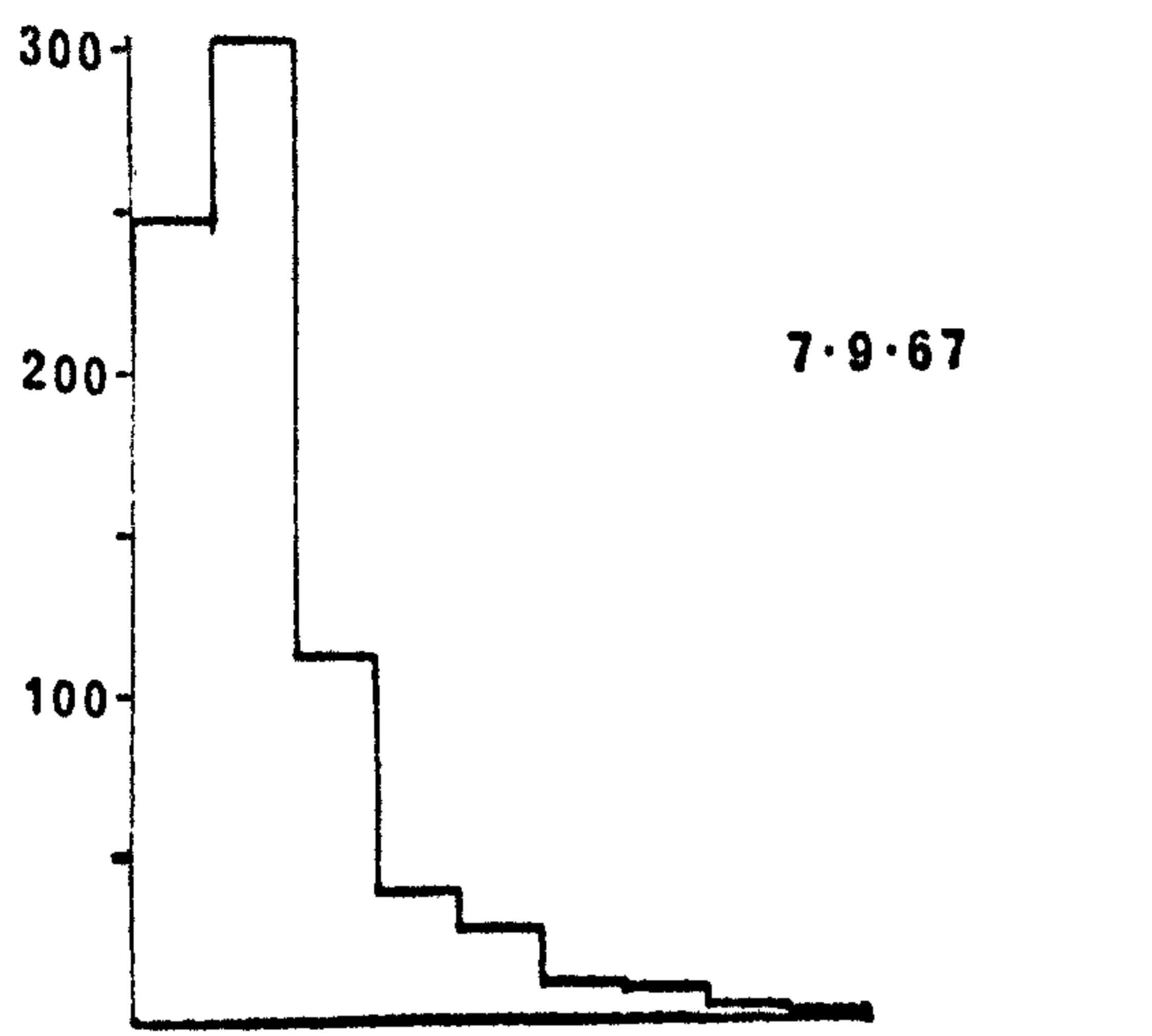
The variance of the parasite index rose from 0.021 on 29.10.66 to 0.03 on 19.11.66 and 10.12.66. It fell to 0.022 on 1.1.67 then rose to 0.025 on 18.2.67. There was then a steady decrease to 0.012 on 21.4.67 followed by an increase to 0.023 on 7.6.67. There was another decrease to 0.014 during July, then another increase to 0.024 on 7.9.67. The value decreased steadily reaching 0.011 on 1.1.68. There was a high value of 0.017 on 15.1.68 then an increase from 0.011 on 1.2.68 to 0.016 on 25.3.68. Finally the variance decreased to 0.012 on 9.4.68.

C. Weight of individual plerocercoids

The individual weights of all plerocercoids in all the fish in a sample gave a useful indication of changes in the Schistocephalus population. Means were calculated and plotted for each sample. Also frequency distributions of weights were formed by collecting worms into groups. The

FIG. 30 Plerocercoid wts





-.01 .1 .2 .3 .4 .5

-.01 .1 .2 .3 .4 .5

-.01 .1 .2 .3 .4

first of these was for worms whose weights were ≤ 0.01 g. These small worms were taken separately so that the appearance of new infections was obvious. Other groups were 0.02-0.05 g, 0.06-0.10 g, 0.11-0.15 g etc. The frequencies of the first four groups were plotted against date of sample (Fig. 31).

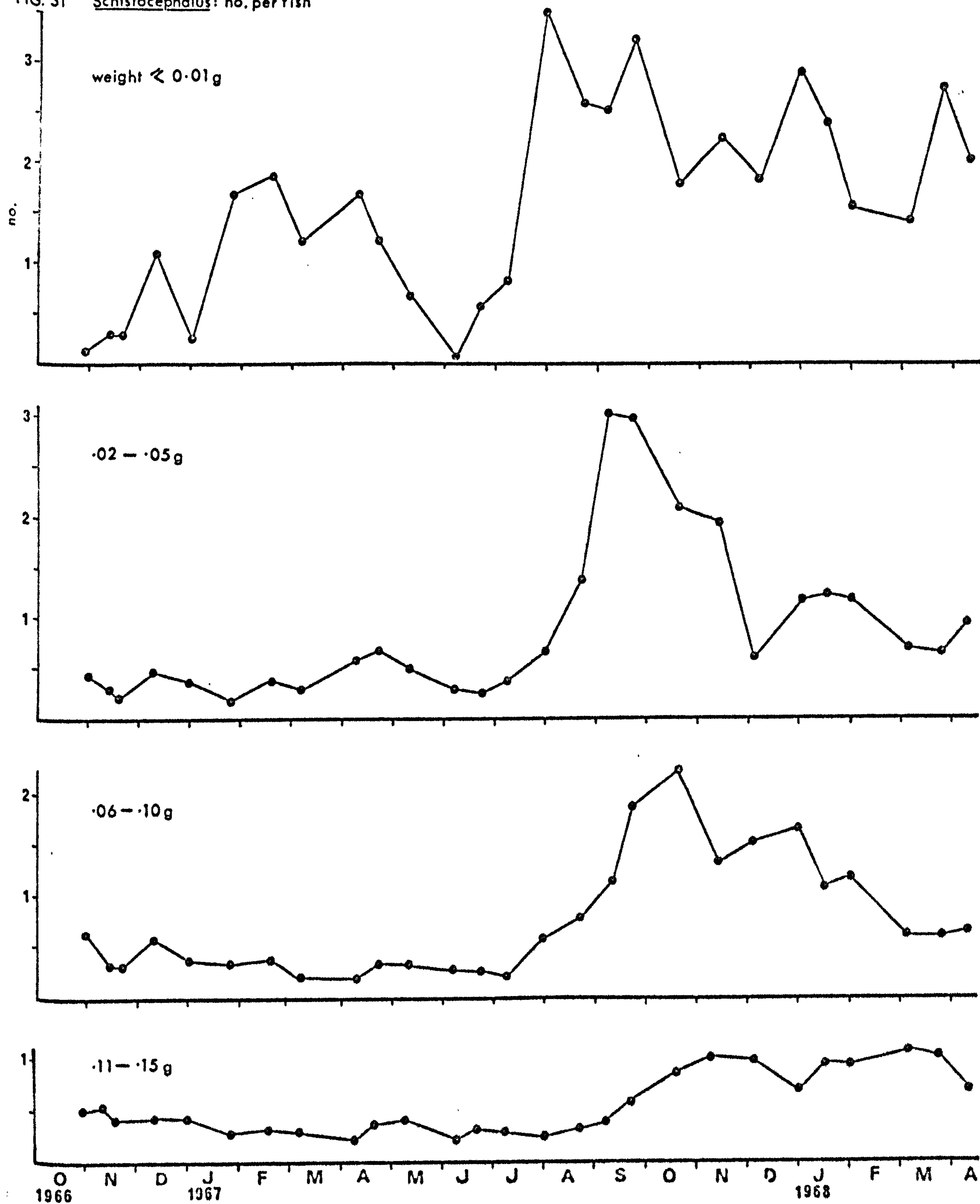
1. Mean (Fig. 28c)

The mean weight of all plerocercoids was 0.078 g. The mean plerocercoid weight decreased from 0.145 g on 29.10.66 to 0.073 g on 10.12.66. There was a high value of 0.125 g on 1.1.67 followed by a decrease to 0.078 g on 18.2.67. There was a fairly steady increase to a maximum of 0.152 g on 7.6.67 followed by a steady decrease to a minimum of 0.051 g on 31.7.67. The mean increased slowly to 0.077 g on 4.12.67, fell to 0.065 g on 1.1.68 and then rose again to 0.091 g on 4.3.68. There was a final decrease to 0.066 g on 25.3.68 and then a slight increase to 0.072 g on 9.4.68.

2. Frequency distributions (Figs. 30, 31.)

Initially most plerocercoids weighed between 0.02 and 0.2 g, and there were very few small ones. In December there was an increase in numbers of worms weighing up to 0.01 g. There were fewer in this group on 1.1.67, but more again on 25.1.67 and 18.2.67. The rest of the distribution was fairly flat with a long tail, that is there were some worms with high

FIG. 31 Schistocephalus: no. per fish



weights. In March and April there were fewer worms in the first group but more weighing 0.02-0.05 g, due to growth of the plerocercoids. The numbers of small worms then decreased until 7.6.67 after which there was a marked increase in numbers of worms weighing up to 0.01 g until the end of July. Heavier worms increased in numbers gradually as growth occurred; group 0.02-0.05 g reached a maximum in September, 0.06-0.1 g in October and 0.11-0.15 g in November. After these maxima the numbers in each group declined as the worms increased in size further. In January 1968 and again in March the number of plerocercoids weighing up to 0.01 g increased, with decreases in February and April. Numbers of larger worms increased as growth proceeded.

IV Discussion

Initially the level of infection was quite high although there were few small worms, showing that there had not recently been a new wave of infection. In November 1966 there was a decrease in the level of infection; the number, and more particularly the weight, of Schistocephalus per fish decreased. This could have been due either to heavily infected fish dying, or being eaten by predators, or to the plerocercoids themselves dying within the fish. A number of dead fish was picked up at this time and they had a higher mean number and weight of plerocercoids than the living ones (see p. 48). This was not just due to their being older and

larger as the parasite index was also greater. The mean weight of the individual worms was about the same, however. This shows that the decline in parasite index and mean numbers and weights of plerocercoids per fish was due to heavily infected fish dying. Conditions would have been becoming more difficult in autumn as food became scarcer and the temperature fell. More fish were probably also taken by predators as they would have been weakened and therefore easier to catch.

In December there was an increase in the mean and variance of the numbers of plerocercoids and a decrease in the individual weights, with a large number of small worms appearing. This indicates a new wave of infection, although it was not a very large one for the percentage of infected fish and the mean weight per fish continued to decrease; the new infection was not enough to balance the decrease due to heavily infected fish being removed from the population.

In January 1967 the percentage of fish infected did increase showing that the infection was continuing. At the same time the plerocercoids picked up earlier were growing and their mean weight increasing. The mean number of plerocercoids decreased and so did the variance, and the distribution shows that this was due to a decrease in the number of fish with many plerocercoids. There was no decline in numbers of fish with a high weight of Schistocephalus, however. This suggests that large numbers of small worms are more deleterious than a few

large ones of the same total weight. (See also p. 70). This could be the case as smaller worms would have a higher growth rate and larger surface area for absorption of food.

Therefore the decrease in numbers of fish with large numbers of plerocercoids was due to death of the fish rather than to death of the plerocercoids within the fish. Hopkins and Smyth (1951) suggest that this occurs but provide no evidence to support the theory.

The mean number of parasites per fish increased once again in the latter part of January and in February, although the percentage infection remained more or less constant so that fish must still have been dying. The variance increased rapidly, but these high values were due largely to single very heavily infected fish. The infection was continuing at this time as the mean weight per fish increased slightly while the mean plerocercoid weight decreased; there were many very small worms.

This infection continued throughout March and April and the percentage of infected fish also rose showing that fewer heavily infected ones were being removed from the population. The mean number and weight per fish and the parasite index were fairly constant suggesting that the infection was only light.

During May the male fish were setting up territories around the edge of the pond and beginning to breed. These fish

were lightly infected (see p. 43) and the decreases in percentage infection, mean numbers and weights at this time were probably due to change in behaviour of the fish, resulting in a biased sample, rather than to true changes in the infection. In June and July the infection rose again as breeding was completed and the non-breeding fish returned to the catching area.

At the end of July, and continuing until September, there was a rapid and large rise in the infection. The percentage of fish infected, already high, rose to about 100%. The mean and variance of the numbers rose rapidly; the overdispersion was lower than at other times when the variance was high showing that the increase in numbers of Schistocephalus was due to a general increase in the number in each fish rather than only to an increase in the numbers of fish with many parasites. The mean weight per fish and the parasite index also increased rapidly, but lagged slightly behind the numbers, not reaching their maxima until October. The mean plerocercoid weight was very low. The parasite index did not increase as much as would have been expected from the increase in weight per fish showing that the larger fish were taking relatively more of the parasite burden. The scatter diagrams of parasite index vs. length and weight of fish (see p. 97) show that this was because the parasite index decreased with size of fish in July but was more or less equal in all sizes in September. Hopkins and Smyth (1951) also found large

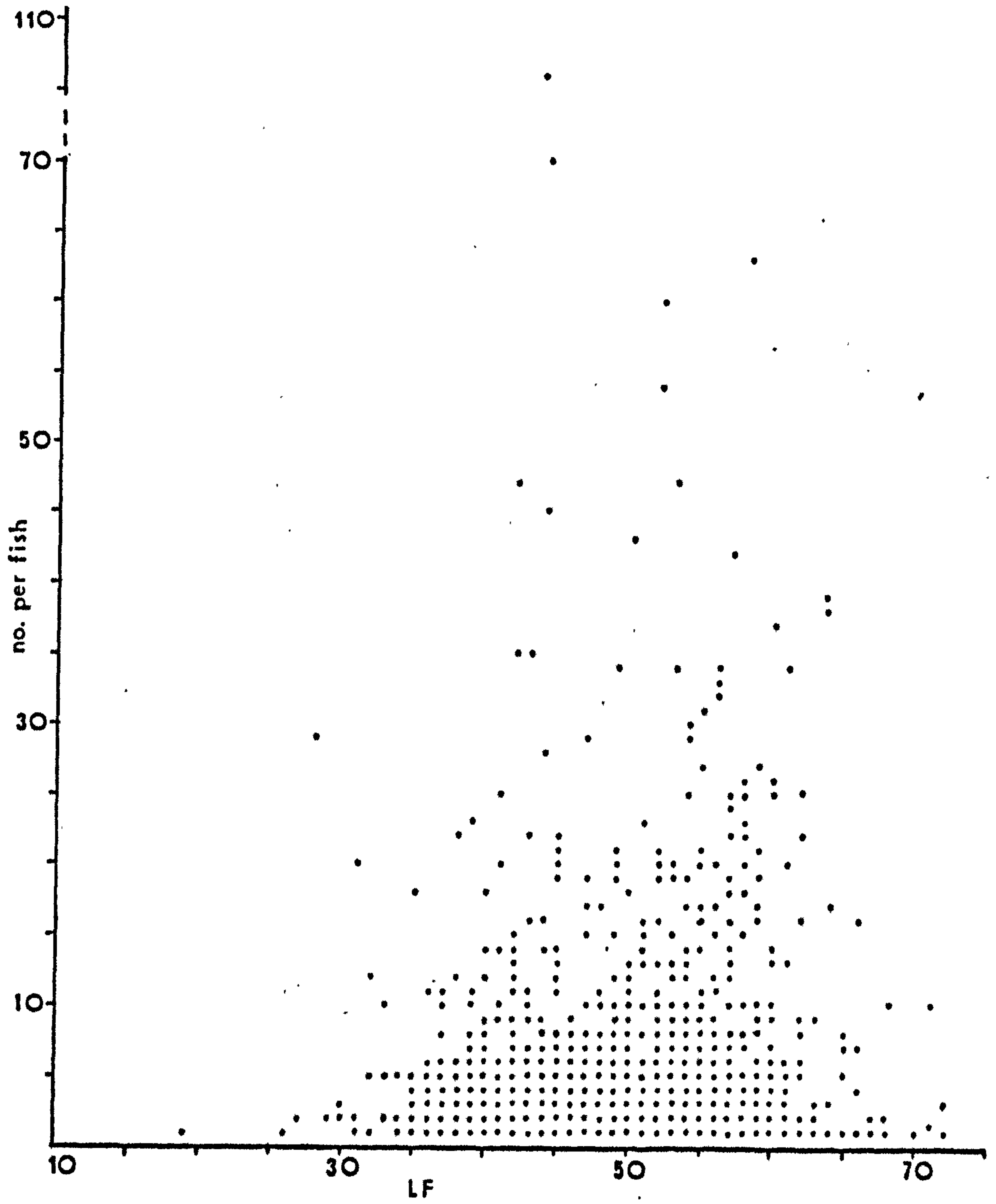
numbers of plerocercoids appearing in their sticklebacks in August.

During the autumn there was a general decline in the numbers and weights of worms per fish due to decrease in the numbers of parasites, particularly smaller ones. At the same time the plerocercoids were growing so that the decrease in mean weight must have been caused by heavily infected fish dying. This is confirmed by the fall in the variances of numbers and weights. Numbers of dead or dying fish were found at this time; the body walls of these fish were very often broken and it was apparent from the distended shape that Schistocephalus had once been present. Of those with intact body walls the mean numbers and weights of plerocercoids were not greater than those of living fish. It would be expected, however, that the larger the bulk of worms the easier it would be for them to break out of a dead fish.

There were two further infections: in January and March 1968. This was shown by the increases in numbers of plerocercoids weighing up to 0.01 g, and decreases in the mean plerocercoid weight. The mean number of worms and the variance increased. Between these infections there was once again a decrease in the mean number and variance, and in the mean weight of plerocercoids per fish. This was due to heavily infected fish dying: the pond was often frozen during these months. Most of the dead fish found were in age group

IV, showing that older fish were affected more than younger ones. Hence the decrease in mean weight was greater as the larger fish had a greater mean weight. This is borne out by the fact that the parasite index remained more or less constant.

FIG. 32 Schistocephalus



DISTRIBUTION IN FISH OF DIFFERENT SIZES

The distributions of the numbers and weights of Schistocephalus among sticklebacks of different lengths and weights were also considered. Scatter diagrams were plotted by the computer for each sample for the following pairs of variables: LF vs NS, LF vs WS, LF vs P.I., WF vs WS, and WF vs P.I.

1. Fish of different lengths

(a) Numbers of Schistocephalus

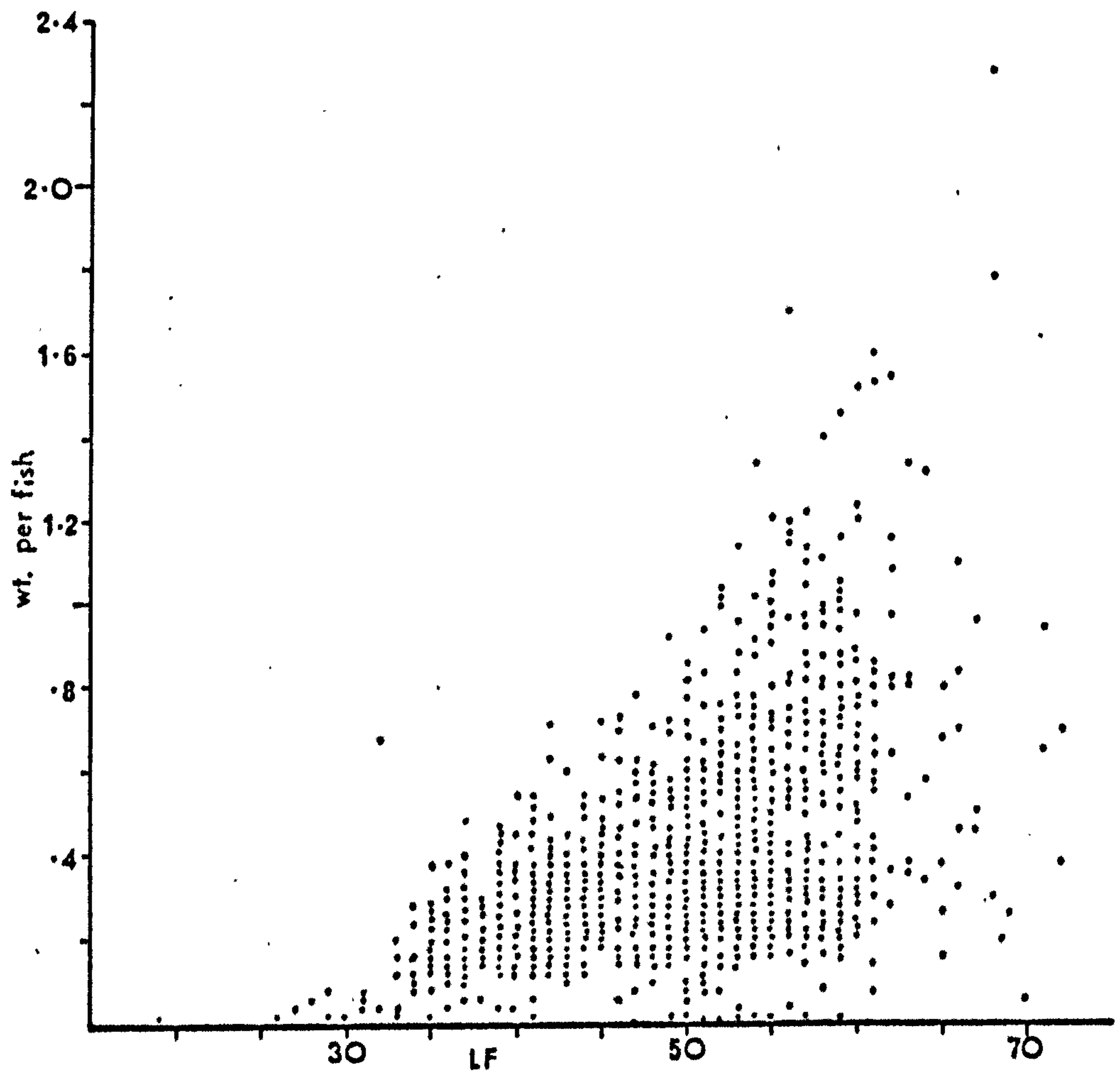
Fig. 32 is a scatter diagram for all fish; each point may represent several fish. Only one fish shorter than 25 mm was infected. Fish between 25 and 35 mm contained small numbers of Schistocephalus, those from 35 - 60 mm had larger numbers, the average increasing slightly with length. In fish longer than 60 mm there was a steady decline in the numbers of plerocercoids.

The maximum number per fish rose fairly steadily to about 60 in fish of 50-60 mm, except for two exceptionally heavily infected fish, one of 43 mm with 106 and one of 44 mm with 70 plerocercoids. The maximum number decreased in longer fish.

(b) Weight of Schistocephalus

The scatter diagram for all fish is shown in Fig. 33. The weight of Schistocephalus rose fairly steadily with length

FIG. 33 Schistocephalus



of fish and there was only a slight decrease in mean in the longest fish. There was a noticeable dearth of fish with less than about 0.1 g of Schistocephalus, due to the rapid growth of plerocercoids in the fish.

The maximum weight rose steadily with length. When this was compared with the maximum weight of fish, including uninfected ones, it was seen that the maximum Schistocephalus weight was slightly less than the maximum fish weight for nearly all lengths; this difference was greater in longer fish.

(c) Parasite index

Fish of all sizes had about the same range of parasite indices. The maximum for fish between 30 and 60 mm was greater than 0.5, and in a few cases greater than 0.6. There were few fish from 30-50 mm with a very low parasite index; the minimum was between 0.1 and 0.2. Fish between 50 and 60 mm more often had a parasite index of less than 0.1.

2. Fish of different weights

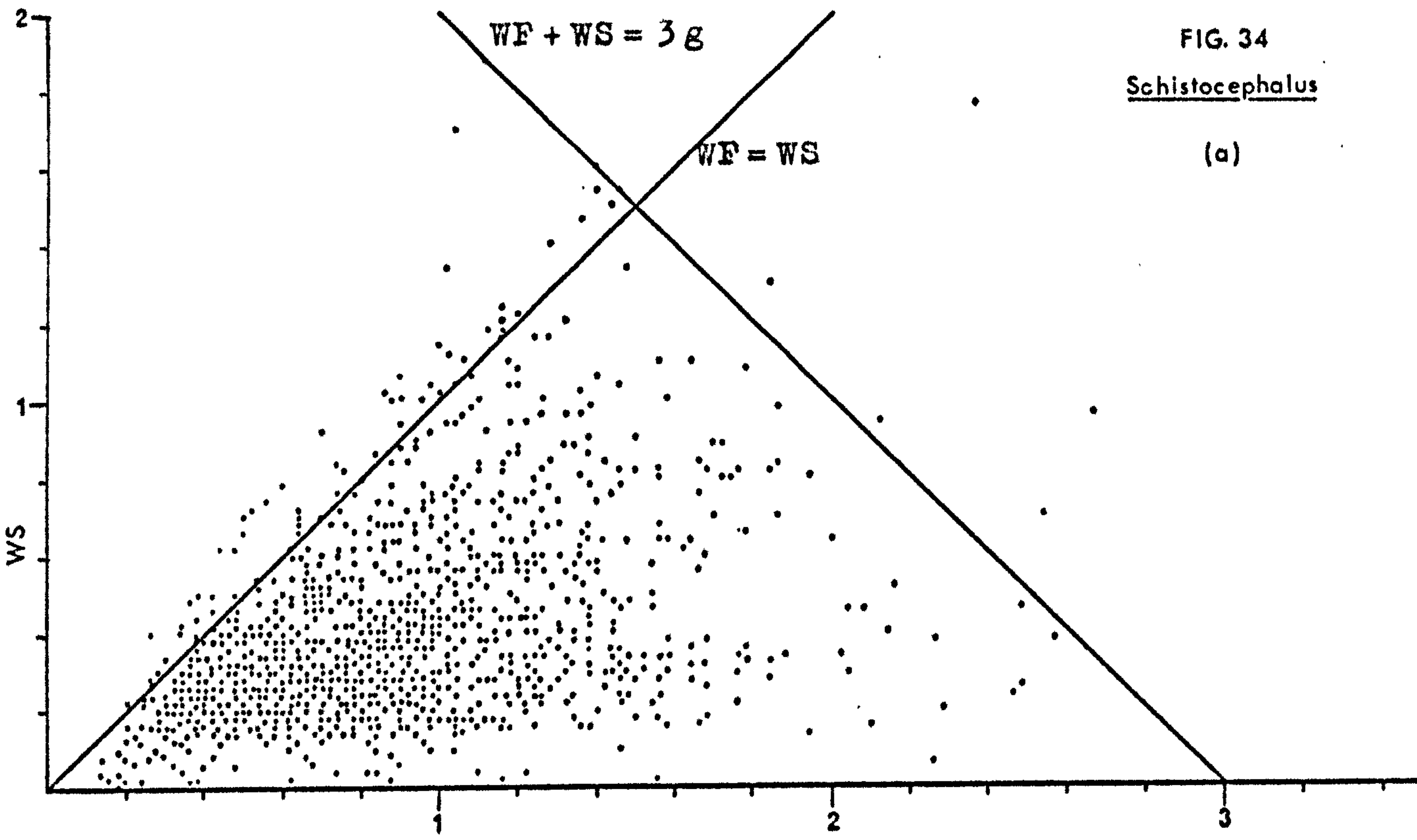
(a) Weights of Schistocephalus

The weight of fish is plotted against weight of Schistocephalus for all fish in Fig. 34a. The maximum weight of Schistocephalus rose steadily with weight of fish, being slightly higher, until the weight was 1.5 g. There was then a steady decrease in the maximum as the fish weight increased, except for a few cases. The value of WF + WS was less than

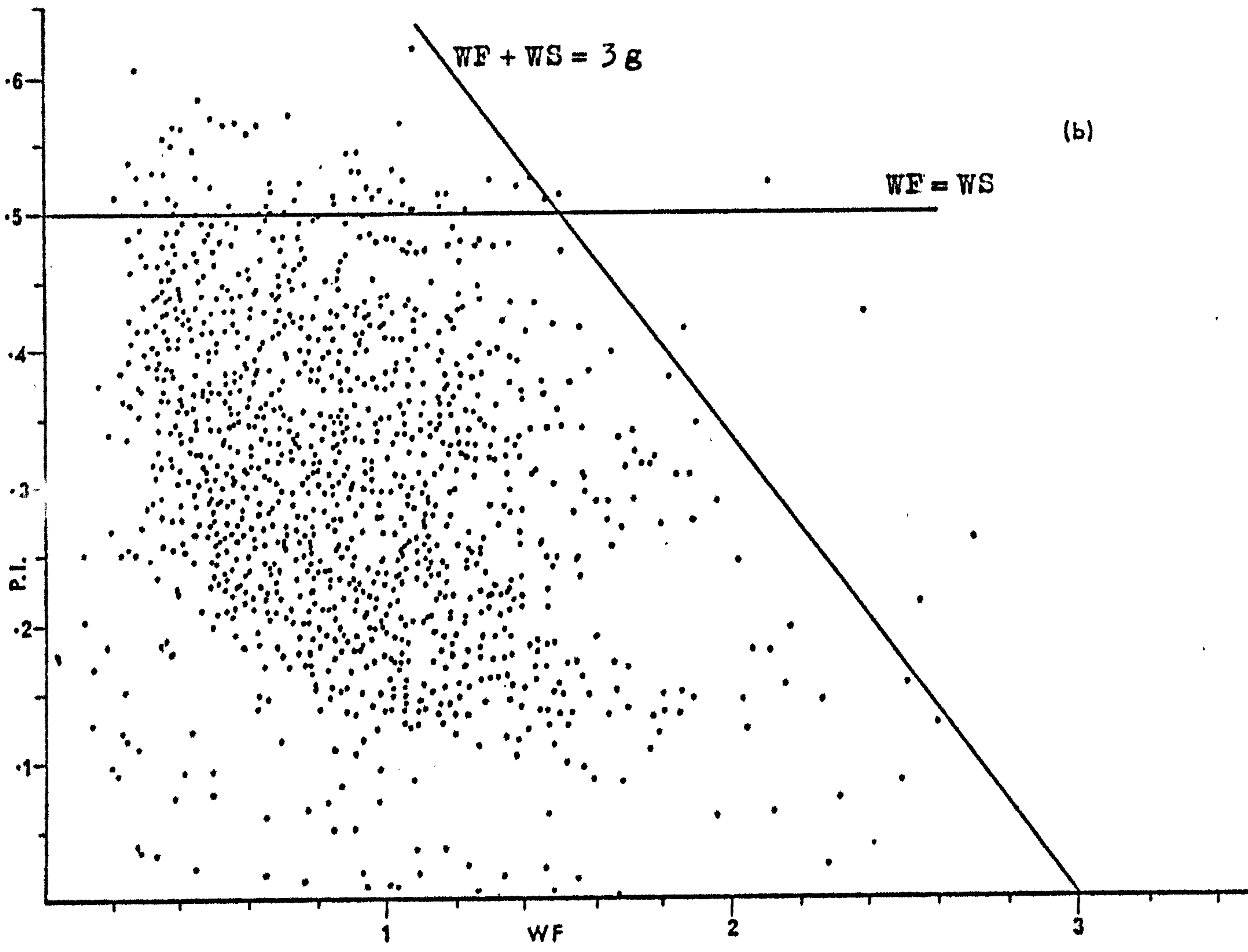
FIG. 34

Schistocephalus

(a)



(b)



3 g in all but 6 infected fish; the maximum weight of an uninfected fish was 3.13 g.

The minimum weight of Schistocephalus increased with weight of fish; otherwise the points were fairly evenly distributed up to the maximum, for all weights of fish.

(b) Parasite index

The scatter diagram for all fish is shown in Fig. 34b. There were few fish with weights less than 0.2 g and these all had low values of the parasite index. The maximum P.I. was at its highest in fish weighing between 0.4 and 0.8 g; it then decreased slightly in fish up to 1.5 g. There was a more rapid fall in the maximum P.I. in fish heavier than this. Once again it can be seen that the maximum WF + WS rarely exceeded 3 g.

Fish weighing 0.2 g mostly had a P.I. greater than 0.25. As the weight of fish increased the lower value of the P.I. decreased until in fish of 0.8 g it was about 0.1, after which it remained about the same. Thus in fish heavier than 0.2 g the P.I. decreased as fish weight increased.

Therefore the sticklebacks could not support a weight of Schistocephalus very much greater than their own weight. Once the weights were about equal the parasites were taking so much food that the fish was no longer able to maintain its own weight and thus became emaciated and eventually died.

It was also found that the total weight of fish plus parasites was rarely greater than 3 g. This limit was imposed by the total amount of food which a fish was able to find and digest. Thus a very large fish was able to support only a small weight of Schistocephalus because its own requirements were such that there was little excess food available for the parasites.

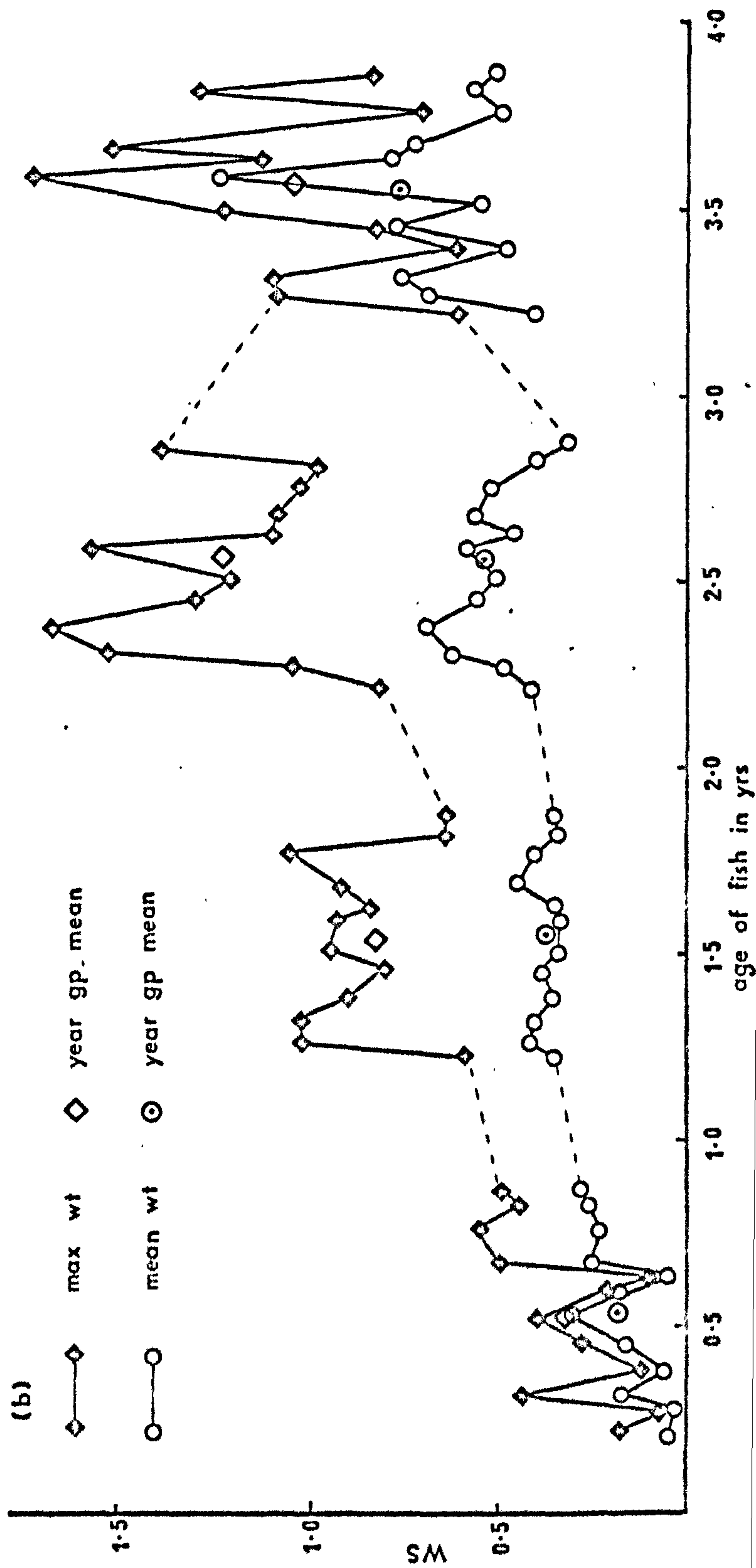
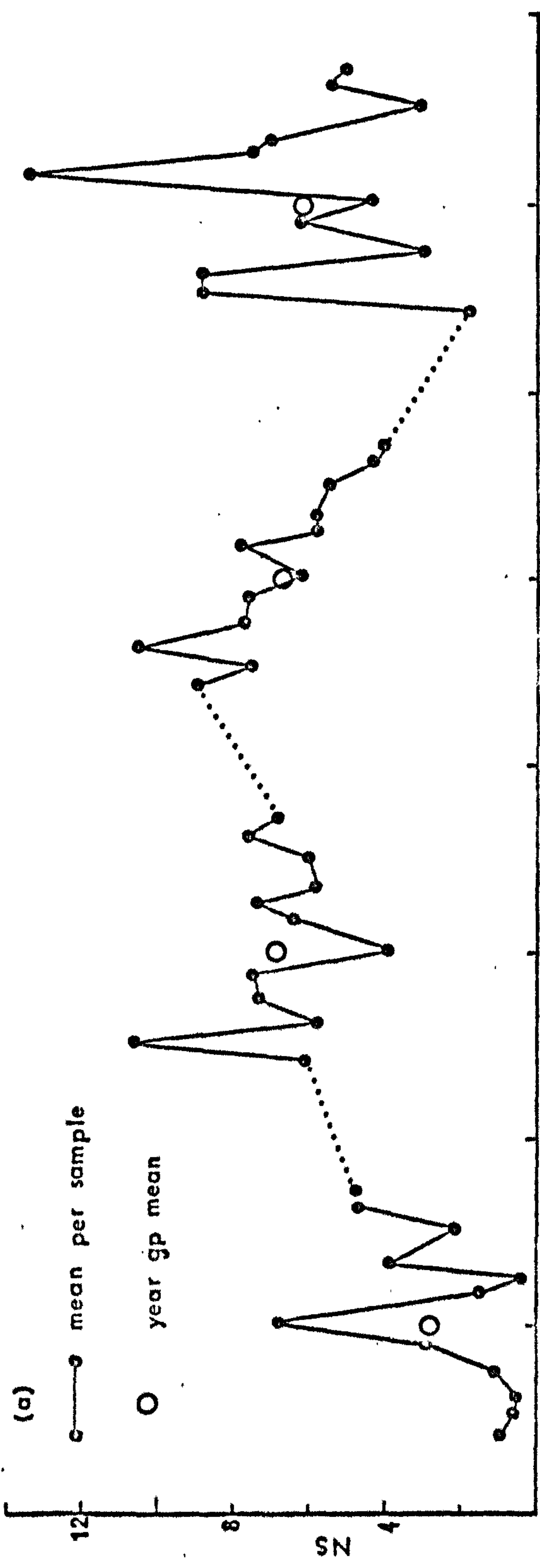
Arme and Owen (1967) found that the numbers of Schistocephalus tended to decrease with increasing size of stickleback, although this is not a very clear trend due to their size-groups being rather broad. It is, however, obvious that the largest fish did have fewer worms, as was found in the Priddy fish.

Their data also show a decrease in P.I. with increasing weight of fish. In the first sample of June 1962 when the infection was exceptionally heavy (see also p. 58) the mean P.I. decreased steadily from 0.65 in fish weighing less than 2 g to 0.33 in fish weighing over 5 g. All other samples showed similar decreases, though the levels were lower. Very few fish had a P.I. of less than 0.1. From their table 3 it is seen that few fish had weights of more than 3 g, except in the first exceptional sample where 75% of the sticklebacks weighed over 3 g.

Thus in general the relationships between size of sticklebacks and numbers and weights of Schistocephalus were

the same in the data of Arme and Owen as in those from Priddy.

FIG. 35 *Schistocephalus*



DISTRIBUTION IN FISH OF DIFFERENT AGES

(a) Numbers of Schistocephalus

The mean number of plerocercoids per fish was calculated for each age group of each sample and is plotted in Fig. 35a. The mean number increased with age in age group I, remained fairly constant in group II and decreased in groups III and IV. This shows that the decrease in population mean occurring at this time was due largely to the death of heavily infected fish in age groups III and IV. The overall mean for each age group was higher in group II than group I and then decreased in groups III and IV.

(b) Weight of Schistocephalus

The mean weight of Schistocephalus for each age group of each sample is plotted in Fig. 35b. The value of the mean increased with age in age group I, was more or less constant in group II and increased then decreased in group III. The values for group IV were rather variable as the numbers of fish were small, but decreased in the last six samples. The mean for the whole population increased between August and October 1967 (the first four aged samples) and then decreased until April 1968. The increase was due to increases in all groups except II, and the decrease to decreases in only the last two groups. This shows that fish in groups III and IV with large weights as well as large numbers of Schistocephalus

were dying between November 1967 and April 1968. The overall mean for each age group increased steadily with age.

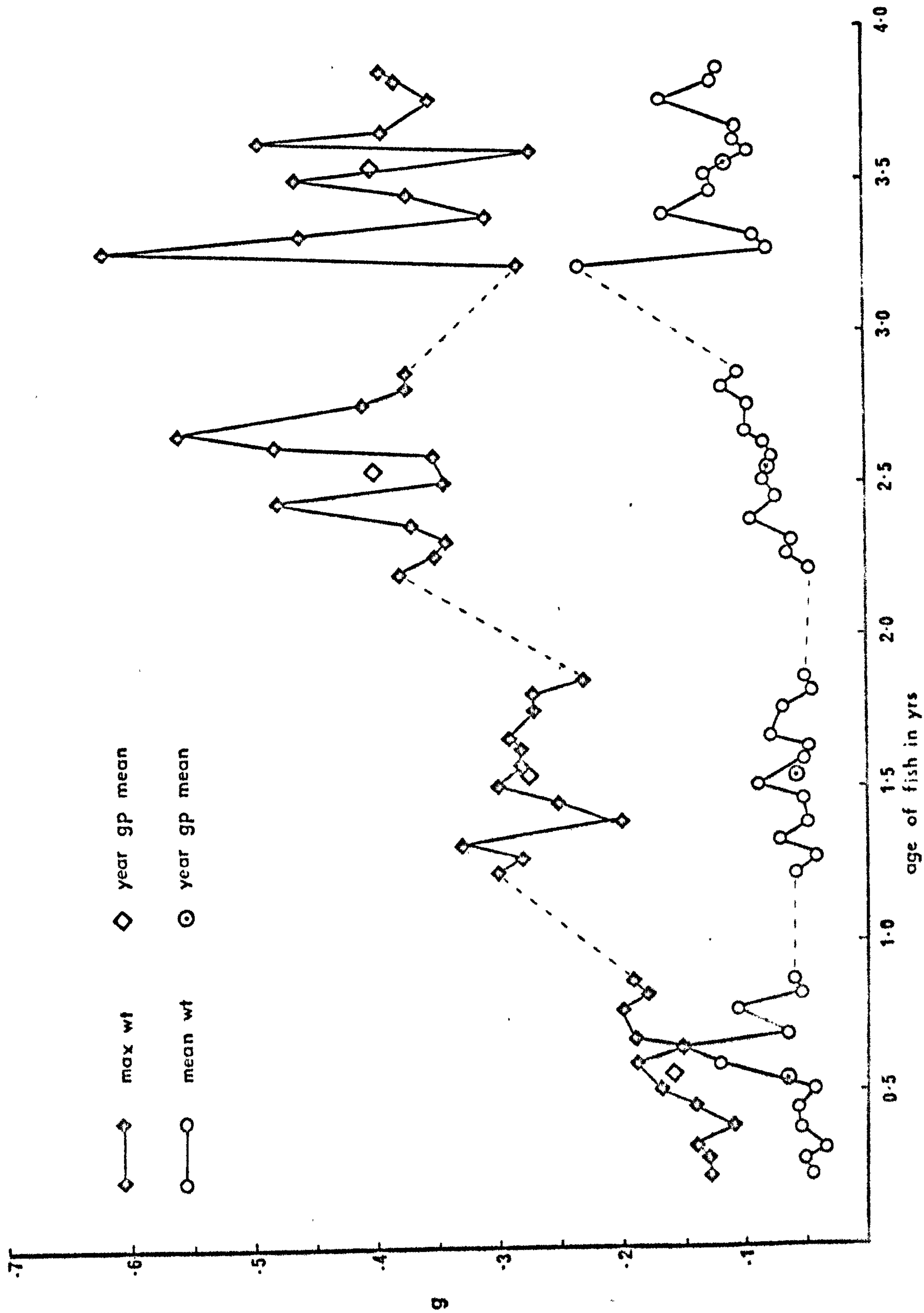
The maximum weight of Schistocephalus for each age group of each sample is also plotted in Fig. 35b. This followed a similar pattern to that of the mean, except that variations from sample to sample tended to be larger. The decrease in maximum in the last two groups again showed that the number of heavily infected fish was declining. The mean maximum per age group increased in the first three groups and was then lower in age group IV. This shows that the largest weights of Schistocephalus were not found in the oldest fish.

(c) Plerocercoid weight

The mean weight of individual plerocercoids for each age group of each sample is plotted in Fig. 36. The weight tended to increase with age in all age groups, although I and IV had quite large fluctuations; the increase was most marked in group III. There was a small decrease in the last one or two samples. This was the pattern for the population as a whole: a steady increase until March 1968 and then a slight decrease. The overall mean for each age group was higher in group I than group II, but then increased in III and IV, although the differences were small.

The maximum plerocercoid weights are also plotted in Fig. 36. In age group I there was a steady increase with

FIG. 36 Pteroceroid wts



age, in groups II-IV there were fairly large fluctuations but no very clear trends. The average maximum for each age group increased in the first three groups and was then about the same in the final two.

Thus the weight of individual plerocercoids increased with age, at least up to age group III, showing that the worms could live for up to three years in a fish, and continued to grow throughout this time. The maximum weight gave an indication of growth rate of the plerocercoids although the maximum rate was probably higher as most fish were multiply infected.

Thus the numbers of Schistocephalus increased with size and age of fish up to a certain point, and then decreased again. The largest and oldest fish could not support the greatest numbers of plerocercoids.

The mean weight of Schistocephalus increased fairly steadily with length and age of fish, but with weight only up to 1.5 g after which it decreased steadily. However the maximum weight was lower in the longest and oldest fish as well as in the heaviest. The length and age of fish therefore have little effect on the proportional weight of Schistocephalus that can be supported, except that older fish are less able to support very high weights. However, as the total WF + WS could not exceed 3 g the weight of Schistocephalus decreased steadily as weight of fish increased after 1.5 g.

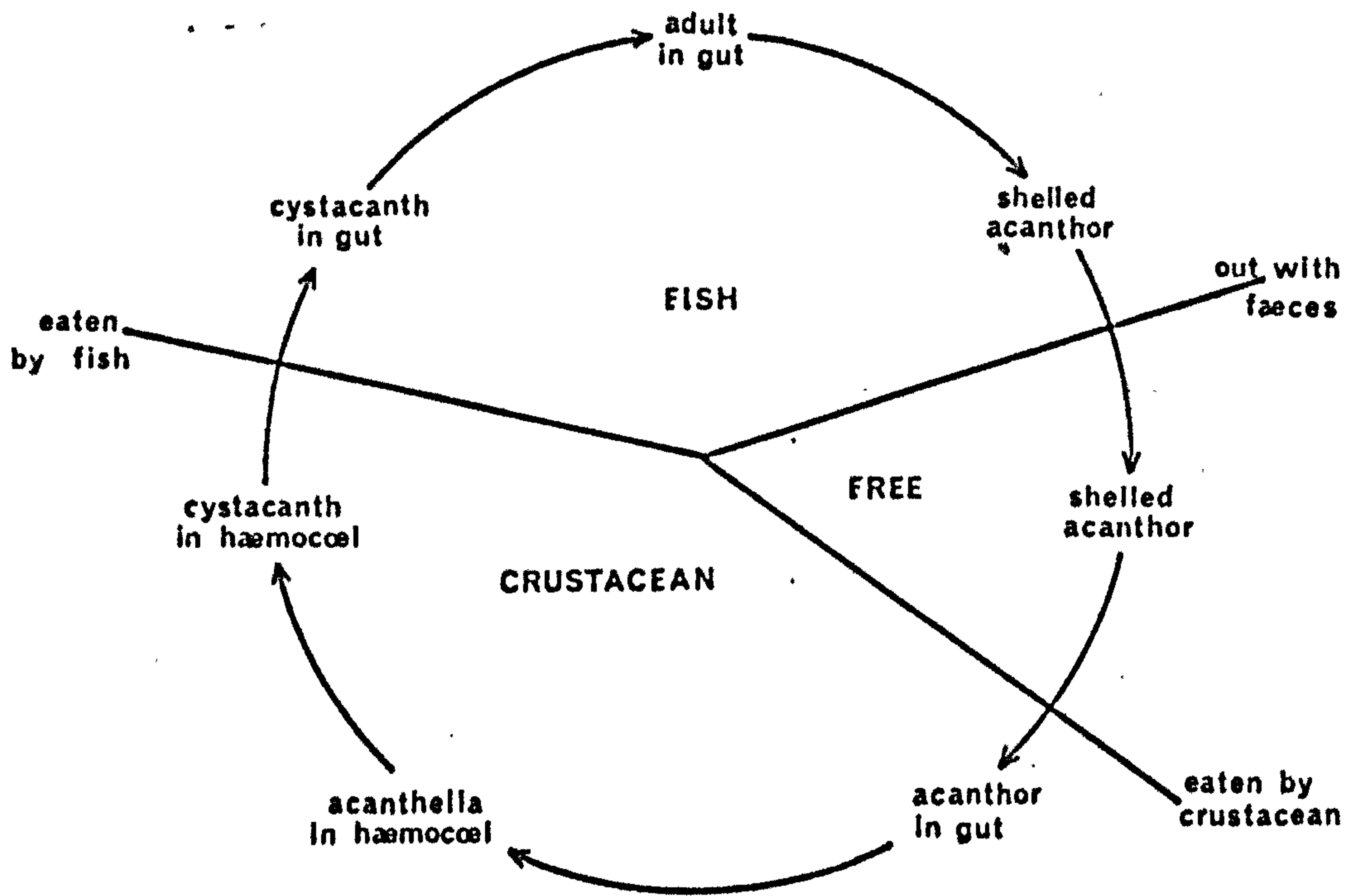
III ECHINORHYNCHUS CLAVULA (Dujardin, 1845) nec Hamann, 1892

LIFE CYCLE

This is an Acanthocephalan of the family Echinorhynchidae. It is the only one of the three parasite species found for which Gasterosteus is the definitive host. The worm lives as an adult in the intestine of the fish with its spiny proboscis embedded in the epithelium. The sexes are separate and copulation occurs. Males have a shorter life-span than females and are therefore less numerous; they may die after one copulation (Chubb, 1964). Unlike some Acanthocephala Echinorhynchus clavula lives for some time in its definitive host.

Fertilised eggs develop into shelled acanthors in the female and pass out with the faeces of the fish. The acanthors hatch quickly if the eggs are ingested by the intermediate host. The acanthor bores through the gut and develops in the body cavity, first into an acanthella and finally to a cystacanth. Six to twelve weeks are required for complete development. Chubb (1964) found cystacanths in Asellus meridianus and states that Gammarus pulex pulex and Pontoporeia affinis have been recorded as intermediate hosts. As none of these three species was found at Priddy, either in the pond or in the fish's guts, the identity of the intermediate host is not certain. However, Asellus was present in the pool in large numbers shortly before this study was

LIFE CYCLE of. ECHINORHYNCHUS



commenced (see p. 40), and was probably still there in small numbers.

If the crustacean host is then eaten by a stickleback the adult develops. Other fresh water fish can also act as the definitive host; Chubb found them in grayling, pike, roach and eels in Bala lake. He found that predatory fish could become infected by eating an infected fish.

PATHOLOGY

The spines on the proboscis cause physical irritation of the gut, but Chubb (1964) found that there was no inflammatory or other reaction by the epithelium. The worms must also take a certain amount of the fish's food, but this is probably significant only in heavy infections.

SEASONAL DISTRIBUTION

The measurements made on the Echinorhynchus were numbers of males and females per fish, and hence total numbers, length of each worm, and presence or absence of shelled acanthors in females. The figures are given in appendix 2 d.

I Percentage infection (Fig. 37a)

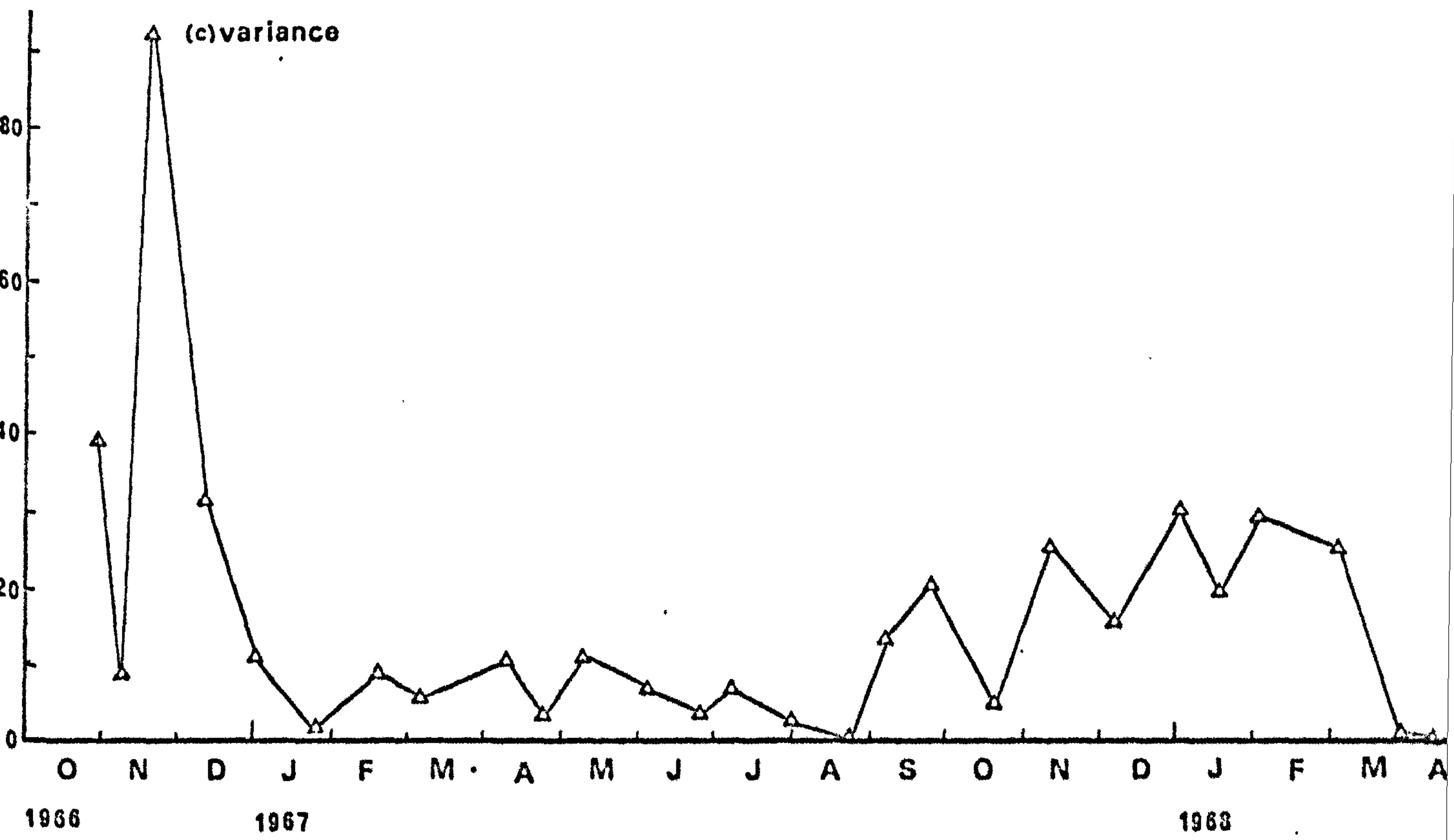
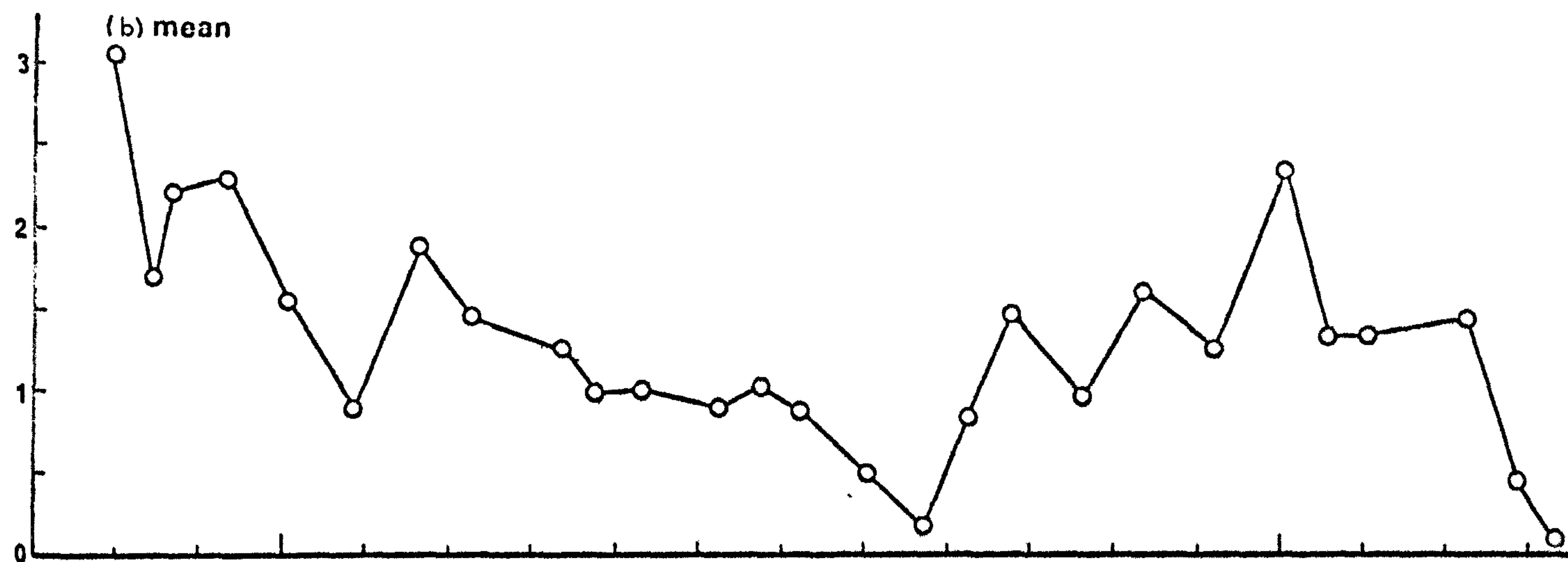
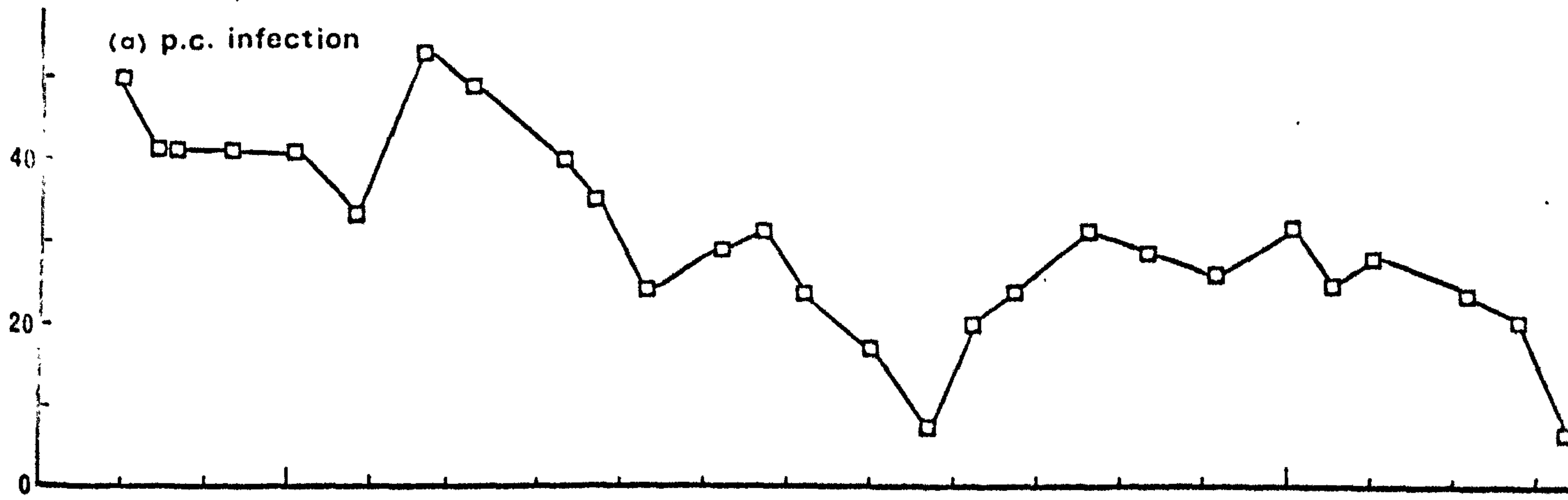
The percentage of all fish infected was 31.5%. 50% of sticklebacks were infected with Echinorhynchus on 29.10.66. The percentage fell to about 40% during November and December and then declined further to 33.3% on 25.1.67. There was then a rise to 52.7% on 18.2.67 followed by a fairly steady fall to 7.6% on 21.8.67. The percentage of fish infected rose to a level of around 30% by October and then fluctuated about this level until January 1968 when it fell rapidly once more, to 6.6% on 9.4.68, about the same level as in the preceding August.

II Numbers of Echinorhynchus per fish

A. Total numbers

The mean and variance of the total numbers of Echinorhynchus per fish were calculated for each sample. The figures were collected into frequency distributions which were plotted in log x 2 classes expressed as percentages. Theoretical distributions were calculated and compared with the originals.

FIG. 37 Echinorhynchus nos.



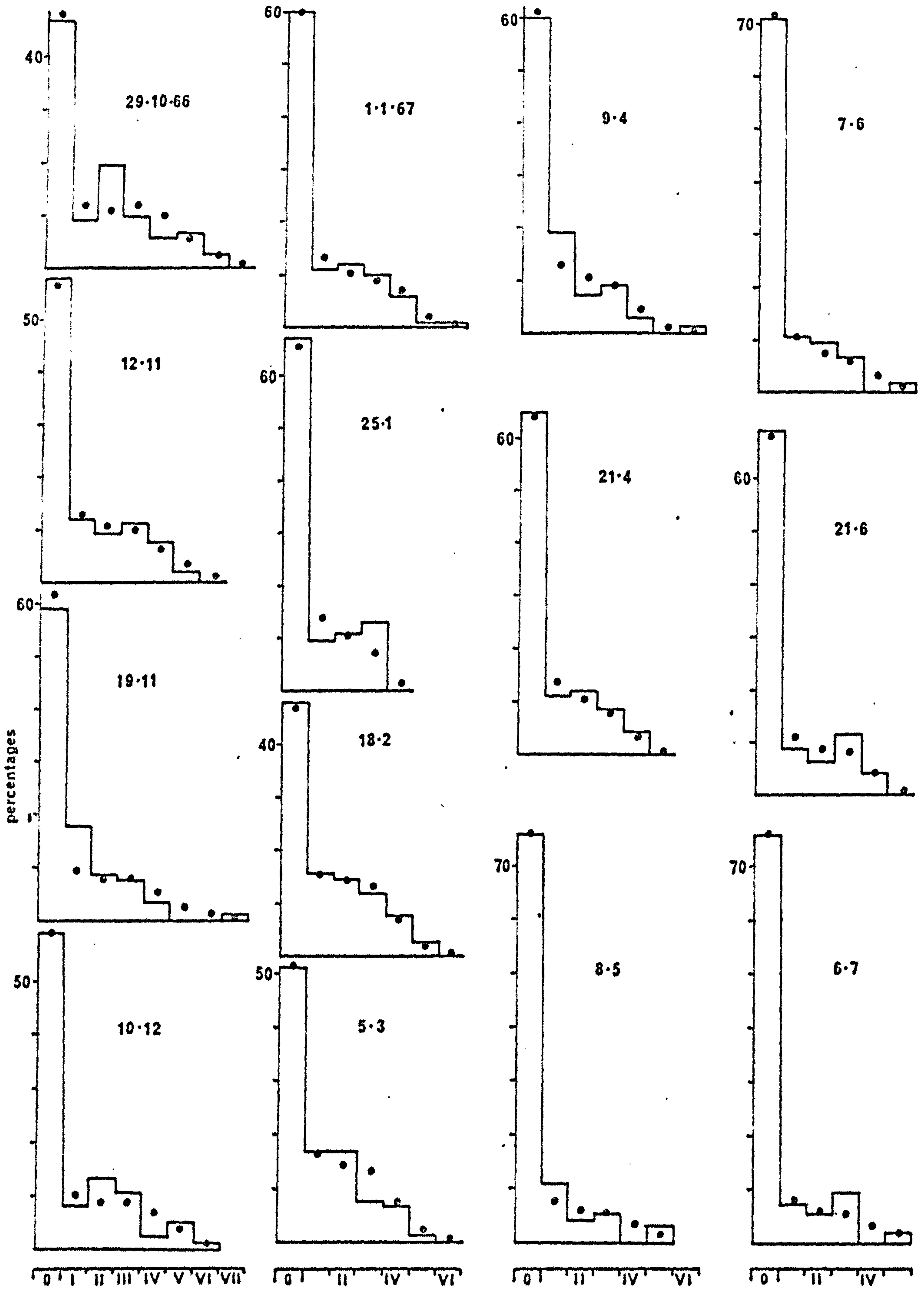
1. Mean (Fig. 37b)

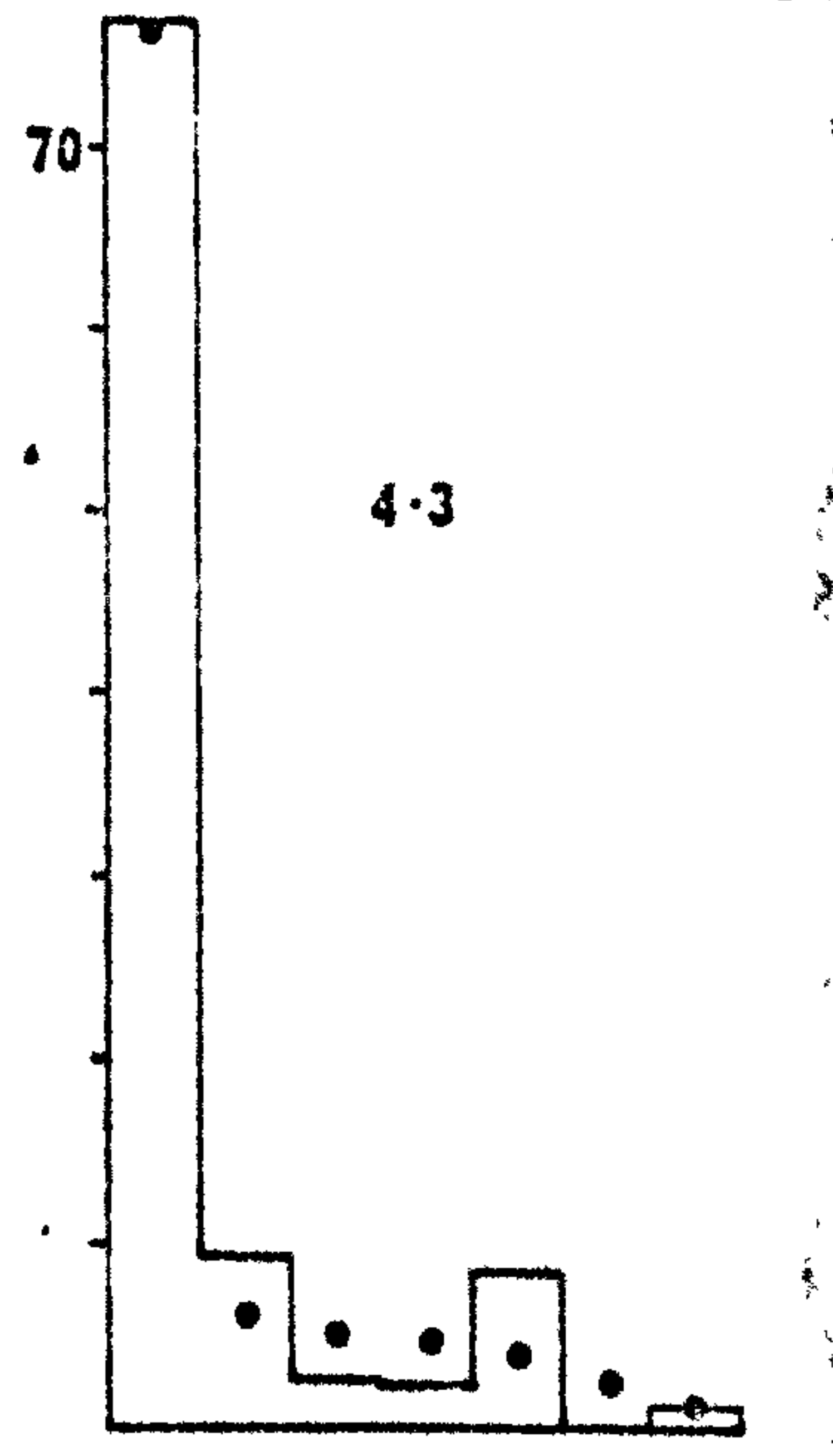
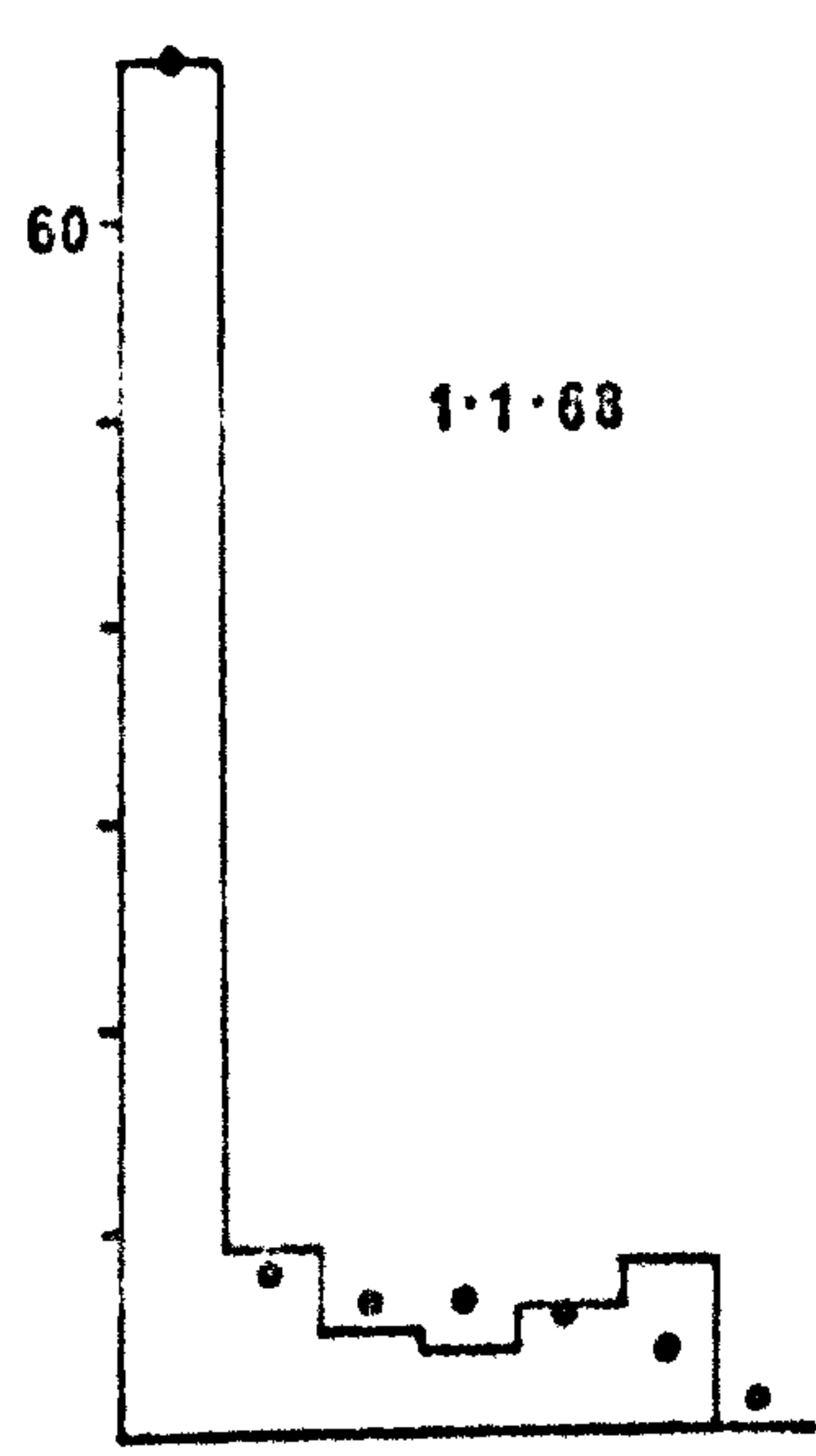
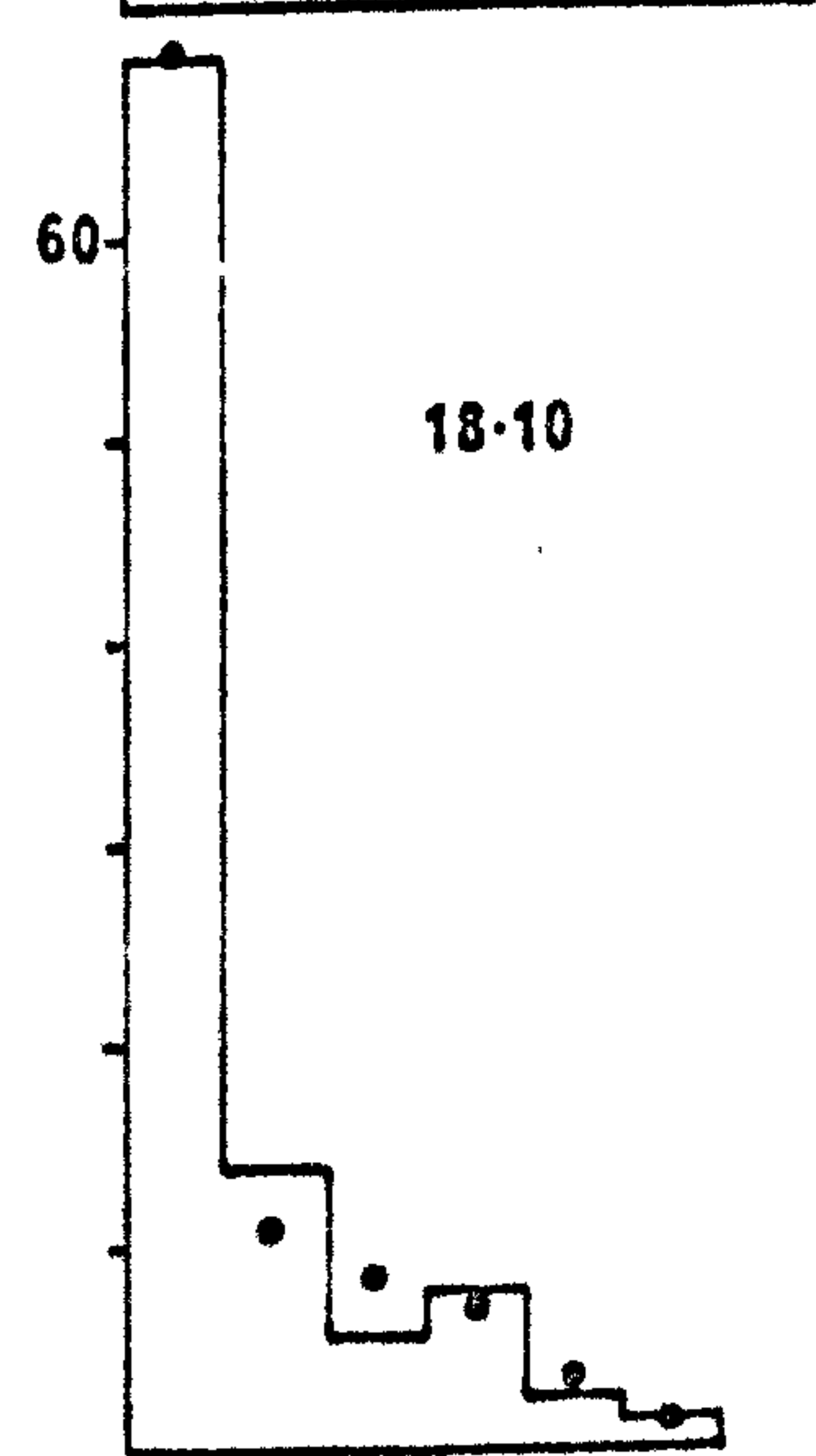
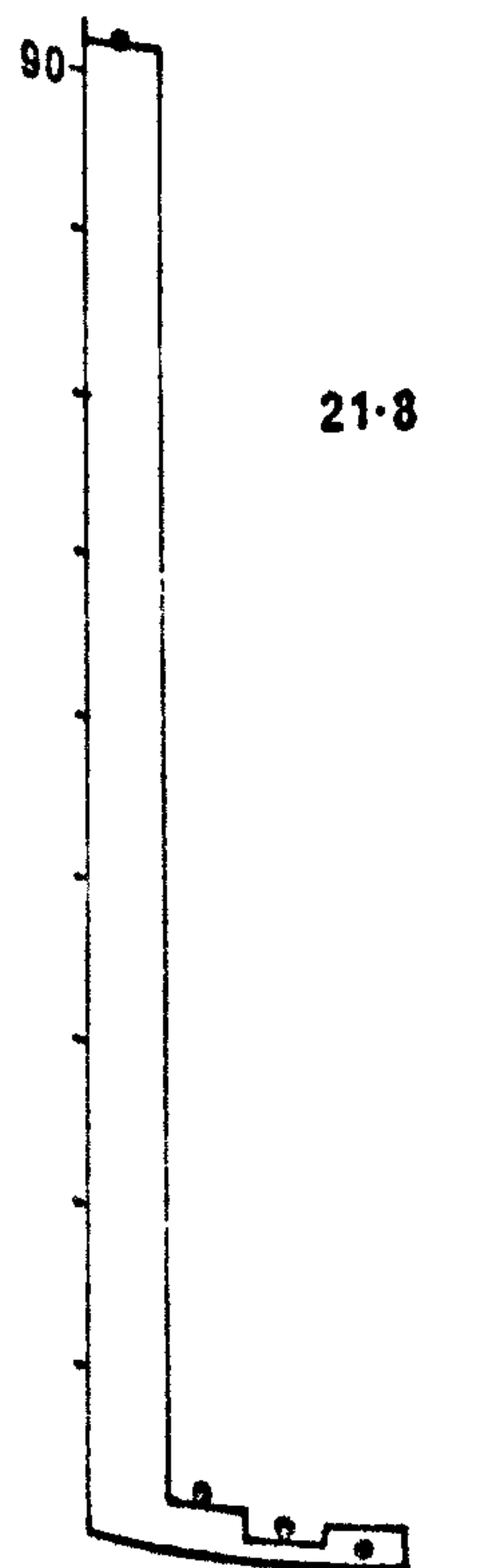
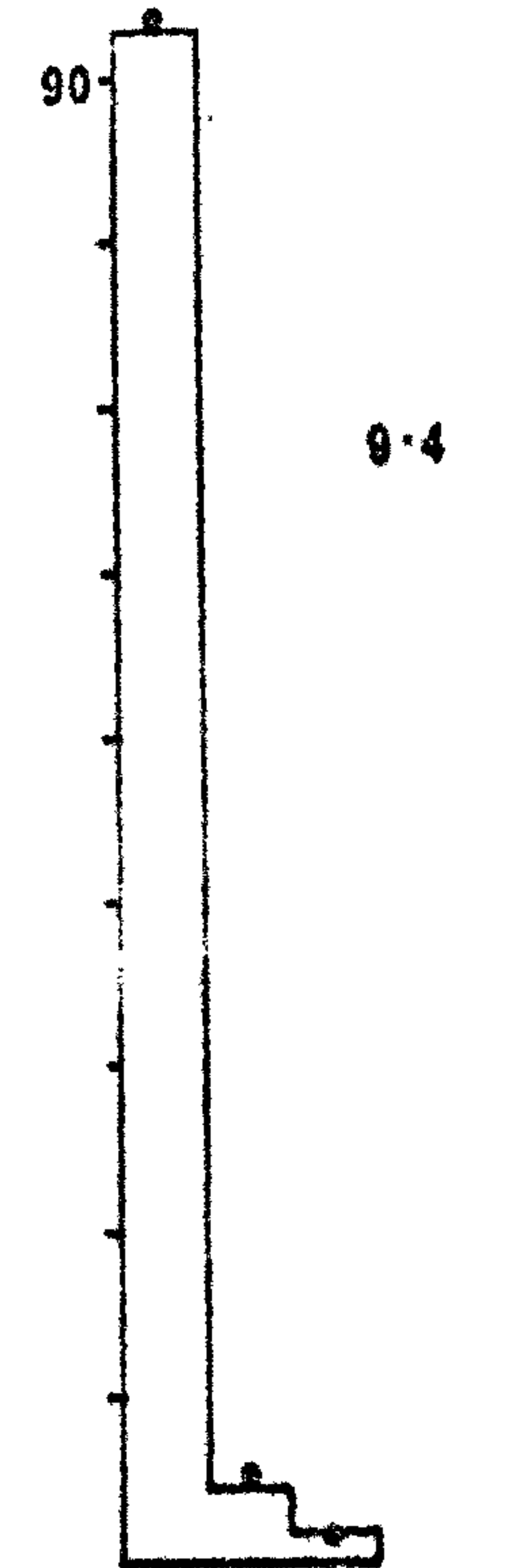
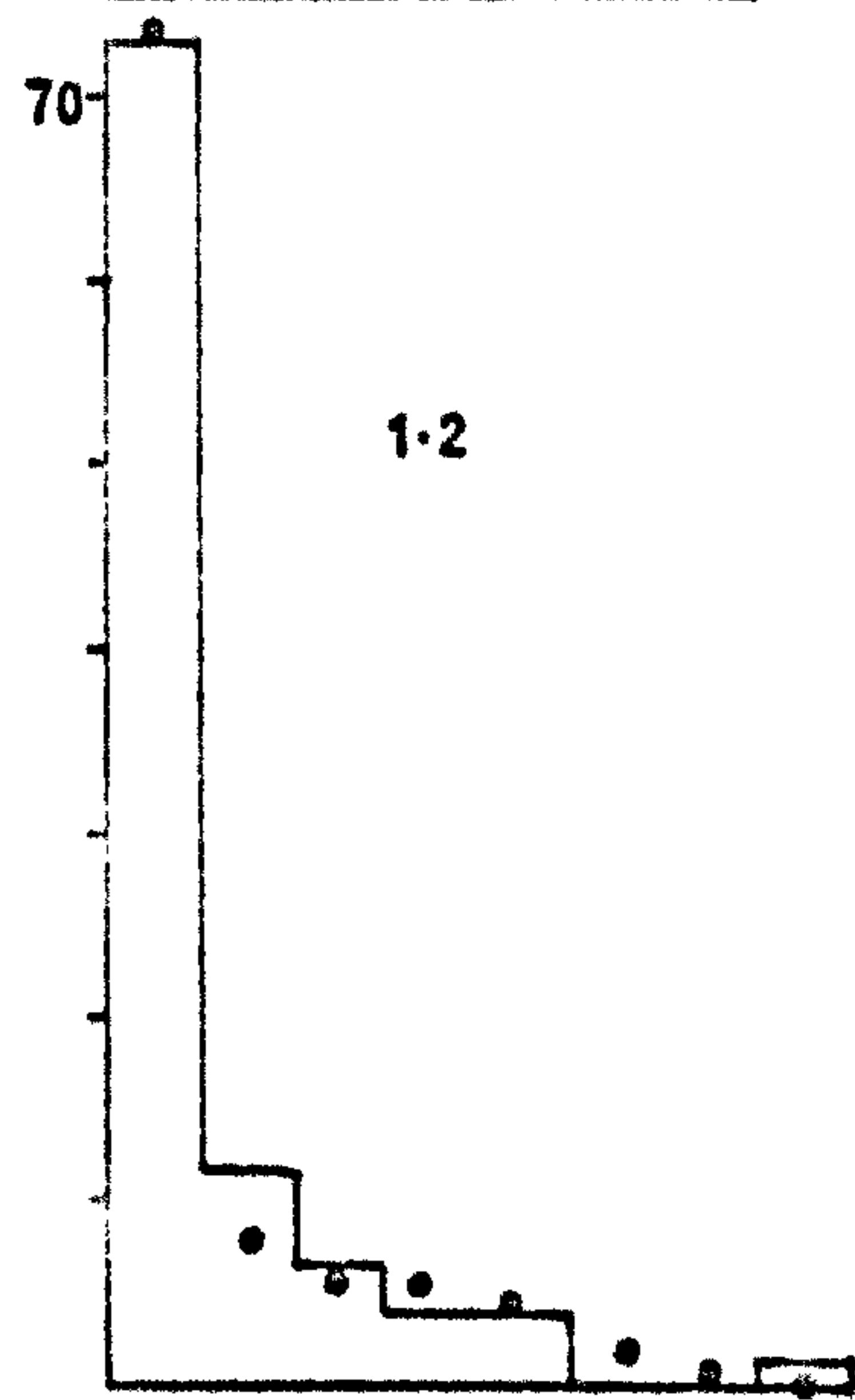
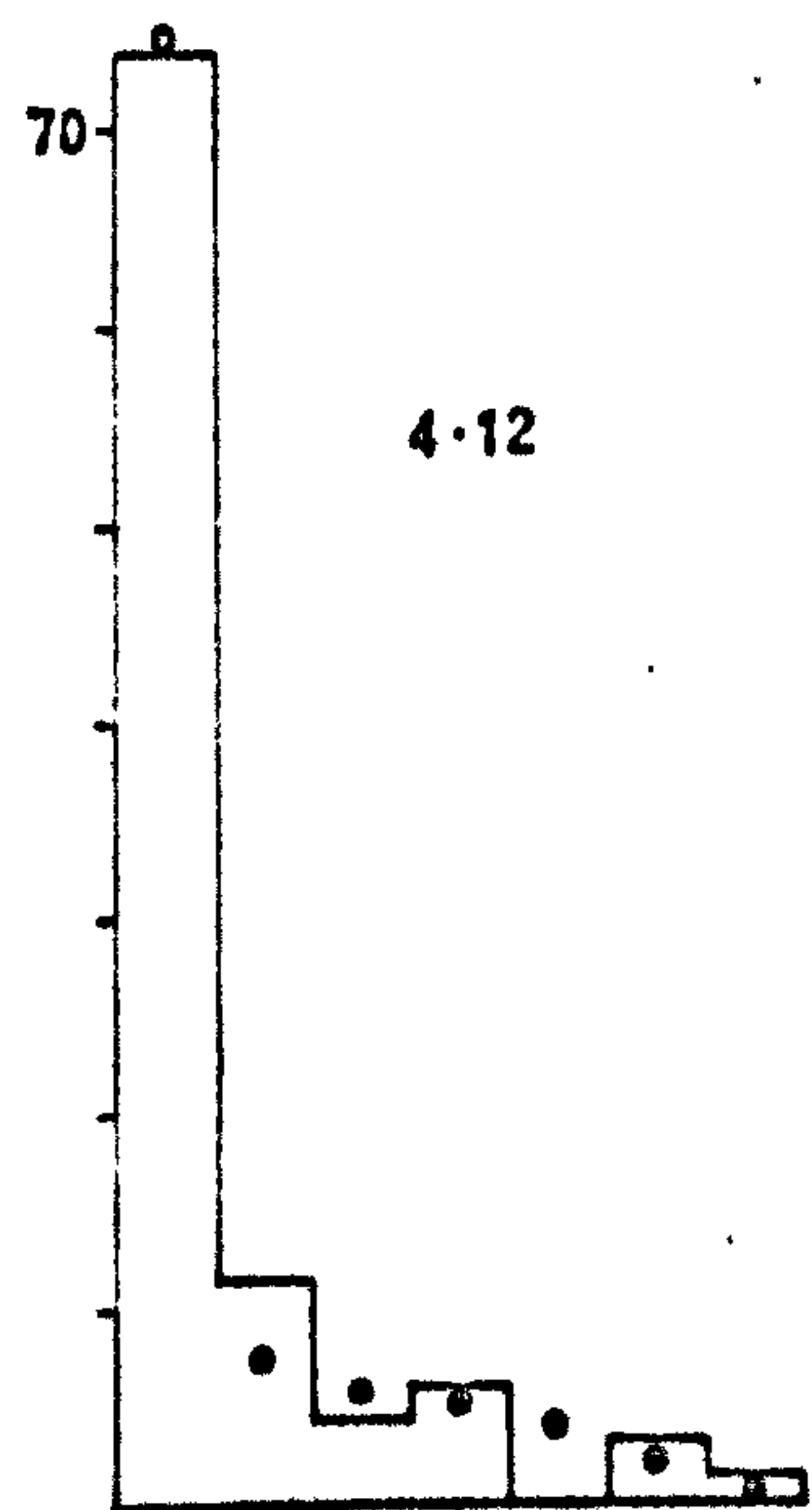
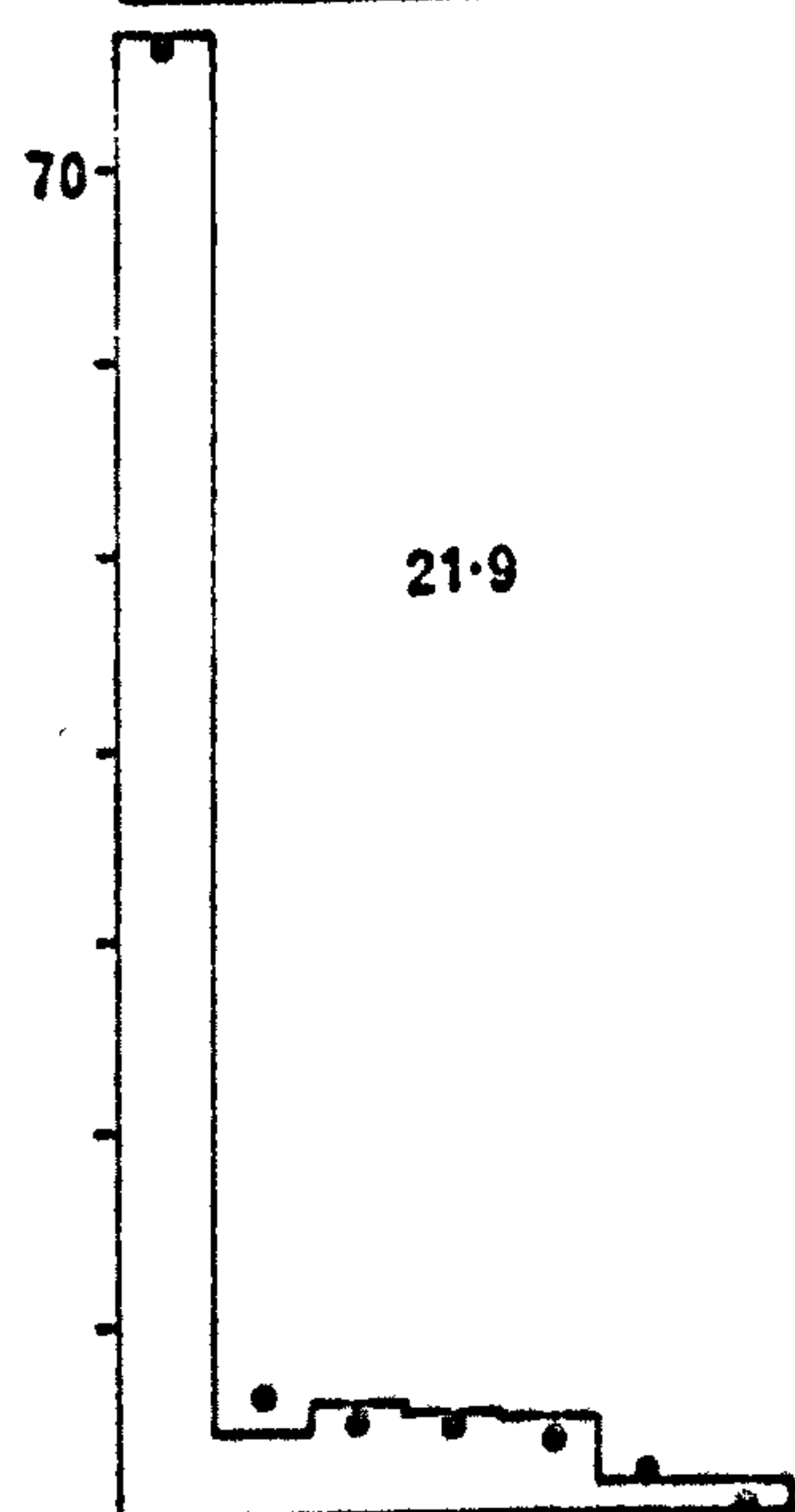
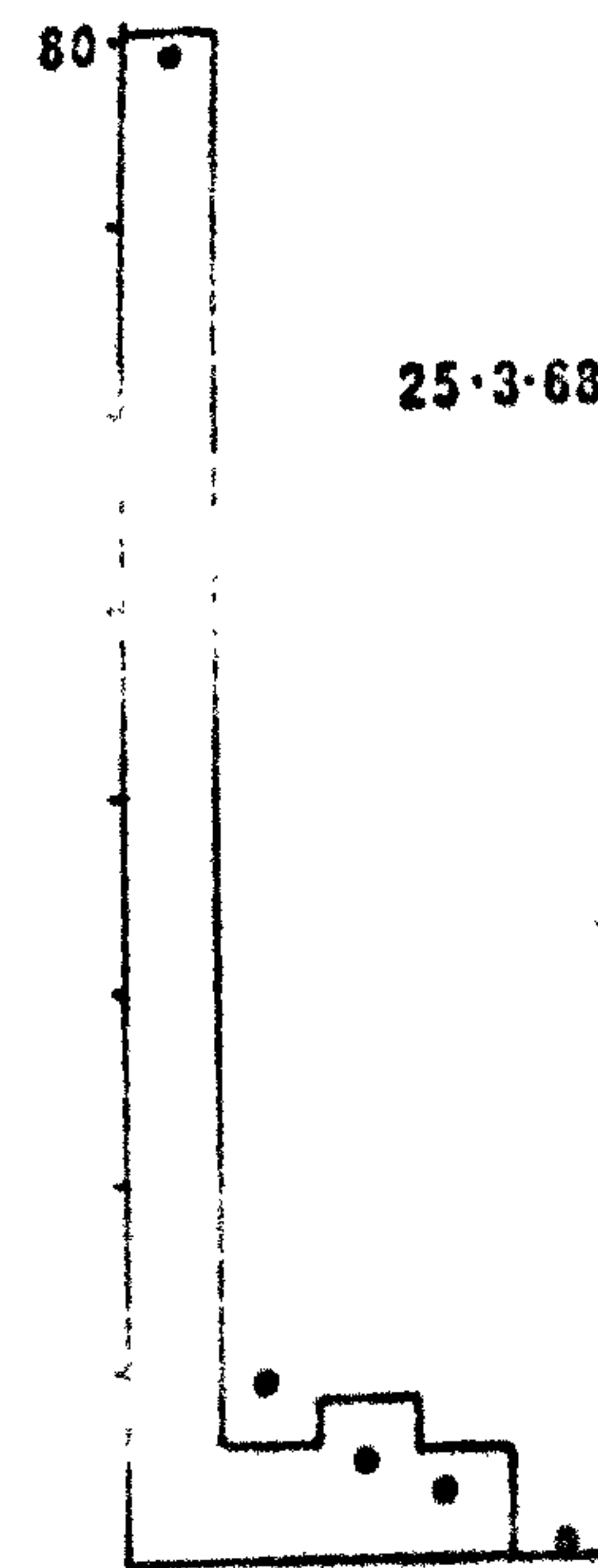
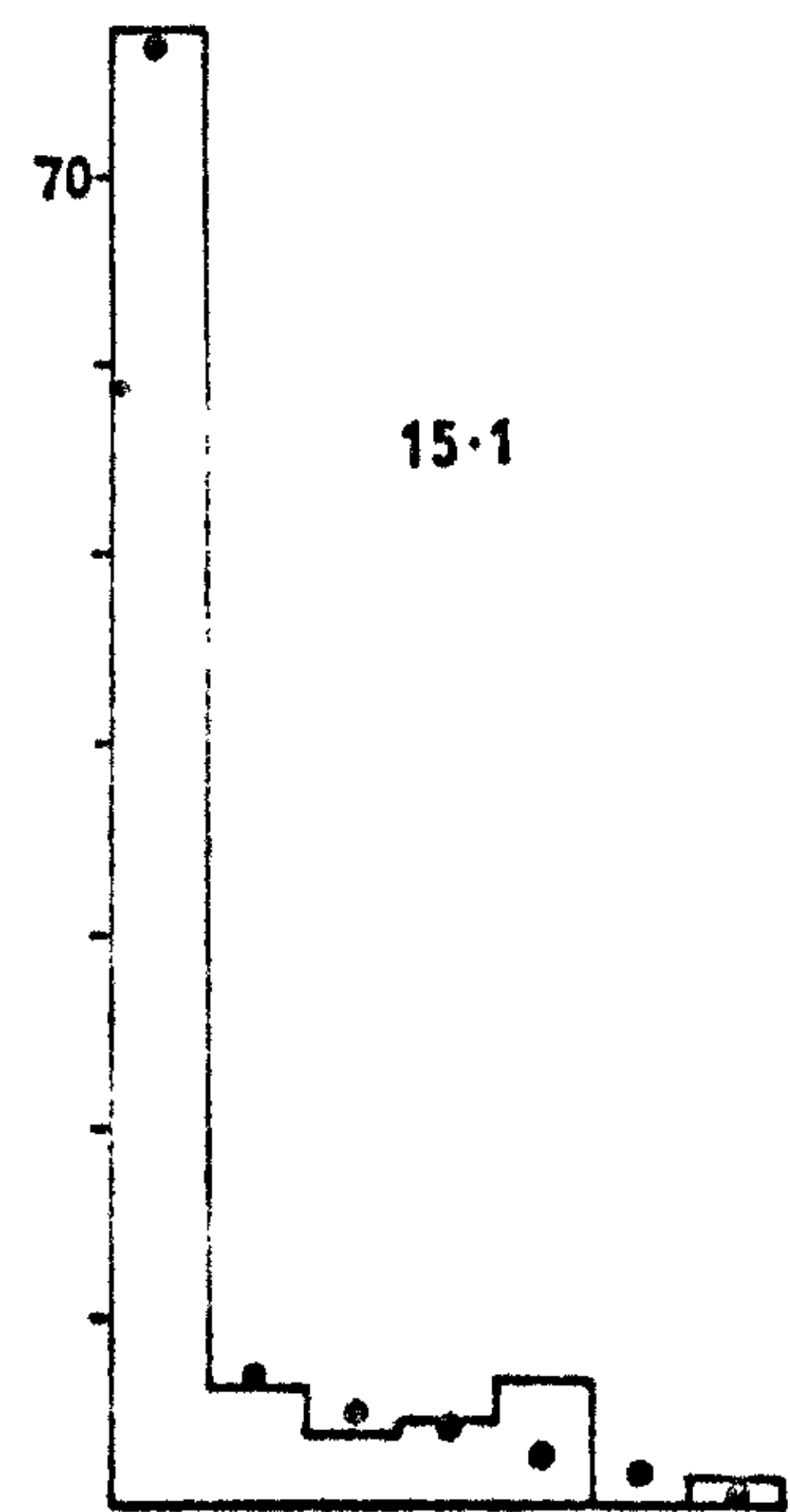
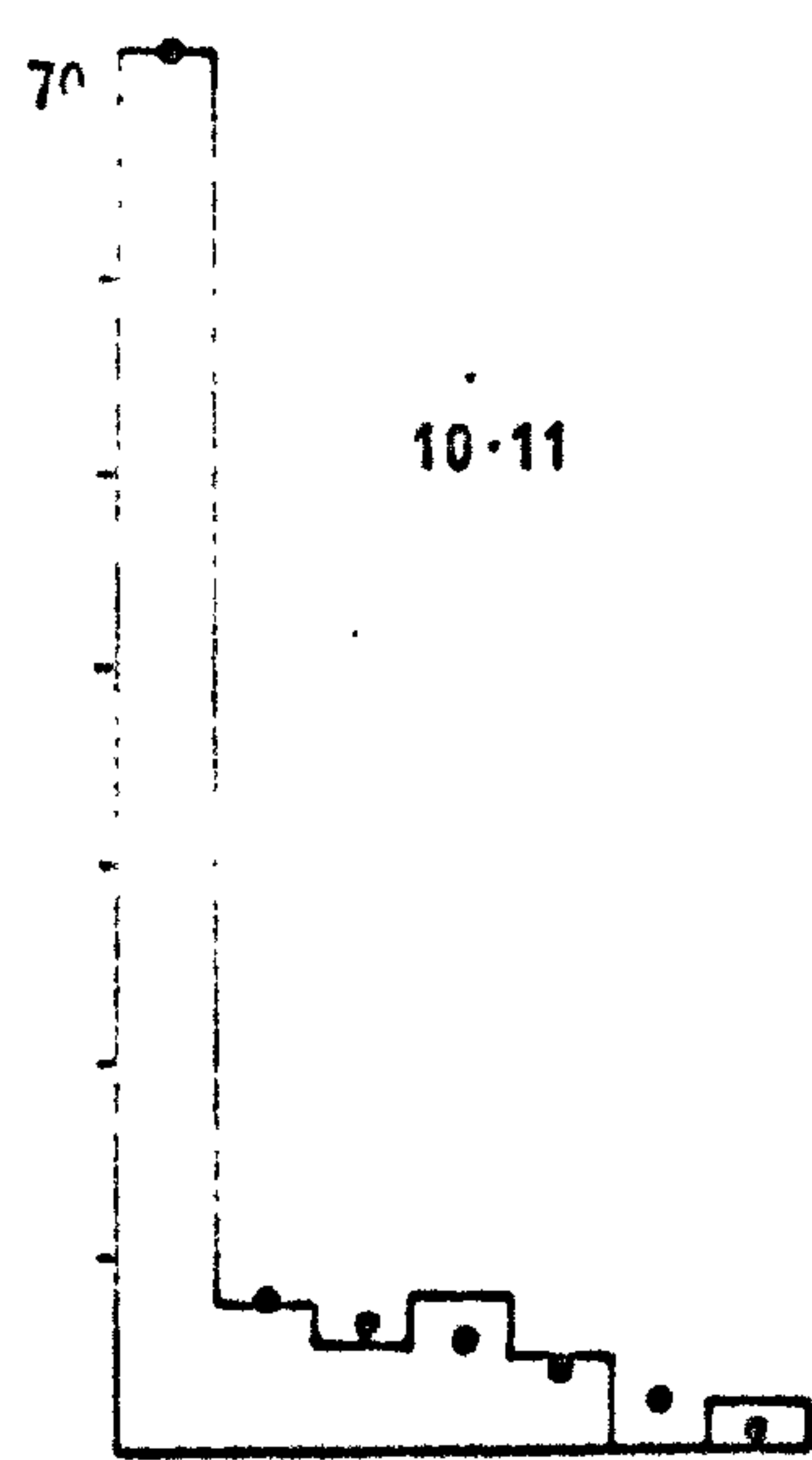
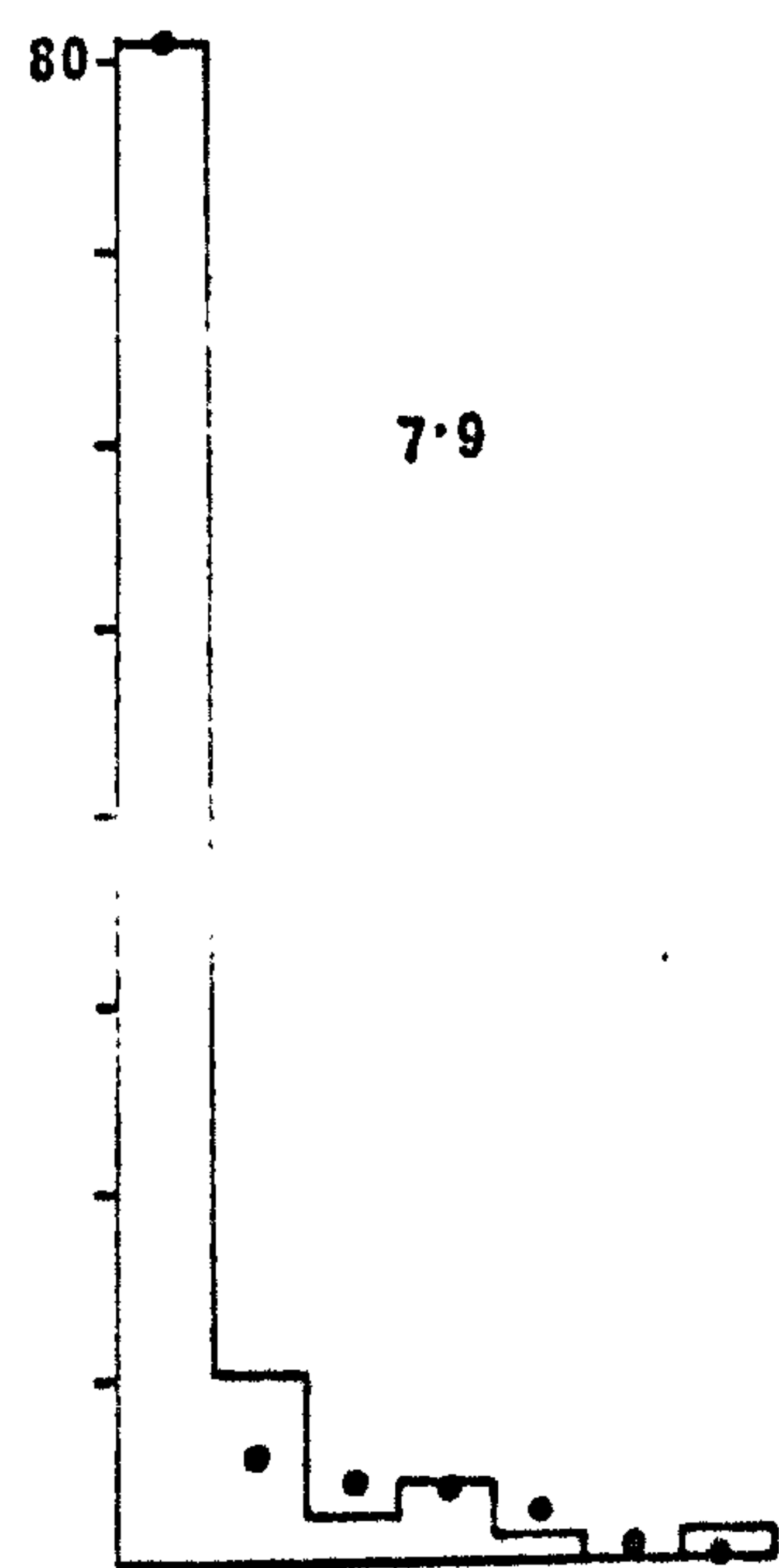
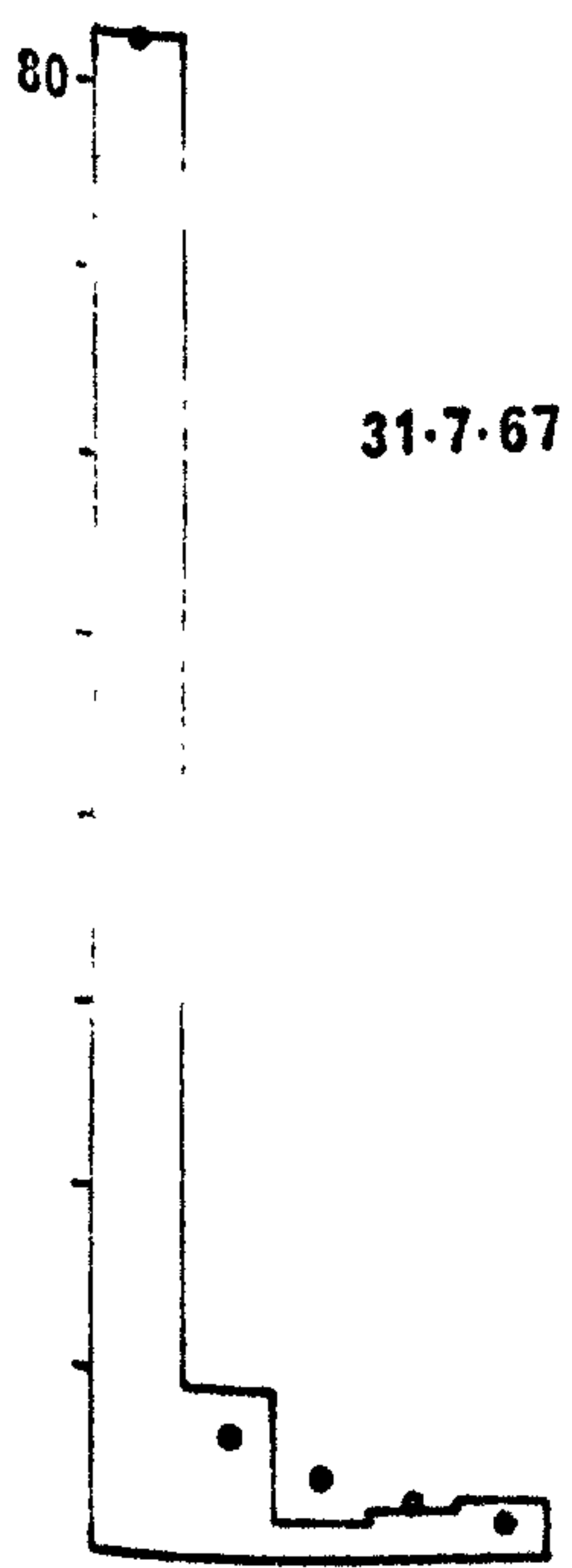
The mean number of Echinorhynchus in all fish was 1.34. There were larger fluctuations between successive samples than in the percentage infection. The mean number of parasites per host decreased from 3.05 on 29.10.66 to 0.88 on 25.1.67. There was then a rise to 1.9 on 18.2.67 followed by a decrease to 0.15 on 21.8.67. The mean then increased again and by October had reached a level of 1.2-1.5 about which it varied until February 1968. There was then a decrease to 0.08 by 9.4.68, again similar to the value in the August before.

2. Variance (Fig. 37c)

The overall value of the variance was 16.89. As with the mean there were fairly large fluctuations from one sample to the next. The value was 39.7 on 29.10.66; there was then a decrease to 9.3 on 12.11.67 followed by a very large value of 93.8 on 19.11.67 due to one exceptionally heavily infected fish with 83 worms. This shows how greatly the variance is affected by just one high value. There was then a decline to a lower level, with fluctuations between 2.4 and 11.1 until July 1967 when there was a further decrease to 0.36 by 21.8.67. The variance then rose to a level of 20-30 by September; it fluctuated about this level until March 1968 when it decreased rapidly to 0.1 on 9.4.68.

FIG. 39 Echinorhynchus Tug A-Z classes





0 I II IV

0 I II IV

0 I II IV VI

0 I II IV VI

0 I II IV VI

3. Overdispersion (Fig. 38d)

The ratio of variance: mean for all fish was 12.61. The overdispersion was very similar in pattern to the variance - fluctuations in the mean having little effect. The initial value was 13.0; there was then a low one of 5.5 on 12.11.66 and a high one of 42.4 on 19.11.66. The level then decreased and from January to August 1967 was around 5, varying between 2.4 and 11.1. There was a rise to about 15 in September, followed by a slight increase with fluctuations between 22.8 and 5.4 until 4.3.68 when the value decreased, to 1.3 on 9.4.68.

4. Frequency distributions (Fig. 39)

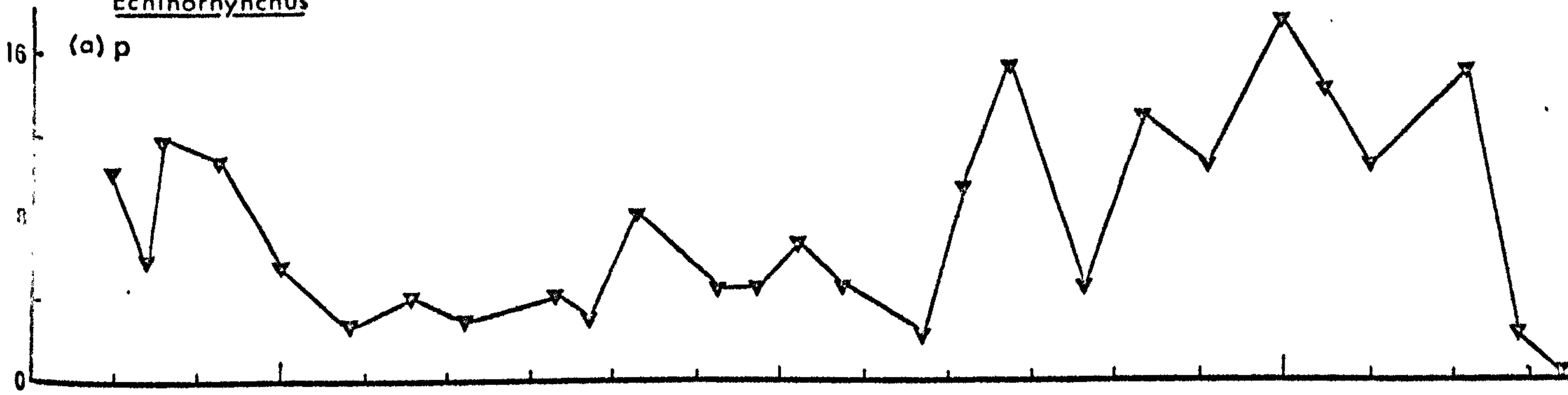
The zero class was always the greatest, generally by a large amount. There were few fish with more than 12 parasites, although several had over 30, one had 46, and one 83.

The data for each sample were fed into the computer programs calculating the negative binomial and log series distributions. The negative binomial fitted better than the log series and had the added advantage of taking into account the number of fish with no parasites, often a large proportion of the sample. R^2 was calculated as a measure of the efficiency of the fit of the theoretical distribution. For the negative binomial R^2 was always greater than 0.95, and in 85% of the samples greater than 0.99. The closeness of the fit can be seen in Fig. 39 where the negative binomial distributions are

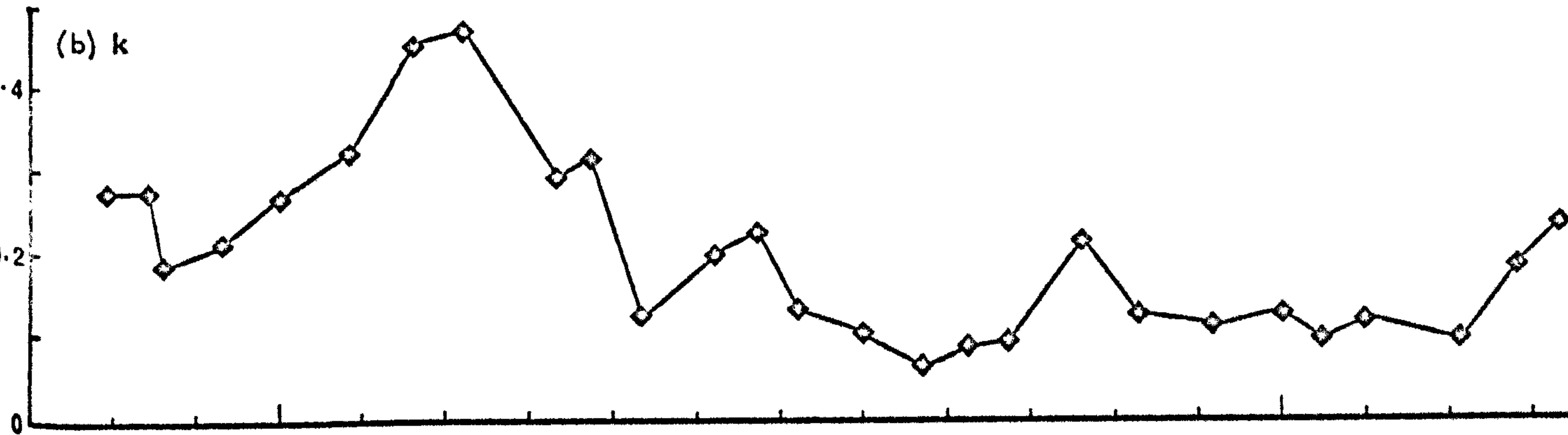
FIG. 38

Echinorhynchus

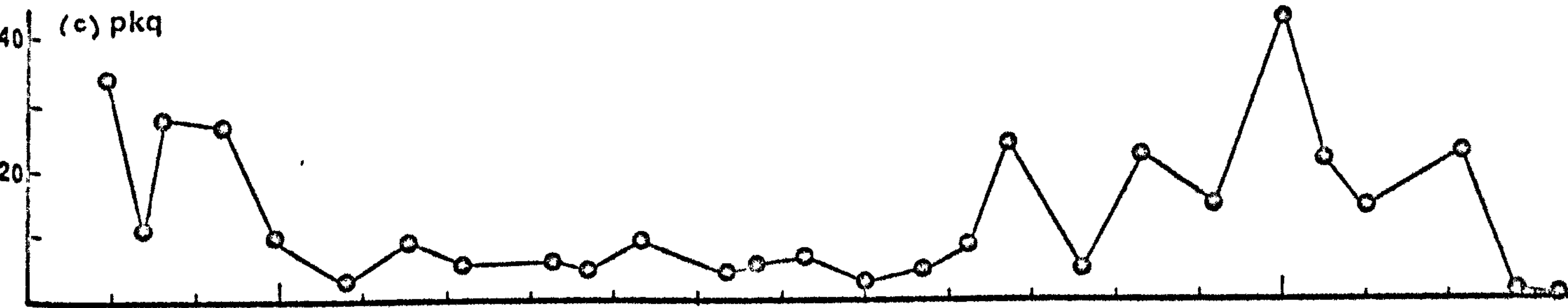
(a) p



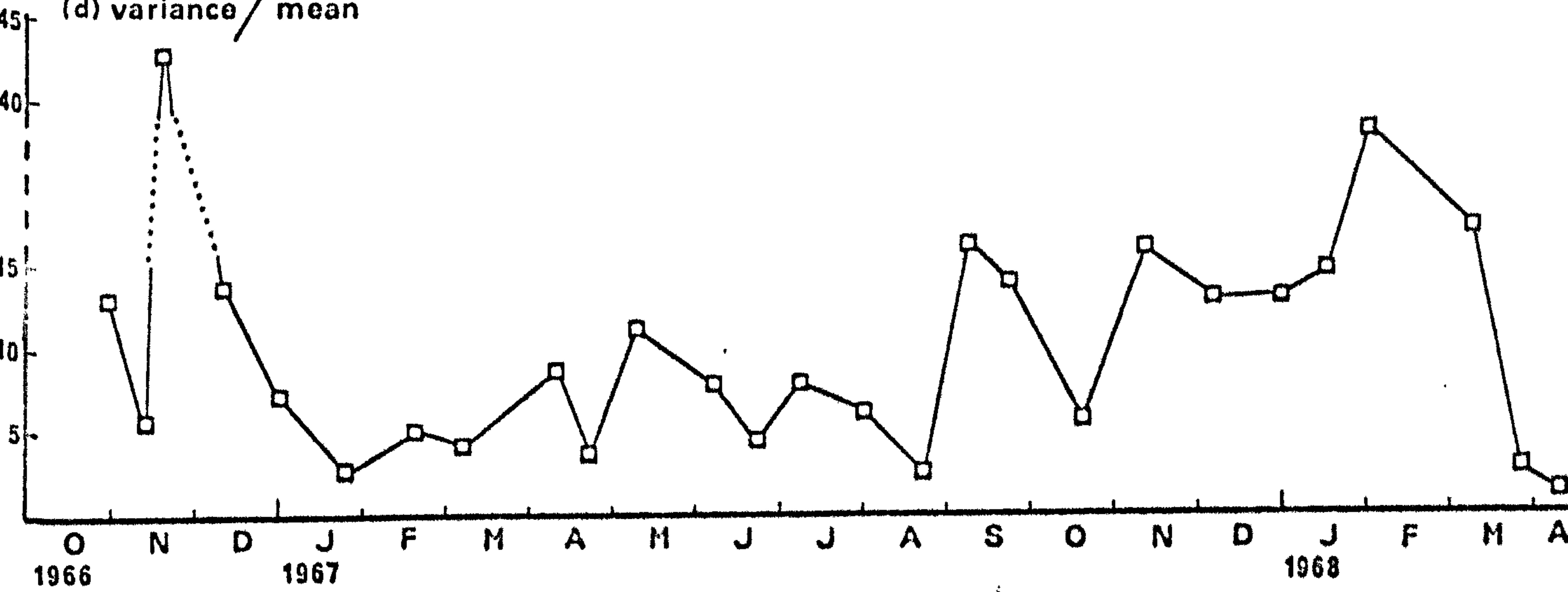
(b) k



(c) pkq



(d) variance / mean



plotted with the originals.

Parameters of negative binomial

p (Fig. 38a)

The value of p averaged over all samples was 7.57. The value decreased from 10.1 on 29.10.66 to 5.9 on 12.11.66, rose to 11.8 on 19.11.66 and then fell steadily to 2.7 on 25.1.67. p then remained at a low level with fluctuations between 8.2 and 2.3, until 21.8.67. There was then a sharp increase to 15.5 on 21.9.67, followed by fluctuations around a level of about 12 until March 1968, and finally a drop to 0.32 on 9.4.68.

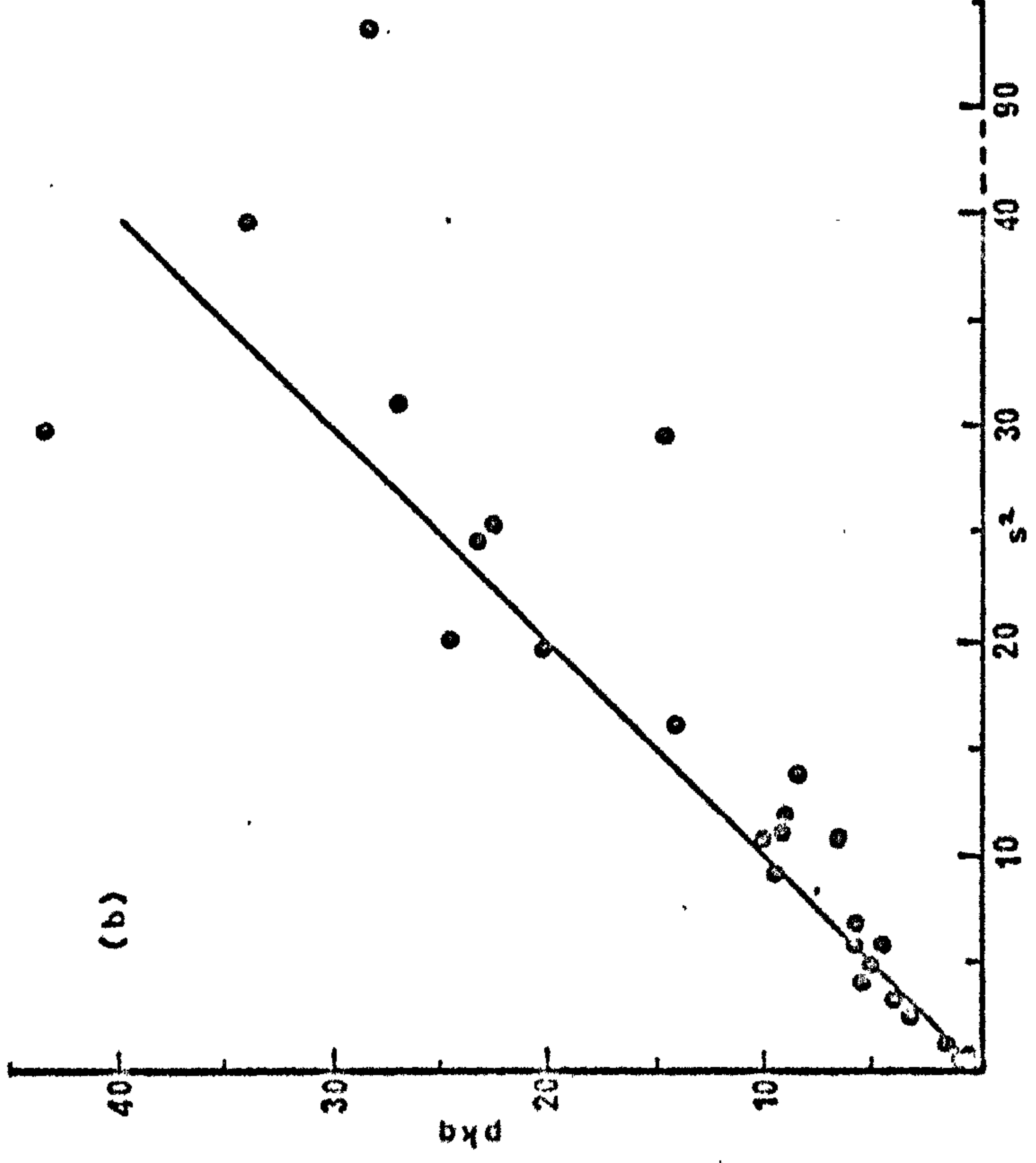
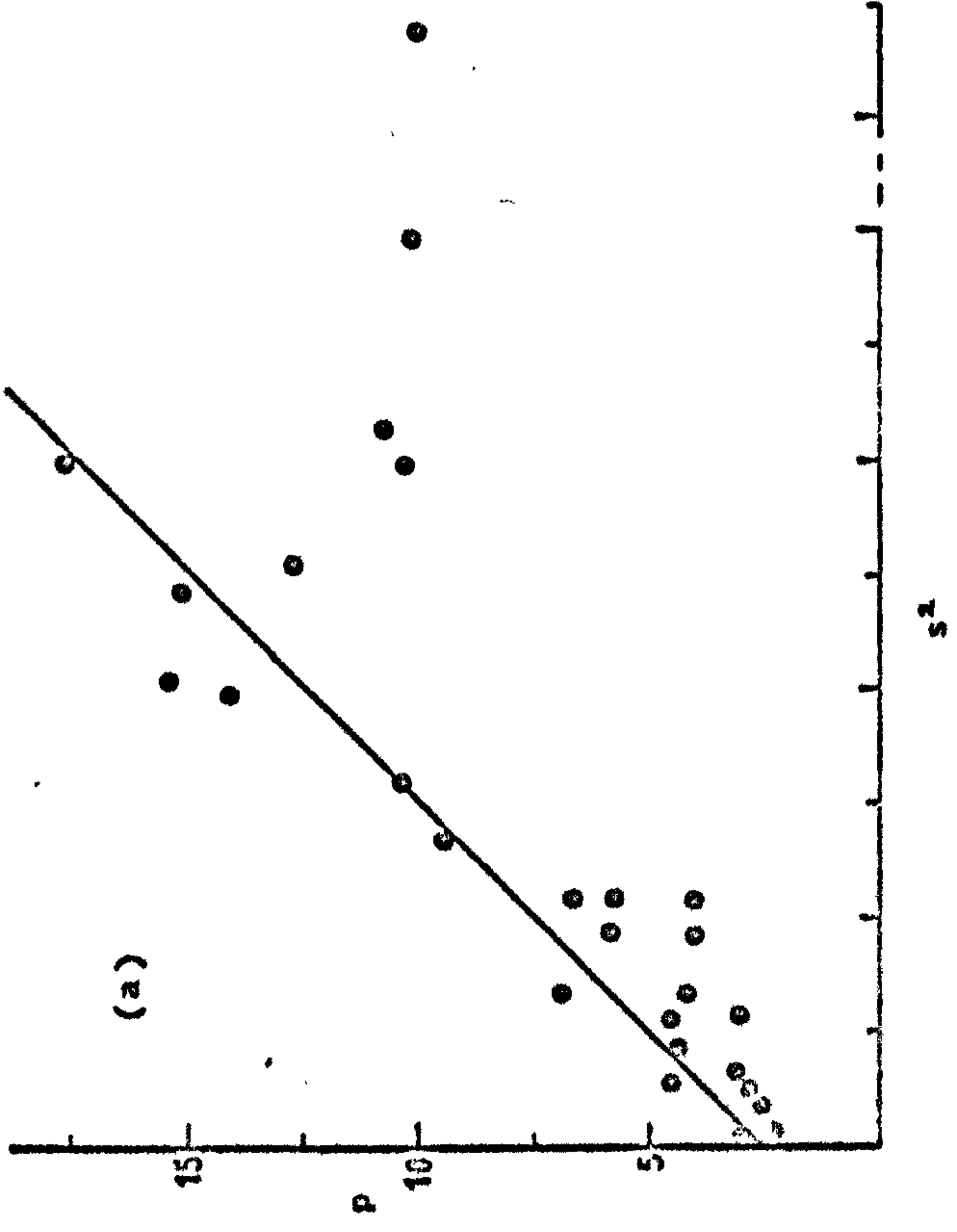
k (Fig. 38b)

The value of k averaged over all samples was 0.204. The value was always less than one. Initially k was 0.3; it fell to 0.19 on 19.11.66 and then rose steadily to 0.47 on 5.3.67. There was then a fairly steady decrease to 0.12 on 8.5.67, followed by an increase to 0.23 on 21.6.67 and a further decrease to 0.07 on 21.8.67. k increased to 0.13 on 10.11.67 and then remained more or less constant until March 1968 when it finally increased to 0.24 on 9.4.68.

pkq (Fig. 38c)

The value calculated from the average values of p and k for all samples was 13.2. The value of pkq was initially

FIG. 40 Echinorhynchus



34.2. It decreased to 3.25 on 25.1.67 and then remained more or less constant, fluctuating between 9.4 and 0.49, until 7.9.67. There was a general increase in level to 20-25 which was maintained, with large fluctuations, until 4.3.68. The value then decreased to 1.01 on 9.4.68.

Relationships between p and k and the parameters of the original distribution

Values of p and k for each sample were plotted against the parameters calculated from the original data. The following five pairs showed the closest relationships.

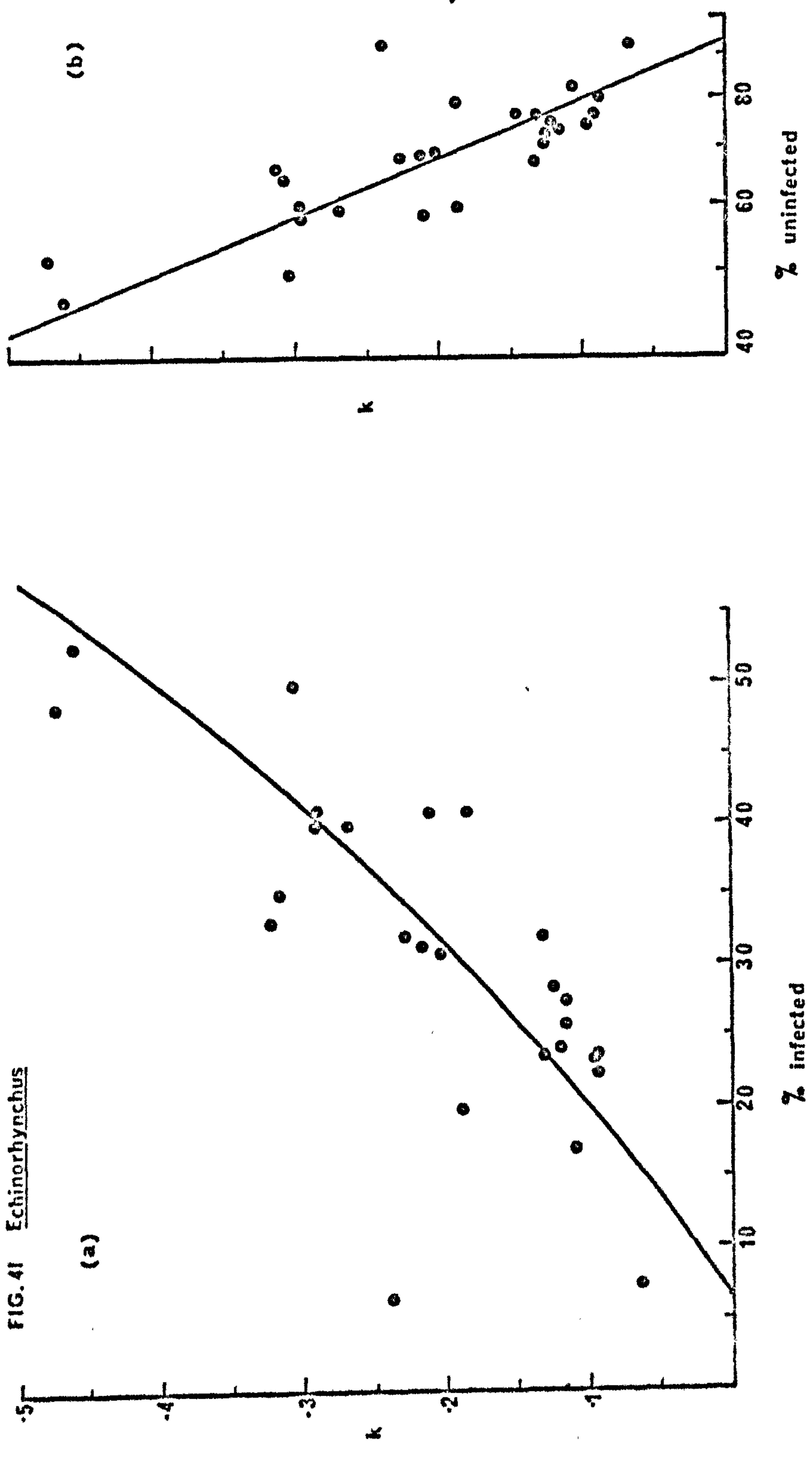
1. p vs. s^2/\bar{x} (Fig. 40d)

As expected (see p. 19) the line $s^2/\bar{x} = 1 + p$ fitted the points well, except for three values. The points for two samples (19.11.66 and 1.2.68) had too high a value of s^2/\bar{x} for the value of p , due to a high variance caused by a single heavily infected fish. This was aggravated in the latter case by a low mean. One sample (1.1.68) had a low value for the overdispersion because of the lack of any heavily infected fish in an otherwise heavy infection.

2. p vs. s^2 (Fig. 40a)

The points again lay on a fairly straight line, except for a few with a very high variance. If this was due to a high general level of infection rather than to a single heavily infected fish then the mean was also high and the

FIG. 41 Echinorhynchus



point did not deviate from the above line.

3. p vs \bar{x} (Fig. 40c)

The relationship between p and the mean was approximately linear, but the points were very widely scattered.

4. pkq vs s^2 (Fig. 40b)

The variance of the negative binomial was close to the calculated variance in all but three samples: 19.11.66, 1.2.68 and 1.1.68. As has already been described under (1) above the first two of these had an exceptionally high variance and the third an exceptionally low one.

5. k vs percentage infection (Fig. 41a)

The points did not lie on a straight line but on a curve. The scatter was fairly wide, one point in particular being a long way off; this was the sample for 9.4.68 in which the infection was very light. A straight line was obtained by plotting k against $\log p_0$ where p_0 is the percentage of uninfected fish (Fig. 41b). This had equation

$$k = -1.5 \log_{10} p_0 + 2.95 \quad \dots(95)$$

This is also drawn on the original graph where it is a curve fitting the points quite well.

Thus in general p varied with the variance, or more closely with the overdispersion, and k with the percentage infection. p tended to vary inversely as k . From February-

August 1967 the mean was changing in a similar way to the percentage infection and therefore to the value of k . From September-April 1968 the mean and variance both had similar patterns and were followed by the value of p . The value of k rose less than expected for the increase in the percentage infection and this was compensated by the large rise in the value of p caused by the high overdispersion,

B. Numbers of males and females

In 23 out of the 27 samples there were more female than male Echinorhynchus. In all 1860 fish there were 1436 females and 1047 males - a significantly larger number of females. This difference is due to the longer life of the females.

The ratio of numbers of males: numbers of females in each sample was calculated, and plotted in Fig. 42c. The ratio increases when new infections occur and decreases when males die.

The sex ratio was 1.02 on 29.10.66; it fluctuated, with an overall decrease, until 25.1.67 when the value was 0.47. There was then an increase to 0.85 on 5.3.67 with a sudden decrease to 0.4 on 9.4.67. The value rose fairly steadily to 0.86 on 6.7.67 and then fell again to 0.60 on 21.8.67. It then rose to about 0.8 and remained at this level until 4.12.67 when there was a sharp increase to 1.33 by 15.1.68. The ratio then fell rapidly to 0.2 on 25.3.68 and finally rose

to 1.0 on 9.4.68 when there were only six worms in all.

III Sizes of Echinorhynchus

The means and variances of the lengths of the Echinorhynchus were calculated separately for males and females. The lengths were also collected into frequency distributions with class interval 0.5 mm.

1. Mean (Fig. 42a)

The mean length of the female worms was always greater than that of the males. The mean of all females was 4.49 mm, significantly greater than the mean of 3.08 mm for all males.

The mean length of the female worms fluctuated irregularly between 4.2 and 5.2 mm from October 1966 to August 1967 with a slight decrease in the level. There was a high value of 6.28 mm on 21.8.67 but there were only five female worms in this sample. The level then decreased and remained more or less constant at around 4.2 mm until January 1968. There was a minimum mean length of 3.7 mm on 1.2.68 followed by an increase to 4.2 mm in the final two samples.

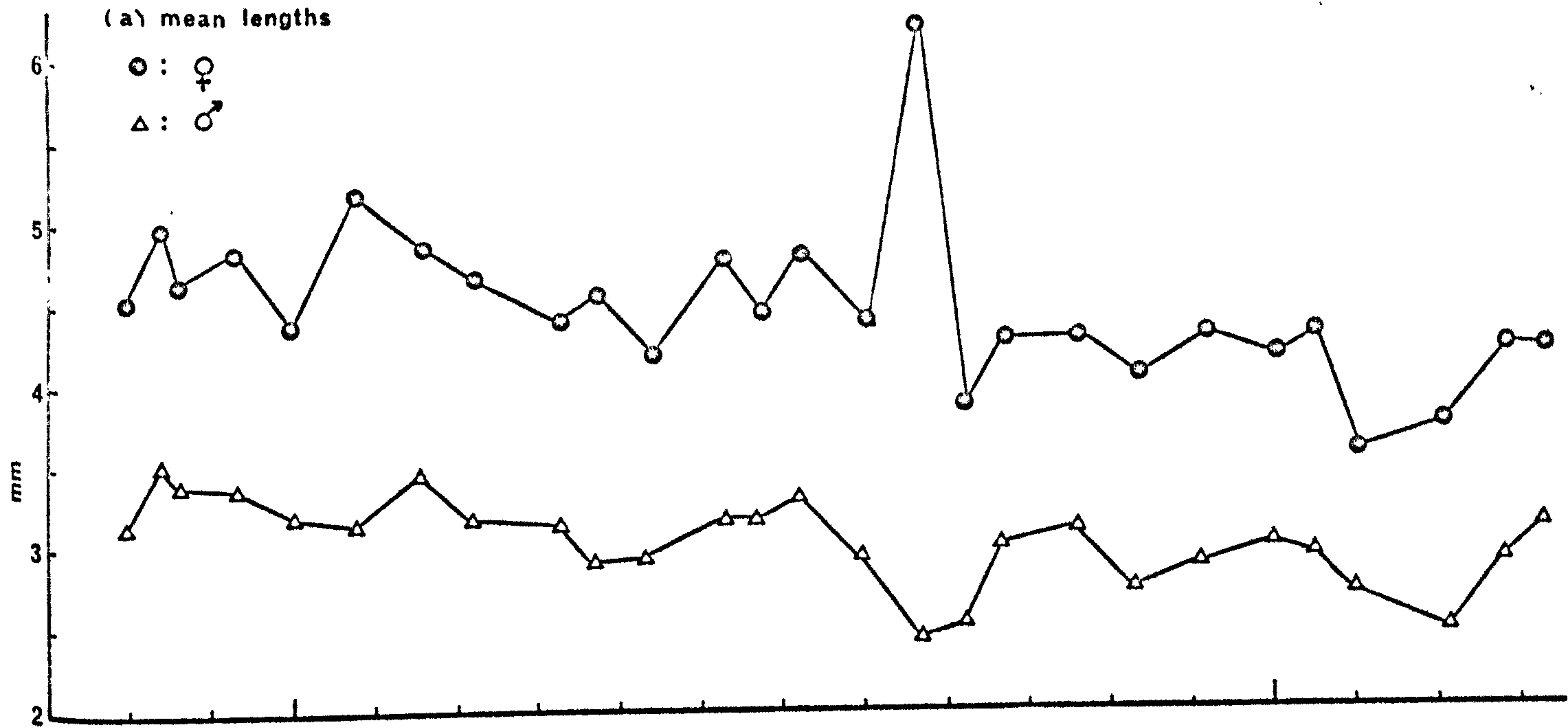
The mean length of the male worms showed a similar pattern. From October 1966 to April 1967 there were small fluctuations, between 2.9 and 3.45 mm, with a decrease in the general level, then a slight increase until July when there was a decrease to a minimum of 2.4 mm on 21.8.67. This

FIG. 42

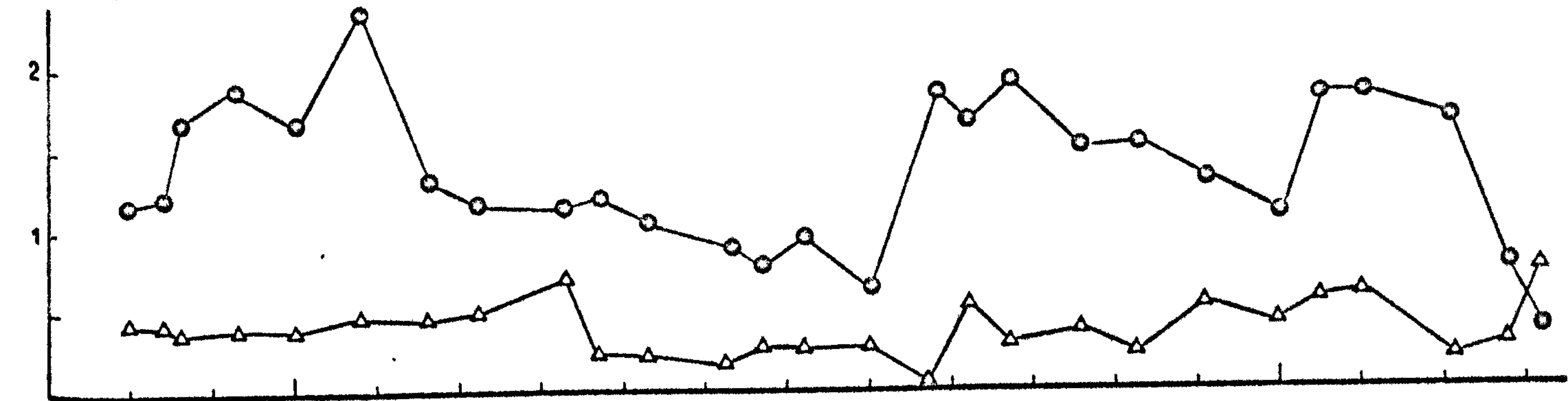
Echinorhynchus

(a) mean lengths

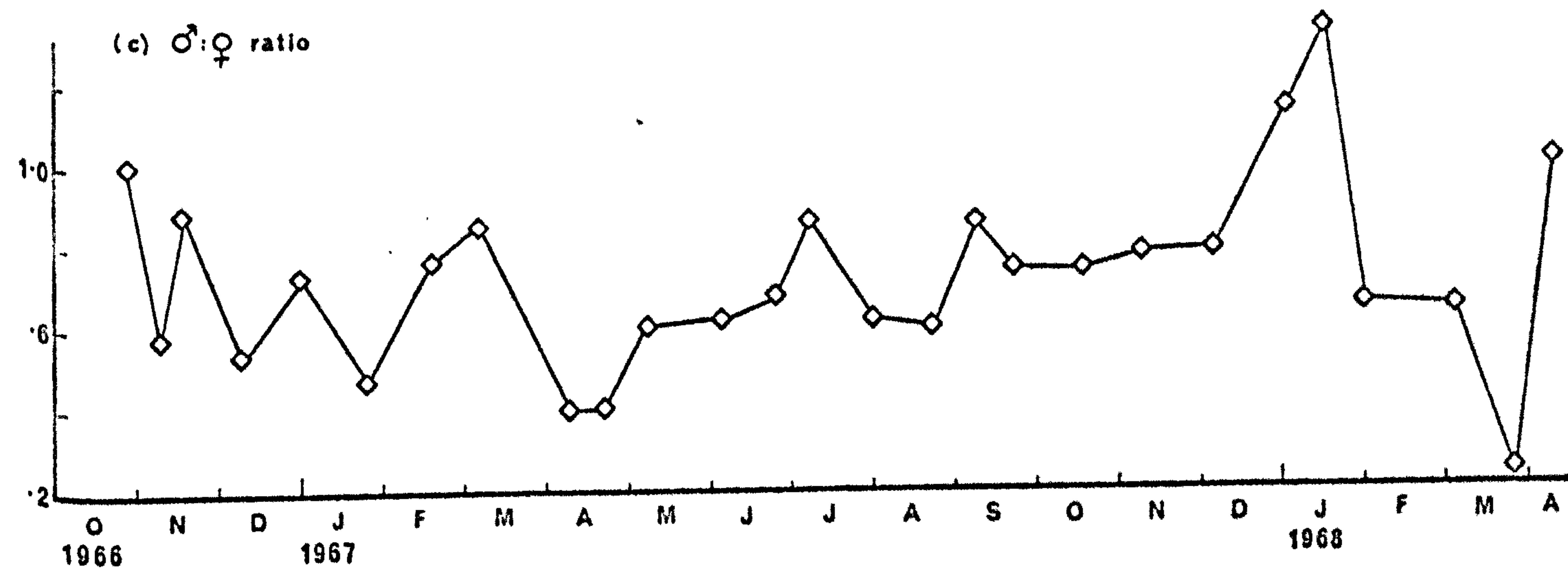
○ : ♀
 △ : ♂



(b) variances



(c) ♂:♀ ratio



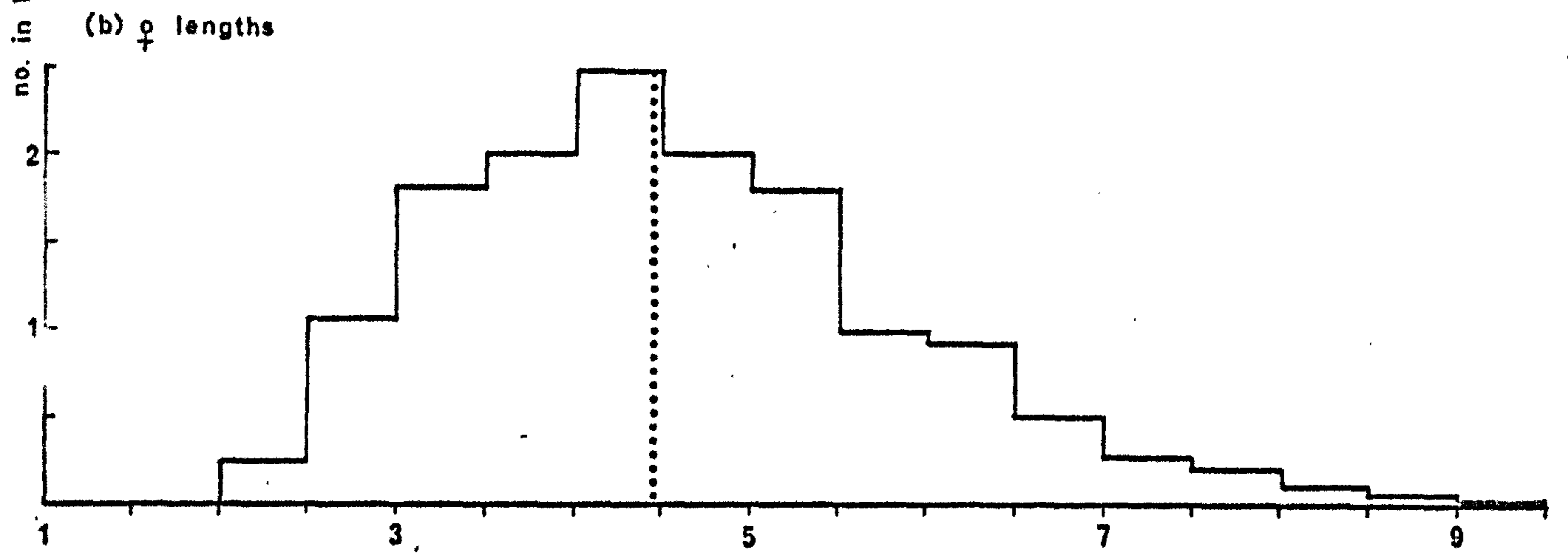
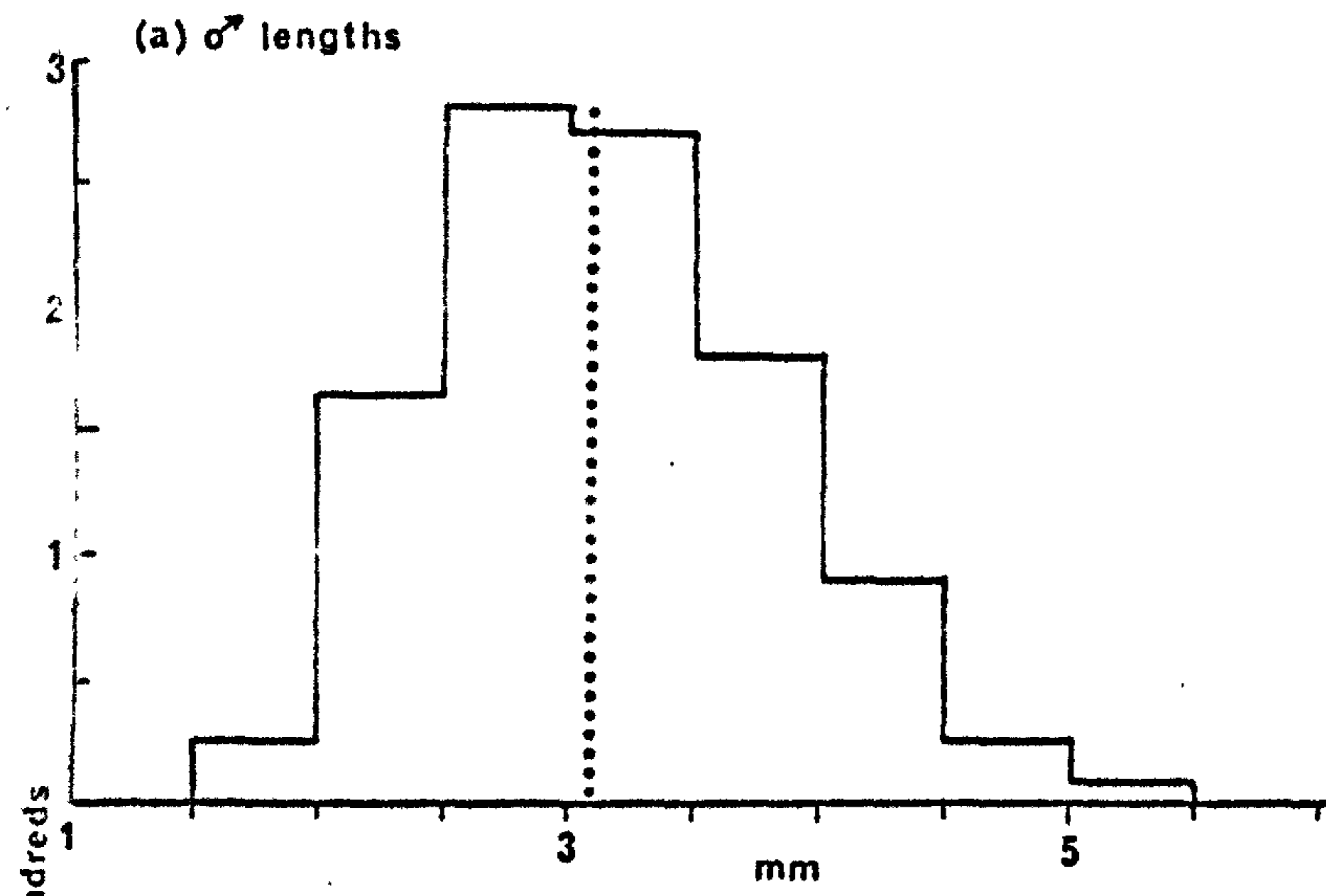
was followed by an increase to a more or less constant level of just below 3 mm. There was a decrease during January and February 1968 to 2.46 mm on 4.3.68, then finally an increase to 3.1 mm on 9.4.68.

2. Variance (Fig. 42b)

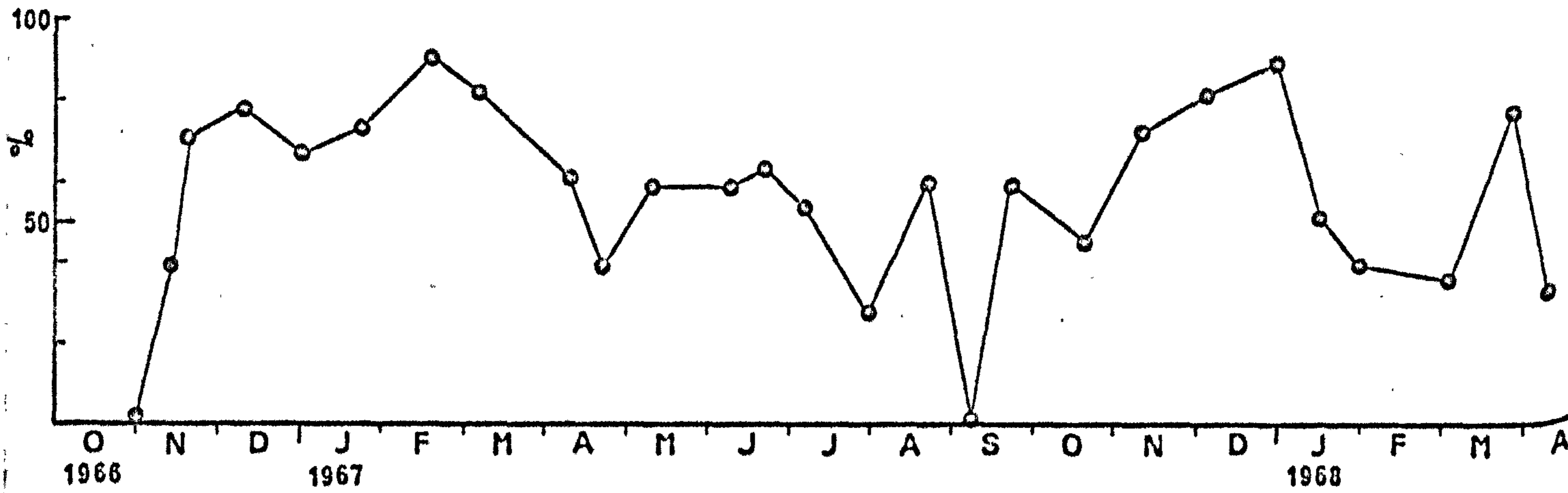
The variance of the lengths of the females was greater than that of the males except in the final sample where there were only 3 worms of each sex.

The variance of the female lengths was initially 1.2, then rose to 1.9 on 10.12.66. There was a high value of 2.4 on 25.1.67, but otherwise a steady decrease to 0.64 on 31.7.67. There was a sudden increase to 1.84 on 21.8.67, then a gradual decline to 1.09 on 1.1.68. There was another increase to 1.82 on 15.1.68 followed by a decrease to 0.38 on 9.4.68.

The variance of the male lengths was about 0.4 from October 1966 to February 1967; it then rose slightly to 0.71 on 9.4.67 and fell to a level of around 0.25 on 21.4.67 which was maintained until July. There was a very low value of 0.02 on 21.8.67, then an increase, with fluctuations, to a value of 0.58 on 1.2.68. There was a decrease to 0.2 on 4.3.68 followed by an increase to 0.75 on 9.4.68.



(c) % ♀ with shelled acanthors



3. Distributions (Fig. 43a & b)

The length distributions for both male and female Echinorhynchus were positively skewed. The range of sizes for the male worms was 1.5-5.5 mm and that for the females 2-9.5 mm. The female distribution had a much longer right-hand tail than the male distribution. This was due to the longer life-span of the females giving a greater time for growth. Females also started off slightly longer; this enables them to produce a large volume of eggs.

IV Percentage of females with shelled acanthors (Fig. 43c)

The percentage of female Echinorhynchus containing shelled acanthors was calculated for each sample and then plotted. For all worms the percentage was 55.71%. The percentage rose from 2% on 29.10.66 to 70.8% on 19.11.66. There was then a more gradual increase to 91.1% on 18.2.67 followed by a decrease to 39.2% on 21.4.67. The level increased to about 60% where it remained until July when there was another decrease, to 0% on 7.9.67. There was a high value of 60% on 21.8.67 but there were only five female worms in this sample. The percentage rose fairly steadily to 89.1% on 1.1.68; it then fell to 33.3% on 9.4.68 with a high value of 77.3% on 25.3.68.

V Discussion

As new worms are acquired by the fish the mean number and variance will increase while the sex ratio, mean and variance of the length of the worms, and the percentage of females with acanthors will all decrease. The new worms will then grow causing the mean lengths to increase, copulation will occur and the females will start to produce shelled acanthors. Then the males will die, reducing the sex ratio; females will continue to grow so that their mean length will increase. Finally the females will become senescent, ceasing production of shelled acanthors and eventually dying, causing a decrease in the mean and variance of the length.

About a third of all the fish were infected with Echinorhynchus although the mean number per fish was quite low. There were large variations at different times.

The first sample had the highest mean number of parasites and almost the highest percentage of infected fish. This, together with the high male: female ratio of the worms, their small size and the low percentage of females with shelled acanthors shows that there had recently been a new wave of infection.

From November 1966 to January 1967 there were decreases in the mean and variance of the numbers of Echinorhynchus; the percentage infection decreased slightly. The decrease in numbers of parasites could have been due either to death of the worms or to death of heavily infected fish.

The mean length of male worms decreased slightly but there was no change in the variance. This shows that some were dying, but not large numbers. The percentage of female worms with shelled acanthors increased, then levelled off: as smaller worms matured so larger ones became senescent. The mean length of the females did not change appreciably, although the variance increased, as the number of large worms was increasing due to growth, and some were dying. The male:female ratio decreased showing that more males than females died.

The competition for food between worms would be greater in a heavily infected fish and so more worms would die causing a decline in the number of heavily infected fish. Dead fish picked up at this time did not have a higher mean number of Echinorhynchus than living ones, although a higher percentage was infected. It is probable however that heavily infected fish were more susceptible to predation; as food supplies decreased the effect of large numbers of Echinorhynchus would become greater and the fish would be weakened. There was thus a combination of different factors acting to cause the decrease in infection.

There was an increase in the mean number and percentage infection in February due to a new infection. The sex ratio and size of worms decreased, but the variance of the numbers was hardly affected showing that only small numbers of worms were involved.

There was then another decrease in the level of infection from March to May. The mean, percentage infection, and sex ratio decreased. This was due to a decrease in the number of heavily infected fish brought about by the death of large worms. The mean worm length decreased as growth of individuals did not counteract the death of large ones.

A further infection occurred in June and July with an increase in the percentage of fish infected, the sex ratio of the Echinorhynchus, and the numbers of small worms. The mean number and size of worms was more or less constant as the number of small ones acquired was balanced by the number of large ones dying.

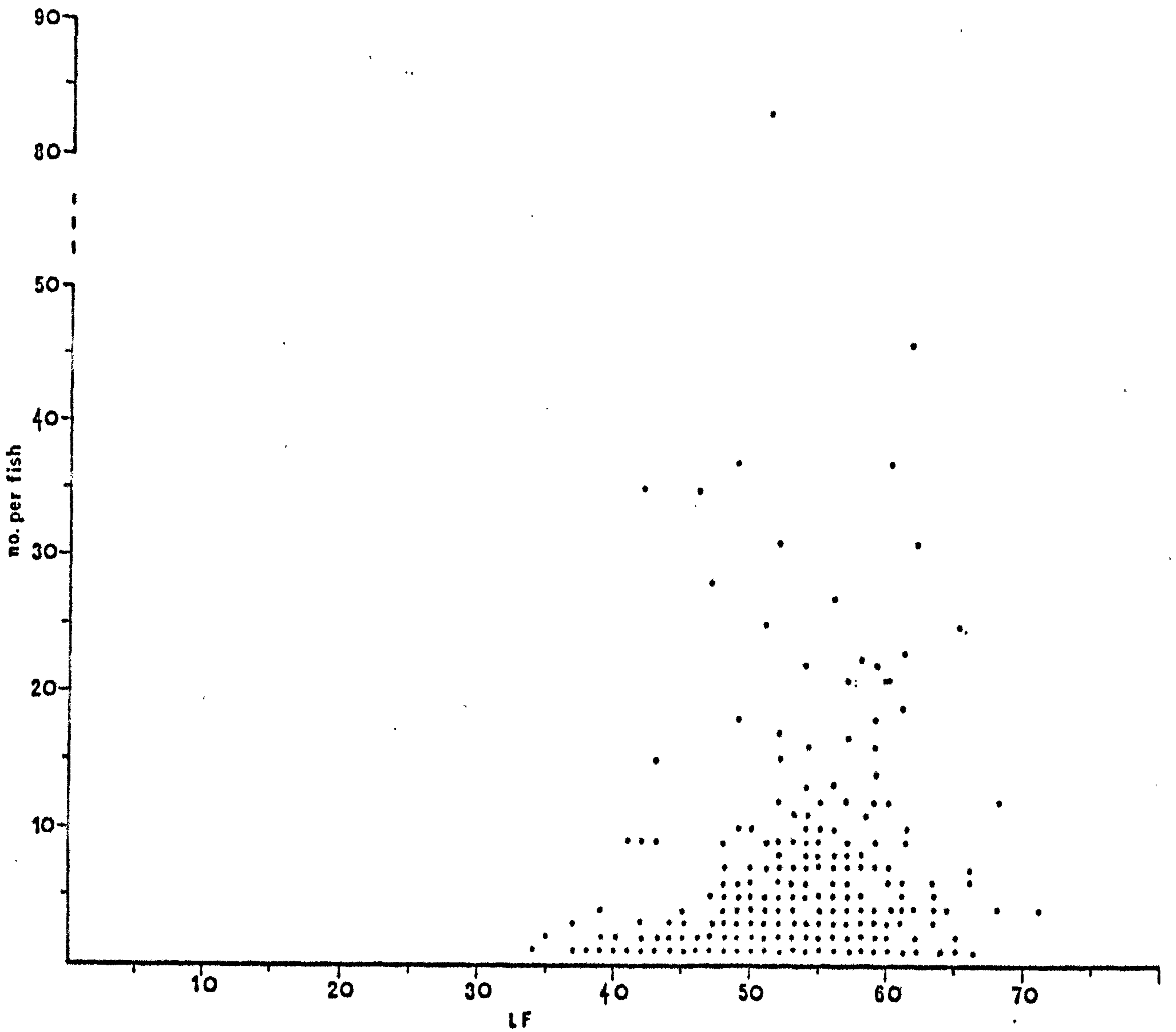
At the end of July and in August the infection decreased to a very low level. In September and October the mean number and variance increased rapidly and the percentage infection more slowly. The sex ratio was high and the mean sizes of the worms low. Thus a new infection occurred at this time. The high percentage infection was maintained until February, and the mean and variance of the numbers continued to increase showing that more worms were being acquired. The mean length remained low because of this, but the number of large worms increased and the percentage of females with shelled acanthors rose as the worms grew and matured. In January 1968 there was a larger infection: the sex ratio rose to its highest level and the mean number of

parasites per fish was also high, while the percentage of females with acanthors and the mean length of worms decreased.

In March there was a decrease in the percentage infection, mean number and variance due to heavily infected fish dying. Dead ones picked up in March, after heavy frosts, had a higher mean number of Echinorhynchus than living ones. More fish were probably being eaten by predators. The mean length of the worms increased showing that no new ones were being acquired and few large ones lost. The decrease in infection was therefore due to heavily infected fish dying rather than to death of the worms themselves, as the large decrease in variance of numbers also shows.

Although the general level of infection was lower in the winter of 1967-8 the pattern was similar to that in the preceding year. The infection increased in October then remained more or less constant, with a slight increase in January or February, and a decrease in March and April. The difference in level was probably due to the fact that the winter of 1966-7 was milder than that of 1967-8. There was also probably a higher infection in 1966, before this study was started, when there were more Asellus in the pond.

FIG. 44 Echinorhynchus

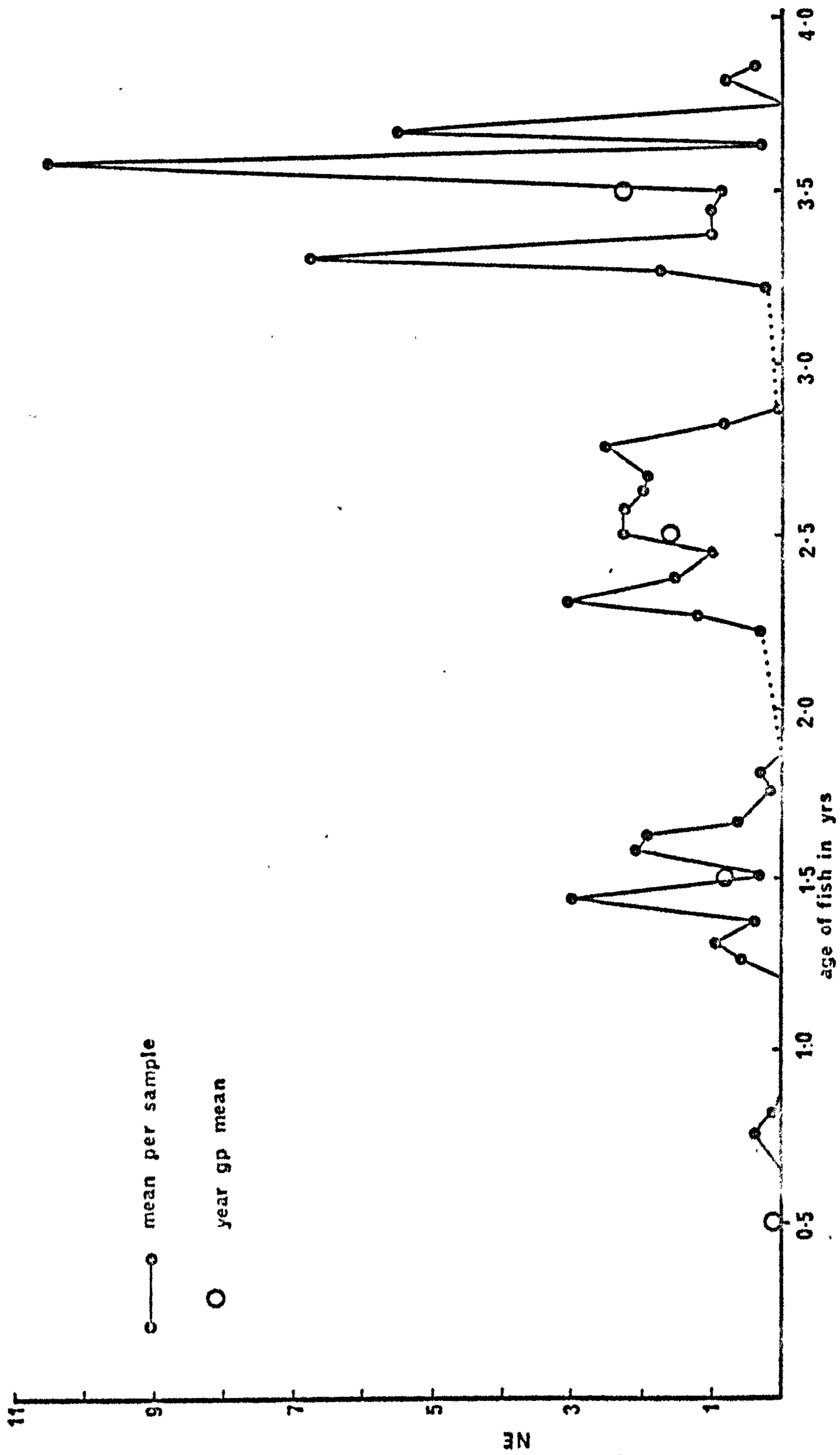


DISTRIBUTION IN FISH OF DIFFERENT LENGTHS

The distribution of Echinorhynchus in fish of different lengths was also considered. The number of worms per fish was plotted against the length of the fish for each sample, using the computer. The scatter diagram for all fish together is shown in Fig. 44.

The number of Echinorhynchus per fish increased steadily with the length of the fish to about 55 mm, then decreased again. The maximum number was more or less constant at 30-40 in fish of between 40 and 65 mm; it was very low in shorter fish and decreased steadily in longer ones.

FIG. 45 Echinorhynchus



DISTRIBUTION IN FISH OF DIFFERENT AGES

The mean numbers of Echinorhynchus in fish of each age group of each sample from 21.8.67 onwards were calculated, and are plotted in Fig. 45. There were only two fish in age group I with any worms. The mean number per fish then increased steadily with age, though it varied as the level of infection changed. Values for age group IV were erratic as there were only small numbers of fish of this age.

Data for fish of each age group of each sample were also collected into frequency distributions. Thus one of the factors which could have been causing the distributions to be negative binomial - non-homogeneity of the host population - was eliminated. In general the resulting distributions were based on very small numbers of fish, but it was obvious that they were still overdispersed.

The percentage of infected fish rose steadily with age: 2% in age group I, 16.6% in II, 30.5% in III, and 36.5% in group IV.

IV DIPLOSTOMUM (D.) GASTEROSTEI Williams, 1966

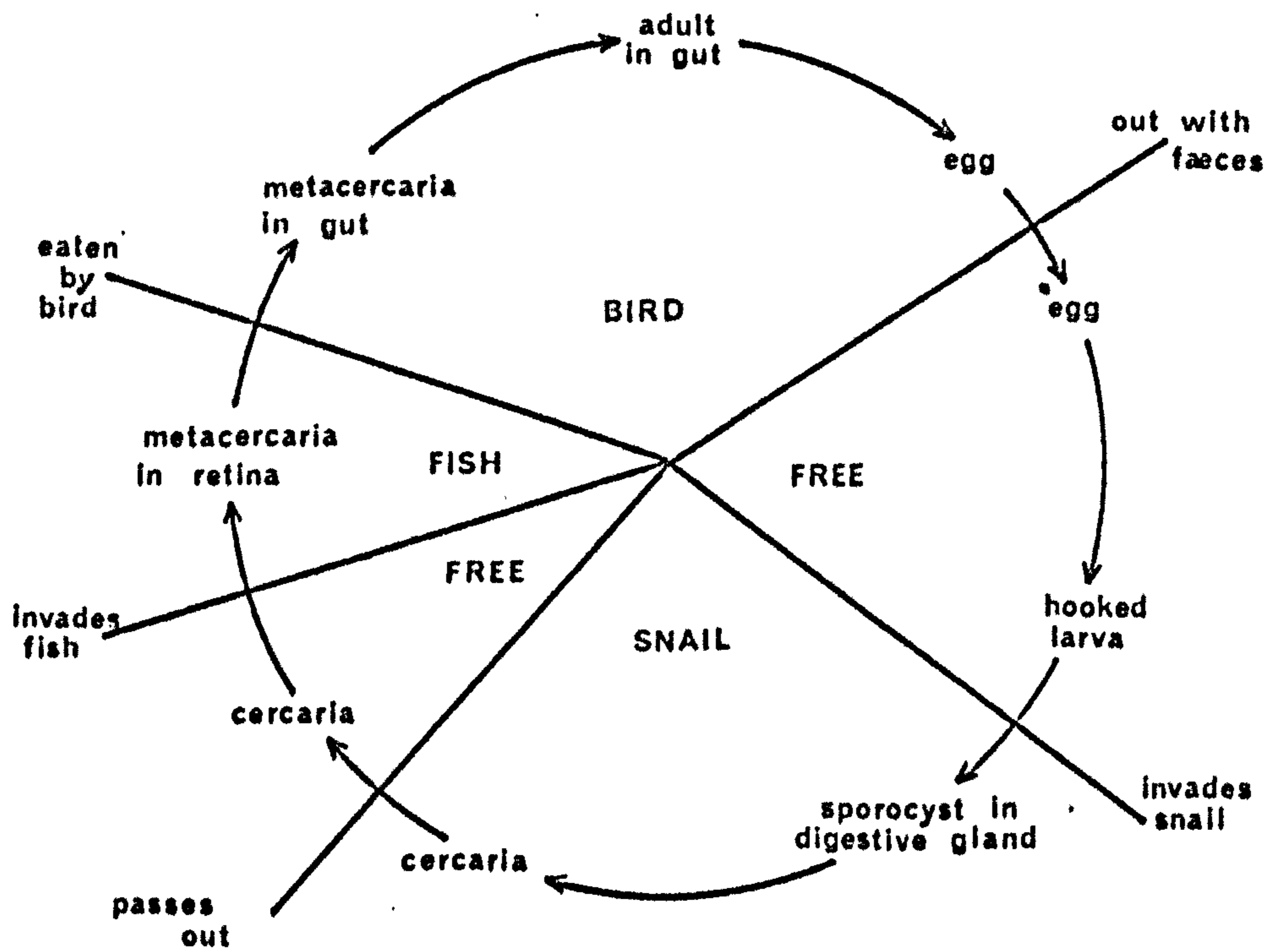
LIFE CYCLE

Diplostomum gasterostei is a digenetic trematode of the family Strigeidae. The metacercarial larva, or diplostomulum, is found in the retinal layer of the eyes of Gasterosteus. This species has only recently been described and named by Williams (1966), although it had previously been recognised by Berrie (1960) as being distinct from D. spathaceum (Rud.) whose metacercarial stage is found in the lenses of sticklebacks. Unlike spathaceum the diplostomulum of gasterostei does not encyst.

Williams found that the definitive host was a duck and not a gull as it is in spathaceum, but Berrie cites ducks and gulls as definitive hosts of both species. No fish-eating ducks were seen at Priddy so it seems probable that gulls are acting as the definitive host. This suggests they may also be the definitive hosts for Schistocephalus.

The adult fluke lives in the bird's gut and produces eggs which are passed out with the faeces and hatch to hooked larvae. The first intermediate host is Limnaea pereger which is invaded by the hooked larva; this develops into a sporocyst in the digestive gland of the snail and produces fork-tailed cercariae which pass out of the snail. These enter the fish, losing their tails on contact, penetrate

LIFE CYCLE of DIPLOSTOMUM



the tissues and migrate to the eyes. This can take as little as three hours.

Williams (1966) examined 550 Limnaea pereger and found only one of them infected with cercariae of D. gasterostei although nearly all sticklebacks from the same pond were harbouring the diplostomulum. Also Pike (1968) found Diplostomum sp. in 78% of Gasterosteus and 64% of Pygosteus but no cercariae in 1467 L. pereger. Fifty L. pereger were collected at Priddy in the first year of the study and only one was infected. There were few snails to be found in winter but the numbers were higher in spring and summer. Because of the very large numbers of cercariae produced by each infected snail it would seem that only a small number needs to be infected to maintain a high level of infection in the stickleback population.

PATHOLOGY

There must be some interference with vision when there are large numbers of metacercariae in the eyes. The flukes are quite transparent, however, and the movement of potential predators is probably clearly visible. There was no evidence that the food-finding capacity was significantly reduced; there were not large numbers of dead fish with higher than average numbers of Diplostomum.

SEASONAL DISTRIBUTION

The numbers of Diplostomum in the right and left eyes of each fish were counted and hence the total number per fish known. The figures are given in appendix 2 e .

I Percentage infection (Fig. 46a)

56.1% of all fish were infected with Diplostomum. The percentage rose from 45% on 29.10.66 to 55% on 10.12.66. It then remained at about the same level until February 1967 after which it decreased to 18.9% on 21.4.67. There was a rapid rise to 88.2% on 21.6.67. The highest value, of 91.4%, occurred on 31.7.67 and was followed by a gradual decline to 63.6% on 18.10.67. The level then remained more or less the same, with fluctuations between 60 and 73%, until March 1968; the percentage decreased to 50% on 25.3.68 and increased slightly to 52.6% in the final sample.

II Numbers of Diplostomum per fish

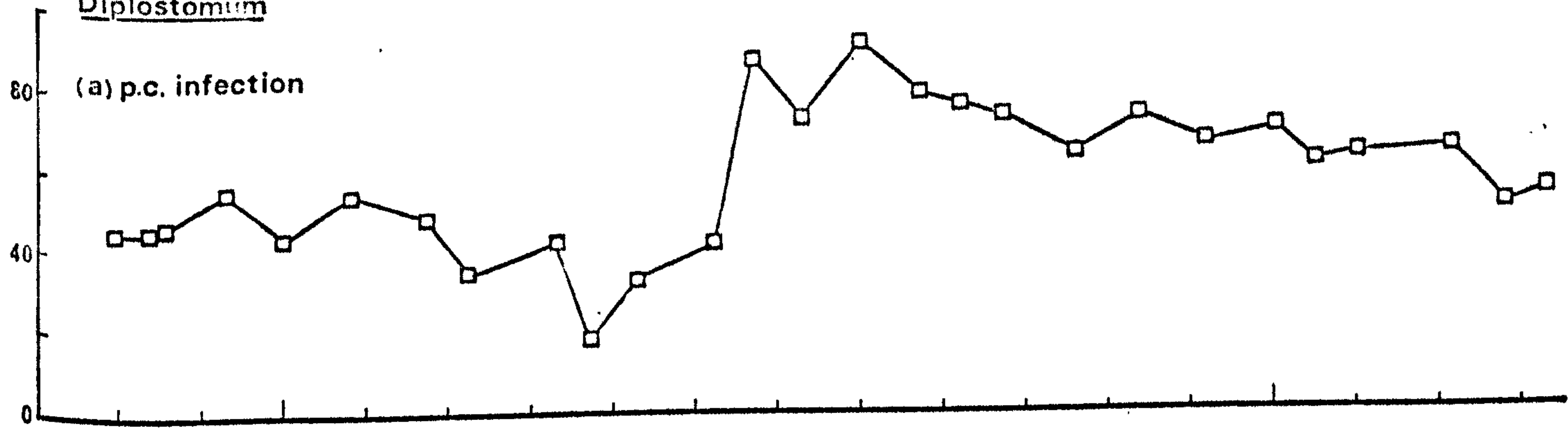
A. Total numbers

The mean and variance of the total numbers of Diplostomum per fish were calculated for each sample. The figures were collected into frequency distributions which were plotted in log x2 classes expressed as percentages. Theoretical distributions were calculated and compared with the originals.

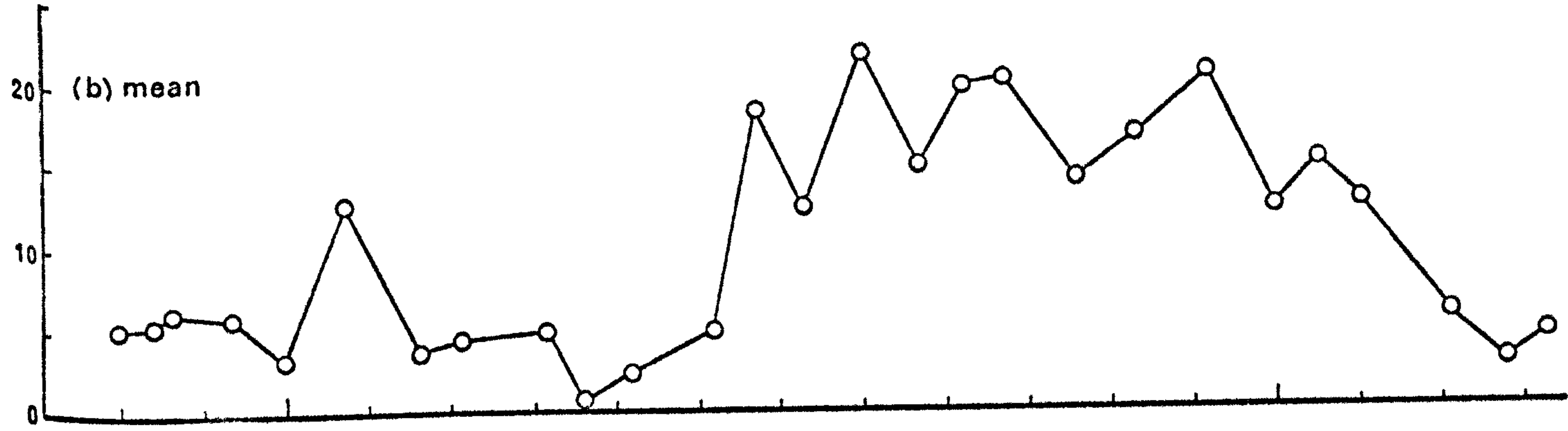
FIG. 46

Diplostomum

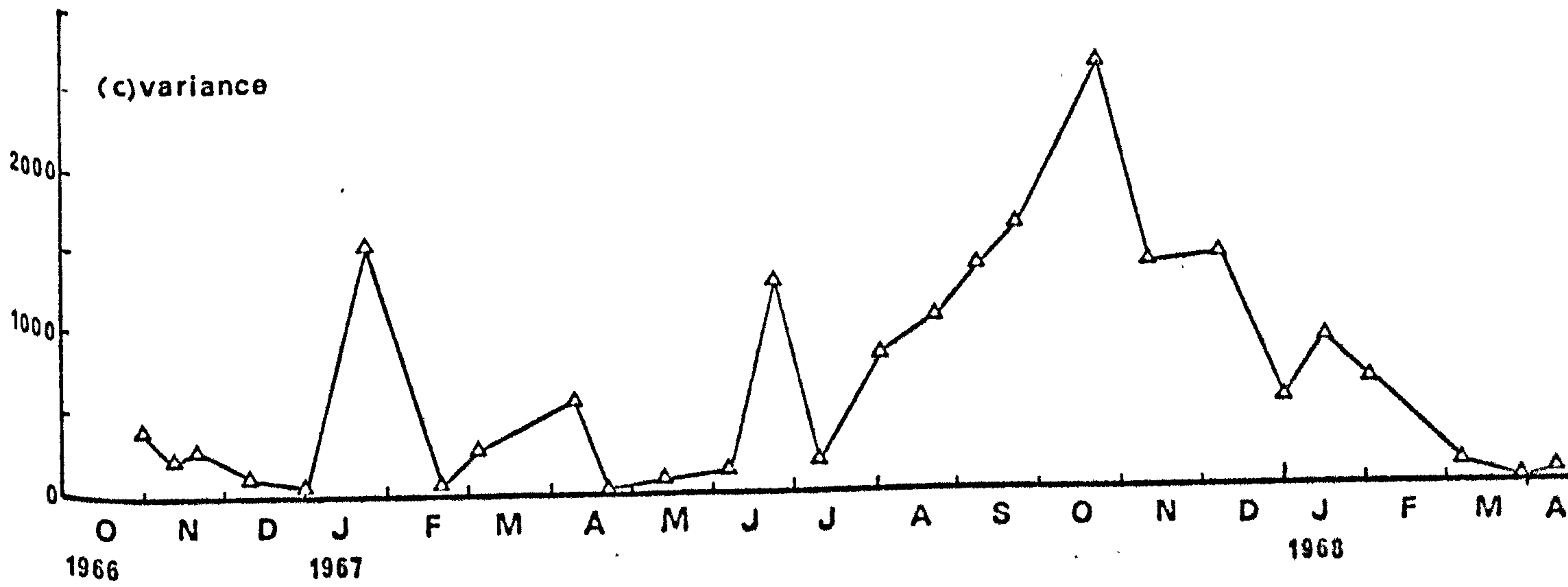
(a) p.c. infection



(b) mean



(c) variance



1. Mean (Fig. 46b)

The mean number of Diplostomum in all fish was 9.35. The mean increased from 5.3 on 29.10.66 to 6.3 on 19.11.66, then fell to 3.4 on 1.1.67. There was a high value of 12.8 on 25.1.67, due to one fish with 275 parasites, followed by a steady rise from 3.6 on 18.2.67 to 4.9 on 9.4.67, and then a minimum of 0.72 on 21.4.67. There was a steady rise to 18.4 on 21.6.67. The mean fluctuated about this level until January 1968, varying between 12.1 and 21.9, then decreased fairly steadily to 2.9 on 25.3.68. Again there was a slight rise in the final sample, to 4.3.

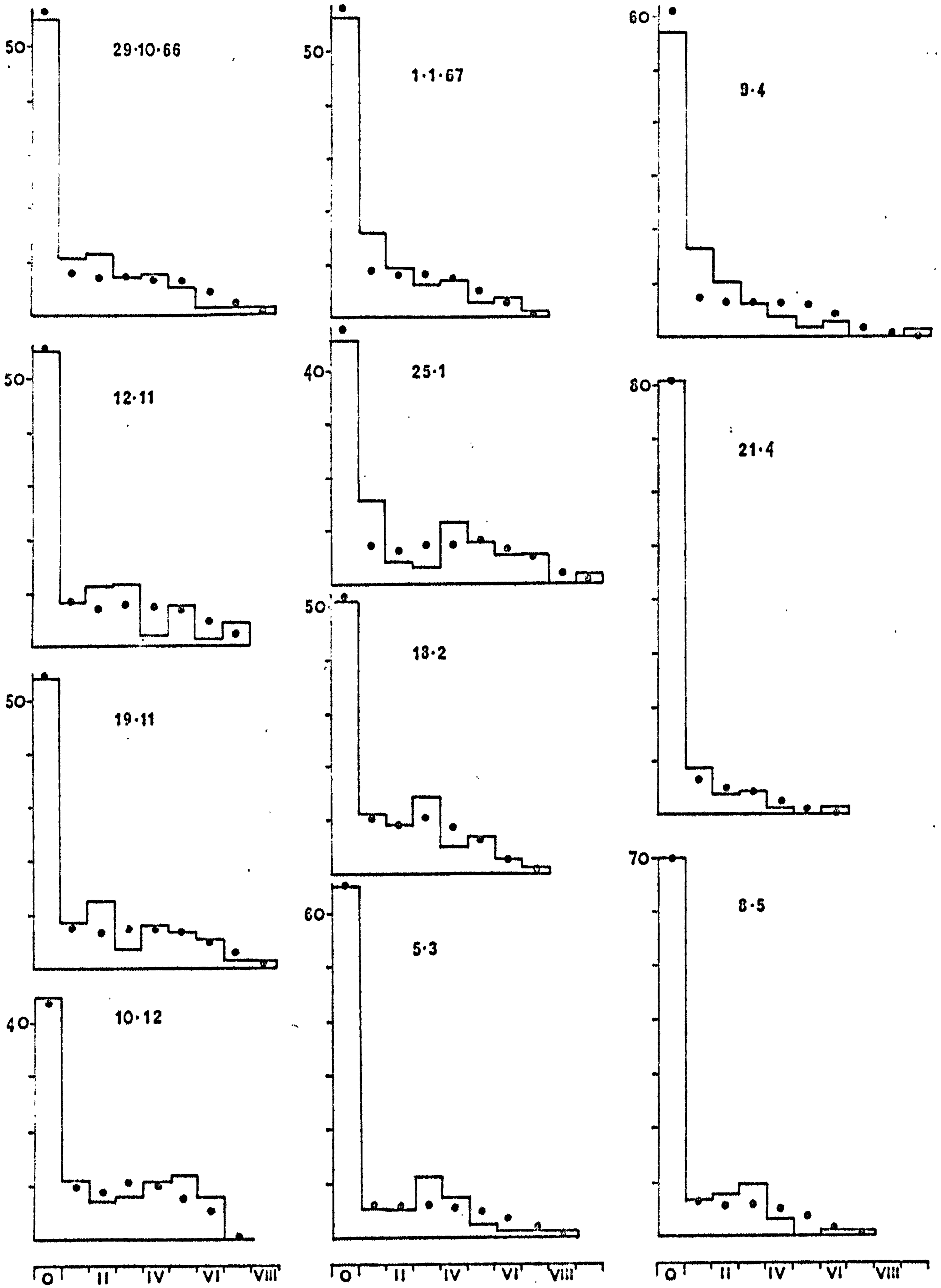
2. Variance (Fig. 46c)

The variance for all fish was 592.6. The value was 316 on 29.10.66; it then fell fairly steadily to 68 on 18.2.67, except for a high value of 1520 on 25.1.67 due to the single fish with 275 Diplostomum. The variance rose to 545 on 9.4.67, fell to 8.2 on 21.4.67 and then increased again to 228 on 6.7.67. There was a peak of 1286 on 21.6.67, due partly to one fish with 243 parasites, then a faster steady rise to a maximum of 2637 on 18.10.67, followed by a fairly steady decrease to 28 on 25.3.68. There was a small rise to 59 in the final sample.

3. Overdispersion (Fig. 47d)

The ratio of variance:mean for all fish was 63.38.

FIG.48 Diplostomum log x 2 classes • -ve binomial



The variations in the value of the overdispersion were very similar to those in the value of the variance. The overdispersion was initially 59.5; it then decreased to 11.5 on 21.4.67, with two large peaks of 119 on 25.1.67 and 112 on 9.4.67. There was then a rise to a level of about 25 in May which was maintained until July, except for a peak of 70 on 21.6.67. The value then increased rapidly to a peak of 187 on 18.10.67 followed by a fairly steady decrease to 9.7 on 25.3.68 with a slight rise to 13.9 in the final sample.

4. Frequency distributions (Fig. 48)

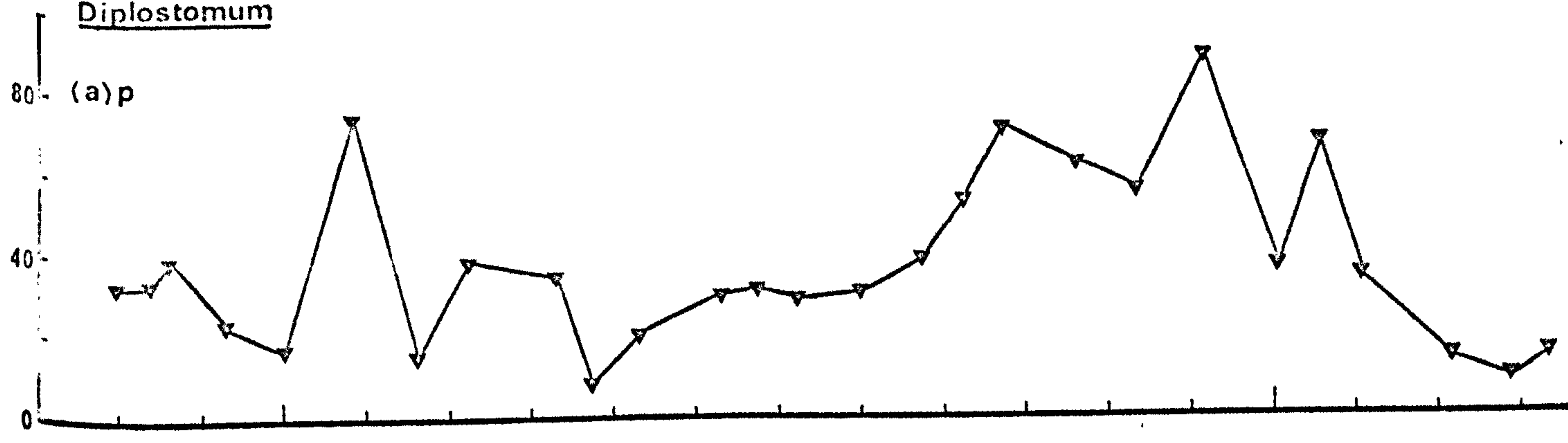
The zero class was the largest in all but one of the distributions. The tail was often very long: there were many fish with over 50 parasites and the maximum was 443. However, only 16 fish, 1.5% of those infected, had more than 120 Diplostomum.

Negative binomial and log series distributions were calculated, using the computer, for each sample. The former fitted closely for most samples, though R^2 was not as high as for the Echinorhynchus distributions. R^2 was greater than 0.96 for 14 samples, but less than 0.9 for samples between 21.6.67 and 21.8.67, when the percentage infection was high, and also on 21.9.67 and 10.11.67 when there were too many low values. For these samples the log series was a worse fit. The log normal was also tried but did not fit any better.

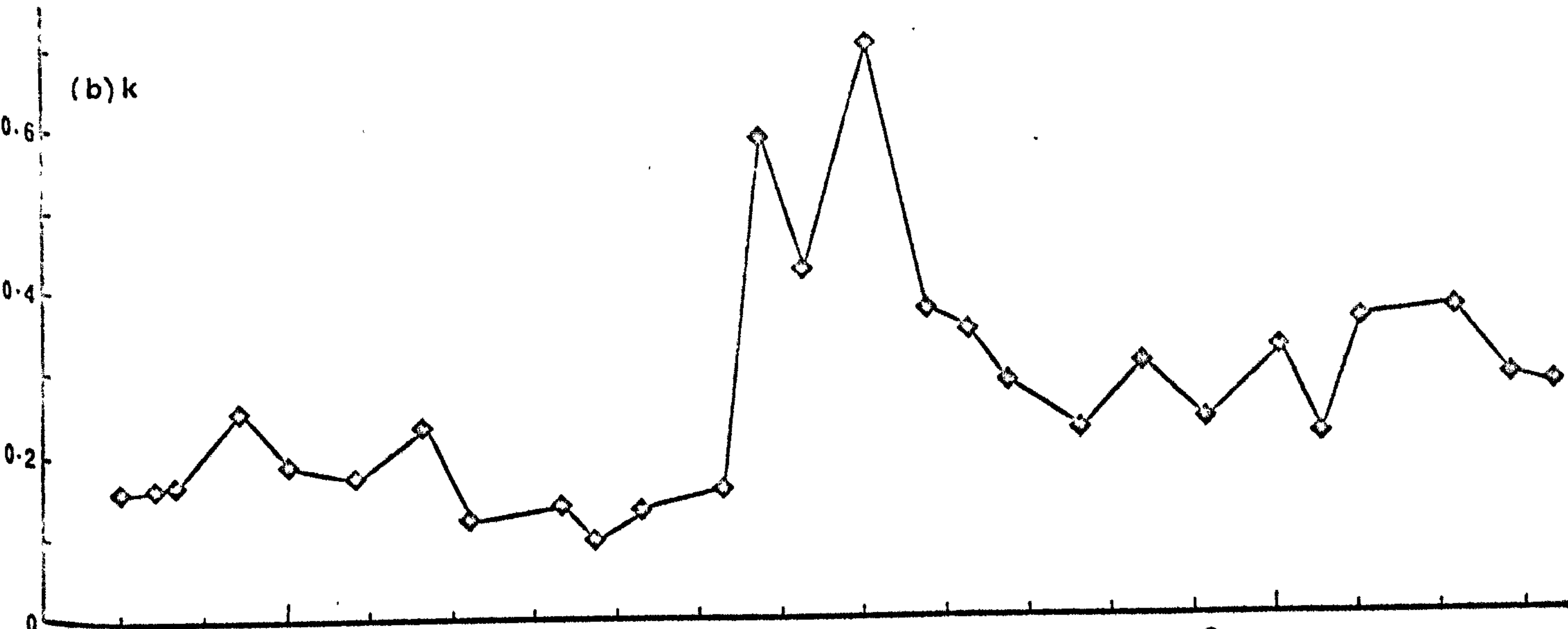
FIG. 47

Diplostomum

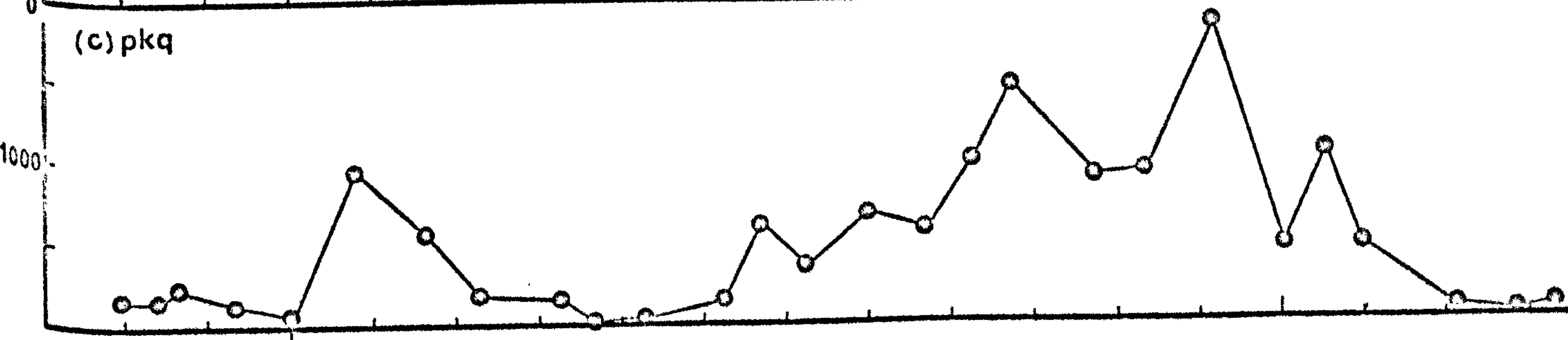
(a) p



(b) k



(c) pkq



(d) variance / mean



The negative binomial distributions are plotted with the originals in Fig. 48, and it can be seen that the fit was reasonable for most samples although the shapes varied quite widely.

Parameters of the negative binomial

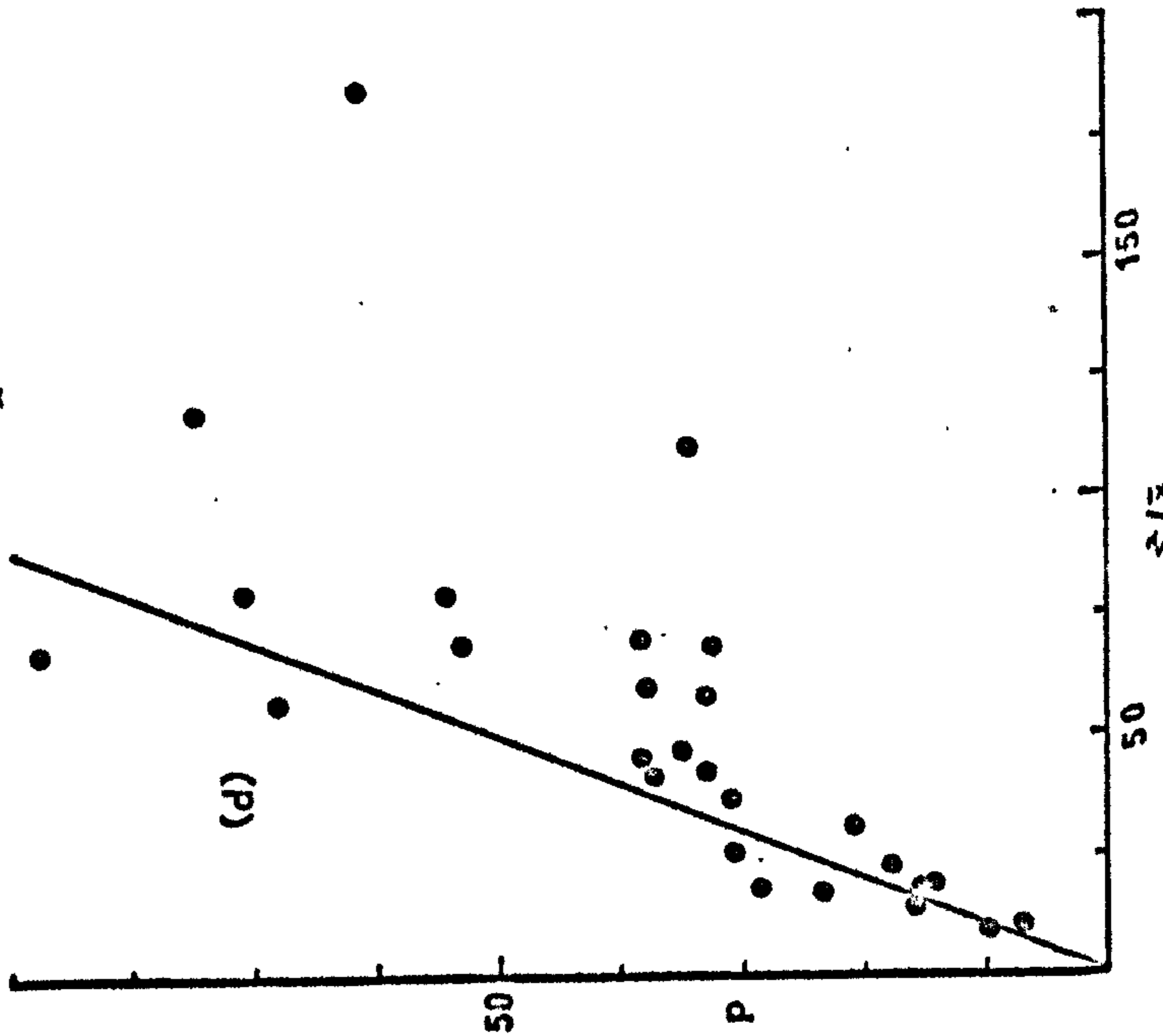
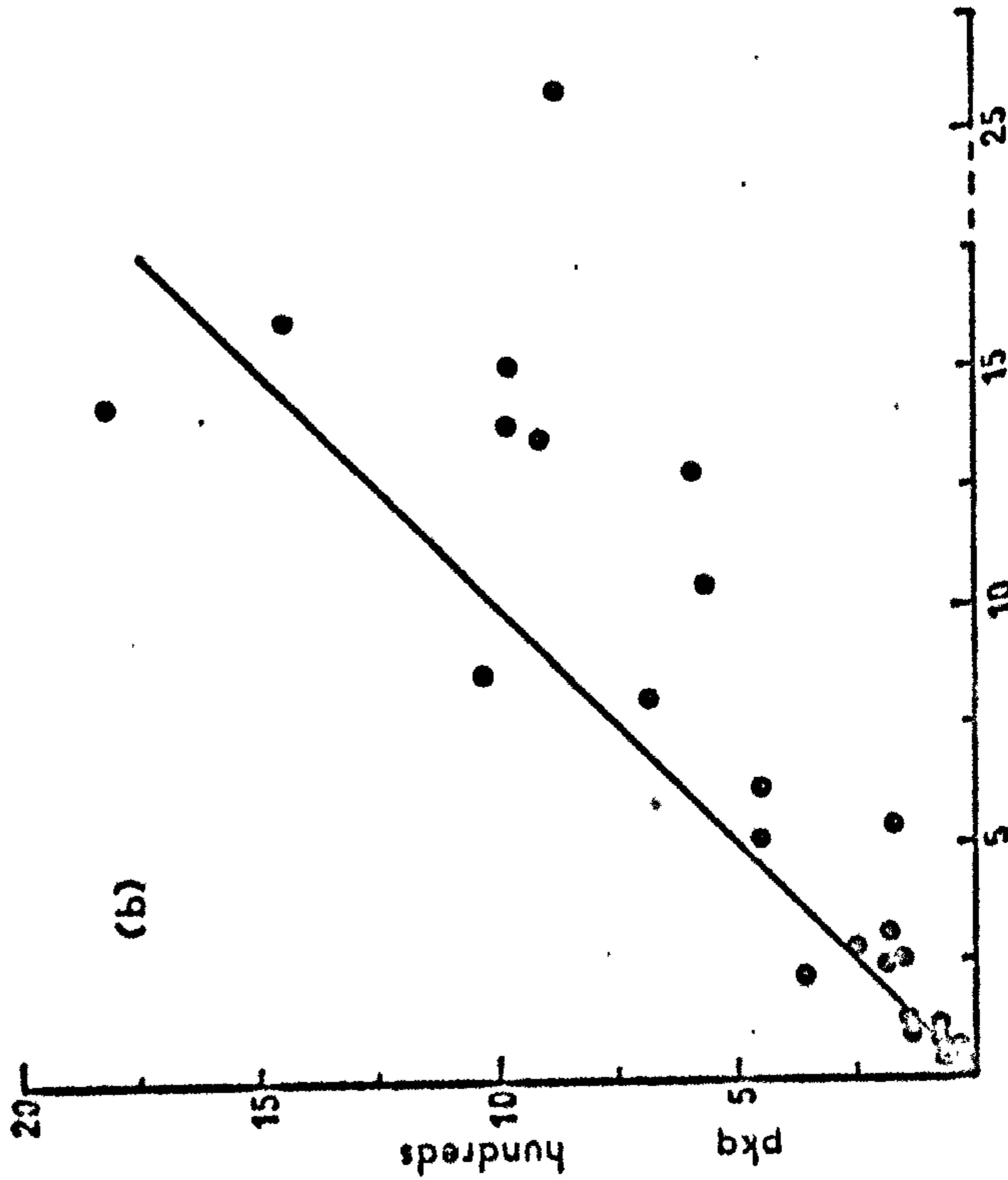
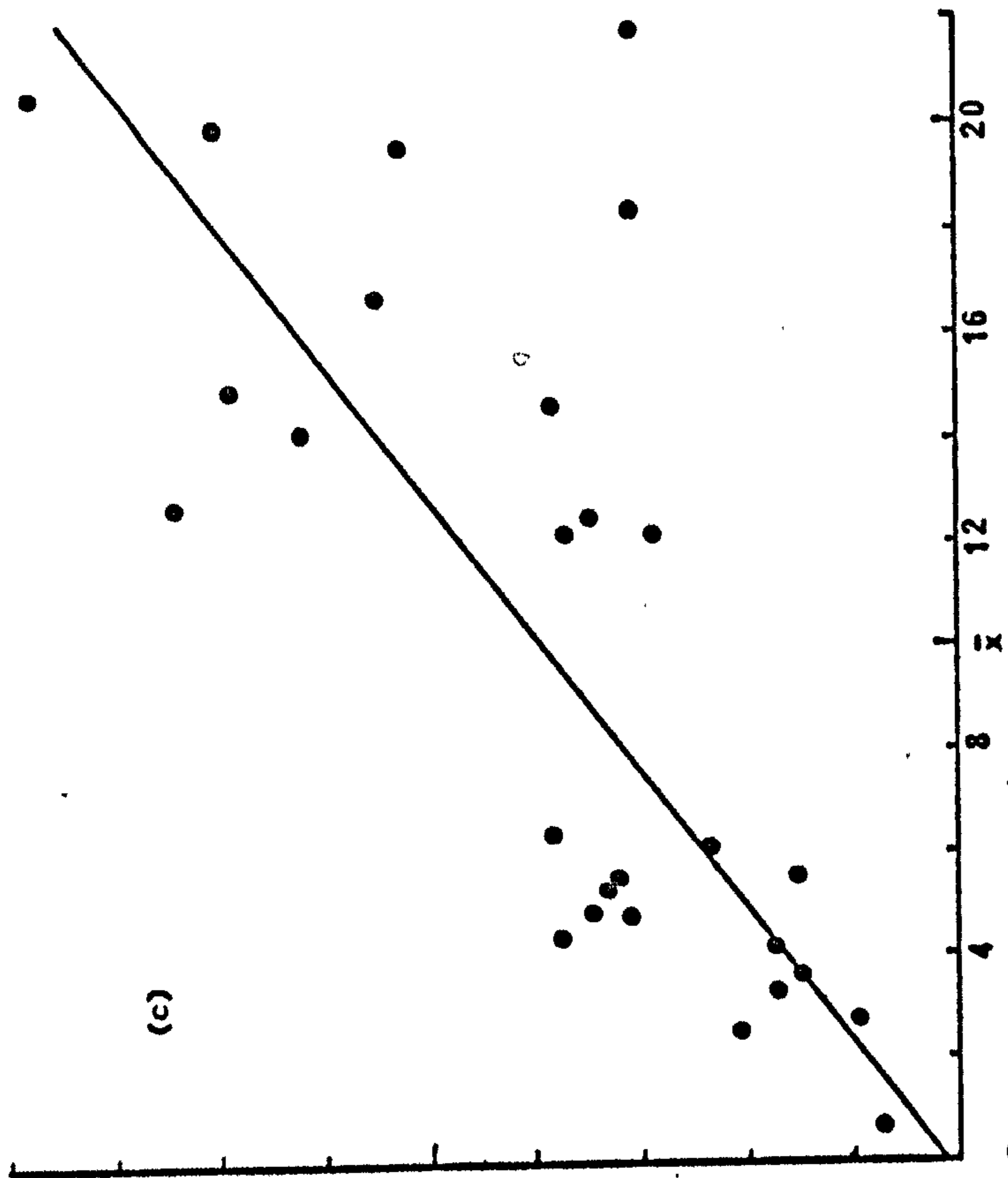
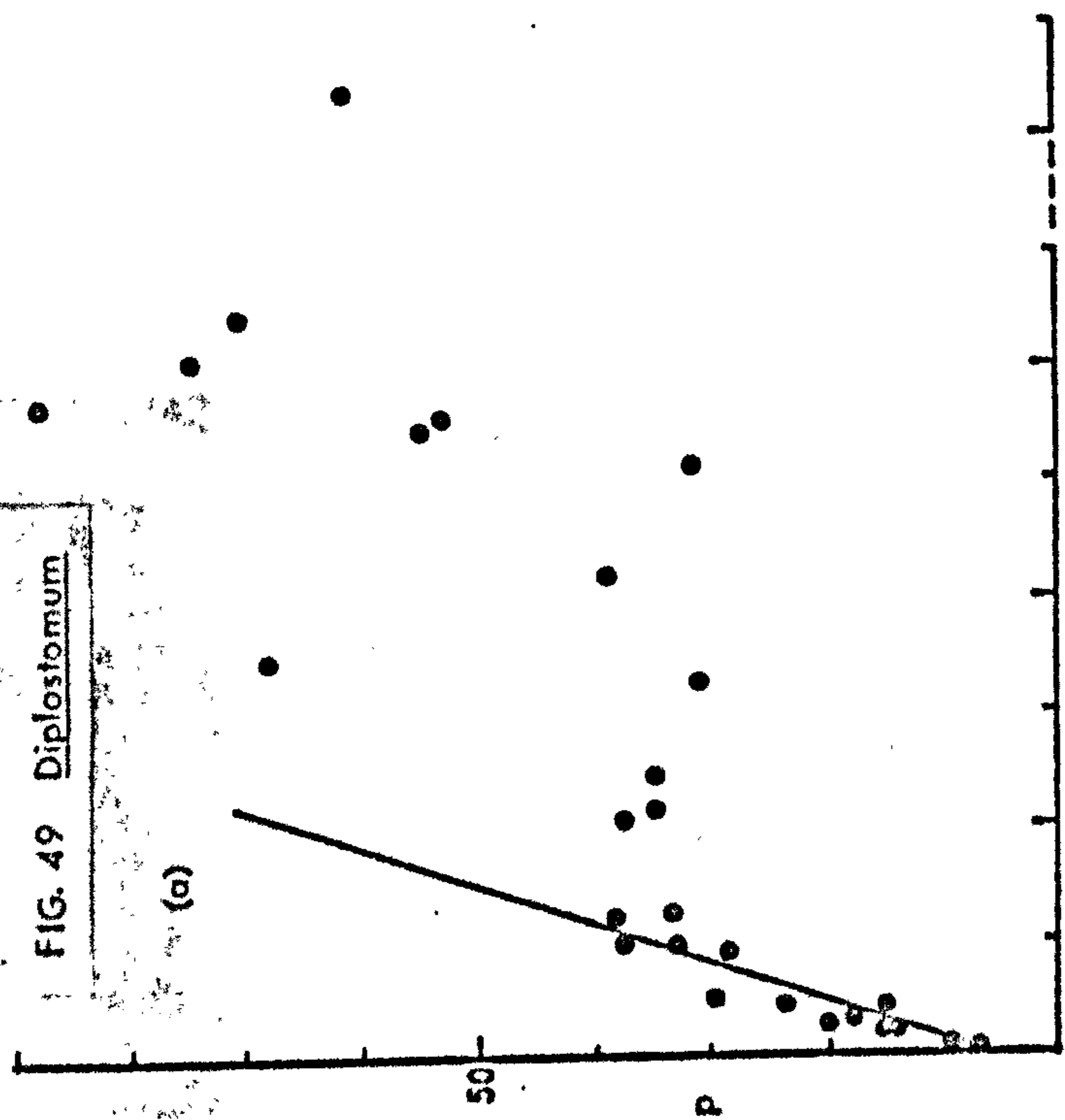
p (Fig. 47a)

The value of p averaged over all the samples was 37.2. p fell from 33.1 on 29.10.66 to 15.4 on 18.2.67, except for a peak of 74.7 on 25.1.67. There was then an increase to 37.9 on 5.3.67, followed by a decrease to a minimum of 7.4 on 21.4.67. The value increased to 30.6 on 7.6.67 and then remained fairly constant until 31.7.67 after which it rose steadily to 70.1 on 21.9.67. The value then fluctuated widely, between 87.7 and 37, though with a tendency to decrease, until January 1968; then it fell steadily to 9.7 on 25.3.68. There was a slight rise to 15.3 on 9.4.68.

k (Fig. 47b)

The value of k averaged over all the samples was 0.27. The value was fairly constant until 7.6.67, fluctuating between 0.26 and 0.10. It then increased suddenly to 0.59 on 21.6.67, followed by a decrease to 0.42 and then a maximum of 0.71 on 31.7.67. There was a steady decrease to 0.23 on 18.10.67. The level remained about the same, with fluctuations between 0.22 and 0.32, until 15.1.68 when it rose to 0.37 on

FIG. 49 Diplostomum



4.3.68, and then fell to 0.28 on 9.4.68.

pkq (Fig. 47c)

The value of the theoretical variance calculated from the average values of p and k was 383. The value decreased from 185 on 29.10.66 to 64 on 1.1.67. There was then a sudden increase to 965 on 25.1.67 followed by a steady decrease to 11.5 on 21.4.67. The value then rose fairly steadily to 1425 on 21.9.67. There was a decrease to a level of about 900 during October and November followed by a peak of 182 on 4.12.67. The value of pkq then fell to 28 on 25.3.68 with a final rise to 70.

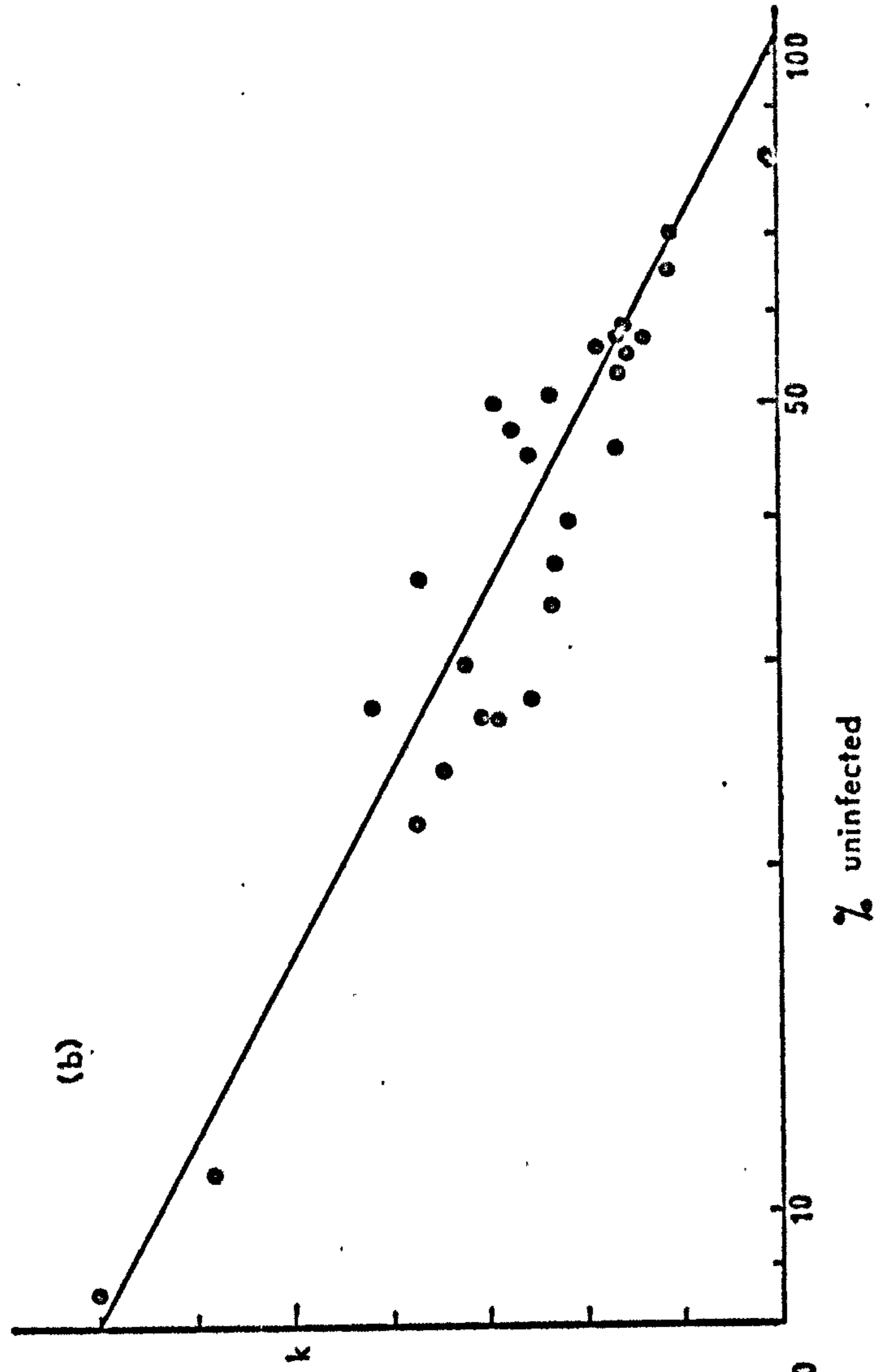
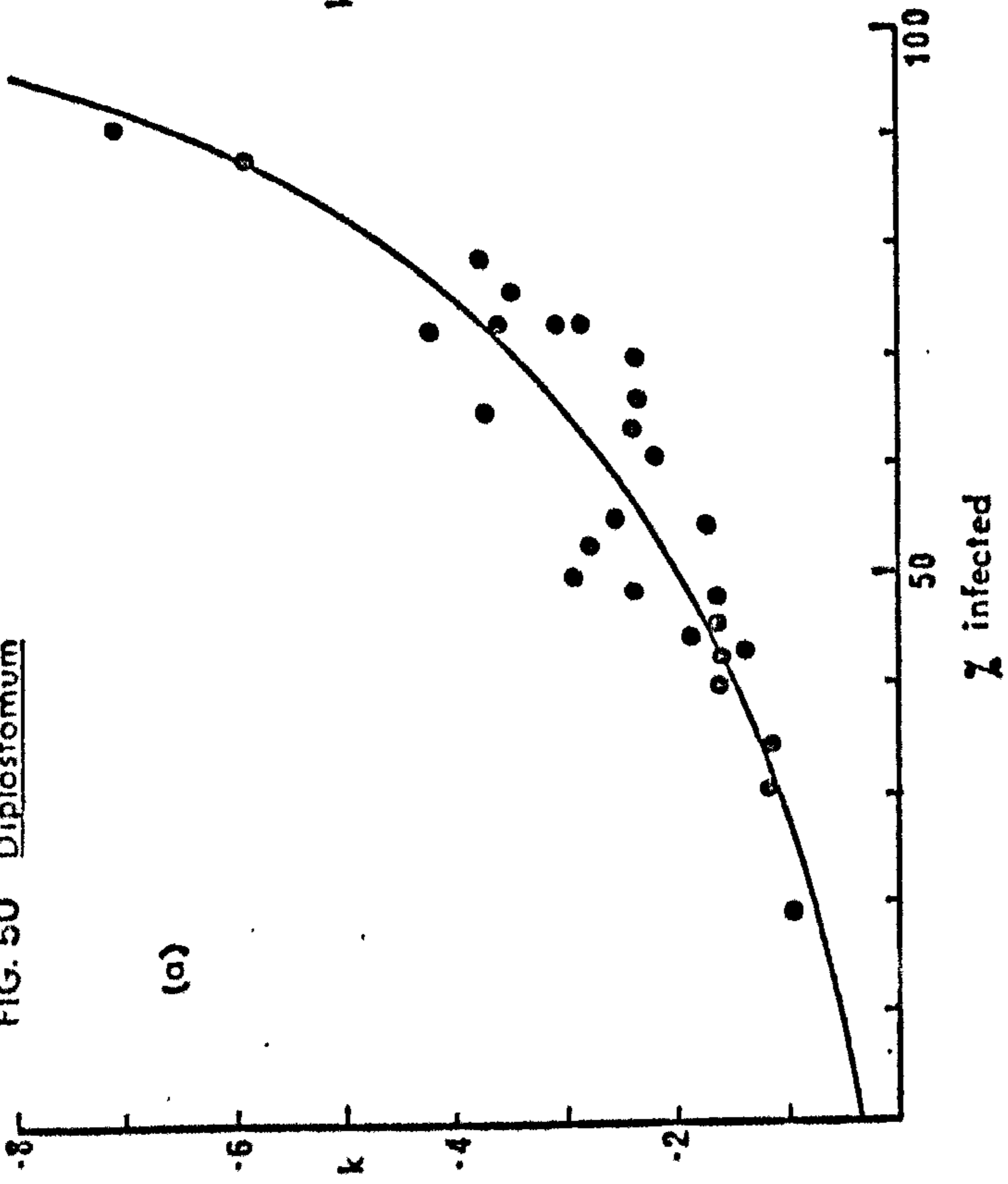
Relationships between p and k and the parameters of the original distribution

Values of p and k were plotted against the parameters calculated from the original data for each sample. The following five pairs showed the closest relationships, as with the Echinorhynchus distributions.

1. p vs s^2 / \bar{x} (Fig. 49d)

Once again the line $s^2 / \bar{x} = 1 + p$ fitted the points quite well. The points for three samples, 25.1.67, 9.4.67, and 18.10.67 had too high a value of the overdispersion due to the variance being raised by single heavily infected fish, with 275, 191 and 443 Diplostomum respectively.

FIG. 50 Diplostomum



2. p vs s^2 (Fig. 49a)

These points were widely scattered except for those with low variance (less than 250). As some fish had very large numbers of parasites the variance was often very high. If the mean was also high, when there was a high general level of infection, then the overdispersion was not exceptionally large and the points did not deviate from the above line.

3. p vs \bar{x} (Fig. 49c)

The points were widely scattered about an approximately straight line.

4. pkq vs s^2 (Fig. 49b)

In general s^2 was greater than pkq , particularly for higher values. This was again due to the high variances caused by small numbers of heavily infected fish. The point for 18.10.67 was a long way from the line $s^2 = pkq$; this sample contained the most heavily infected fish found, with 443 Diplostomum.

5. k vs percentage infection (Fig. 50a)

The points lay on a curve which was converted into a straight line by plotting k against $\log p_0$ where p_0 is the percentage of uninfected fish (Fig. 50b). The line

$$k = -1.2 \log_{10} p_0 + 1.93 \quad \dots(96)$$

fitted the curve quite closely and no points were very far off.

Thus in general k varied as the percentage infection and p as the overdispersion. p and k tended to vary inversely with each other.

Between October and April 1966-7 the percentage infection, mean and variance were all fairly low and tended to decrease; p and k were also low and decreased in April. In May and June the percentage infection and mean increased rapidly while the variance increased very slowly. This increase was largely represented by an increase in k , although the value of p increased slightly. The percentage infection then decreased steadily until October while the mean remained at the same high level and the variance rose steadily to a high level. As the mean remained constant so did the product of p and k , but their individual values changed: k decreasing with the percentage infection and p increasing with the variance.

From November to April 1968 the percentage infection was more or less constant and so therefore was k . The mean was constant until December, then decreased, and the variance decreased steadily. The value of p was about the same until December while the mean was constant, then decreased as both mean and variance fell.

B. Number in left and right eyes

For all the fish the mean number of Diplostomum per

right eye was 4.83 and the mean number for the left eye 4.53. This difference was not significant.

56.1% of all fish were infected; 40.4% had Diplostomum in both eyes, 8.4% only in the right eye, and 7.4% only in the left. There were 10.5% of fish with only one parasite, which was in the right eye in 5.3% of fish and in the left in 5.2%. Thus very few fish had a single eye infected with more than one parasite, and in all of these the numbers were small. The fish with both eyes infected had approximately equal numbers in each eye even when the numbers were large. In 19 out of the 27 samples there were more Diplostomum in the right than in the left eyes of the fish, although the difference was often very small.

Therefore at each infection some flukes generally found their way to each eye although there was a slight bias towards the right.

III Discussion

Just over half of all the fish were infected with Diplostomum and the mean number per fish was quite high: 9.4. The variations in the pattern of infection over the study period were considerable.

Initially the level of infection was fairly constant. On 25.1.67 the mean and variance were raised by the presence of one very heavily infected fish, with 275 parasites. Apart

from this there was a slight decrease in mean and variance in December 1966 and January 1967, although the percentage infection did not fall until February. This shows that the number of heavily infected fish was decreasing but that relatively few fish were involved. It is probable that, as conditions became harsher in autumn, selection against heavily infected fish increased. As dead fish picked up at this time did not have a higher mean number of Diplostomum than living ones predation must have been the chief cause of death. It was of course advantageous for the Diplostomum that infected fish should be eaten by a bird, so that the life cycle could be completed; and the more heavily infected the fish the more Diplostomum matured.

There was a slight increase in mean and more particularly in the variance in March, due to a new wave of infection. Only a small number of fish was involved however, for the percentage infection did not increase. As large numbers of cercariae were produced from one infected snail it was usual for a few fish to pick up large numbers of Diplostomum.

In April the mean, variance and percentage infection all decreased to a low level due to decrease in numbers of heavily infected fish. In May and June there was a sudden increase in the mean and percentage infection as many fish acquired new infections. At this time the snail population was increasing and many cercariae being released. The variance

increased only slowly at first showing that the cercariae were quite widely distributed and many fish were picking up small numbers.

Between July and October the mean number levelled off, while the percentage infection decreased slightly, and the variance increased rapidly. A few fish were picking up large numbers of Diplostomum showing that the distribution of cercariae was patchier.

There was then a sharp decrease in the variance while the mean and percentage infection remained more or less constant. Once again heavily infected fish were being removed from the population, largely due to predation. As the mean did not decrease a light infection was continuing. In January the variance continued to decrease rapidly and so did the mean; the percentage infection fell slightly. Thus heavily infected fish were still being removed but no new infection was occurring. In the final sample there was a slight increase in the percentage infection, mean, and variance, indicating the start of a new wave of infection.

There were large differences in the level of infection in the two winters studied: in 1966-7 the infection was very much lower than in 1967-8. The percentage infection followed a similar pattern in the two years; it was constant in winter and decreased in spring, but the level remained higher in 1968.

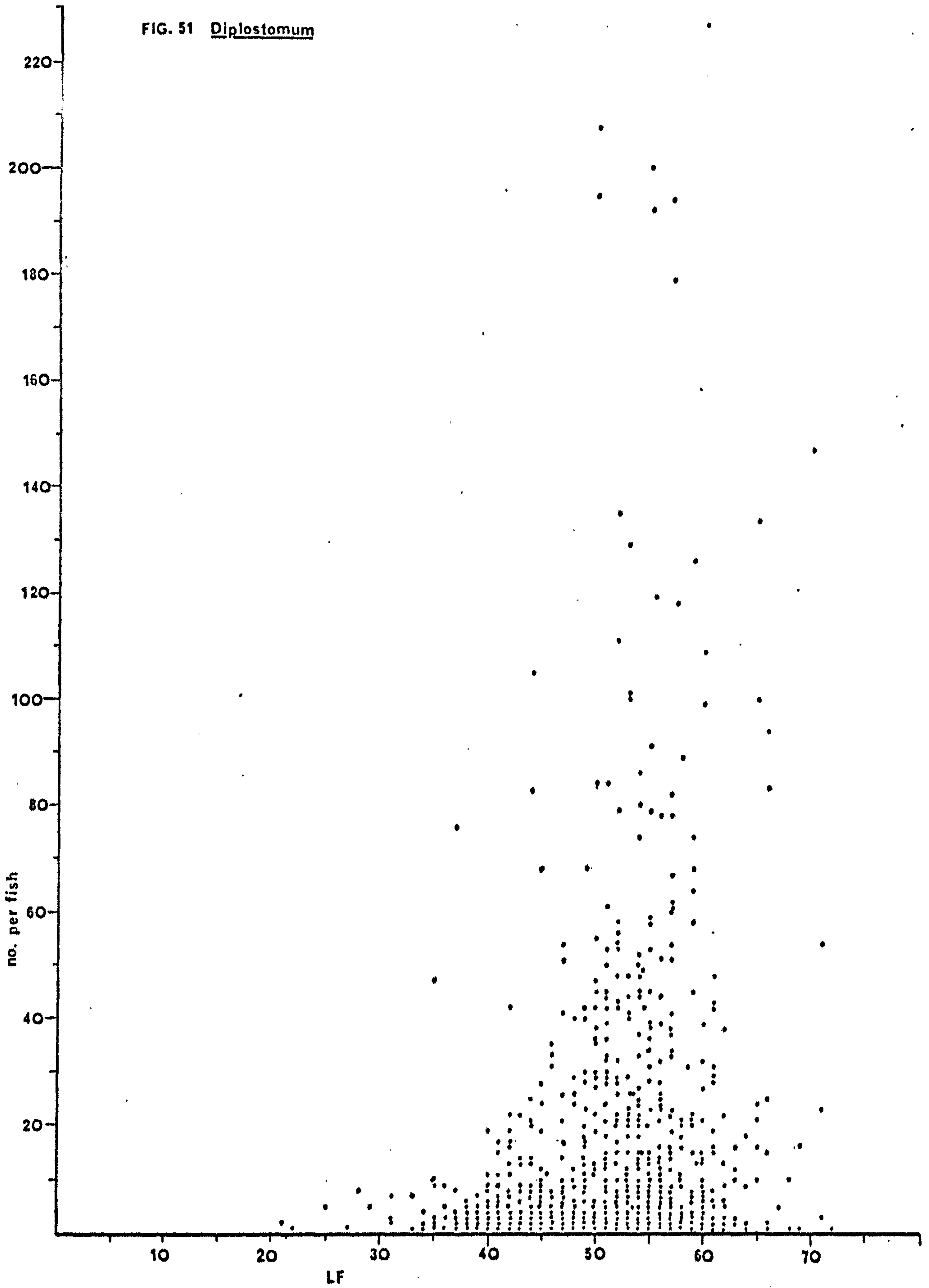
The mean was more or less constant from October 1966 to April 1967, but in the second year was constant only until December 1967, at a higher level, then decreased rapidly in the spring of 1968 bringing the value to about the same level as that in spring 1967. The variance decreased fairly steadily in both years, though with some fluctuations. However in 1967-8 the fall was much faster, as the value was initially much higher, but it ended up at about the same level.

A much larger infection must therefore have occurred in summer 1967 than in summer 1966. This could have been due to a difference in the size of the snail population or to other physical or biological factors affecting the life cycle of the Diplostomum. Although the percentage of fish infected remained higher in the second year the mean and variance decreased to about the same level as in the previous spring. The fish were unable to sustain such a large parasite population, particularly in the cold weather of spring 1968.

Probert (1966) studied the incidence of larval trematodes in various species of freshwater snail. He found that adult Limnaea pereger spawned and died in late spring so that there was a large decrease in the percentage of snails infected. As the young snails grew the infection increased, reaching a peak in late summer. Rees (1932) found peaks of infection in May and September in L. pereger.

Although the Priddy sticklebacks picked up light infections over much of the year by far the largest numbers of Diplostomum were acquired in May and June. There must therefore have been a single peak of infection in the L. pereger population at this time. This is similar to the situation found by Probert, although the timing is closer to the first peak found by Rees.

FIG. 51 Diplostomum



DISTRIBUTION IN FISH OF DIFFERENT LENGTHS

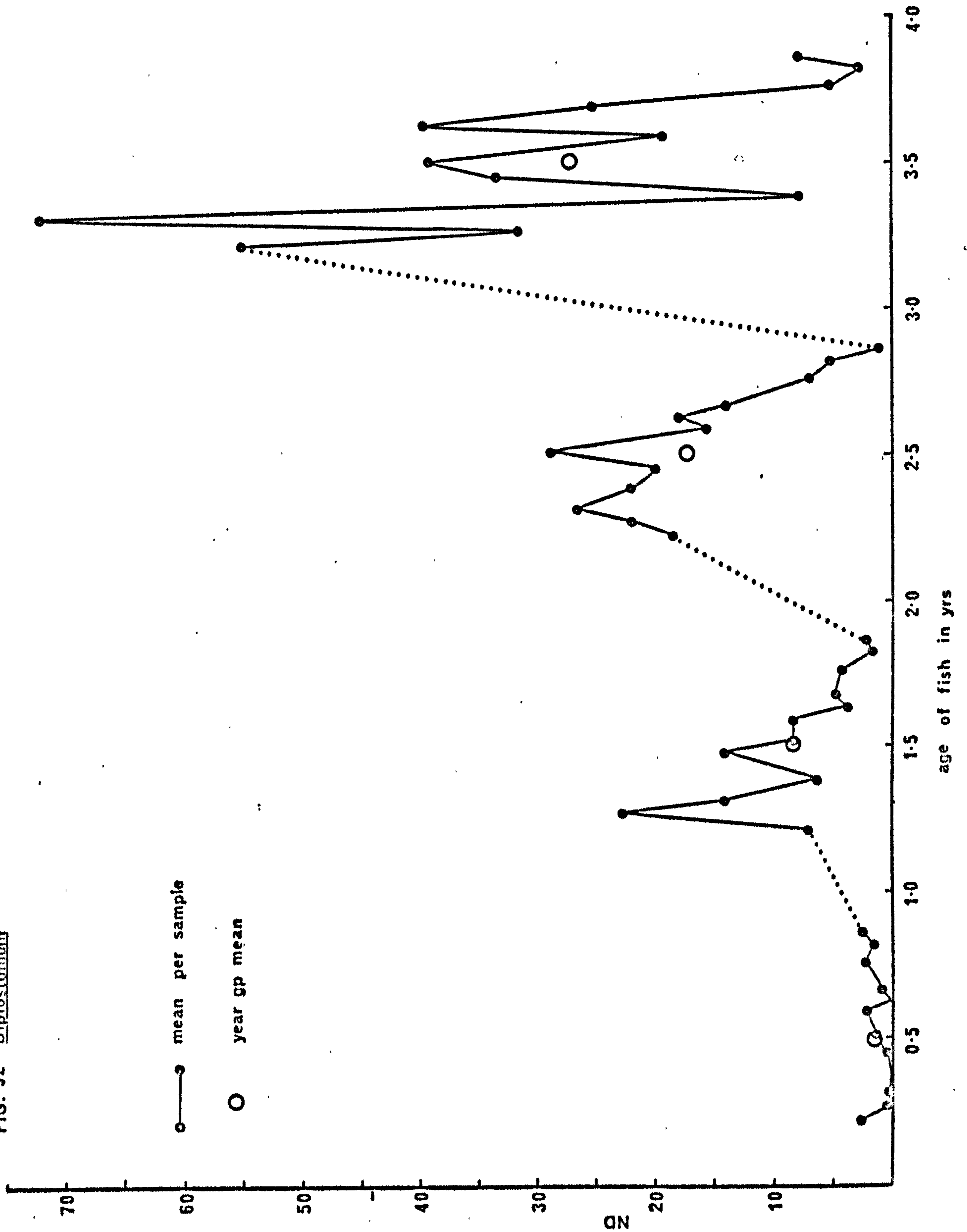
The number of Diplostomum per fish was plotted against length of fish for each sample, using the computer. The scatter diagram for all fish together is shown in Fig. 51.

Few fish shorter than 35 mm were infected with Diplostomum and those that were never had more than 8 worms. The number of worms per fish increased steadily with length in fish from 35-55 mm, then decreased again in longer fish. The maximum number of Diplostomum per fish increased slowly in fish up to 50 mm. There was then a sudden increase, the fish with most worms (443) being 53 mm long. The maximum then decreased more slowly in longer fish.

Fish between 50 and 60 mm in length were therefore best able to withstand high infections with Diplostomum.

Williams (1966) found no Diplostomum in fish under 2 cm in length; fish between 2 and 6 cm were infected and the average number of diplostomula increased with size. He examined no fish longer than 6 cm. Thus he found a similar pattern of infection amongst fish of different sizes as was found at Priddy.

FIG. 52 Diplosfomum



DISTRIBUTION IN FISH OF DIFFERENT AGES

The mean numbers of Diplostomum in fish of each age group of each sample, from 21.8.67 onwards, were calculated and are plotted in Fig. 52. The mean increased steadily with age of fish. In general the fluctuations in each age group were the same as those for the population as a whole. In age group I however the mean increased in spring 1968 when the population mean was decreasing. Thus young fish were acquiring worms while older ones died from heavy infections. In group IV the mean was very variable due to the small size of the samples.

Data for each sample were collected into frequency distributions for each group; the distributions were still overdispersed.

The youngest fish were infected but the percentage of infected fish increased with age: 45% in age group I, 59.4% in II, 77.1% in III, and 77.7% in group IV.

Although the mean number of Diplostomum per fish was higher in age group IV than in group III, there were more heavily infected fish in the latter group. This suggests that older fish are killed sooner by heavy infections.

V COMPARISON BETWEEN THE THREE SPECIES OF PARASITE

Table 3

	<u>Schistocephalus</u>	<u>Echinorhynchus</u>	<u>Diplostomum</u>
1. % infection	88.3% 70.5-100	31.5% 6.6-52.7	56.1% 18.9-91.4
2. Maximum no.	106	83	443
3. Mean no per fish	4.40 1.87-8.95	1.34 0.08-3.02	9.35 0.72-21.93
4. Variance	45.08 2.25-154.0	16.89 0.10-93.77	592.6 8.21-2636.6
5. Overdispersion	10.25 1.61-41.2	12.60 1.25-42.4	63.38 9.73-187.0
6. Frequency distribution	log normal	negative binomial	negative binomial
& parameters	g 2.14 0.74-4.35	p 7.57 0.32-17.67	p 37.19 7.39-87.71
	s ² 11.84 6.81-22.09	k 0.204 0.09-0.47	k 0.270 0.097-0.705

Table 3 gives a summary of the data for the three species of parasite: the figures for all fish together are given above with the minimum and maximum values for individual samples below.

It can be seen that the percentage infection was highest for the Schistocephalus whereas the Diplostomum had the highest maximum and mean numbers per fish, variance and overdispersion. The Echinorhynchus had the lowest percentage infection; the range did not even overlap with that for the Schistocephalus. The maximum and mean numbers of Echinorhynchus per fish and the variance were also the lowest, but the overdispersion was higher than that of the Schistocephalus.

Despite the differences in the numbers of parasites per fish both Diplostomum and Echinorhynchus were distributed as a negative binomial. The parameters, p and k , were both higher for the Diplostomum distributions, as expected. The difference in k was small and the value was always below one, showing that the zero class was always the largest. The value of p was considerably higher for the Diplostomum than for the Echinorhynchus distributions although the ranges overlapped.

Thus, although k tended to vary as the percentage infection in sample to sample variations in the distributions of both these parasites, the larger overall percentage in the Diplostomum was not accompanied by a high k . This is because the variance was very much greater than in the Echinorhynchus distributions and this caused p to be much greater, which also raised the percentage infection a sufficient amount.

The very high percentage infection combined with

relatively low mean and overdispersion in the Schistocephalus infection meant that the negative binomial did not fit the distributions in most cases. The log normal was found to be a better fit.

These differences can be related to the life histories of the parasites and the different ways in which they infect the stickleback.

Schistocephalus is acquired by the fish when it eats a cyclops infected with the proceroid larva. Each cyclops can support only a small number of proceroids so that the fish picks up only a few at a time - although several infected cyclops may be eaten in a short time if the infection is high. Hence large numbers of fish become infected with a relatively small number of plerocercoids.

Once inside the body cavity of the fish the plerocercoids grow rapidly, attaining a very large bulk and weight in relation to those of the host. Therefore fish with very large numbers are soon unable to support them all, and are killed. (The Schistocephalus remain in the fish for its lifetime.) This further reduces the variance and mean while having a small effect on the percentage infection. Thus the distribution is truncated: this was found when fitting the log normal. It is not simple numerical truncation, however, for fish with small numbers but large weights of Schistocephalus are also killed.

The sticklebacks also become infected with Echinorhynchus by eating an organism containing a larval stage: in this case an acanthella in Asellus. As the Asellus is larger than a cyclops it may harbour quite a large number of acanthellae so that a fish is more likely to pick up many Echinorhynchus from a single Asellus. At the time of the study Asellus were uncommon and did not form an important item in the fish's diet. Thus small numbers of fish were becoming infected with a relatively large number of parasites. This explains the fact that the overdispersion was greater than that of the Schistocephalus while the mean and percentage infection were much lower. The adult Echinorhynchus lived in the gut of the fish for a considerable time, particularly the females, but eventually died and passed out. Thus the infection was reduced by loss of individual parasites rather than death of heavily infected fish.

The Diplostomum was not acquired in the food of the fish, but penetrated the skin directly. Cercariae were released from the previous host, Limnaea pereger, in very large numbers; they were dispersed to a certain extent by water movements and their own swimming, but fish still tended to encounter large concentrations and become infected with very large numbers. This gave rise to a very high maximum number per fish, variance and overdispersion. The mean was also much higher than for either of the other two parasites although the percentage infection was relatively low.

The fish were exposed to continual waves of infection by all three parasites and the level of infection tended to build up as successive waves attacked. The Schistocephalus and Diplostomum populations were reduced in the stickleback population by heavily infected fish being eaten by predators. In both these species the fish was an intermediate host and the life cycle was completed only if the fish was eaten by a bird. It was therefore to these parasites' advantage to render the fish more susceptible to predation. In the case of the Echinorhynchus the adult lived in the stickleback so that it was not to the parasite's advantage to kill its host. Echinorhynchus died and passed out of the fish, reducing the infection without the fish dying. This enabled newly acquired worms to mature and reproduce without raising the infection to a lethal level.

VI CORRELATION BETWEEN THE THREE SPECIES OF PARASITE

Cole's (1949) coefficient, C_7 , was used to test whether a fish infected with any one of the three parasites was more or less likely to be infected with one of the others than an uninfected fish. This is calculated as follows:

		species B		TOTAL
		present	absent	
species A	present	a	b	a + b
	absent	c	d	c + d
	TOTAL	a + c	b + d	N

where a, b, c and d are the numbers of fish in a sample which are infected or uninfected with the two parasites, A and B.

If the association is positive, $ad \geq bc$, then

$$C_7 = \frac{ad - bc}{(a+b)(b+d)} \dots(97)$$

$$\text{and } \chi^2 = \frac{C_7^2}{\frac{(a+c)(c+d)}{N(a+b)(b+d)}} \dots(98)$$

If the association is negative, $ad < bc$, then

$$C_7 = \frac{ad - bc}{(a+b)(a+c)} \quad \dots(99)$$

$$\text{and } \chi^2 = \frac{C_7^2}{\frac{(b+d)(c+d)}{N(a+b)(a+c)}} \quad \dots(100)$$

The value of χ^2 is looked up in tables to determine whether it is significant and therefore whether there is positive or negative association between the two species.

No significant deviations from random association were found for any pair of the three species of parasite.

The above method considers only presence and absence of the parasites and not the numbers of each within the host. Thus a second test, based on a contingency table, was carried out. A computer program was used to collect the numbers of each parasite into log x2 frequency classes, each class being subdivided according to the numbers of a second parasite. This was done for each pair of parasites for each sample. A table was thus formed; as shown in Table 4.

Table 4

		species B						TOTAL
		0	1	2	4	8	...	
species A	0	$a_{0,0}$	$a_{0,1}$	$a_{0,2}$	$a_{0,3}$	$a_{0,4}$		$\sum a_{0,y}$
	1	$a_{1,0}$	$a_{1,1}$	$a_{1,2}$	$a_{1,3}$	$a_{1,4}$		$\sum a_{1,y}$
	2	$a_{2,0}$	$a_{2,1}$	$a_{2,2}$	$a_{2,3}$	$a_{2,4}$		$\sum a_{2,y}$
	4	$a_{3,0}$	$a_{3,1}$...				⋮
	8	$a_{4,0}$...					
	⋮							
TOTAL		$\sum a_{x,0}$	$\sum a_{x,1}$	$\sum a_{x,2}$...			N

The row and column totals were then used to compute the expected frequency of each of the combinations, for example:

$$A_{1,2} = \frac{(\sum a_{1,y})(\sum a_{x,2})}{N} \dots(101)$$

and a table of expected frequencies ($A_{x,y}$) was built up. The actual and expected frequencies were then compared by means of a χ^2 test:

$$\chi^2 = \sum_{x=0} \sum_{y=0} \frac{(A_{x,y} - a_{x,y})^2}{A_{x,y}} \dots(102)$$

If the table had r rows and c columns then χ^2 had $(r-1) \cdot (c-1)$ degrees of freedom.

In no sample was χ^2 significant for any pair of parasite species showing that there was no tendency for any of them to be associated.

It has already been noted (p.145) that both Diplostomum and Schistocephalus caused the death of fish when present in large numbers. It would therefore be expected that if both were present the lethal levels would be lower. Between October 1967 and March 1968 both these species were decreasing in the fish population due to death of heavily infected fish. It would therefore be expected that fish with large numbers of Diplostomum would have a lower parasite index than ones with smaller numbers. This was found to be the case for most samples during this period. As both these species require that the fish host be eaten by a bird for completion of their life cycles this interaction results in more of both species reaching maturity.

Thus there is no association between the three species of parasite except that large number of Schistocephalus and Diplostomum are not found together.

DISCUSSION

The aim of this study was to describe, in quantitative terms, the relationship between host and parasite populations.

Various studies have been made on pairs of interacting populations and the relationships generally expressed in terms of the logistic curves of each:

$$\frac{dN}{dt} = \frac{r \cdot N (k - N)}{k} \quad \dots(103)$$

where r is the intrinsic rate of natural increase and k is the number of organisms at saturation point. Slobodkin (1961) discusses competition and predator-prey interactions from this angle. Host-parasite systems are discussed by Watt (1959) who describes a number of models proposed by different workers, and puts forward a new one, applicable to parasitic wasps etc. attacking larvae of other insects. This is more comparable to a predator-prey interaction as each host has only one parasite and is always killed by it.

Paperna (1963) has studied a population of the Monogenean Dactylogyrus vastator on the gills of carp fry from a viewpoint more similar to that taken in the present investigation. He studied infections in different rearing ponds and found that the dynamics of Dactylogyrus on the fish were determined by

- a) Rate of initial parasite contamination in the pond.
- b) Growth rate of the fry - this depended on the density of fish in the pond and determined whether gill regeneration was fast enough for the fish to survive.
- c) The time between hatching of the fish and the contamination of the pond with parasites.

Only young fish were infected and if they survived the early infections the parasites were thrown off. New infections built up each spring and the parasite survived the winter as a diapausing egg. This is different from the parasites found in the Priddy sticklebacks where the infections continued to build up in fish of all ages. Older fish were less able to survive large infections.

There are few studies involving the species found at Priddy. A certain amount of information is available about Schistocephalus infections as this species has been used in many studies of tapeworm metabolism. The quantitative data described by Arme and Owen (1967) has already been discussed (p.58, 100). Threlfall (1968) describes a mass mortality of Gasterosteus. He found 439 dead fish, 99% of which were infected with Schistocephalus; each fish had between 1 and 12 worms which were 4-36 mm long. This does not appear to be an exceptionally heavy infection although no details of weights are given. However 45% of the fish were also infected with a copepod, Thersitina gasterostei, on the gills and there were many Argulus. Thus the deaths

of the sticklebacks had probably been caused by the combination of these three parasites.

A comparison with the Echinorhynchus infection is provided by a study of Acanthocephalus ranae in frogs by Lees (1962). He found that only 18.1% of all the frogs collected over a four-year period were infected, compared with 31.5% of the sticklebacks infected with Echinorhynchus. This is probably due to the fact that the level of infection declined while the frogs were hibernating. The infection increased again in the spring and summer and the mean number of parasites was higher in the frogs (1.9) than in the sticklebacks (1.3).

The different factors found to affect the fish and parasite populations, and the interactions between host and parasites, are discussed below. These effects are considered first in general terms and then related to the distributions of the parasites amongst the fish. The effects of the life cycle on the form of the distribution, and hence on the survival of the parasite, are discussed.

(a) General effects

The factors found to affect the Priddy stickleback population are: the availability of food, the ambient temperature, the number of fish, the parasites, and the predators. The effects of these factors are modified by interaction with each other.

The amount of food which a fish can obtain affects its growth rate and breeding capacity. If food is short the fish loses weight and is more easily caught by a predator, or may die. The amount of food available to each fish depends upon many other factors, including temperature and number of fish. When the temperature is low food is in short supply and competition amongst the sticklebacks may be significant in determining whether each can obtain enough food to survive. Competition with other species may also be significant at times of food shortage; for example newts eat the same types of food. As the temperature increases the metabolic rate of the fish increases and it requires more food. The high temperature will also cause the numbers of food organisms to increase more rapidly, but there may be a time lag during which there is insufficient food for all fish. Temperature also acts directly on the sticklebacks as they cannot survive when the water freezes.

The number of fish eaten by a predator depends not only on the number of predators, but also on the food supply of the fish. The presence of parasites also tends to increase the susceptibility of a fish to predation.

The effects of the three species of parasite on the sticklebacks, and the factors affecting their own populations, are discussed in detail below. All three species have other hosts besides the sticklebacks and transference

between one host and the next is one of their chief problems.

In Schistocephalus the time taken for the egg to hatch depends upon the temperature. The larva must then be eaten by the correct species of Cyclops which must live for at least 25 days for the proceroid larva to develop, and then be ingested by a stickleback. Development to an infective plerocercoid is rapid and if the fish is then eaten by a bird the adult Schistocephalus can develop. Eggs are produced after about three days and the bird must remain at the pond, or return to it, for reinfection to occur; or the infection may be introduced to another pond with Cyclops and Gasterosteus populations.

Most of the sticklebacks at Priddy were found to be infected with Schistocephalus although few had large numbers of plerocercoids. Peaks of new infection occurred in February and March and in August and September, probably corresponding to peaks in the Cyclops population. The fish continued to acquire new infections throughout their lives, but the oldest ones were killed by a lighter infection than younger ones.

The Schistocephalus took food which would otherwise have been available to the fish, and the larger the infection the greater was this effect. The fish became weakened and died, or was eaten by a predator, when the infection was so large that it could no longer find and/or digest enough food

for itself and the parasites. Bauer (1961) states that fish heavily infected with Schistocephalus are easy prey to piscivorous birds. As larger fish have a slower growth rate a larger proportion of their food is required for maintenance and there is a smaller surplus available for the parasites. The Schistocephalus also causes a distortion of the body of the fish which has an adverse effect on the swimming efficiency and further decreases the capacity to find sufficient food and increases the susceptibility to predation.

As the Schistocephalus requires the fish host to be eaten by a bird for completion of its life cycle it is to its advantage to increase the fish's chances of being eaten. As this effect is greater in more heavily infected fish a large number of parasites reaches the final host.

At the time of the study the Schistocephalus infection was high, and increasing, and the effects on the fish population were very great. Many fish were dying, particularly older ones, thus reducing both host and parasite populations. Many fish were also prevented from breeding which did not directly reduce the level of infection but caused the stickleback population to decline rapidly. As the density of fish is thus reduced so the Schistocephalus infection will decrease and this in turn will allow the fish numbers to increase again. The Schistocephalus

therefore causes cyclic changes in both its own and the stickleback population and this controls the numbers of both. Other external factors, such as temperature and food supply, modify these fluctuations.

Echinorhynchus has a less complicated life cycle than Schistocephalus. Shelled acanthors hatch if eaten by an Asellus and develop into the acanthella and then the cystacanth in six to 12 weeks. If the Asellus is then eaten by a stickleback the adult Echinorhynchus develops.

The infection in the Priddy sticklebacks was fairly low, and was lower in 1967-8 than in the previous year, probably because the Asellus population decreased. New infections occurred mostly in January and February, June and July, and September and October. New infections were acquired by sticklebacks of all ages and older fish had more Echinorhynchus than younger ones, although they were killed by a smaller infection.

As the fish is the definitive host it is advantageous to the parasite that it should cause the least damage possible so that its host is not killed or eaten by a predator. However, the Echinorhynchus inevitably takes a certain amount of food otherwise available to the fish and when the infection was high fish were killed. As with the Schistocephalus older fish were killed by a relatively low infection as their growth rate was lower. Death of heavily infected fish

reduced the parasite population so that the infection in the fish population was kept down to a low level. The infection was also reduced by individual parasites dying at the end of their useful life: in the males after copulation, and in the females after egg-production had ceased. The short life-span of the males meant that they did not take resources otherwise available for the females to produce eggs.

The Diplostomum again has three hosts. Eggs hatch to larvae which bore into a Limnaea pereger; large numbers of cercariae are produced, pass out of the snail, and bore into a stickleback. If the fish is eaten by a gull or a duck the adult Diplostomum develops within three days. As with the Schistocephalus the bird must return so that Diplostomum eggs passing out with its faeces reinfect the pond.

The infection in the Priddy sticklebacks was quite low in the first year, but much higher in autumn and winter 1967-8. New infections occurred mostly between May and July but continued until October. This was when there were most snails producing cercariae. The infection in the fish population fell in winter and spring, reaching about the same level by April in both years. This seasonal distribution tends to keep the parasite population to a moderate size. As with the other two parasite species the largest fish were

less able to support a large number of Diplostomum than smaller ones, although new infections were acquired by fish of all ages, and the percentage infection and mean number increased with age of fish.

The Diplostomum must also have taken a certain amount of the fish's food, but its greatest effect was interference with vision. This decreased the food-finding capacity of the stickleback and increased its chances of being eaten by a predator. Thus fish heavily infected with Diplostomum tended to be eaten by birds and this resulted in many parasites being able to continue their life cycle.

(b) Frequency distributions

The type of host-parasite system studied here is different from other systems of pairs of interacting species, such as predators and prey, in that the individuals of one (the parasite) are distributed amongst those of the other (the host) in a certain mathematical pattern or frequency distribution.

The form of the frequency distribution can be related to the life cycle of the parasite, and the mechanisms by which it controls its numbers and transfers from one host to the next. The shape of the distribution also provides a basis for analysis of changes in the populations with time. For example the time of new infections with parasites can be

determined, whether decreases in the level of infection are due to death of heavily infected hosts or to death of the parasites, and so on.

Williams (1964) analysed frequency distributions of various types from the data of a number of workers. Much of this was concerned with distributions of individuals amongst species, species amongst genera and so on. The parasitological data were mostly of external parasites such as fleas and mites which are not comparable as they can move freely from host to host, or with laboratory studies in which conditions are obviously very different.

He shows that the eggs of a tachinid fly in larvae of Prodemia litura (Lepidoptera) had a log normal distribution. Copepods in mussels from a number of localities on British shores were distributed as a negative binomial, with $k = 0.81$. This distribution could, however, have arisen due to the pooling of samples taken from different populations and at different times and not been the pattern found at any one place at any one time. Distributions of copepods and branchiurans in fish from a number of East African lakes were found to be log series. The negative binomial also fits these data, however. Williams used an inefficient method of fitting the negative binomial ((b) on p. 13) and often found that the log series fitted better because of this.

This shows that other host-parasite distributions are similar to those studied here although the life cycles of the parasites are very different. It is interesting also that the form of the distribution often stays the same with widely differing levels of infection, as in the Diplostomum population, although the parameters may be different. Also similar distributions are found to apply to a wide range of different biological situations: Williams (1964) found for example that number of species per genus, number of genera per family, number of parasites per host were all distributed as the log series.

Thus it is usual for the distribution of parasites amongst their hosts to be overdispersed. The greater the overdispersion the more parasites there are in the host population for a given percentage infection. For a random, or Poisson, distribution the proportion of hosts infected, P, is given by:

$$P = 1 - e^{-m} \quad \dots(104)$$

$$\text{or } \ln P = m \cdot \ln e \quad \dots(105)$$

$$\therefore m = \ln P \quad \dots(106)$$

For a negative binomial distribution

$$P = 1 - \frac{1}{q^k} \quad \dots(37)$$

where q is a measure of the overdispersion.

$$\text{hence } \ln P = k \cdot \ln q \quad \dots(107)$$

$$\text{or } k = \frac{\ln P}{\ln q} \quad \dots(108)$$

$$\text{but } p \cdot k = m \quad \dots(11)$$

$$\text{and } p = q - 1 \quad \dots(12)$$

$$\therefore m = \frac{\ln P}{\ln q} \cdot (q - 1) \quad \dots(109)$$

If the percentage infections are equal the ratio of the means:

$$\frac{m_{NB}}{m_P} = \frac{q - 1}{\ln q} \quad \dots(110)$$

As $(q-1) > \ln q$ for all $q > 1$ the ratio is always > 1 , that is the mean of the negative binomial is greater than the mean of the Poisson. For example if $q=20$, the ratio is 6.3; in other words there are 6.3 times as many parasites in the negative binomial as in the Poisson.

Conversely, for a given mean the percentage infection is greater in a Poisson than in a negative binomial:

$$\frac{\ln P_P}{\ln P_{NB}} = \frac{q - 1}{\ln q} \quad \dots(111)$$

For example, for a mean of 1.0 and an overdispersion of 20, the percentage infection of a Poisson is 63.2% and of a negative binomial 45.7%.

This means that a larger number of parasites is accommodated in a smaller number of hosts so that there is less effect on the host population. As Bauer (1961) states, "every parasite is harmful to its host", and the more parasites there are in a host the larger are the adverse effects. With an overdispersed distribution there will be a small number of hosts with many parasites and these may die. This reduces the parasite population by many more individuals than it does the host population and so the parasites are kept to a moderate level. For example if the mean is 10 and hosts with more than 25 parasites are killed, in a random distribution 0.024% of hosts will die and these will contain 0.028% of the parasites. If the overdispersion = 11 then, with a negative binomial, 8.4% of hosts, containing 31.8% of the parasites, will die, or if the overdispersion is 100 then 10.3% of the hosts with 81.7% of the parasites will be lost. Therefore with an overdispersed distribution the parasite population is prevented from becoming too large and causing the death of large numbers of hosts.

On the other hand heavily infected hosts may not die but may be eaten by a predator. This is advantageous to the parasite if it requires its host to be eaten for the

development of the next stage in the life cycle.

If the parasite had no effect on the host each host would have an equal chance of being eaten by a predator, regardless of the number of parasites it contained. Each parasite would therefore have an equal chance of entering its next host and the form of the frequency distribution would be irrelevant. If, however, the host has an increasingly greater chance of being eaten as the number of parasites with which it is infected increases, then the form of the distribution will affect the chances of a parasite being in a host which is eaten. In general the more parasites there are in the host the greater its chance of being eaten, but if there are only very few hosts with large numbers of parasites then the chances of the predator finding these will be slight even if the susceptibility to predation is greatly increased. Also if there are too many parasites in the host it may die before it can be eaten. There is thus an optimum shape for the distribution in which a large proportion of the parasites is in a fairly small proportion of the hosts.

It is assumed, for example, that fish with more than 25 parasites have an increased chance of predation and that the number of parasites per host is 10. In a negative binomial distribution with an overdispersion of 50, 70% of the parasites will be in hosts with over 25 parasites and

will therefore have an increased chance of entering the next host. 12% of the hosts are affected. In a random distribution 70% of the parasites are in hosts with only 10 or more parasites and thus each parasite must have a greater adverse effect on the host for it to have the same chance of entering the next host. 55% of the hosts will be affected.

Thus if the distribution is overdispersed each parasite needs to have a smaller adverse effect on the host, to ensure that it has a large chance of entering the next host, than if the distribution is random. Not only are the effects on the individual host smaller, but fewer hosts are affected.

An overdispersed distribution can therefore be advantageous to both host and parasite in ensuring that the parasite continues its development and in keeping the infection to a moderate level with only small losses to the host population. The ways in which such distributions can arise, and their effects on the host and parasite populations, are discussed in relation to the sticklebacks and their parasites studied here.

The Schistocephalus was generally distributed as a log normal and the overdispersion was fairly low (10.3). The overdispersion arose because there were several waves of non-random infections, but was not high as only small numbers

of parasites were acquired from each infected Cyclops. The overdispersion was also reduced because fish with many Schistocephalus died; this resulted in a truncated distribution in some samples. The form of the distribution was variable, however, as it was weight rather than number of plerocercoids which was significant in the amount of damage caused to the fish.

The chances of an individual parasite being in a fish which was eaten were therefore increased both by its being associated with other individuals and by its growing rapidly. In general fish with a weight of parasites greater than their own weight could not survive. The mean fish weight was 0.86 g and the mean plerocercoid weight was 0.078 g. Thus fish with more than 11 plerocercoids on average had a larger weight of parasites than they could support. There were 8.4% of all the fish with more than 11 plerocercoids and these contained 40.9% of the parasites. Thus the overdispersion was high enough to ensure that each parasite had a large chance of being in a fish with an increased susceptibility to predation, although this was not a very great proportion of the fish population.

The larger the weight of an adult Schistocephalus the greater is its egg-producing capacity. As a heavier plerocercoid has a greater chance of entering a bird, because of its effects on the fish, this results in a large number of

eggs being produced.

The Echinorhynchus was distributed as a negative binomial with a fairly low over-dispersion (12.7). This arose because there was a number of waves of infection, each of which attacked non-randomly. Only a small number of parasites was acquired by the fish from each infected Asellus.

As the fish is the definitive host it is to the parasite's advantage to cause the least possible ill-effects so that the host is not killed. However, the parasites inevitably affect the fish to a certain extent and it is therefore advantageous for there to be as few heavily infected fish as possible. In a random distribution there is a minimum of fish with large numbers of parasites, but the method by which the Echinorhynchus infects the fish gives rise to an overdispersed distribution. The number of parasites in a fish is reduced by individuals dying and passing out of the fish; this may also reduce the overdispersion slightly as more parasites may die in a heavily infected fish, due to competition for food.

Some fish are, however, killed by the Echinorhynchus, particularly when the infection is high. Assuming that fish with over 15 parasites are increasingly likely to die and that the mean = 1.5, the number of fish with over 15 parasites increases with increasing overdispersion, reaching a maximum of 2.5% at an overdispersion of 20. At an overdispersion of

12.7 there are 2% of fish with over 15 parasites, and these contain 35% of the parasites. 1.5% of the fish caught had over 15 Echinorhynchus and these harboured 30% of the parasites. Thus fish with over 15 parasites were tending to die, particularly those with larger numbers. This reduces the level of infection, as a high proportion of the parasites is lost while only a very small proportion of the fish population dies.

The overdispersed distribution prevents the parasite population from increasing to a level at which many fish would be killed. The parasite is thus enabled to control its own numbers while having only a small effect on the host population.

In Diplostomum the frequency distribution was again a negative binomial, although the overdispersion and percentage infection were much higher than in the Echinorhynchus distributions. The negative binomial arose because there were several waves of non-random infections. The high overdispersion arose because one snail releases very large numbers of cercariae in a small area; small numbers of fish are thus liable to pick up very heavy infections.

Diplostomum also relies upon the fish host being eaten by a bird for the completion of its life cycle, and it is therefore to its advantage to render the fish susceptible to predation. As the effects of individual parasites are much smaller than in Schistocephalus the level of infection at which this occurs is much higher.

The shape of the frequency distribution will determine what chance a Diplostomum has of being in a fish which is eaten by a bird; the probability that a fish will be eaten depends upon the number of Diplostomum which it harbours.

The probability (D_x) of a Diplostomum being in a fish with x parasites depends upon the proportion of such fish in the population (P_x), as well as on the value of x :

$$D_x = \frac{P_x \cdot x}{m} \quad \dots(112)$$

where m is the mean number of Diplostomum per fish. The value of P_x depends on the frequency distribution; in a negative binomial with low k and high overdispersion (q) it decreases steadily with increasing values of x :

$$P_x = P_{x-1} \cdot R \cdot \frac{(k + x - 1)}{x} \quad \dots(22)$$

where $R = \frac{q - 1}{q} \quad \dots(23)$

The susceptibility of a fish to predation (S_x) increases as the number of parasites with which it is infected increases. It is assumed here that the susceptibility is significantly increased when x is greater than 20, and increases linearly with further increases in x :

$$S_x = \frac{x - 20}{400} \quad \dots(113)$$

The probability of a Diplostomum entering a bird, B_x , is then

$$B_x = S_x \cdot D_x \quad \dots(114)$$

There will be a certain value of x for which B_x is a maximum.

This occurs when successive values are equal:

$$B_x = B_{x-1} \quad \dots(115)$$

or $S_x P_x \cdot x = S_{x-1} P_{x-1} \cdot x \quad \dots(116)$

i.e. $R \cdot (k + x - 1) = \frac{(x - 21)}{(x - 20)} \cdot (x - 1) \quad \dots(117)$

The value of x for the maximum value of B_x increases as the overdispersion increases; as k increases the peak is sharper.

For all values of the parameters found in the Diplostomum distributions this maximum occurred between 40 and 90 parasites per fish. The highest chance of a Diplostomum entering a bird was thus if it was in a fish with between about 35 and 120 parasites. 6.3% of all the fish were so infected and they harboured 38.6% of all the Diplostomum. A further 15.8% of parasites were in fish with over 120 parasites but these had a reduced chance of being eaten because of the small number of fish (0.7%). A large proportion of the Diplostomum population thus had an increased chance of entering a bird, while only a small proportion of the fish population was lost by predation.

The effect of the overdispersion on the proportion of

hosts with over 35 parasites was investigated. For a negative binomial distribution with a mean of 10 this was at a maximum when the overdispersion was between 50 and 70. The overall value of the overdispersion for the Diplostomum was 63.4, well within this range. Thus a maximum number of fish had an increased chance of predation. With an overdispersion of 63.4 the proportion of fish with over 35 parasites was calculated to be about 10% and these harboured about 58% of the parasites. Only 7% of the fish collected had more than 35 Diplostomum, however, and these contained 54% of the parasites, showing that heavily infected fish were indeed being removed from the population.

The form of the frequency distribution thus ensures that a Diplostomum has a large chance of being in a fish which is eaten by a bird. This leads to a large number of parasites entering the next host with only a small loss to the fish population. The distribution arises largely because of the method by which the Diplostomum infects the fish.

As both Schistocephalus and Diplostomum require the fish host to be eaten by a bird it would appear to be to their mutual advantage if they were positively associated; this was not found. However, this association would cause a fish to be eaten when infected with fewer parasites of each species. This would reduce the overall chances of individuals of either species being in a fish which was eaten and so would

not be advantageous to either.

Thus each of the three species of parasite was adapted to live in the stickleback with the minimum ill-effects on the host while maximum numbers of the parasite survived. Although heavily infected fish died this was advantageous to the host population as a whole as it reduced the level of infection with the parasite, which was also to the parasite's advantage. The Echinorhynchus and Diplostomum both had efficient mechanisms for controlling their own numbers, particularly the former, and had little effect on the numbers of sticklebacks. Schistocephalus had a less efficient mechanism for controlling its own numbers and tended to increase until many sticklebacks were killed or prevented from breeding; it therefore had a large effect on the numbers of fish.

The form of the frequency distribution of the parasites amongst the sticklebacks was such as to enable the above mechanisms to work. The distributions arose largely because of the types of life cycle and these were therefore well adapted to the needs of the parasite populations.

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REFERENCES

- ARME, C. & OWEN, R.W. (1967). Infections of the three-spined stickleback, Gasterosteus aculeatus L., with the plerocercoid larvae of Schistocephalus solidus (Müller, 1776), with special reference to pathological effects. Parasitology, 57: 301-314.
- AVERY, R. A. (1968). Food and feeding relations of three species of Triturus (Amphibia Urodela) during the aquatic phases. Oikos, 19: 408-412.
- BAILEY, N. T. J. (1959). Statistical methods in biology. English Universities Press. London.
- BAUER, O. N. (1961). Relationships between host fishes and their parasites. In Parasitology of fishes, ed. Dogiel, V.A., Petrushevski, G.K. & Polyanski, Yu.I. Oliver and Boyd. London.
- BEALL, G. (1940). The fit and significance of contagious distributions when applied to observations on larval insects. Ecology, 21: 460-474.
- BERRIE, A. D. (1960). Two Diplostomulum larvae (Strigeida, Trematoda) in the eyes of sticklebacks (Gasterosteus aculeatus L.). J. Helminth., 34: 211-216.
- BERTIN, L. (1925). Recherches bionomiques, biométriques et systématiques sur les Epinoches. Annls Inst. océanogr., Monaco, N.S. 2 fasc. 1.

- BLISS, C. I. & FISHER, R. A. (1953). Fitting the negative binomial distribution to biological data, with a note on the efficient fitting of the negative binomial. Biometrics, 9: 176-200.
- BRASS, W. (1958). Simplified methods of fitting the truncated negative binomial distribution. Biometrika, 45: 59-68.
- BRÅTEN, T. (1966). Host specificity in Schistocephalus solidus. Parasitology, 56: 657-664.
- CASSIE, R. M. (1954). Some uses of probability paper in the analysis of size frequency distributions. Aust. J. mar. Freshwat. Res., 5: 513-522.
- CASSIE, R. M. (1962). Frequency distribution models in the ecology of plankton and other organisms. J. Anim. Ecol., 31: 65-92.
- CHUBB, J. C. (1964). Occurrence of Echinorhynchus clavula (Dujardin, 1845) nec Hamann, 1892 (Acanthocephala) in the fish of Llyn Tegid (Bala Lake), Merionethshire. J. Parasit., 50: 52-59.
- CLARKE, A. S. (1954). Studies on the life cycle of the pseudophyllidean cestode Schistocephalus solidus. Proc. zool. Soc. Lond., 124: 257-302.

- COLE, L. C. (1949). The measurement of inter-specific association. Ecology, 30: 411-424.
- FISHER, R. A. & YATES, F. (1963). Statistical tables for biological, agricultural and medical research. Oliver and Boyd. Edinburgh.
- HEUTS, M. J. (1947). Experimental studies on adaptive evolution in Gasterosteus aculeatus L. Evolution, 1: 89-102.
- HOPKINS, C. A. & McCAIG, M. L. O. (1963). Studies on Schistocephalus solidus. 1. The correlation of development in the plerocercoid with infectivity to the definitive host. Expl Parasit., 13: 235-243.
- HOPKINS, C. A. & SMYTH, J. D. (1951). Notes on the morphology and life history of Schistocephalus solidus (Cestoda: Diphyllbothridae). Parasitology, 41: 283-291.
- JONES, J. W. & HYNES, H. B. N. (1950). The age and growth of Gasterosteus aculeatus, Pygosteus pungitius and Spinachia vulgaris as shown by their otoliths. J. Anim. Ecol., 19: 59-73.

- KERR, T. (1948). The pituitary in normal and parasitised roach (Leuciscus rutilus Flemm.). Q. Jl microsc. Sci., 89: 129-137.
- LEES, E. (1962). The incidence of helminth parasites in a particular frog population. Parasitology, 52: 95-102.
- McCAIG, M. L. O. & HOPKINS, C. A. (1963). Studies on Schistocephalus solidus. II. Establishment and longevity in the definitive host. Expl Parasit., 13: 273-283.
- NEYMAN, J. (1939). On a new class of "contagious" distributions, applicable in entomology and bacteriology. Ann. math. Statist., 10: 35-57.
- ORR, T. S. C., HOPKINS, C. A. & CHARLES, G. H. (1969). Host specificity in Schistocephalus solidus. Parasitology, 59: 683-690.
- PAPERNA, I. (1963). Dynamics of Dactylogyrus vastator Nybelin (Monogenea) populations on the gills of carp fry in fish ponds. Bamidgeh, 15: 31-50
- PARKER, R. R. & LARKIN, P. A. (1959). A concept of growth in fishes. J. Fish. Res. Bd Can., 16: 721-745.

- PIKE, A. W. (1968). The distribution and incidence of larval trematodes in the fresh water fauna of the Wentloog level, S. Wales. J. Zool. Lond., 155: 293-309.
- PROBERT, A. J. (1966). Studies on the incidence of larval trematodes infecting the fresh water molluscs of Llangorse Lake, S. Wales. J. Helminth., 40: 115-130.
- REES, F. G. (1932). An investigation into the occurrence, structure and life histories of the trematode parasites of four species of Lymnaea (L. truncatula (Müll.), L. pereger (Müll.), L. palustris (Müll.) and L. stagnalis (L.)) and Hydrobia jenkinsi (Smith) in Glamorgan and Monmouth. Proc. zool. Soc. Lond., 1932: 1-32.
- SLOBODKIN, L. B. (1964). Growth and regulation of animal populations. Holt, Rinehart and Winston. New York.
- SMYTH, J. D. (1952). Studies on tapeworm physiology. VI Effect of temperature on the maturation in vitro of Schistocephalus solidus. J. exp. Biol., 29: 304-309.
- SMYTH, J. D. (1962). Introduction to animal parasitology. English Universities Press. London.

- SNEDECOR, G. W. (1946). Statistical methods. Iowa State College Press. Iowa.
- THRELFALL, W. (1968). A mass die-off of three-spined sticklebacks (Gasterosteus aculeatus L.) caused by parasites. Can. J. Zool., 46: 105-106.
- WATT, K. E. F. (1959). A mathematical model for the effect of densities of attacked and attacking species on the number attacked. Can. Ent., 91: 129-144.
- WILLIAMS, C. B. (1944). Some applications of the logarithmic series and the index of diversity to ecological problems. J. Ecol., 32: 1-44.
- WILLIAMS, C. B. (1964). Patterns in the balance of nature. Academic Press. London and New York.
- WILLIAMS, M. O. (1966). Studies on the morphology and life-cycle of Diplostomum (Diplostomum) gasterostei (Strigeida: Trematoda). Parasitology, 56: 693-706.
- WOOLDRIDGE, R. & RACTLIFFE, J. F. (1963). An introduction to ALGOL programming. English Universities Press. London.

APPENDIX 1

COMPUTER PROGRAMS

Programs were written in the Elliott variety of ALGOL (Wooldridge and Ractliffe, 1963) and run on the University of Bristol's Elliott 503 computer. Programs and data were punched on cards as this enabled modifications to be made easily. Results were printed on the lineprinter or graphs drawn on the graph plotter.

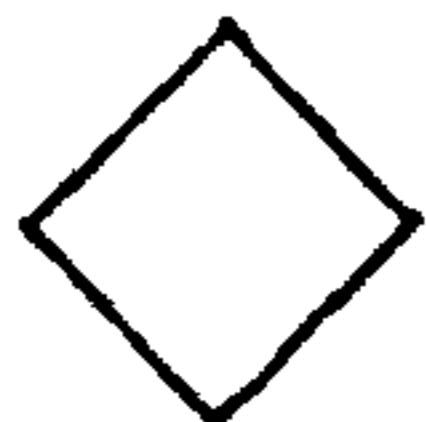
Some of the programs used are represented here as flow diagrams, in which the following symbols appear:



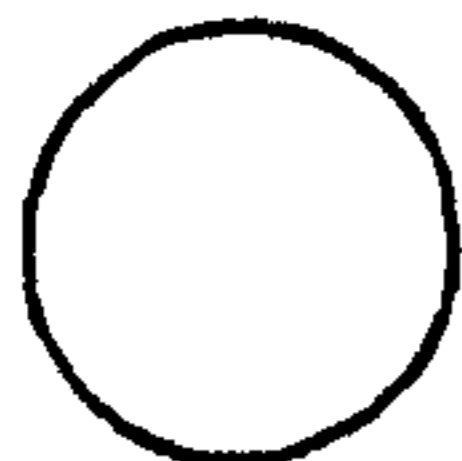
input and output statements



statements to be executed



alternatives for different routes to be followed



procedures utilised. Thus a standard sub-program can be included in several other programs.

$:=$ becomes. e.g. $x := x + 1$ means that the value of x is increased by one.

\uparrow raise to the power of. e.g. $x \uparrow 2$ means x^2

$*$ multiply by

Other signs have their usual meanings.

Standard functions

sqrt (x) square root of x

exp (x) exponential function of x: e^x

ln (x) natural logarithm of x

abs (x) modulus of x

entier (x) integral part of x, e.g. if $x = 3.6$, $\text{entier}(x) = 3$

Matrices or "arrays" were used extensively. These can have any number of dimensions, each represented by a subscript; the limits of each dimension must be declared at the head of the program. For example a two-dimensional array, A [i,j] where i has limits from 0 to 10 and j from 1 to 12 is declared

array A [0:10, 1:12]

A number of procedures was available for performing different operations on two-dimensional arrays and the following were used:

printmx (A) prints array A by rows

formmx (A, x, i, j) A [i, j] becomes x for all i,j

mxprod (A, B, C) multiplies arrays B and C and puts the result in A. $A := B * C$

mxdiff (A, B, C) $A := B - C$

mxcopy (A, B) $A := B$

mxtrans (A, B) A becomes the transpose of B

mxquot (A, B, C) A becomes B to the minus one times C: the set of simultaneous equations $B x A = C$ is solved.

(a) MVAR

This program calculates the mean and variance of a frequency distribution. Data are read in in the form $x, f_x \dots$ and terminated by $-1, -1$ (as x is never negative). The data are stored in an array $f [0:xmax]$ where $xmax$ is the maximum value of x .

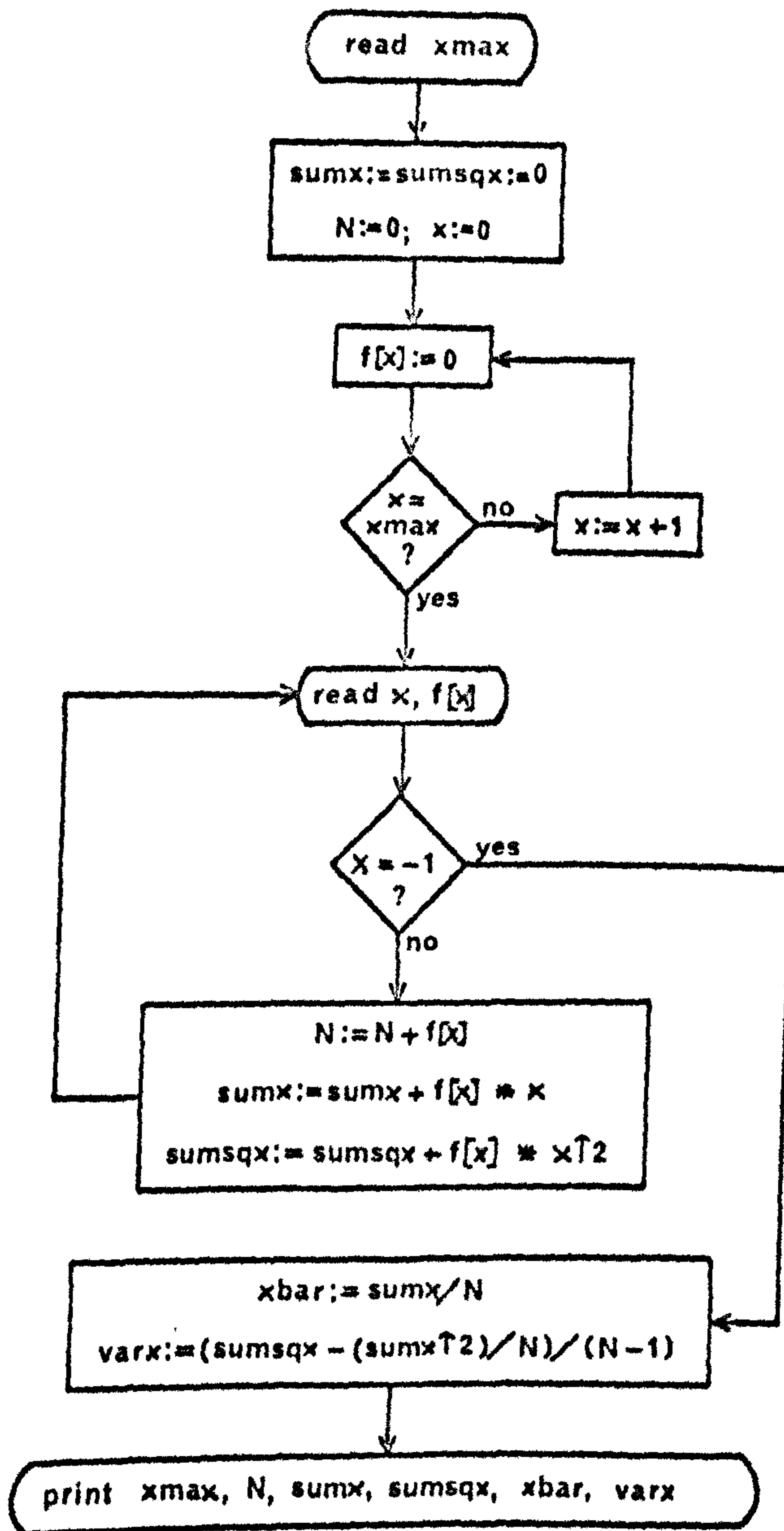
$$N = \sum f_x$$

$$\text{sumx} = \sum f_x \cdot x$$

$$\text{sumsqx} = \sum f_x \cdot x^2$$

$\text{xbar} = \text{mean of } x$

$\text{varx} = \text{variance of } x$



(b) NEGATIVE BINOMIAL

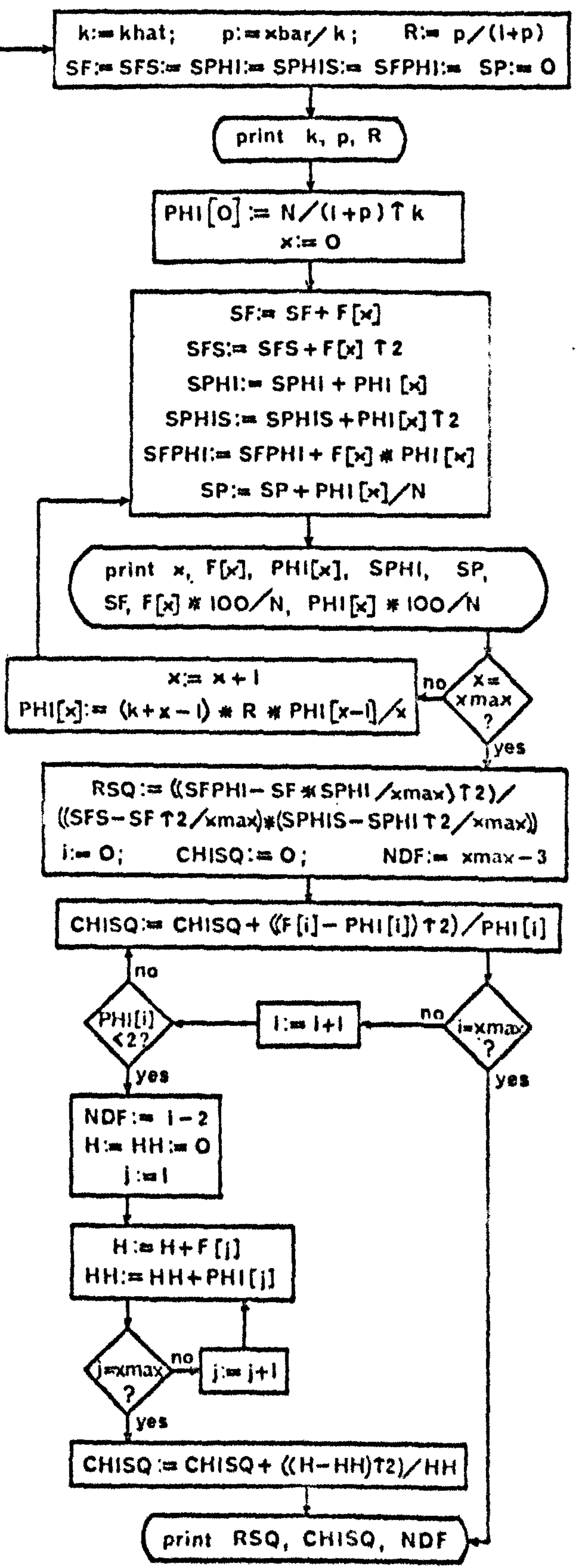
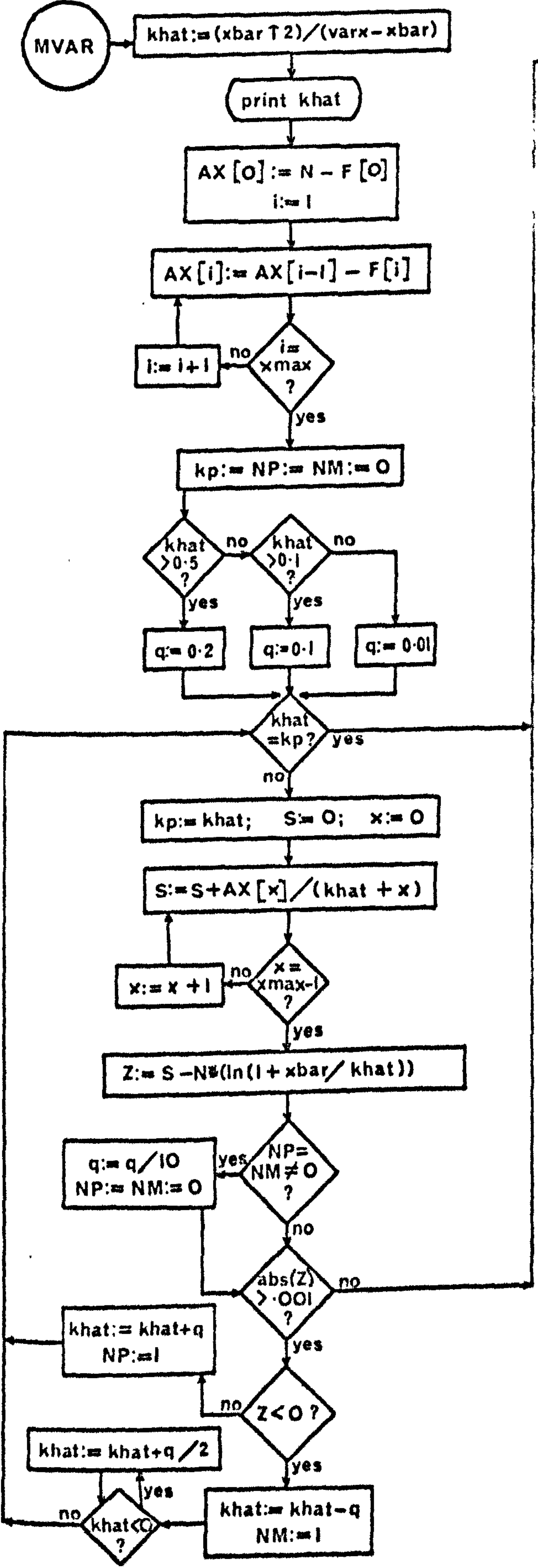
This program estimates the value of the negative binomial parameter, k , by a reiterative procedure and the best value is used to calculate the theoretical distribution. The method is described on p. 13.

\hat{k} and k_p are successive estimates of k .

SF, SFS, SPHI ... are sums of f_x , f_x^2 , ϕ_x ...

arrays F, PHI, AX [0:xmax]

χ^2 (CHISQ) and R^2 (RSQ) are calculated to test the efficiency of the fit of the theoretical distribution to the original.

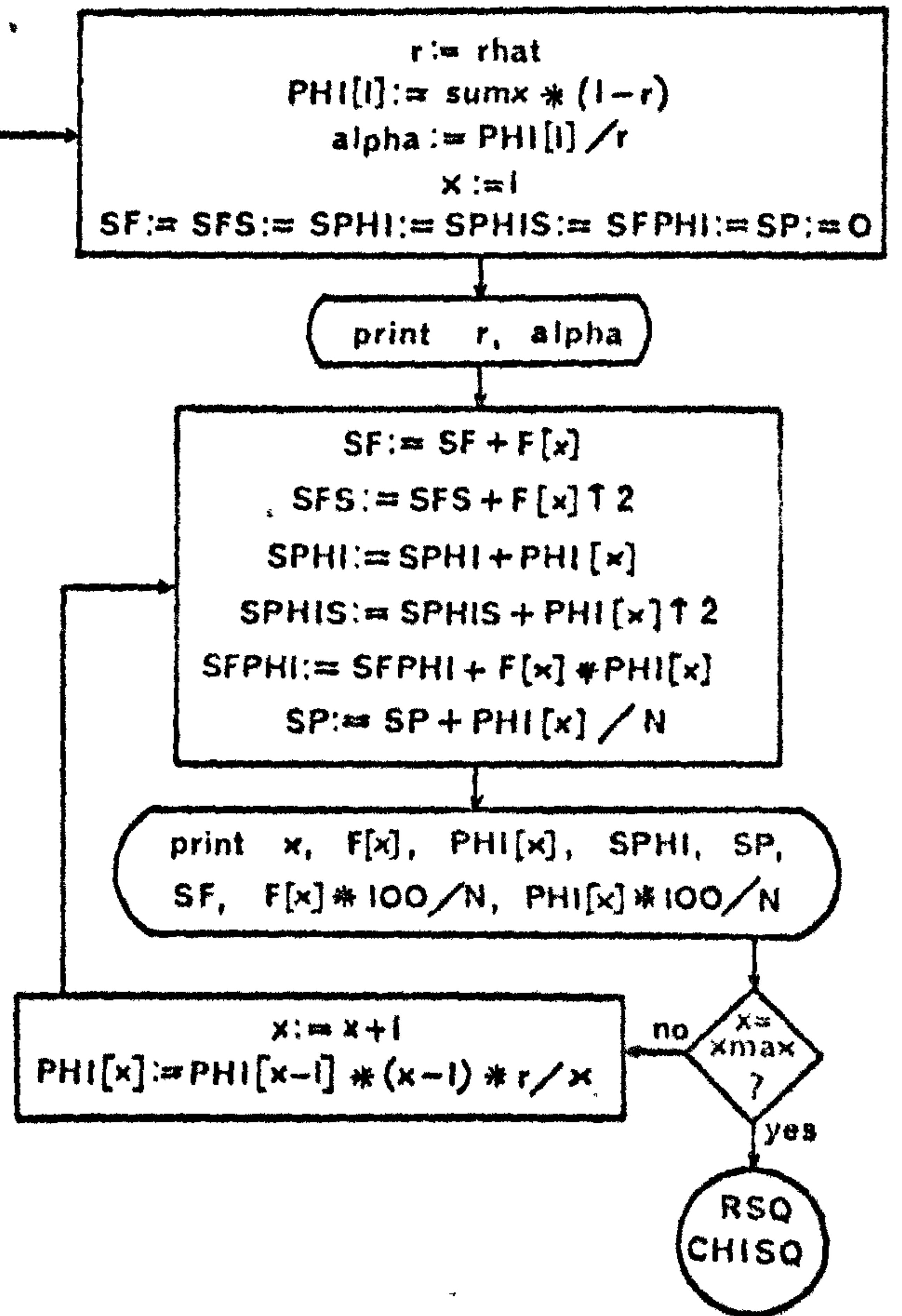
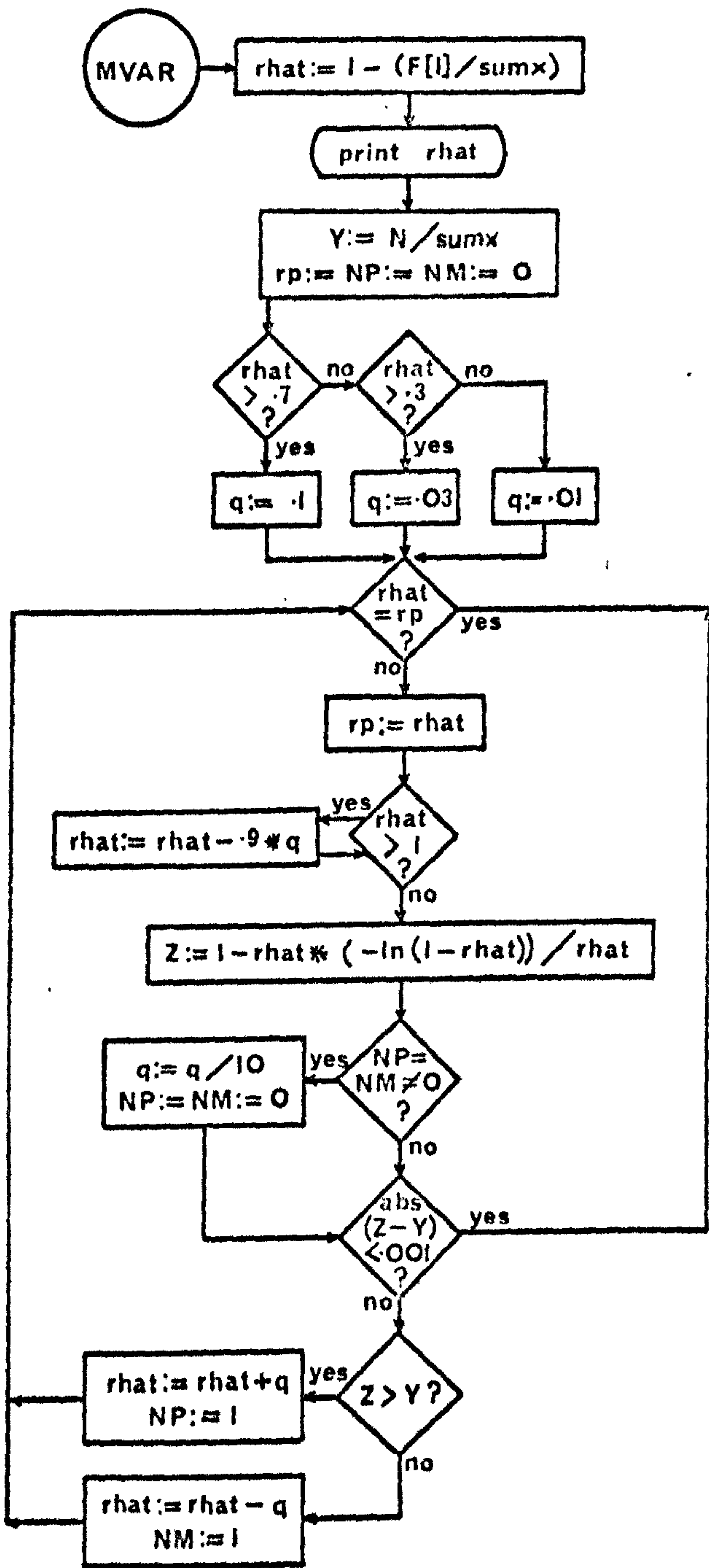


(c) LOG SERIES

The best value of the parameter, r , is estimated as described on p.24 and the theoretical distribution calculated. R^2 and χ^2 are calculated as shown in the flow diagram of the negative binomial.

\hat{r} and r_p are estimates of r

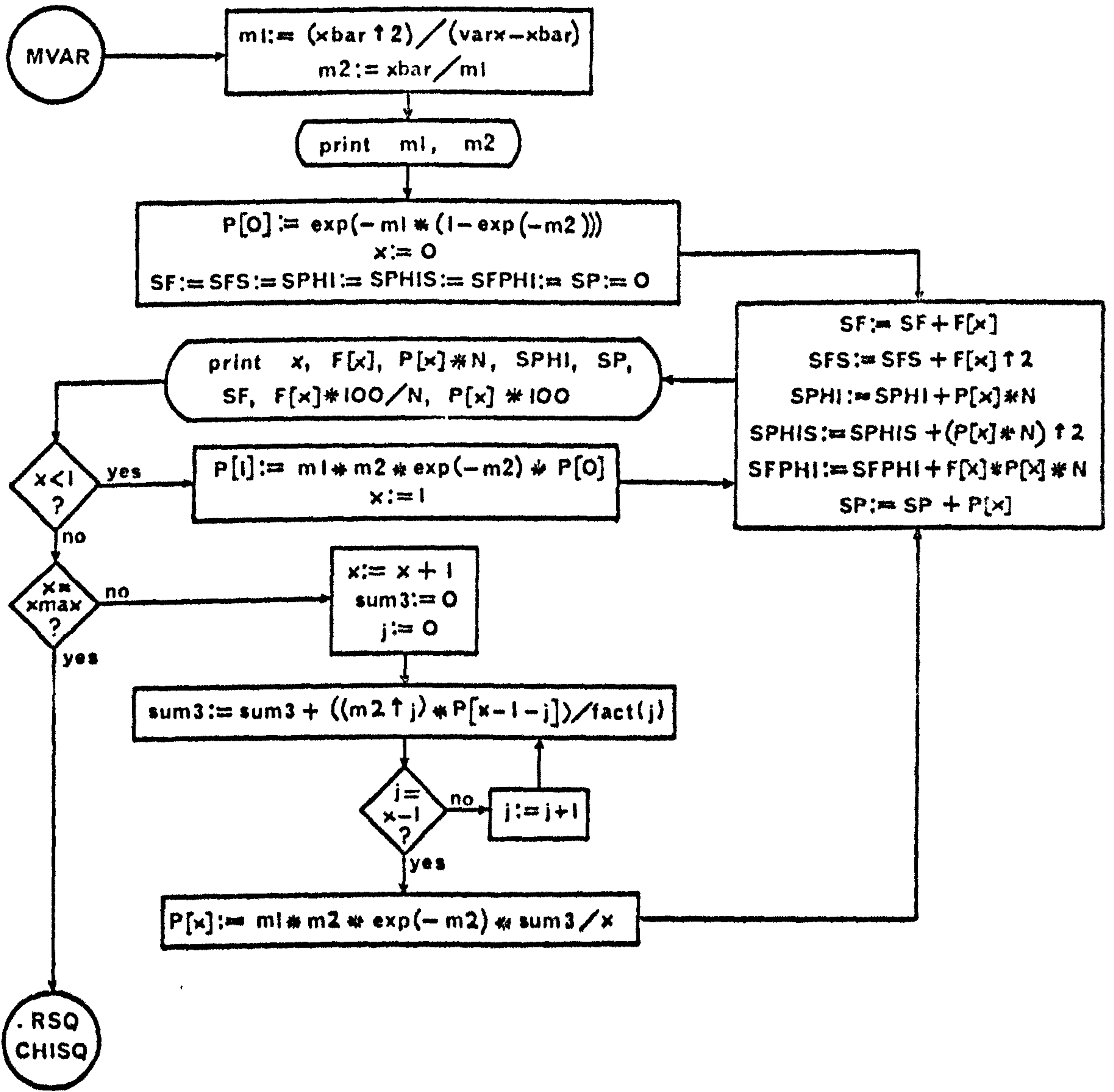
arrays F, PHI [1:xmax]



(d) NEYMAN A

The parameters m_1 and m_2 are calculated from the mean and variance, and hence the distribution computed (see p. 27). R^2 and χ^2 are again calculated. A procedure, `fact (x)`, was declared at the start of the program to calculate the factorial of x .

arrays F, P [0:xmax]



(e) POLYNOMIAL CURVE FITTING

This program calculates a polynomial curve of any order, n , to fit any number, N , of points (x,y) . The pairs of co-ordinates are read in and stored in an array $XY [0:N, 0:1]$. At this point the data may be transformed:

e.g. $XY [i,0] := \ln (x); XY [i,1] := 1/y;$

only one program card requiring alteration.

A series of equations with order $n=nmin$ to $n=nmax$ can be calculated, provided that $n \leq N-1$. Two-dimensional arrays are used throughout so that standard matrix operations can be performed.

arrays $SXX, Sxx, CF [1:n+1, 1:n+1]$
 $Sx, c [1:n, 1:n]$
 $SX, XN [1:n+1, 1:1]$
 $Sy, B, C, D, sB [1:n, 1:1]$
 $Xbar, Sytr [1:1, 1:n]$
 $Syhatsq, KXbar [1:1, 1:1]$

The constant, $K1$, and the coefficients, $B [i,1]$, of x^i for $i=1$ to $i=n$, were printed, with 95% limits. A set of co-ordinates $(x1, y1)$ of the curve were also printed, and plotted on a graph together with the original points. xe is the increment added to $x1$ in the calculation of successive points on the curve. Details of plotting the graph and its axes are not shown.

read nmin, nmax, xmin, xmax,
ymin, ymax, N, xe

formmx (XY, 0, i, j)
m:=0

read x, y

XY [m, 0] := x
XY [m, 1] := y

plot x, y

m=N ?
no m:=m+1
yes

n:=nmin

formmx (SX, 0, i, j)
formmx (SXX, 0, i, j)
m:=0

i:=1

XN [i, 1] := XY [m, 0] ↑ i

i=n ?
no i:=i+1
yes

XN [n+1, 1] := XY [m, 1]
i:=1

SX [i, 1] := SX [i, 1] + XN [i, 1]
j:=1

SXX [i, 1] := SXX [i, 1] + XN [i, 1] * XN [i, 1]

j=n+1 ?
no j:=j+1
yes

i=n+1 ?
no i:=i+1
yes

m=N ?
no m:=m+1
yes

i:=1

j:=1

CF [i, 1] := (SX [i, 1] * SX [1, i]) / N

j=j+1
j=n+1 ?
no
yes

i=i+1
i=n+1 ?
no
yes

i:=1

Xbar [i, 1] := SX [i, 1] / N

i=i+1
i=n ?
no
yes

Ybar := SX [n+1, 1] / N
mxdiff (Sxx, SX * X, CF)
mxcopy (Sx, Sxx)
i:=1

Sy [i, 1] := Sxx [i, n+1]

i=i+1
i=n ?
no
yes

mxquot (B, Sx, Sy)
i:=1

j:=1

j=1 ?
no
yes

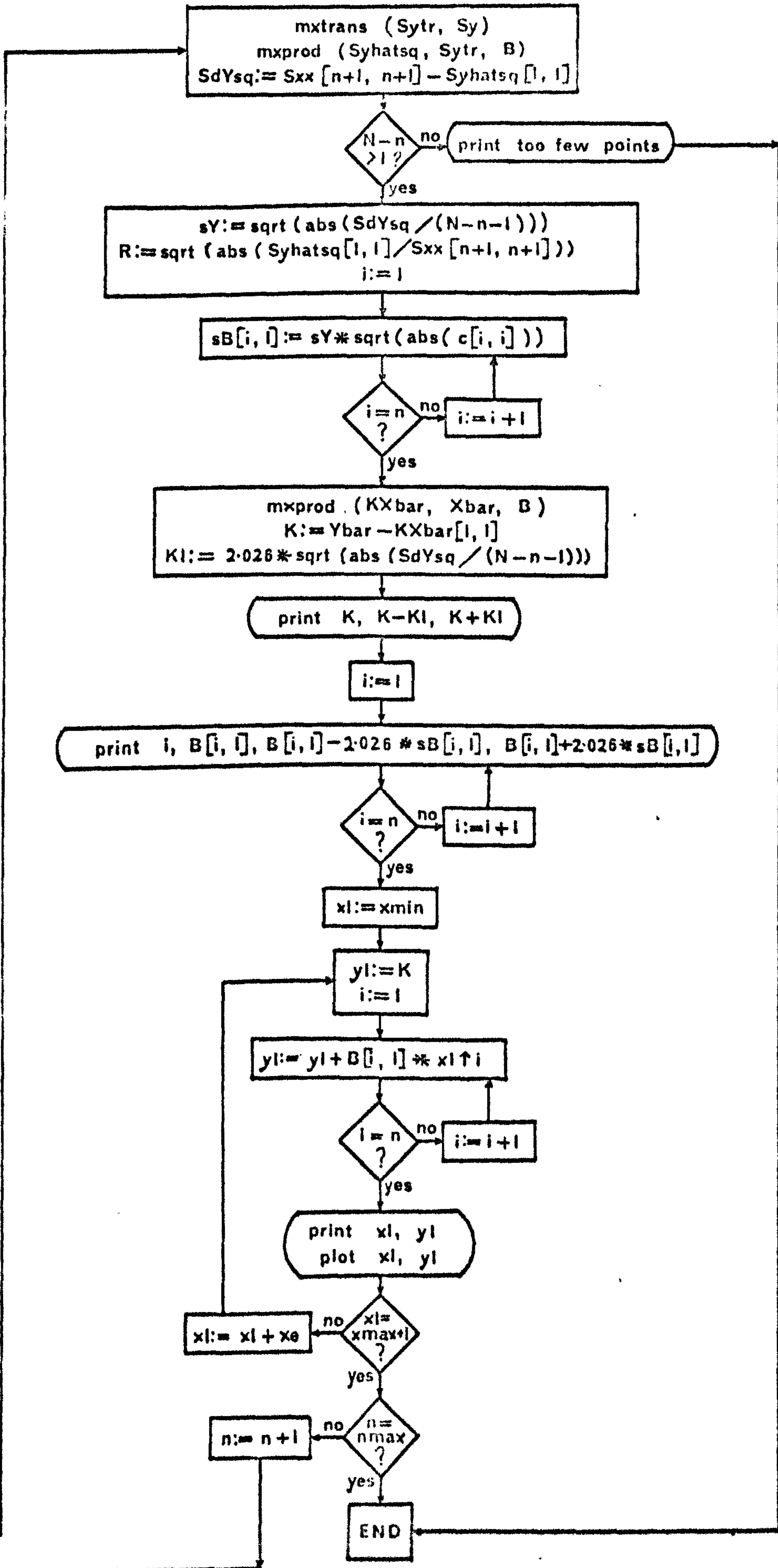
D [j, 1] := 0
D [j, 1] := 1

j=j+1
j=n ?
no
yes

mxquot (C, Sx, D)
j:=1

c [j, 1] := C [j, 1]

i=i+1
i=n ?
no
yes
j=n ?
no
yes
j:=j+1



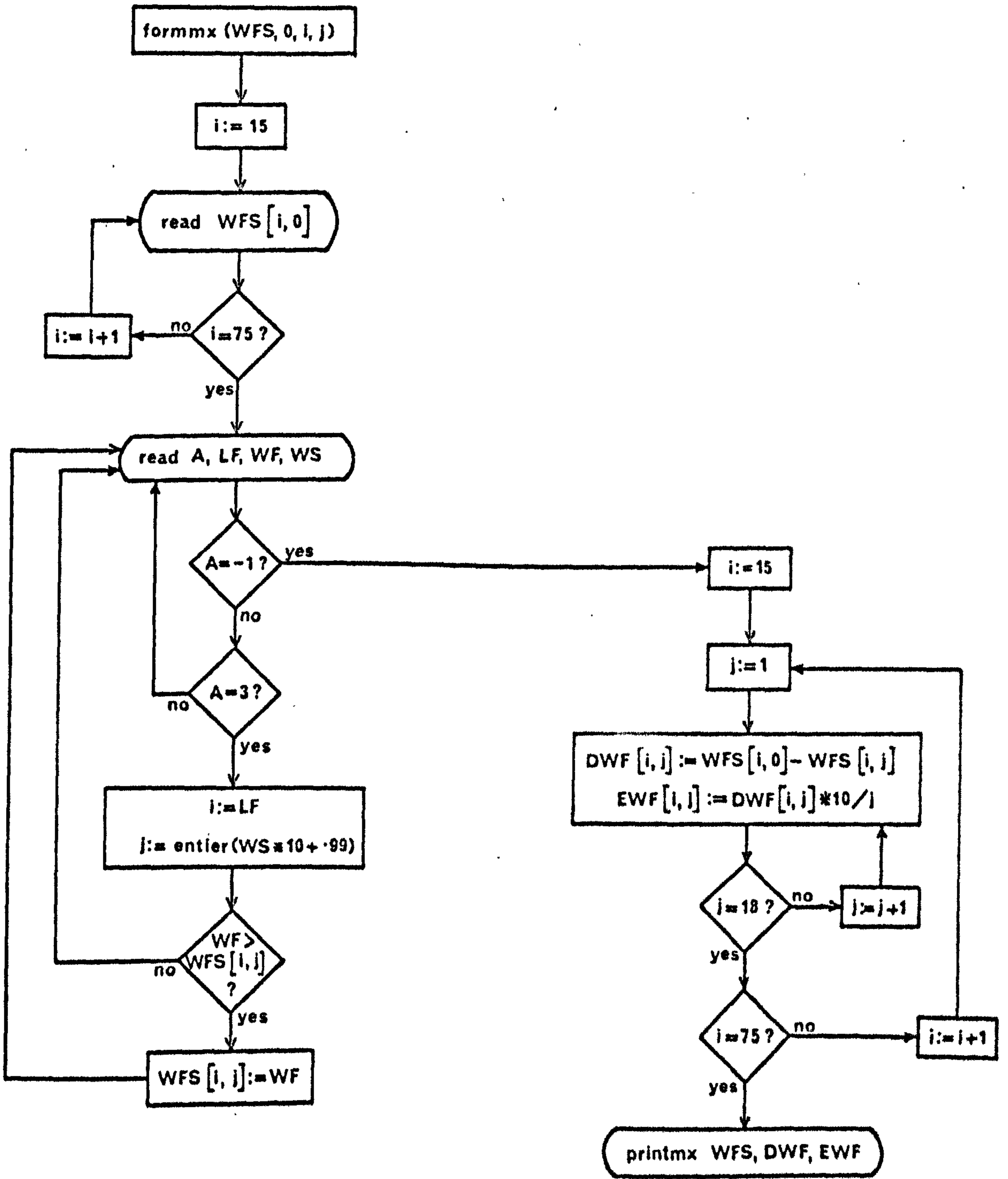
(f) MAX WFS

This program calculates the loss of weight of fish caused by the presence of different weights of Schistocephalus (see p. 67). Data were read in from the cards for each fish (p. 38), the age of the fish, A, length of fish, LF, weight of fish, WF, and weight of Schistocephalus, WS, being the relevant items. Each age group was dealt with separately - in the flow diagram shown fish of age group III were selected.

The maximum weights of uninfected fish of each length were also read in, and stored in the first column of the array WFS [15:75, 0:10]. The maximum weights of fish for each length (rows) and for each weight of Schistocephalus in intervals of 1g (columns) are stored in the remainder of this array.

The second and subsequent element of each row of WFS is then subtracted from the first element of that row and the result stored in a new array DWF [15:75, 1:10]. Thus the loss of weight of fish caused by each weight of Schistocephalus for each length of fish is found.

A third array, EWF [15:75, 1:10] is then formed in which each element represents the loss of weight of fish which would have been caused by 1 g of Schistocephalus, for each length of fish and weight



of Schistocephalus.

The three arrays are printed.

APPENDIX 2

(a) Figures for Gasterosteus - all ages

date	n u m b e r s			f i s h l e n g t h				f i s h w e i g h t			
	total	♂	♀	total		♂ mean	♀ mean	total		♂ mean	♀ mean
				mean	var.			mean	var.		
1966											
29.10	78	20	58	48.7	79.0	50.3	48.8	.834	.154	.906	.829
12.11	97	45	49	48.3	61.6	47.5	50.0	.918	.170	.876	.991
19.11	76	35	41	47.0	59.4	47.4	46.8	.812	.178	.829	.797
10.12	78	33	43	47.0	100.8	47.8	47.1	.841	.230	.892	.832
1967											
1.1	115	45	68	48.3	56.4	48.9	48.1	.824	.133	.862	.812
25.1	57	25	31	48.8	43.5	49.8	48.3	.866	.133	.925	.833
18.2	74	29	40	50.1	48.4	50.9	50.8	.927	.192	.945	.986
5.3	86	48	37	50.4	49.8	49.5	51.9	.935	.158	.876	1.031
9.4	70	27	37	47.9	80.9	51.0	48.1	.844	.201	.977	.845
21.4	74	30	42	47.2	50.5	48.3	47.1	.800	.136	.814	.814
8.5	66	33	30	49.4	63.5	50.0	49.5	.917	.261	.987	.882
7.6	52	28	24	49.7	33.7	51.1	48.0	.872	.084	.953	.779
21.6	51	22	28	51.2	51.4	52.8	50.4	.968	.174	1.090	.894
6.7	51	30	20	47.7	47.7	49.3	46.6	.794	.102	.880	.701
31.7	58	26	28	48.6	94.6	49.7	50.5	.828	.231	.839	.909
21.8	53	25	16	44.7	120.0	50.9	47.4	.685	.149	.800	.746
7.9	62	32	23	45.8	158.1	47.6	51.9	.740	.176	.749	.943
21.9	60	27	30	48.8	85.4	49.6	50.5	.837	.154	.848	.898
18.10	77	31	44	48.6	64.4	47.6	50.4	.795	.102	.765	.844
10.11	74	35	37	48.9	66.2	48.7	49.7	.771	.103	.775	.787
4.12	62	32	30	51.4	49.7	51.0	51.9	.938	.155	.903	.975
1968											
1.1	50	25	25	52.4	46.9	51.5	53.4	.978	.158	.909	1.046
15.1	58	35	20	51.0	70.6	52.5	51.3	.858	.155	.914	.858
1.2	77	34	41	53.6	44.2	52.9	54.6	.956	.112	.915	1.013
4.3	68	29	39	52.6	58.5	50.7	54.1	1.004	.194	.894	1.086
25.3	60	32	26	48.1	67.2	48.6	48.8	.831	.224	.823	.880
9.4	76	34	41	49.5	58.3	49.4	49.9	.916	.187	.897	.944
overall mean	69	31	35	49.1	69.2	49.7	49.8	.863	.166	.882	.890

(b) Figures for Gasterosteus - age groups - including weights of Schistocephalus

age- group	21.8	7.9	21.9	18.10	10.11	4.12	1.1	15.1	1.2	4.3	25.3	9.4	
I	12	9	4	4	6	4	4	3	8	13	15	10	7.67
no. II	13	22	36	32	26	23	19	19	16	12	22	31	22.6
III	22	27	15	39	38	29	25	29	41	37	17	26	28.8
IV	4	4	4	2	3	6	2	7	12	6	5	8	5.3
mean I	27.4	21.2	29.0	31.3	33.5	40.8	42.5	30.7	41.9	41.9	40.7	40.0	35.6
LF II	44.3	46.5	47.5	44.6	44.8	47.4	48.6	45.4	47.9	47.0	45.3	46.3	46.4
III	51.8	51.1	53.2	53.4	53.3	53.8	56.1	54.6	55.9	56.9	55.6	54.4	54.3
IV	57.2	62.0	61.5	55.5	56.7	62.7	62.5	59.9	60.8	61.0	61.6	62.0	60.7
mean I	.153	.080	.265	.250	.262	.413	.538	.190	.448	.472	.460	.440	.343
WF II	.599	.710	.734	.622	.579	.746	.786	.581	.699	.688	.630	.700	.675
III	.930	.869	1.01	.972	.945	1.02	1.14	.979	1.04	1.21	1.21	1.17	1.037
IV	1.13	1.52	1.63	1.20	1.13	1.65	1.69	1.39	1.34	1.50	1.73	1.65	1.475
calc. I	.180	.099	.358	.283	.355	.527	.628	.222	.554	.575	.563	.550	.422
mean II	.617	.904	.923	.804	.764	.920	.952	.754	.912	.887	.800	.869	.849
WF III	1.20	1.15	1.33	1.28	1.27	1.31	1.44	1.26	1.35	1.51	1.50	1.44	1.330
IV	1.56	2.02	2.12	1.66	1.65	2.13	2.29	1.88	1.84	1.90	2.21	2.13	1.951
mean I	.045	.029	.173	.055	.162	.300	.180	.050	.248	.229	.256	.277	.177
YS II	.350	.421	.410	.364	.384	.343	.325	.347	.451	.413	.340	.347	.365
III	.420	.487	.627	.701	.555	.514	.590	.466	.562	.522	.495	.412	.535
IV	.410	.685	.763	.485	.777	.550	1.25	.781	.725	.493	.658	.596	.662

(c) Figures for Schistocephalus

date	% fish infected	mean	var.	var/ mean	log normal		weight per fish		parasite index		pleroc. weight
					mean	var.	mean	var.	mean	var.	mean
1966											
29.10	89.7	2.82	5.5	1.87	1.61	7.90	.409	.080	.299	.021	.145
12.11	75.3	2.08	8.2	3.93	0.88	9.55	.248	.054	.197	.024	.119
19.11	72.4	1.87	4.6	2.42	0.92	8.64	.241	.045	.221	.030	.129
10.12	70.5	3.14	23.2	7.37	1.19	14.3	.228	.066	.197	.030	.073
1967											
1.1	81.7	2.12	10.3	4.86	0.91	8.94	.268	.071	.243	.022	.126
25.1	78.9	3.21	85.6	27.0	1.14	7.40	.258	.033	.235	.024	.080
18.2	78.4	3.74	154.0	41.2	1.25	9.99	.296	.055	.240	.025	.078
5.3	81.4	3.00	36.5	12.2	0.94	19.0	.292	.051	.239	.021	.097
9.4	91.4	3.51	35.7	10.2	1.35	12.1	.273	.031	.241	.017	.078
21.4	95.9	3.49	17.8	5.08	1.53	10.4	.293	.029	.271	.012	.084
8.5	86.4	2.55	8.0	3.17	1.23	9.80	.244	.026	.229	.018	.096
7.6	71.2	1.40	2.3	1.61	0.74	6.81	.213	.042	.186	.023	.152
21.6	82.4	1.90	4.4	2.31	0.91	8.94	.237	.035	.199	.015	.125
6.7	92.2	2.35	4.9	2.09	1.18	7.73	.219	.019	.223	.014	.093
31.7	93.1	5.79	76.0	13.1	1.88	20.3	.298	.024	.270	.014	.051
21.8	84.9	5.66	98.3	17.4	2.40	11.7	.309	.058	.275	.022	.055
7.9	88.7	7.66	95.3	12.4	3.45	21.5	.410	.091	.305	.024	.054
21.9	96.7	8.95	103.0	11.5	4.35	21.2	.481	.095	.343	.016	.054
18.10	98.7	7.74	70.5	9.12	4.20	9.92	.522	.129	.365	.015	.067
10.11	97.3	7.34	67.2	9.15	4.05	14.8	.477	.066	.368	.014	.065
4.12	100.0	5.69	30.6	5.38	3.10	9.24	.440	.072	.315	.014	.077
1968											
1.1	100.0	7.42	61.3	8.26	3.40	22.1	.483	.140	.305	.011	.065
15.1	98.5	6.43	33.1	5.15	4.00	9.61	.443	.063	.330	.017	.069
1.2	98.7	6.07	25.6	4.22	4.40	12.4	.532	.077	.349	.011	.088
4.3	98.5	4.87	41.5	8.51	1.40	10.1	.445	.065	.305	.014	.091
25.3	96.6	5.87	46.0	7.84	2.75	7.67	.384	.056	.316	.016	.066
9.4	97.4	5.32	22.8	4.29	2.75	7.67	.382	.047	.298	.012	.072
overall	88.3	4.40	45.1	10.3	2.14	11.8	.343	.071	.266	.024	.078
means											

(d) Figures for Echinorhynchus

date	% fish infect.	number per fish			-ve binomial		lengths of worms				% ♀ with acanth.	
		mean	var.	var/ mean	p	k	male		female			♂:♀ ratio
							mean	var.	mean	var.		
1966												
29.10	50.0	3.05	39.7	13.0	10.1	.305	3.17	.447	4.54	1.17	1.020	1.7
12.11	41.2	1.69	9.3	5.5	5.85	.291	3.44	.410	5.03	1.23	.576	38.5
19.11	40.8	2.21	93.8	42.4	11.8	.187	3.29	.362	4.64	1.09	.887	70.8
10.12	41.0	2.30	31.3	13.6	10.8	.213	3.32	.396	4.86	1.90	.543	78.5
1967												
1.1	40.0	1.54	11.0	7.2	5.72	.269	3.20	.383	4.40	1.67	.735	67.6
25.1	33.3	0.88	2.4	2.7	2.71	.323	3.14	.460	5.17	2.37	.470	73.5
18.2	52.7	1.88	9.4	5.0	4.05	.461	3.45	.443	4.88	1.32	.760	91.1
5.3	48.8	1.44	5.9	4.1	3.04	.474	3.19	.491	4.68	1.16	.850	82.1
9.4	40.0	1.24	10.9	8.7	4.27	.291	3.14	.707	4.42	1.13	.403	61.3
21.4	35.2	0.97	3.4	3.5	3.09	.315	2.91	.231	4.58	1.20	.412	39.2
8.5	24.4	1.00	11.1	11.1	8.19	.122	3.05	.202	4.21	1.05	.609	58.5
7.6	30.8	0.90	6.8	7.6	4.31	.201	3.18	.154	4.79	0.91	.621	58.6
21.6	31.4	1.02	4.3	4.3	4.48	.228	3.17	.251	4.47	0.78	.576	63.6
6.7	23.6	0.88	6.9	7.8	6.66	.132	3.31	.247	4.83	0.95	.857	54.2
31.7	17.4	0.50	2.9	5.8	4.63	.108	2.94	.253	4.42	0.64	.612	27.8
21.8	7.6	0.15	0.4	2.4	2.25	.067	2.43	.015	6.28	1.84	.600	60.0
7.9	19.4	0.84	13.6	16.2	9.40	.089	2.51	.531	3.89	1.66	.857	0.0
21.9	23.4	1.48	20.2	13.7	15.5	.096	3.01	.265	4.30	1.94	.745	58.9
18.10	31.2	0.96	5.2	5.4	4.41	.218	2.98	.368	4.33	1.51	.762	45.2
10.11	28.4	1.62	25.5	15.8	12.8	.127	2.50	.224	4.07	1.54	.790	72.0
4.12	25.8	1.24	16.0	12.8	10.5	.119	2.88	.551	4.32	1.34	.790	81.4
1968												
1.1	32.0	2.34	30.0	12.8	17.7	.132	3.00	.413	4.18	1.09	1.13	89.1
15.1	22.4	1.33	19.7	14.8	14.2	.094	2.96	.554	4.35	1.82	1.33	51.5
1.2	27.3	1.30	29.7	22.8	10.3	.126	2.69	.581	3.71	1.84	.667	40.0
4.3	23.6	1.44	24.7	17.2	15.1	.095	2.46	.196	3.78	1.66	.661	35.6
25.3	20.0	0.45	1.1	2.5	2.40	.188	2.90	.275	4.24	0.77	.227	77.3
9.4	6.0	0.08	0.1	1.3	0.32	.240	3.10	.750	4.23	0.38	1.000	33.3
overall means	31.5	1.34	16.9	12.7	7.57	.204	3.08	.459	4.49	1.56	.729	55.7

(e) Figures for Diplostomum

date	% fish infected	number per fish			-ve binomial		no. per right eye		no. per left eye	
		mean	var.	var/ mean	p	k	mean	var.	mean	var.
1966										
29.10	44.9	5.30	315.5	59.5	33.1	.160	2.55	64.9	2.74	97.0
12.11	45.4	5.42	233.4	43.1	32.9	.165	2.95	70.5	2.47	53.1
19.11	47.4	6.32	294.9	46.8	38.3	.165	3.82	141.9	2.50	33.8
10.12	55.1	6.00	108.3	18.1	23.4	.256	3.01	26.6	2.99	33.0
1967										
1.1	44.3	3.36	81.9	24.4	18.0	.187	1.82	24.5	1.54	20.0
25.1	54.4	12.75	1519.5	119.1	74.7	.171	6.60	476.2	6.16	300.1
18.2	48.7	3.60	68.4	19.0	15.4	.234	1.78	15.7	1.84	21.2
5.3	34.9	4.40	259.6	61.3	37.9	.116	2.63	112.2	1.77	34.6
9.4	42.9	4.87	545.1	112.0	34.9	.140	2.71	142.9	2.16	130.7
21.4	18.9	0.72	8.2	11.5	7.4	.097	0.37	2.7	0.35	1.8
8.5	30.3	2.33	70.3	30.2	20.1	.116	1.17	18.6	1.17	18.4
7.6	42.3	4.83	129.8	26.9	30.6	.158	2.31	31.0	2.52	36.3
21.6	88.2	18.39	1286.3	70.0	31.4	.585	9.43	332.7	8.96	318.3
6.7	72.5	12.14	228.0	18.8	28.9	.420	6.53	73.0	5.61	53.0
31.7	91.4	21.93	817.1	37.3	31.1	.705	11.41	253.0	10.52	173.3
21.8	79.2	14.68	1054.0	71.9	38.7	.376	7.60	289.0	7.08	243.6
7.9	75.9	19.77	1384.7	70.0	53.0	.348	10.29	379.0	9.48	325.2
21.9	73.3	20.10	1615.7	80.4	70.1	.287	9.98	414.9	10.12	406.6
18.10	63.6	14.10	2636.6	187.0	61.5	.229	6.92	530.3	7.18	807.9
10.11	73.0	16.81	1366.8	81.2	54.6	.308	8.55	362.1	8.26	332.2
4.12	66.1	20.57	1428.8	69.4	87.7	.234	9.87	330.3	10.60	408.6
1968										
1.1	70.0	12.02	506.8	42.2	37.4	.322	6.22	154.0	5.80	109.3
15.1	60.4	15.05	863.8	57.4	68.1	.221	7.41	192.9	7.64	250.3
1.2	72.7	12.53	615.8	49.2	35.0	.358	6.48	185.5	6.05	130.7
4.3	64.7	5.62	111.0	19.7	15.2	.371	2.87	25.3	2.75	33.8
25.3	50.0	2.85	27.8	9.7	9.7	.294	1.53	7.8	1.32	6.0
9.4	52.6	4.26	59.3	13.9	15.3	.278	2.50	22.3	1.76	11.7
overall	56.1	9.35	592.6	63.4	37.2	.270	4.83	170.6	4.53	162.5
means										

A Computer Model of the Oxford Great Tit Population

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Functions relating fecundity and mortality of Great tits to various factors are extracted from data given by Lack (1966). A computer program is described which calculates the number of birds in the population over any number of years; it enables the factors affecting fecundity and survival to be tested alone, and in various combinations, for their effects on the population. The results show that the density-independent factors would not control the population for any length of time. The effect of the calculated fecundity functions on the number of tits is shown to be small compared with the effect of the functions relating to juvenile survival.

1. Introduction

This work is an extension of a study on theoretical population models for use in a digital computer (Pennycuick, Compton & Beckingham, 1968) in which the matrix model of Leslie (1945) was extended to include provision for density-dependent fecundity and mortality. One use for such a model is in the testing of different hypotheses concerning regulation of populations. The chief points over which controversy has raged are whether or not a density-dependent mechanism is required, and if so whether this is mediated through mortality, chiefly from starvation (Lack, 1966), or through fecundity by a type of social behaviour or “group selection” (Wynne-Edwards, 1962).

Information about the fecundity and mortality of a population, and how these are affected by various factors, is required as data for the computer model. This information is difficult to obtain and few studies give sufficient detail. However, one recent study which has provided very suitable data is that of a Great tit (*Parus major* L.) population at Oxford. This work, from 1947 until 1964, is reviewed by Lack (1966) and described in detail by Betts (1955), Gibb (1950, 1954*a*, *b*, 1955, 1956, 1957, 1958, 1962), Hartley (1953), Lack (1955, 1958, 1964), Lack, Gibb & Owen (1957) and Perrins (1963, 1965). Kluyver (1951) describes a similar study of a Great tit population in Holland, started in 1912; the picture here is complicated by migrations but much

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useful information about Great tit populations in general has been obtained from this work.

2. Analysis of the Figures

Lack (1966) summarizes and discusses the results and conclusions of the above authors. They have shown that the size of the population is most affected by the survival of the juvenile birds for the first three months after they leave the nest. The most important factors influencing juvenile survival are population density and Beech mast crop. The fecundity and winter survival were found to be relatively unimportant.

TABLE 1

The factors found to affect the fecundity and survival of the birds

Clutch size	dependent upon	(i) density of population (ii) date of laying (iii) age of parents
Nest survival	(a) losses of eggs negligible (b) nestling survival dependent upon	(i) density of population (ii) date of laying (iii) age of parents (iv) size of clutch (v) availability of food
Juvenile survival	dependent upon	(i) density of population (ii) date of laying (iii) age of parents (iv) size of clutch (v) availability of food (Beech mast)
Winter survival	dependent upon	(i) density of population (ii) Beech mast crop (iii) winter cold

Information extracted from Lack's (1966) summary is used here to derive quantitative relationships between fecundity and survival and some of the above factors. The effects of these factors on the size of the population can then be tested alone and in different combinations using the computer model.

Tables 2 and 3 show the yearly figures given by Lack (1966) together with a number of other statistics which have been calculated from them. Particular use has been made of the ratios of juveniles : adults in winter, although these are not available for all years. The method of separating juveniles from adults by colour was not discovered until 1958 and the earlier figures are based only on ringed birds. The mean date of the first egg is the number of days from 1 April = 1. The Beech mast crop is expressed on an arbitrary

scale from 0, crop failure, to 8, abundant crop. The figure for winter cold was obtained from the average daily temperatures at Oxford; it is the sum of all the negative daily averages, in degrees centigrade, expressed as a positive number.

Certain assumptions were made before starting the analysis. First, the clutch and brood sizes given by Lack naturally apply to pairs of birds not individuals. In Leslie's model only the females are represented. Here the

TABLE 2
Fecundity data

No.	Year	Number breeding			Number of eggs			Mean date of first egg
		total	yearling	adult	total	Mean bird	Mean adult	
1	1947	14			78	5.55		34
2	1948	42			258	6.15		10
3	1949	60	28	32	303	5.05	5.1	23
4	1950	62	29	33	284	4.55	4.7	29
5	1951	64			250	3.90		40
6	1952	40	9	31	198	4.95	5.0	23
7	1953	42			204	4.85		33
8	1954	62	35	27	301	4.85	5.0	25
9	1955	54	18	36	270	5.00	5.1	34
10	1956	48			240	5.00		34
11	1957	98			450	4.60		17
12	1958	54	9	45	248	4.60	4.7	35
13	1959	82	49	33	361	4.40	4.6	24
14	1960	102	51	51	424	4.15	4.3	27
15	1961	172	115	57	688	4.00	4.2	21
16	1962	86	14	72	378	4.40	4.45	34
17	1963	78	22	56	362	4.65	4.75	29
18	1964	108	54	54	491	4.55	4.7	34
Means		70.4	36	44	321.5	4.73	4.72	28.1

whole population is included, but it has been assumed that the sex ratio is always exactly 1 : 1 and that all the birds pair and breed. As the Oxford study was made on only the breeding birds during the breeding season this holds at least for the numbers breeding, which is the chief criterion of population size used. Thus the fecundities given here are per bird, i.e. the values per pair are halved. It has also been assumed that there is no adult mortality during the spring and summer; this cannot be entirely true but the error is probably small.

The quantitative relationships between the fecundity and survival of the birds and the different factors described above were investigated. First, pairs

TABLE 3
Survival data

No. Date	No. breeding	Nest survival no. flying	% flying	Summer total no. in summer	juv.:ad. ratio in summer	total number	Autumn no. of juve-niles	% juv. survival	Winter no. of juve-niles	no. of adults	juv.:ad. ratio in winter	% juv. flying which survive to next spring	Beech mast crop	Winter cold
1 1947	14	65	83.4	79	4.6	79	37	17.7	28	32	0.9	13.4	2	13
2 1948	42	209	81.0	251	5.0	251	55	21.2	29	33	0.9	11.1	8	3
3 1949	60	260	85.8	320	4.3	320	19	12.1	9	31	0.3	5.7	1	13
4 1950	62	190	66.9	252	3.1	252	55	21.2	29	33	0.9	11.1	8	10
5 1951	64	157	62.8	221	2.5	221	19	12.1	9	31	0.3	5.7	0	6
6 1952	40	150	75.8	190	3.8	190	55	29.8	35	27	1.3	19.0	3	16
7 1953	42	184	90.2	226	4.4	226	31	11.8	18	36	0.5	14.5	5	35
8 1954	62	262	87.0	324	4.2	324	55	29.8	35	27	1.3	19.0	0	25
9 1955	54	183	67.8	237	3.4	237	31	11.8	18	36	0.5	14.5	0	58
10 1956	48	189	78.8	237	3.9	237	55	29.8	35	27	1.3	19.0	6	5
11 1957	98	225	50.0	323	2.3	323	20	8.7	9	45	0.2	17.0	0	14
12 1958	54	150	60.5	204	2.8	204	81	54.0	49	33	1.5	32.7	4	14
13 1959	82	277	76.6	359	3.4	359	82	29.6	51	51	1.0	18.4	0	6
14 1960	102	274	64.6	376	2.7	376	202	75.1	115	57	2.0	42.0	5	1
15 1961	172	365	53.1	537	2.1	537	34	9.3	14	72	0.2	3.8	0	47
16 1962	86	226	59.8	312	2.6	312	226	100.0	22	56	(2.6 to 0.4)	9.7	4	165
17 1963	78	253	69.9	331	3.2	331	78	30.8	54	54	1.0	21.4	0	15
18 1964	108													
Means	70.4	212.9	71.42	281	3.43	152.9	75	32.3	36.1	43.9	0.85	16.3	2.7	

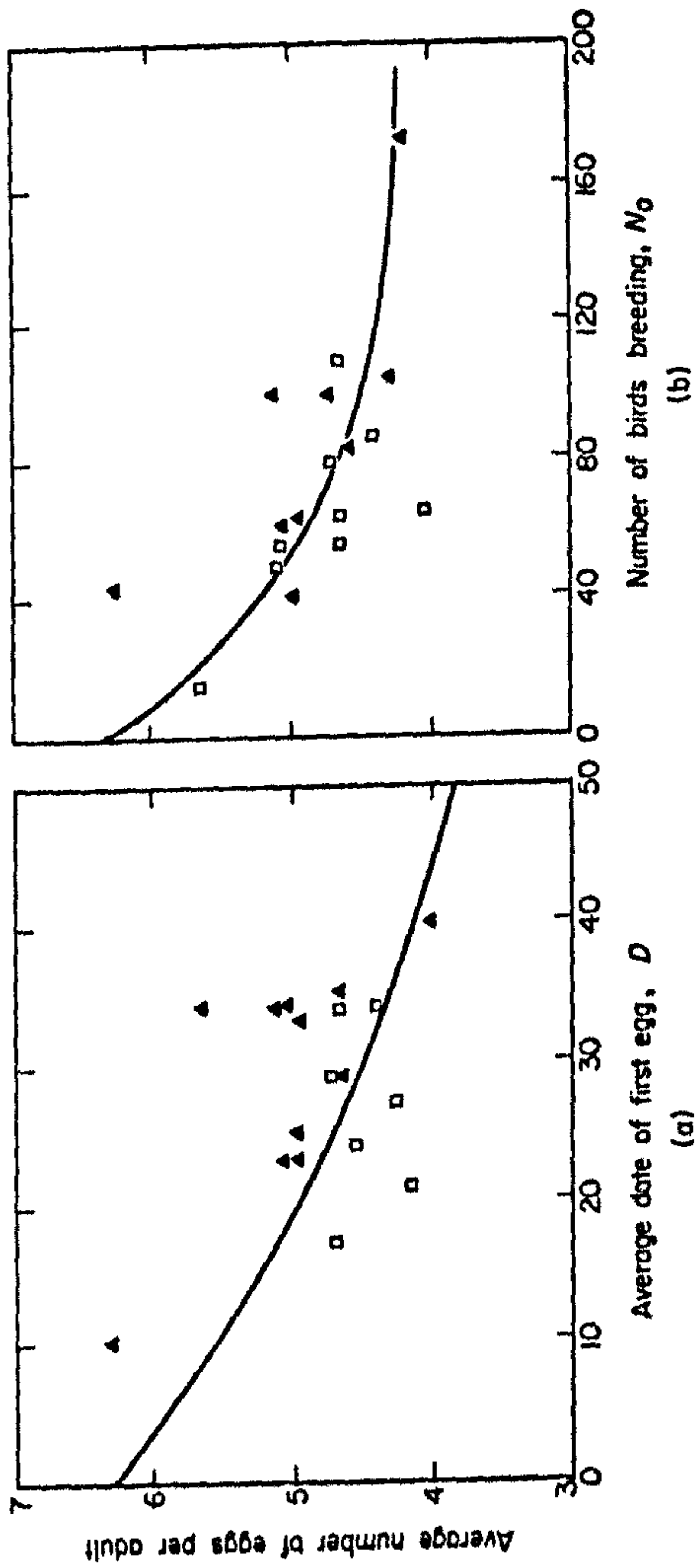


FIG. 1. Fecundity: (a) effect of average date of first egg, D , where 1 April = 1. Curve: $\phi(D) = 504/(80 + D)$, (equation (2)); \square , population density $>$ mean; \blacktriangle , population density $<$ mean.
 (b) Effect of number breeding, N_0 . Curve: $\phi(N_0) = 6.3 - 0.35N_0 + 0.00022N_0^2 - 5 \times 10^{-7}N_0^3$, (equation (1)); \square , date later than mean; \blacktriangle , date earlier than mean.

of values were plotted for each year. Some showed no obvious correlation, for example nest survival with date of laying, and these were therefore not used. A function relating the population statistics to the various factors was calculated for each of the other sets. These functions were not intended to have any biological significance, but simply to describe empirically the situation found. Each set of figures was tested in a computer program calculating a polynomial to second and third order by a multiple regression method, based on Snedecor (1946). In some cases a good fit was obtained, in others not. If the data were very scattered the polynomial did not always

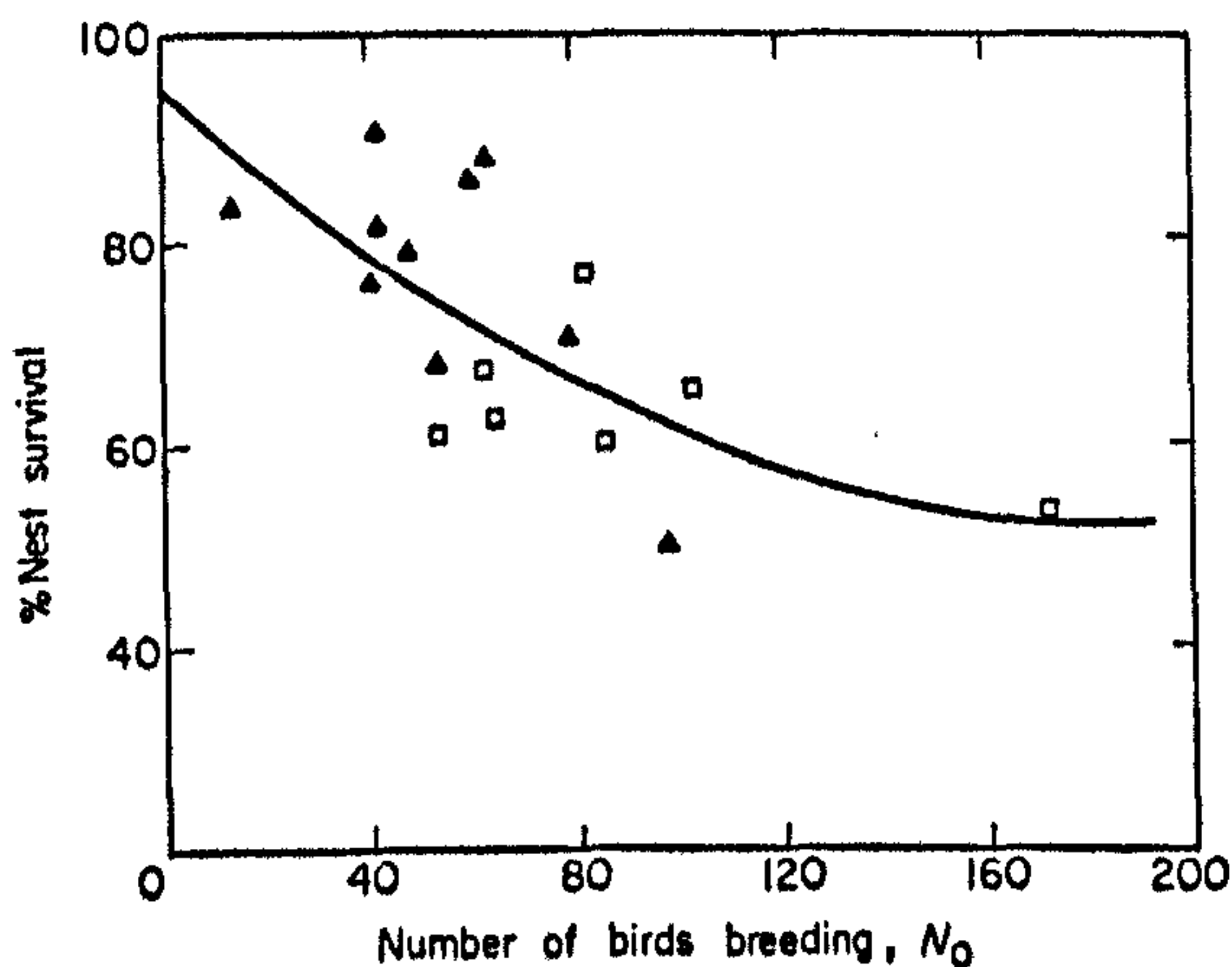


FIG. 2. Nest survival: effect of number breeding, N_0 . Curve: $\phi_2(N_0) = 95 - 0.45N_0 + 0.01N_0^2$ [equation (3)]; □, date later than mean; ▲, date earlier than mean.

give a smooth curve although there appeared to be a correlation; a hyperbolic function was fitted in these cases, using the same multiple regression method. Sometimes a slight modification of the variables used gave a better result: for example juvenile survival was correlated with total summer population rather than the number breeding and so on. For simplicity a few factors which had been found to affect the population were not included, such as the difference in survival of the offspring of adult and yearling parents. Winter cold was not taken into account, although it affected the survival, particularly of the juveniles, when severe.

The functions gave actual values of clutch size and percentage survival and were therefore divided by the mean value concerned to give the proportional effect. For example, the function relating clutch size to population density gave the number of eggs laid per bird; when divided by the mean number of eggs this gave the proportion of the mean for a given population size.

The functions are set out below:

(a) Mean number of eggs per adult versus

(i) total breeding population, N_0 [Fig. 1(a)]

$$\Phi(N_0) = (6.3 - 0.35N_0 + 0.00022N_0^2 - 5 \times 10^{-7}N_0^3)/4.72. \quad (1)$$

(ii) average date of first egg, D [Fig. 1(b)]

$$\Phi(D) = \left(\frac{504}{D+80} \right) / 4.72. \quad (2)$$

(b) Nest survival versus total breeding population, N_0 [Fig. 2]

$$\Phi_2(N_0) = (95 - 0.45N_0 + 0.01N_0^2)/71.4. \quad (3)$$

(c) Three-month juvenile survival versus

(i) total summer population, N_2 [Fig. 3(a)]

$$\Phi(N_2) = \left(\frac{8500}{85 + N_2} \right) / 32. \quad (4)$$

(ii) Beech mast crop, BM [Fig. 3(b)]

$$\Phi(BM) = (15 - 1.8BM + 1.4BM^2)/32. \quad (5)$$

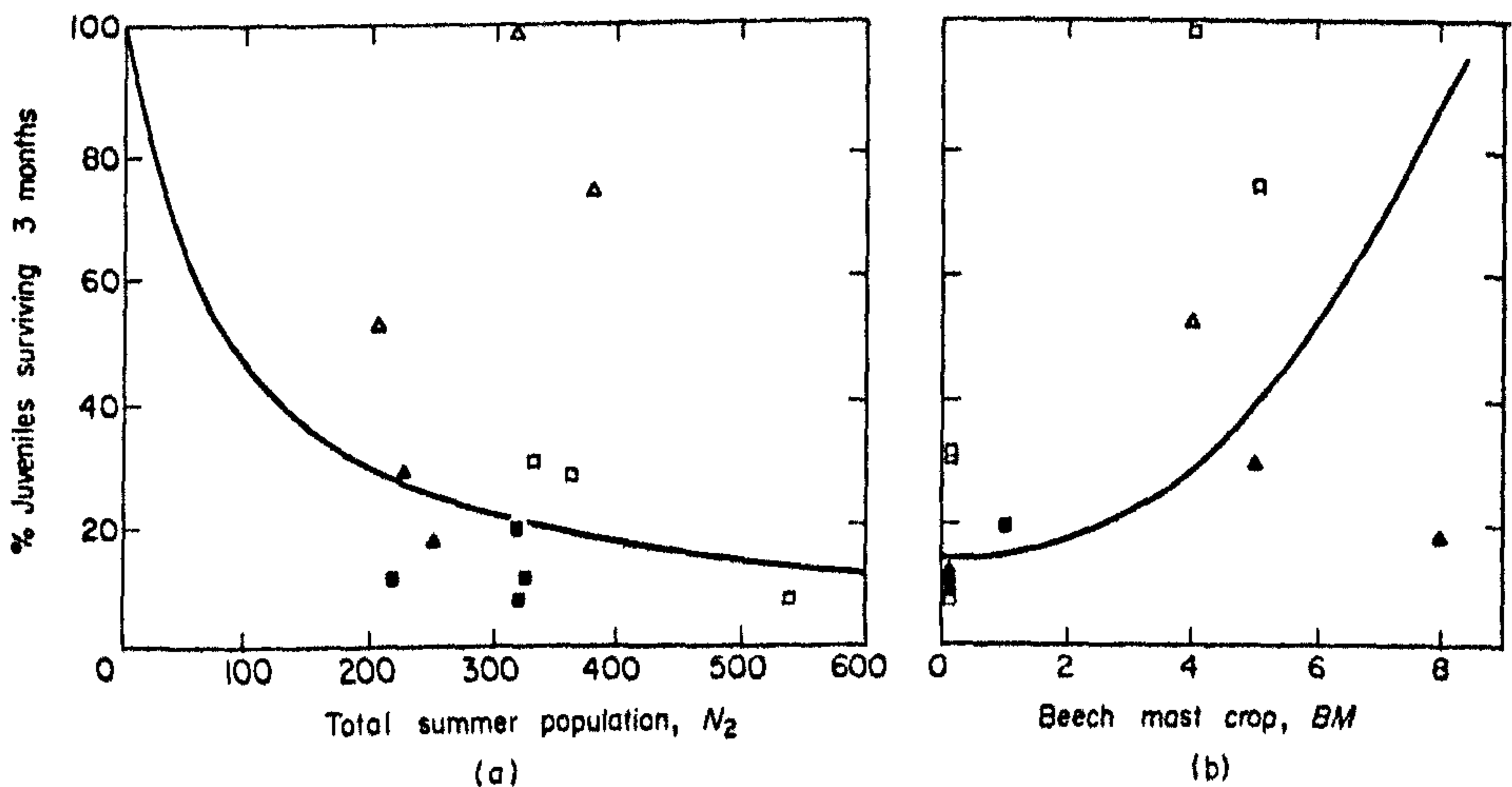


FIG. 3. Three-month juvenile survival: (a) effect of total summer population, N_2 . Curve: $\phi(N_2) = 8500/(85 + N_2)$, (equation (4)); ▲, Δ, Beech mast > mean; ■, □, Beech mast < mean.

(b) Effect of Beech mast crop, BM . Curve: $\phi(BM) = 15 - 1.8BM + 1.4BM^2$, (equation (5)); ▲, Δ, population density > mean; ■, □, population density < mean; solid, 1947 to 1957; hollow, 1958-1963, showing increased survival in later years.

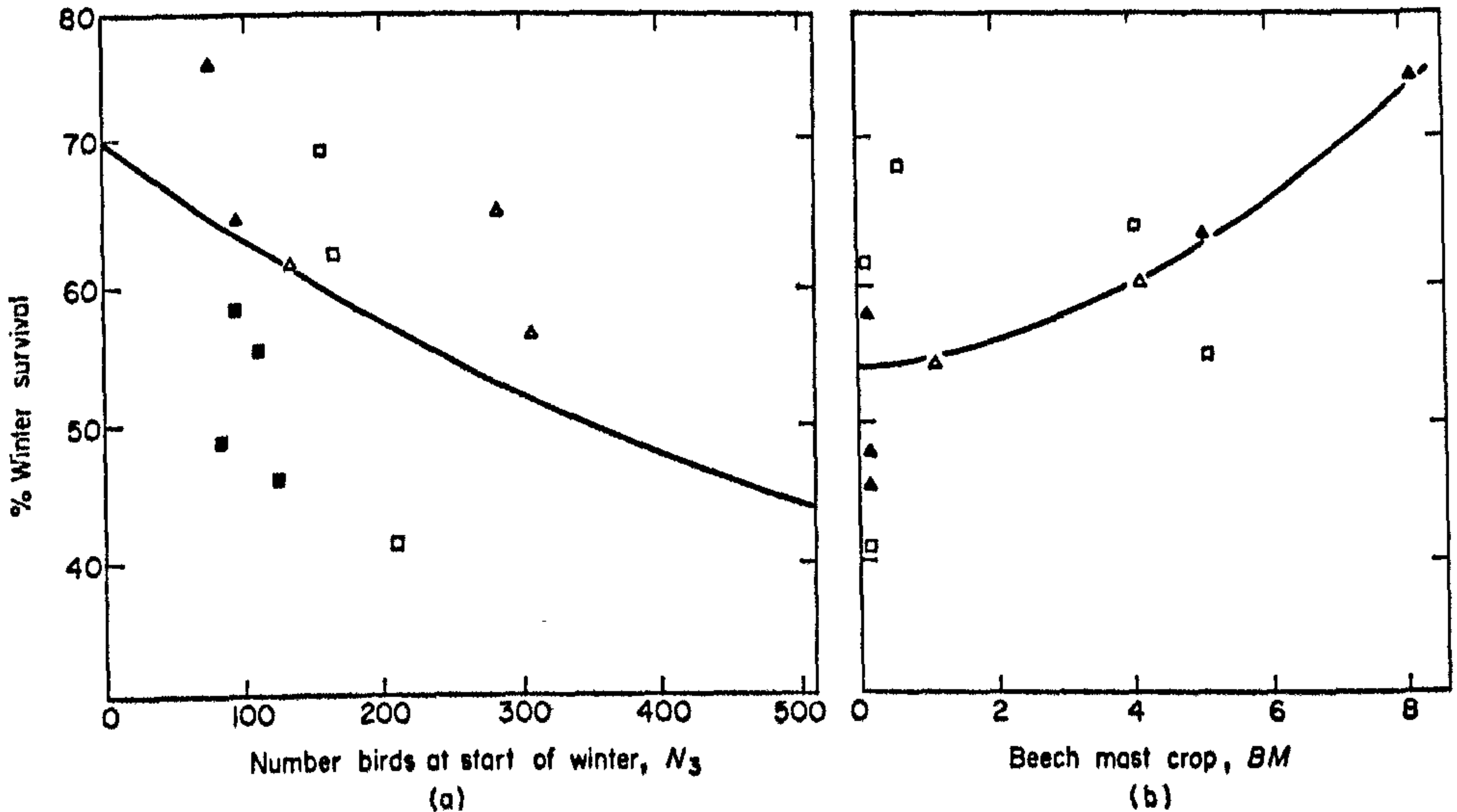


FIG. 4. Winter survival: (a) effect of number of birds at start of winter, N_3 . Curve: $\phi(N_3) = 5600/(800 + N_3)$, (equation (6)); \blacktriangle , \triangle , Beech mast > mean; \blacksquare , \square , Beech mast < mean.

(b) Effect of Beech mast crop, BM . Curve: $\phi_2(BM) = 54 + 0.32BM + 0.29BM^2$, (equation (7)); \blacktriangle , \triangle , population density > mean; \blacksquare , \square , population density < mean; solid 1947 to 1957, hollow 1958 to 1963.

(d) Winter survival versus

(i) number at start of winter, N_3 [Fig. 4(a)]

$$\Phi(N_3) = \left(\frac{5600}{800 + N_3} \right) / 58.7. \quad (6)$$

(ii) Beech mast crop, BM [Fig. 4(b)]

$$\Phi_2(BM) = (54 + 0.32BM + 0.29BM^2) / 58.7. \quad (7)$$

3. Computer Model

In the population calculations it was decided to separate fecundity from mortality and to divide the mortality into three stages: nest, juvenile and winter. These correspond to the stages observed and therefore actual and calculated population sizes can be compared at each stage. This separation was also necessary as the juvenile and winter mortalities depend on the number in the population after the preceding stage.

The breeding population, N_0 , is split into eight age-groups, each of which is represented by an element in a column vector, \mathbf{n}

$$\mathbf{n} = \{n_1, n_2, \dots, n_m, \dots, n_8\}, \tag{8}$$

where n_m is the number of birds at the start of their m th breeding season.

3.1. FECUNDITY

Fecundity is dealt with by premultiplying \mathbf{n} by an 8×8 Leslie-type matrix, \mathbf{F}

$$\mathbf{F} = \begin{bmatrix} F_1 & F_2 & \dots & F_m & \dots & F_7 & F_8 \\ 1 & . & \dots & . & \dots & . & . \\ . & 1 & \dots & . & \dots & . & . \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ . & . & \dots & 1 & \dots & . & . \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ . & . & \dots & . & \dots & 1 & . \end{bmatrix}, \tag{9}$$

in which F_m is the fecundity of age-group n_m . The subdiagonal elements are all equal to unity, representing no adult mortality at this time of year. This could easily be modified by putting the probability of survival of each age-group into the appropriate position. Unfilled elements are valued at zero.

Hence:

$$\mathbf{F}\mathbf{n} = \mathbf{n}', \tag{10}$$

where

$$\mathbf{n}' = \{n'_1, n'_2, \dots, n'_8\}, \tag{11}$$

in which n'_1 is the total number of eggs laid and n'_2 to n'_8 are the breeding birds. It is to be noted that n_8 is multiplied by zero, or birds in their eighth year do not survive. It was calculated that for a population of 70, which was the mean observed, and an average adult survival rate of 60% per annum there would rarely be any birds of this age. Kluyver (1951) also reports the maximum age in the wild to be about eight years.

The fecundity elements in the Leslie matrix (F_1 to F_8) were calculated before each multiplication. F_8 was zero as birds in age-group n_8 did not survive. No difference in fecundity with age was reported, except for yearlings, and therefore F_2 to F_7 were made the same, F_a , where adult fecundity,

$$F_a = f_a \phi(D) \phi(N_0), \tag{12}$$

f_a is the average number of eggs per adult, $\phi(D)$ a function of the average date of the first egg, D , and $\phi(N_0)$ a function of the size of the breeding

population, N_0 . As the yearlings lay on average 0.6 eggs per pair fewer than adults, the yearling fecundity,

$$F_j = F_a - 0.3, \quad (13)$$

when expressed as number of eggs per individual.

3.2. NEST SURVIVAL

The proportion of eggs giving rise to fledged young, or nest survival, was calculated by multiplying the number of eggs by a factor, P_n , where

$$P_n = p_n \phi_2(N_0). \quad (14)$$

p_n is the mean nest survival and $\phi_2(N_0)$ a second function of population size.

Hence

$$P_n n'_1 = n''_1. \quad (15)$$

n''_1 is the number flying and is the first element in a new age-distribution, \mathbf{n}'' in which $n''_m = n'_m$ for $m > 1$. (This could be expressed as a matrix operation, but as only one element in the column vector is operated upon the above system is more economical. For different data it may be desirable to use matrices throughout.) The total summer population was found by summing \mathbf{n}'' to give N_2 .

3.3. JUVENILE SURVIVAL

The survival of the juveniles for the first three months was then calculated by multiplying n''_0 by a factor P_j , where

$$P_j = p_j \phi(N_2) \phi(BM). \quad (16)$$

p_j is the mean juvenile survival, $\phi(N_2)$ a function of the total summer population and $\phi(BM)$ a function of the Beech mast crop.

Hence

$$P_j n''_1 = n'''_1. \quad (17)$$

n'''_1 is the number of young at the start of the winter and is the first element of the new age-distribution, \mathbf{n}''' which has all other elements the same as \mathbf{n}'' . Once again the age-distribution is summed, to give the total population, N_3 , at the start of the winter.

3.4. WINTER SURVIVAL

Finally, the winter survival is computed by premultiplying the age-distribution by a second Leslie matrix, \mathbf{P} ; this is once again square, and the

elements of the principal diagonal represent the proportions of each age-group which survive. Hence:

$$P = \begin{bmatrix} P_1 & \cdot & \cdot & \cdots & \cdot \\ \cdot & P_2 & \cdot & \cdots & \cdot \\ \cdot & \cdot & P_3 & \cdots & \cdot \\ \cdot & \cdot & \cdot & \cdots & \cdot \\ \cdot & \cdot & \cdot & \cdots & P_8 \end{bmatrix}. \quad (18)$$

In this case all the probabilities of survival, P_1 to P_8 , are equal, although this need not necessarily be so.

Winter survival,

$$P_w = p_w \phi_2(BM) \phi(N_3), \quad (19)$$

where p_w is the mean probability of survival, $\phi_2(BM)$ a second function of Beech mast crop, and $\phi(N_3)$ a function of the number in the population at the start of the winter. Hence

$$Pn_i''' = n_{i+1}. \quad (20)$$

The new age-distribution, n_{i+1} , then represents the breeding population for the following year, $i+1$. The calculation can be repeated as many times as required.

The age-distribution and its sum, equal to the number in the population, are printed out after each stage in the calculation, i.e. four times for one yearly cycle. The computer also plotted the number breeding each year on a graph.

The program was written in the Elliott variety of the ALGOL programming language and run on the University of Bristol's Elliott 503 digital computer. The flow diagram of the program is shown in Fig. 5.

It can be seen that there is provision in this system for considerably more detail than was available. It was decided to leave this as it shows how such a model could be used, for example to study the effects of changing age-structure.

4. Calculations

The initial age-distribution was based on the first figure for population size from the Oxford study: 14. No details of the age-structure were available as the study was not begun until the winter of 1946. An arbitrary division into age-groups was therefore made to form the vector n : {1, 6, 3, 2, 1, 1, 0, 0} [see equation (8)]. There is only one yearling as the young birds probably

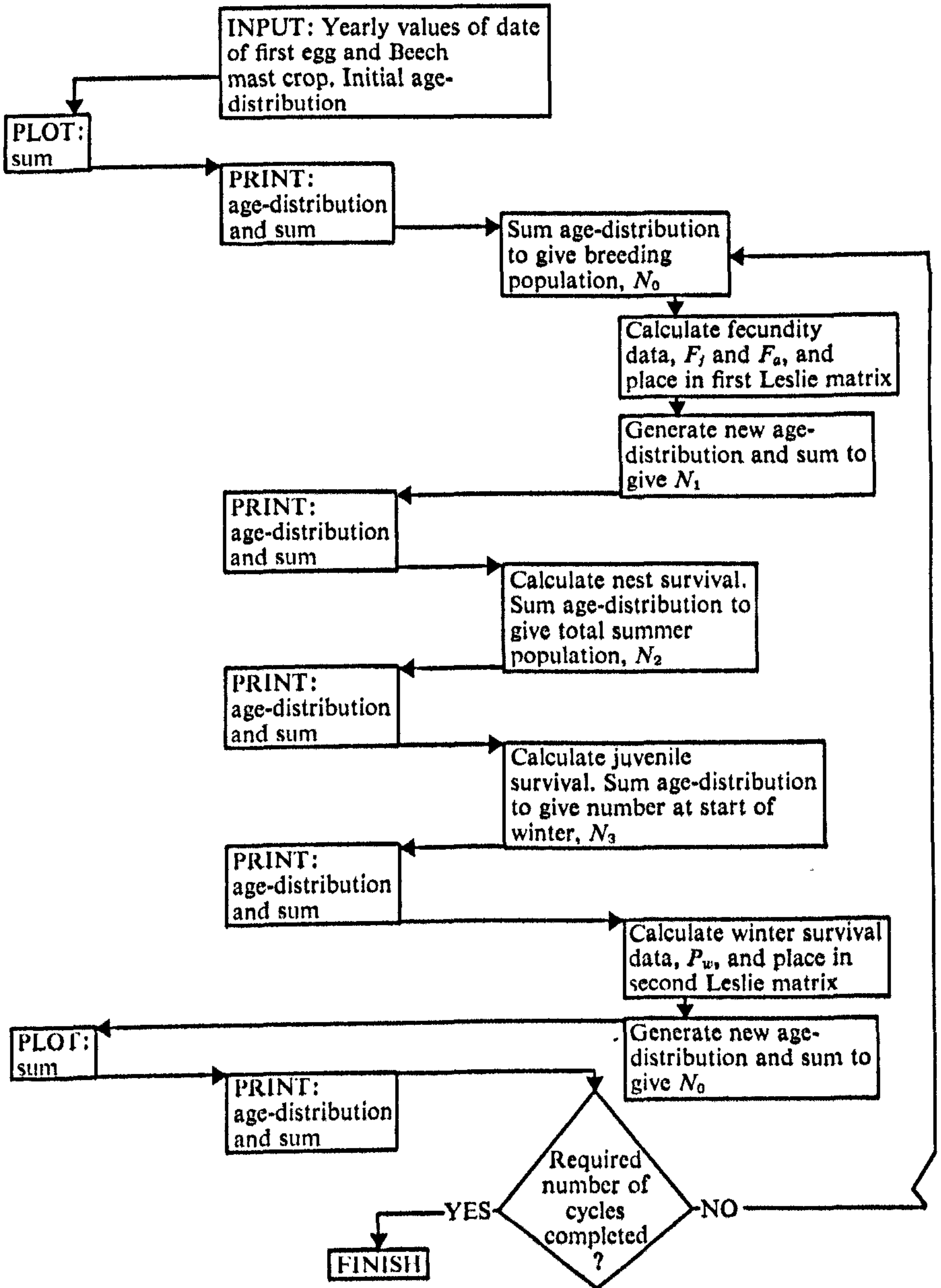


FIG. 5. Flow diagram of computer program.

fared worst in the severe winter of 1946 to 7, while the others are distributed more or less as expected for a 60% survival rate.

The program could calculate any number of years' populations; in most cases 50 years were covered. The values of average date of first egg and Beech mast crop were read in as data. As only 18 and 17 values respectively were available from the actual results the dates were made up from a table of random numbers, including only figures between 10 and 40 as these were the extremes observed; and the Beech mast crop by repeating the observed sequence.

Fecundity and survival could be made to depend on different combinations of the variables which affected them. It was simple to change the functions, $\phi(N_0)$, $\phi(BM)$, etc., used in the calculations. If the effect of the variable

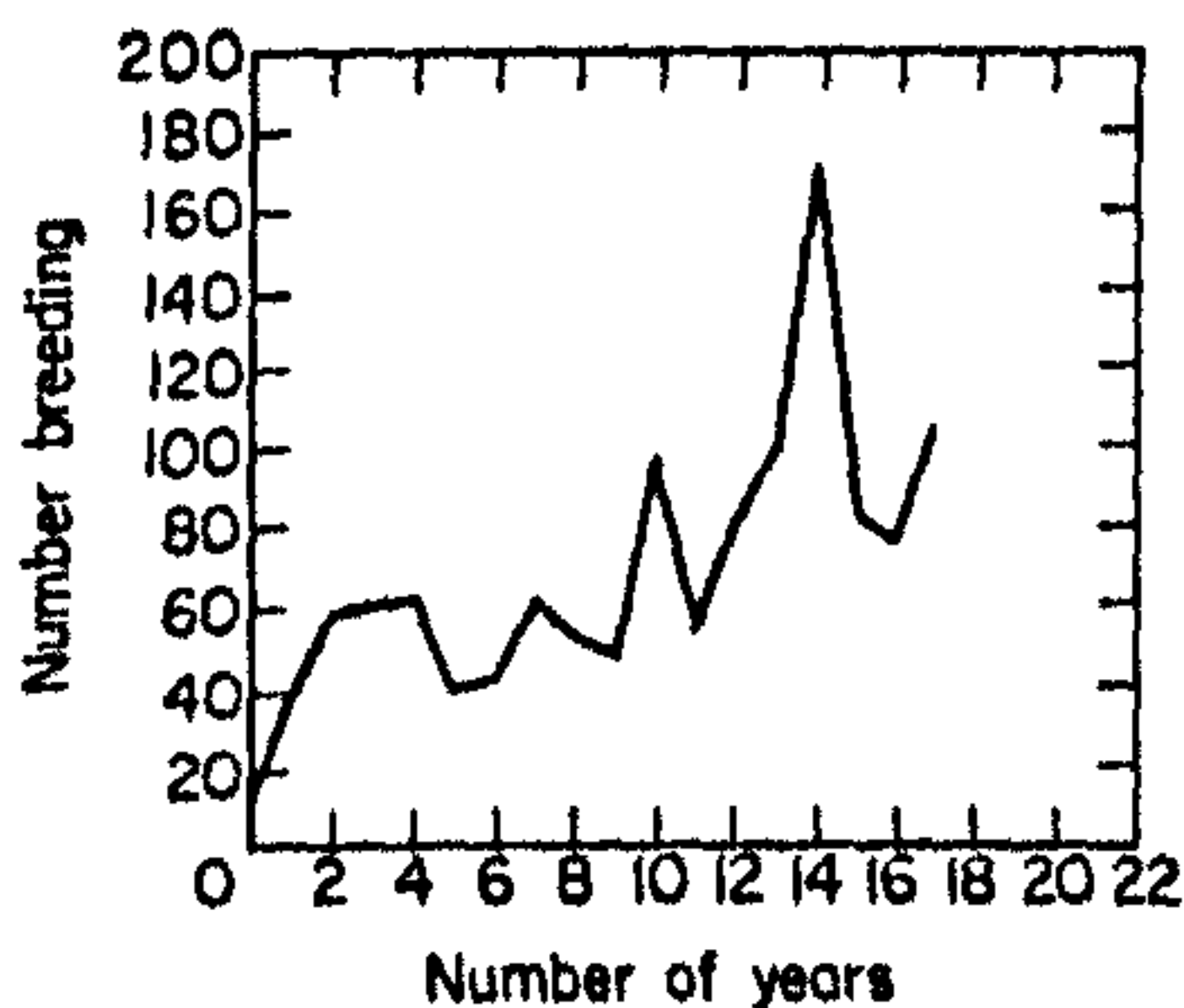


FIG. 6. Changes in size of breeding population of Great tits in Marley wood, 1947 to 1964.

was not required its function was made equal to one, effectively giving the mean value for the fecundity or survival. For example if fecundity was independent of date of first egg, $\phi(D) = 1$, and also independent of density, $\phi(N_0) = 1$, then $F_a = f_a 1 \cdot 1$ [equation (12)], that is, the fecundity has its mean value.

The observed numbers breeding in each year are shown in Fig. 6.

The first calculation was carried out with all the functions equal to one so that there was independence from density, date and Beech mast at all stages. This gave rise to an exponential increase in numbers, as would be expected (see Fig. 7).

The calculated functions [equations (1) to (7)] were then tested separately and in a number of different combinations and their effects on the numbers in the population noted.

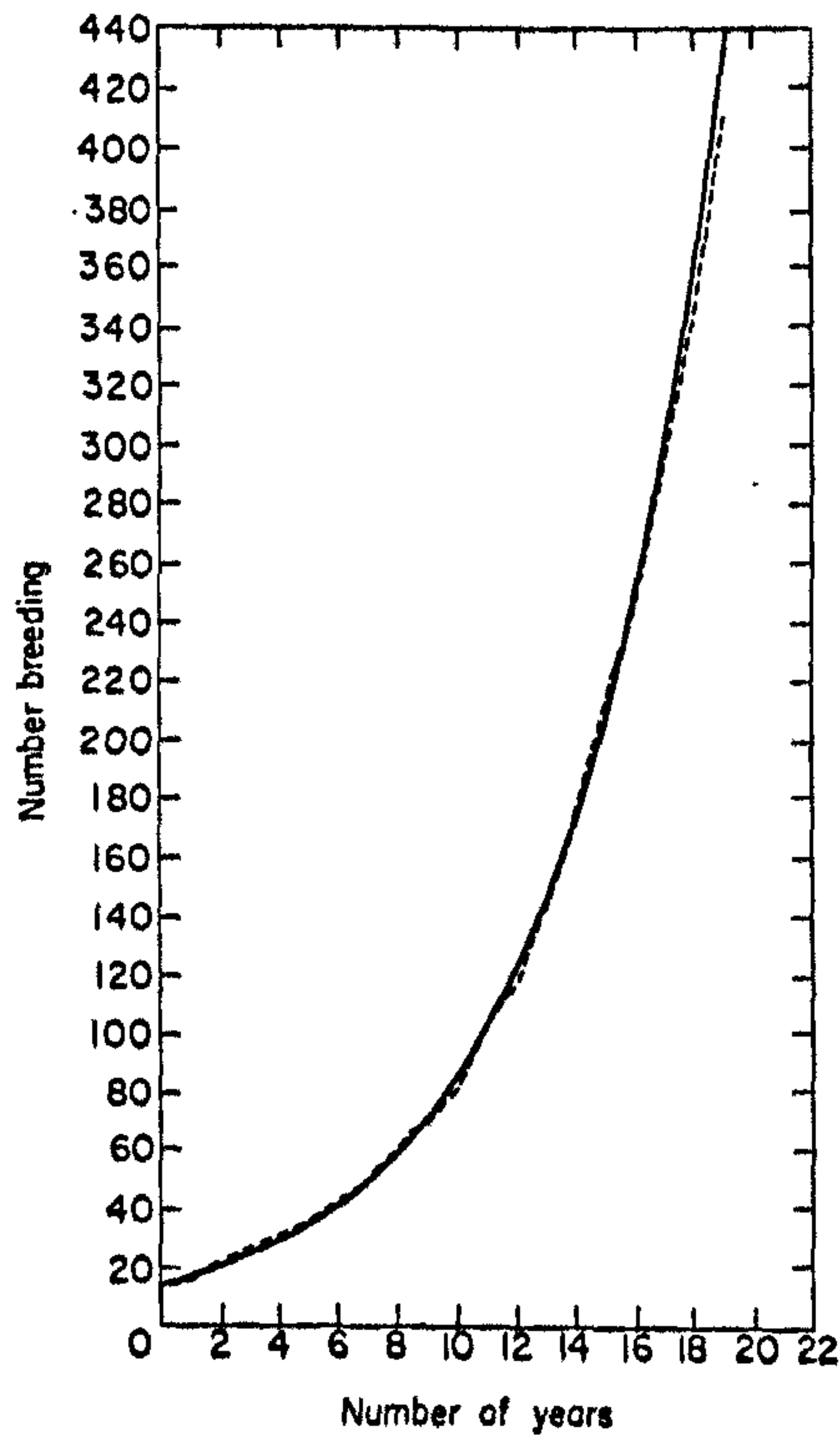


FIG. 7. Calculated changes in breeding population: —, fecundity and survival independent of all variables;, fecundity date dependent.

4.1. DENSITY-DEPENDENT FECUNDITY

If the fecundity of the birds was dependent on the number breeding the population showed a sigmoid growth pattern, rising more steeply than the exponential at first and then levelling off to 266 (Fig. 8).

4.2. DENSITY-DEPENDENT SURVIVAL

If the three phases of survival, nest, juvenile and winter, were all made density-dependent there was a rapid rise to a steady level of 74, shown in Fig. 9. When this was combined with density-dependent fecundity a very similar result was obtained. If only nest survival was density-dependent there was a sigmoid rise to 106; if only winter survival depended on density there was a sigmoid rise to 169 [Fig. 10(a)] and if only juvenile was similarly dependent there was a smooth rapid rise to a steady level of 72 [Fig. 10(b)].

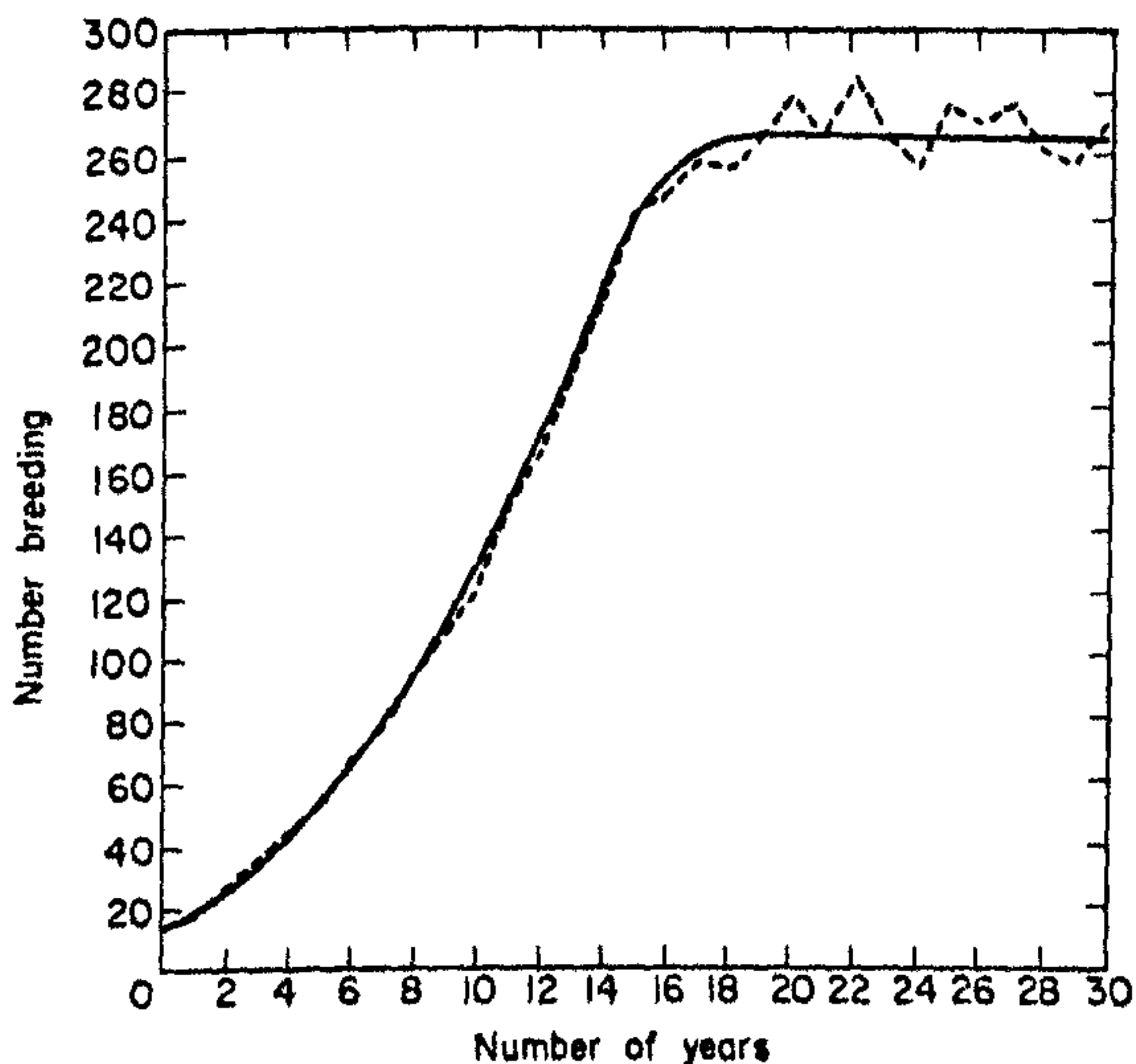


FIG. 8. Calculated changes in breeding population: —, fecundity density dependent;, fecundity date and density dependent.

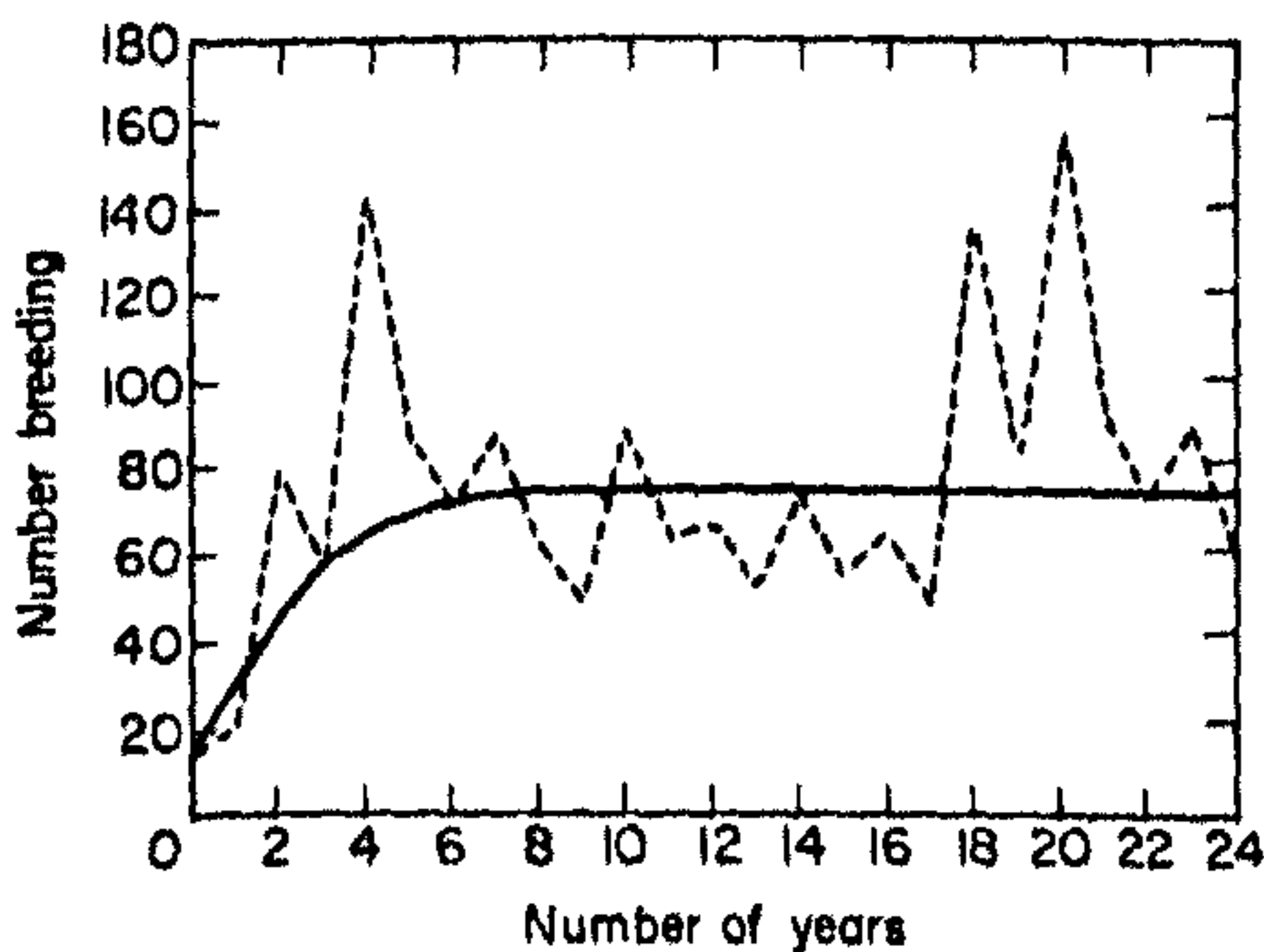


FIG. 9. Calculated changes in breeding population: —, survival density dependent;, survival Beech mast and density dependent.

Thus density-dependent fecundity, or nest or winter survival are not sufficient to hold the population down to the observed level. On the other hand, juvenile survival gives very nearly the right number, 72 against the observed mean of 70.4. This agrees with Lack's conclusion that the survival of the young after leaving the nest is the most critical stage for regulation of numbers. It is seen that the density-dependence of the fecundity can have only a small effect.

The fecundity, winter survival or nest survival could, of course, be given

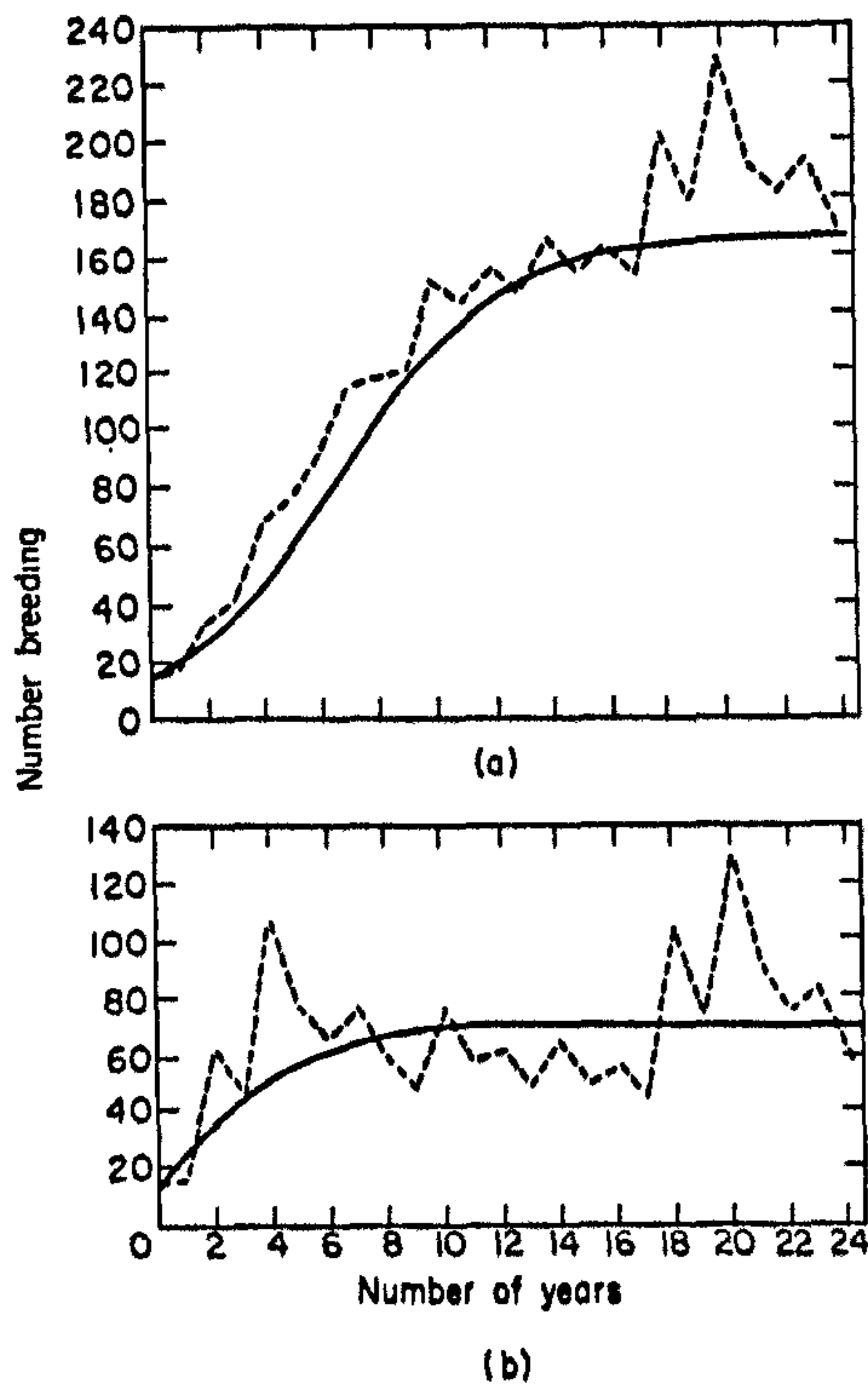


FIG. 10. Calculated changes in breeding population: (a) winter survival: ———, dependent on density; ······, dependent on Beech mast and density; (b) juvenile survival: ———, dependent on density; ······, dependent on Beech mast and density.

density-dependent functions which would make the population stabilize at any desired level. The significance of the result is that the equations (1), (3), (4) and (6) used for the effects of density are not chosen to cause stabilization at any particular level, but to describe the observed relationships.

4.3. DATE-DEPENDENT FECUNDITY

When fecundity was dependent only on the date of laying, the population increased exponentially in a very similar way to that found with no date-dependence, the only difference being a slight irregularity (Fig. 7). Similarly when combined with density-dependent fecundity the effect during the rise was small. Once the stable level was reached, however, fluctuations in the date of the first egg caused quite noticeable fluctuations in population size (Fig. 8). Combined with density-dependent survival the effect of the date was negligible. This is not because the date has a very small effect on the

number of eggs laid; for a population of 70 and a date of 10 there would be 397 eggs, whereas with a date of 40 there would be only 289 eggs. It must therefore be that the other factors have so much more effect on the changes in population size that the effects of date of laying are swamped.

4.4. BEECH MAST DEPENDENT SURVIVAL

If juvenile and winter survival both depended on the Beech mast crop, the population rose exponentially with fairly large fluctuations, as shown in Fig. 11(b). If only juvenile survival was Beech mast dependent the fluctuations were smaller, and if only winter survival was similarly dependent then they were very small [Fig. 11(a)].

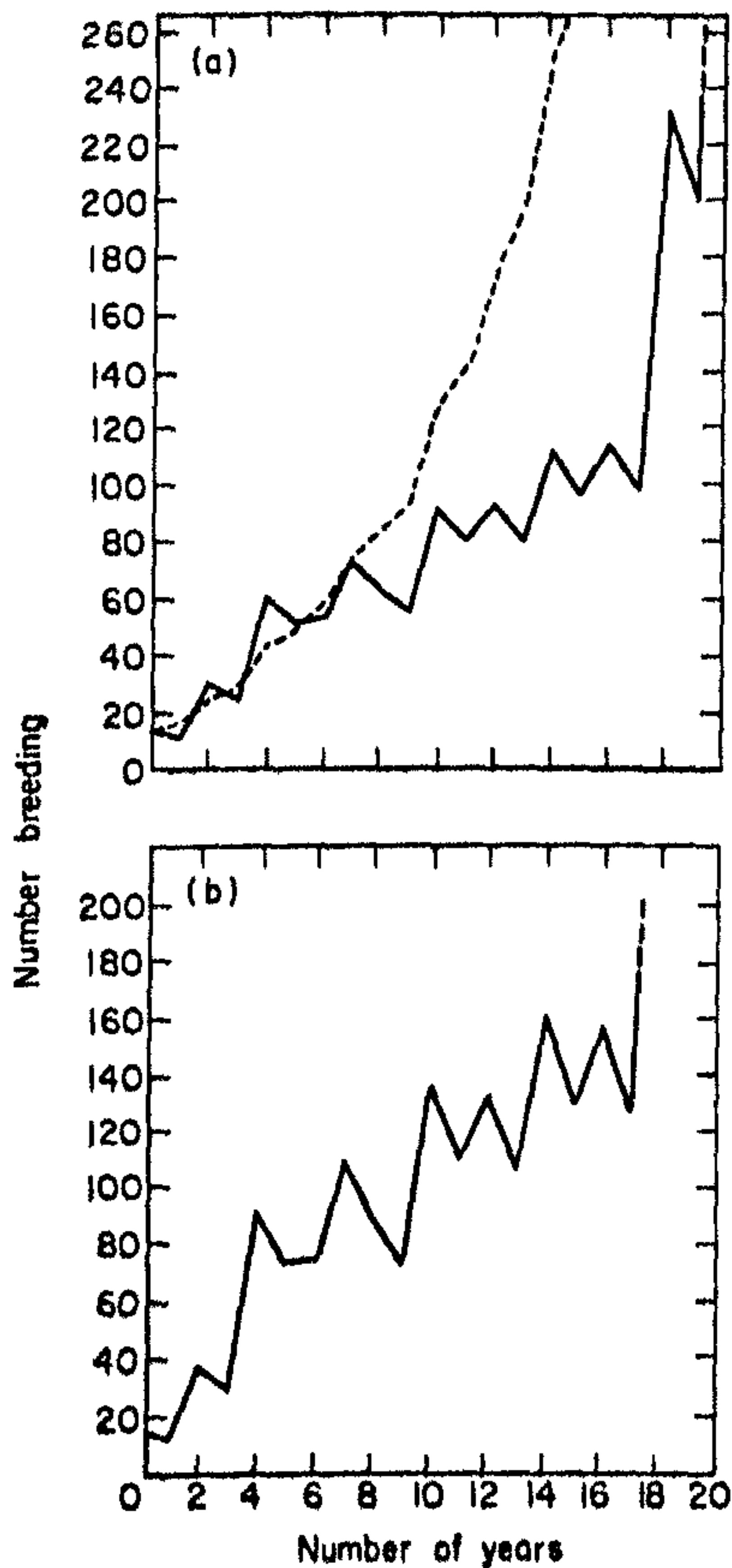


FIG. 11. Calculated changes in breeding population: (a) ———, juvenile survival dependent on Beech mast; , winter survival dependent on Beech mast; (b) juvenile and winter survival dependent on Beech mast.

When combined with density-dependent survival at all three stages fluctuations occurred about a steady level of around 70 and the increases and decreases were nearly all at the right times, but they were not generally of the right size (see Fig. 9). Figure 10 shows the effects of having winter survival dependent on density and Beech mast (a), and the same for juvenile survival (b). It can be seen that the initial rise and the size of fluctuations do not fit the observed curve well.

Thus the two "randomly" varying factors would not keep the population to a steady level. Once again it is seen that the factor affecting survival (Beech mast) has a greater effect on the numbers in the population than that affecting clutch size (date of first egg).

4.5. OTHER COMBINATIONS OF VARIABLES

Many other combinations of the variables were also tested, with varying results, but none fitted the actual curve exactly. The best result was obtained when all the factors were included (Fig. 12), except for the initial rise being too slow and the lack of a large increase in 1961.

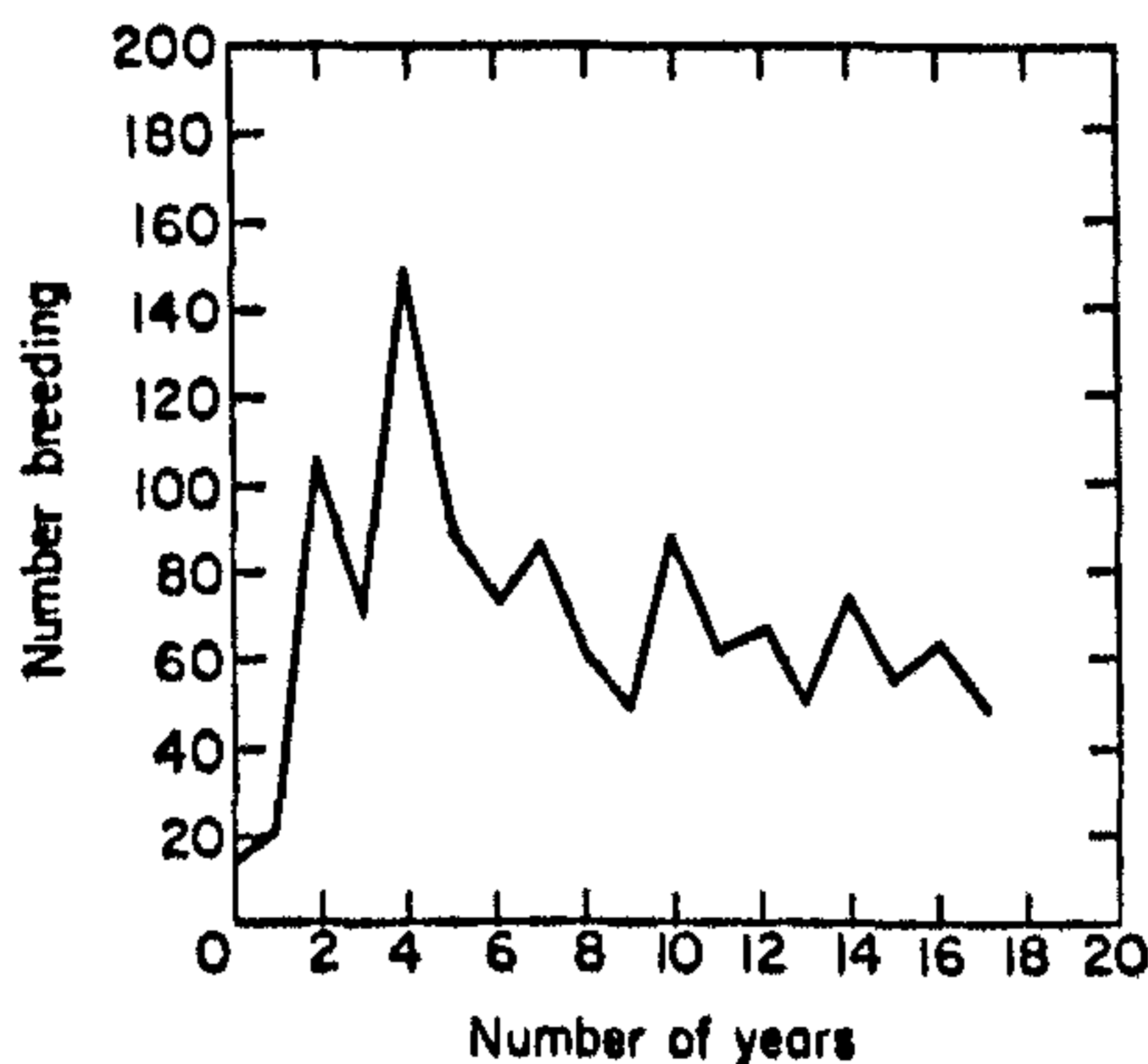


FIG. 12. Calculated changes in breeding population; fecundity and survival dependent on all variables.

It seems probable that some factor affecting mortality has been omitted. The calculated numbers of eggs fit well with the observed figures, and it has been shown that fecundity is relatively unimportant as compared with mortality. It is also probable that the Beech mast functions are incorrect and that the two years with a crop of eight are not so advantageous as they appear. A more complex function, $\Phi(N, BM)$, would possibly describe the situation better than the separate functions, $\Phi(N)$ and $\Phi(BM)$ [equations (4) to (7)]; for each size of Beech mast crop the population would tend towards a different stable level.

A number of factors which were found by the original authors to have some effect have not been included. Winter cold in 1962 to 3 was severe and the juvenile : adult ratio fell from 2.6 to 0.4 during this winter. There was also a steady rise in numbers over the years of the study which is not allowed for, the overall mean having been taken. The rise in number of tits during the first three years may have been affected by the nest boxes which were put up in 1946. This increased the possible nesting sites and tended to reduce any inter- and intra-specific competition. This rise was fitted best by density-dependent juvenile survival on its own, but this is probably a coincidence. The large breeding population in 1961 probably reflects the general rise in numbers, though there were almost certainly more widespread factors involved as well. One thing is clear about the increase in numbers: it is due to decreased mortality rather than increased fecundity, for the fecundity decreases with the greater density.

5. Discussion

The controversy concerning methods of regulation of populations is discussed in relation to the Oxford Great tits by Perrins (1965). Even assuming the necessity for density-dependent control the problem remains as to what causes this control to act about a certain level. Perrins states that in the case of the Great tits it is not availability of nesting holes, as boxes were always in excess, nor space for territories, as the sudden increase in 1961 showed that the area was capable of supporting a far larger population than had previously been supposed. Presumably it must in some way be connected with food supply. Both Lack (1966) and Wynne-Edwards (1962) agree that food is the ultimate controlling density-dependent factor in most cases, but disagree as to the way in which it acts. Lack considers that birds lay a clutch of such a size that they raise the maximum number of offspring and that density-dependent mortality controls the size of the population. Wynne Edwards, on the other hand, thinks that social behaviour acts on fecundity to keep the population below starvation level.

The purpose of the present calculations was to test the effects of some of the factors found to affect the fecundity and survival of the Great tits, alone and in different combinations. It has been shown that the reported density-dependence of the fecundity would not suffice to hold the population to the observed level, whilst the density-dependence of the juvenile survival would. The calculations have also shown that the density-independent factors, date of laying and Beech mast crop, would not hold the population in check. As Solomon (1957) states, the probability of such factors being, by chance, just the right size to hold a population to a steady mean level is very slight indeed.

The date of first egg, although having a fairly large effect on the clutch size, would not cause significant fluctuations in population size. The Beech mast crop, on the other hand, would cause significant fluctuations through its effect on survival; the effect on juvenile survival is greater than that on winter survival. Once again the factor affecting juvenile survival would have the greatest effect on the number of birds.

Density-dependent factors can, of course, act without having a significant effect on the size of the population, for example, fecundity in the case of the Great tits. Under different conditions, if the present controlling factor were removed or reduced, such factors could become the primary controlling force, and then the population would stabilize at a higher mean level.

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REFERENCES

- BETTS, M. M. (1955). *J. Anim. Ecol.* **24**, 282.
 GIBB, J. (1950). *Ibis*, **92**, 507.
 GIBB, J. (1954a). *Bird Study*, **1**, 40.
 GIBB, J. (1954b). *Ibis*, **96**, 513.
 GIBB, J. (1955). *Br. Birds*, **48**, 49.
 GIBB, J. (1956). *Ibis*, **98**, 420.
 GIBB, J. (1957). *Bird Study*, **4**, 207.
 GIBB, J. (1958). *J. Anim. Ecol.* **27**, 375.
 GIBB, J. (1962). *Scient. Rev.* **20**, 20.
 HARTLEY, P. H. T. (1953). *J. Anim. Ecol.* **22**, 261.
 KLUYVER, H. N. (1951). *Ardea*, **39**, 1.
 LACK, D. (1955). *Ardea*, **43**, 50.
 LACK, D. (1958). *Ardea*, **46**, 91.
 LACK, D. (1964). *J. Anim. Ecol.* **33** (Jubilee Suppl.), 159.
 LACK, D. (1966). "Population Studies of Birds". London: Oxford University Press.
 LACK, D., GIBB, J. & OWEN, D. F. (1957). *Proc. zool. Soc. Lond.* **128**, 313.
 LESLIE, P. H. (1945). *Biometrika*, **33**, 183.
 PENNYCUICK, C. J., COMPTON, R. M. & BECKINGHAM, L. (1968). *J. Theoret. Biol.* **18**, 316.
 PERRINS, C. M. (1963). *Proc. Int. Orn. Congr.* **13**, 717.
 PERRINS, C. M. (1965). *J. Anim. Ecol.* **34**, 601.
 SNEDECOR, G. W. (1946). "Statistical Methods" (4th ed.). Ames: Iowa State College Press.
 SOLOMON, M. E. (1957). *A. Rev. Ent.* **2**, 121.
 WYNNE-EDWARDS, V. C. (1962). "Animal Dispersion in Relation to Social Behaviour".
 Edinburgh: Oliver and Boyd.

A QUANTITATIVE STUDY OF HOST AND PARASITE POPULATIONS

(Ph.D. thesis) Linda Pennycook

The study of a population of sticklebacks and their parasites was initially proposed by my supervisor, Dr. H.D. Crofton, who also suggested the use of frequency distributions as a method of analysis.

The computer program for the negative binomial distribution is based on one devised by Professor J.H. Whitlock of Cornell University. All other programs were designed and written by myself.

I carried out all the practical work and analysis of the data, although some aspects were discussed with Dr. Crofton.

Linda Pennycook

A COMPUTER MODEL OF THE OXFORD GREAT TIT POPULATION

J. Theoret. Biol. (1969) 22: 381 - 400. L. Pennycuik.

The analysis described in this paper is based on work which I carried out independently in my first and second years as a post-graduate student at Bristol University.

Wanda Pennycuik